CARNIVORE

Carnivorous Mammals Including Man

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Carnivore is a regular journal devoted to the understanding of carnivory and carnivorous mammals including man. The policy of **Carnivore** is to encourage creative thought about the function and origin of carnivory and carnivorous mammals so as to better comprehend and benefit human life. **Carnivore's** primary emphasis is scientific and philosophic with secondary emphasis on application of knowledge.

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EDITORIAL[1]

WHY CARNIVORE?

In the midst of a terrible crisis as we are, the greatest urgency is clarification of the origin of the crisis and what new worlds are possible. Man is the origin of his crisis: competition for resources, which encompasses the threat of war, is the global crisis facing all of us. The solution lies in accurate perception of our social behavior. The natural and heretofore adaptive response of man to crisis has been construction of theory culminating in a radically new perception of the world, which is philosophy. Idealism and its pious form so prevalent today, intellectualism, are inadequate to save us. There is no authentic love of ideas per se, nor of intellect. What is authentic is the belief in ideas to solve problems which vitally concern us. This, the philosophy of Ortega y Gasset, says that the most radical datum in the universe is that living is problematical. Which is to say that we are selfish at the core. Among all philosophical doctrines ratio-vitalism uniquely parallels the theory of natural selection.

Evolutionary biology has recently postulated the most dramatic idea, which is that social behavior, including morality, is selfish. ("Morality" is derived from "me" or "mine.") It is no mere coincidence that sociobiology appeared at a time when self-interest became necessarily extended to include all of humanity and the entire world. This is the first age in which human social behavior threatens all of humanity. Sociobiology's convergence with ratio-vitalism offers the true psychology, which is necessarily the authentic philosophy. Sociobiology is vitalistic in any sense and as such is the final break from mechanistic or positivistic philosophies of idealism. Natural selection is the foundation of my own thought and the undeniable theme of CARNIVORE; I hope that CARNIVORE will apply natural selection to the solution of vital problems.

To understand man and solve human problems, construction of theory about human origins is essential. I see CARNIVORE as a channel for changing perception about human origins. I refer specifically to the importance of considering man and his present condition in light of his history as a carnivore. In my view carnivory has been the critical niche dimension in the evolution of human behavior. Central to the evolution of carnivory in humans have been carnivores, as predators and competitors. Thus, the drama of human evolution, and the origin of human problems seem to me a matter of adaptation to a niche as a predator, the success of which has been determined by competition with other predators. If this is so then carnivores offer models for testing ideas about human behavior.

The role of carnivores in community structure and function is of special interest to ecology, evolution and resource management. The conservation of carnivores is essential to a number of vital human interests including science. Whether or not readers agree with my reasons for publishing CARNIVORE, it can hardly be denied that there is a need for a publication which gives priority to carnivorous mammals.

In summary, CARNIVORE is intended to be an outlet primarily for ideas about carnivory and carnivorous mammals, including man, and, secondarily, for information about carnivores and solutions for their conservation.

Randall L. Eaton

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[1] *Each issue of* Carnivore *will include an editorial. Readers are encouraged to submit editorials about philosophic, scientific or societal problems. Comments on contributions appearing in* Carnivore *will be published as letters.*

THE COMPARATIVE SOCIO-ECOLOGY OF THE HYAENIDAE

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INTRODUCTION

Socio-ecology is the comparative study of social structure in relation to ecology (Crook, 1970a). This has been studied in various mammalian orders such as primates (Crook, 1970b) and ungulates (Jarman, 1974), as well as birds (Crook, 1965), and has been synthesized for the whole animal kingdom by Wilson (1975).

Among the carnivores socio-ecology has received little attention because few of the families have been studied extensively. The Hyaenidae are a very suitable family for studies of this kind (Kruuk, 1975), as all four species have now been studied to a greater or lesser degree and the members show a wide range of ecological requirements and social organizations.

Unless otherwise stated the data presented here for spotted hyenas *(Crocuta crocuta)* are taken from Kruuk (1972) in northern Tanzania (the Serengeti and Ngorongoro Crater), from Bearder (in press) in the Timbavati Private Nature Reserve, Transvaal, South Africa, and from my own observations in the southern Kalahari. The data for striped hyenas *(Hyaena hyaena)* come from Kruuk (1976) in the Serengeti and Israel, for brown hyenas *(Hyaena brunnea)* from Mills (1976, 1977, and in preparation) in the southern Kalahari, and for aardwolves *(Proteles cristatus)* from Kruuk and Sands (1972) in the Serengeti.

DISTRIBUTION

Figure 1 shows the distributon of the four extant species (Dorst and Dandelot, 1970; Kruuk, 1972 and 1976; Ewer, 1973; Skinner, 1976). The spotted hyena, which is the largest (mass between 50 kg and 80 kg depending on the region), is found throughout Africa south of the Sahara except for the southern parts of South Africa where it has been exterminated and the Congo Basin. The brown hyena (mass approximately 40 kg) occurs in the southern part of the continent, particularly on the west, but excluding the extreme south where it, too, has been exterminated. The striped hyena (mass approximately 25 kg) is found in the northern half of the continent, excluding the Sahara and the west south of 10° N, through the Middle East and southern Asia to the Gulf of Bengal. The aardwolf (mass approximately 9 kg) is confined to the arid and semi-arid regions of southern Africa, northwards on the east into Somalia, Ethiopia, and the Sudan. The ranges of all the species, therefore, except for the brown and striped hyenas, overlap each other to a greater or lesser extent.

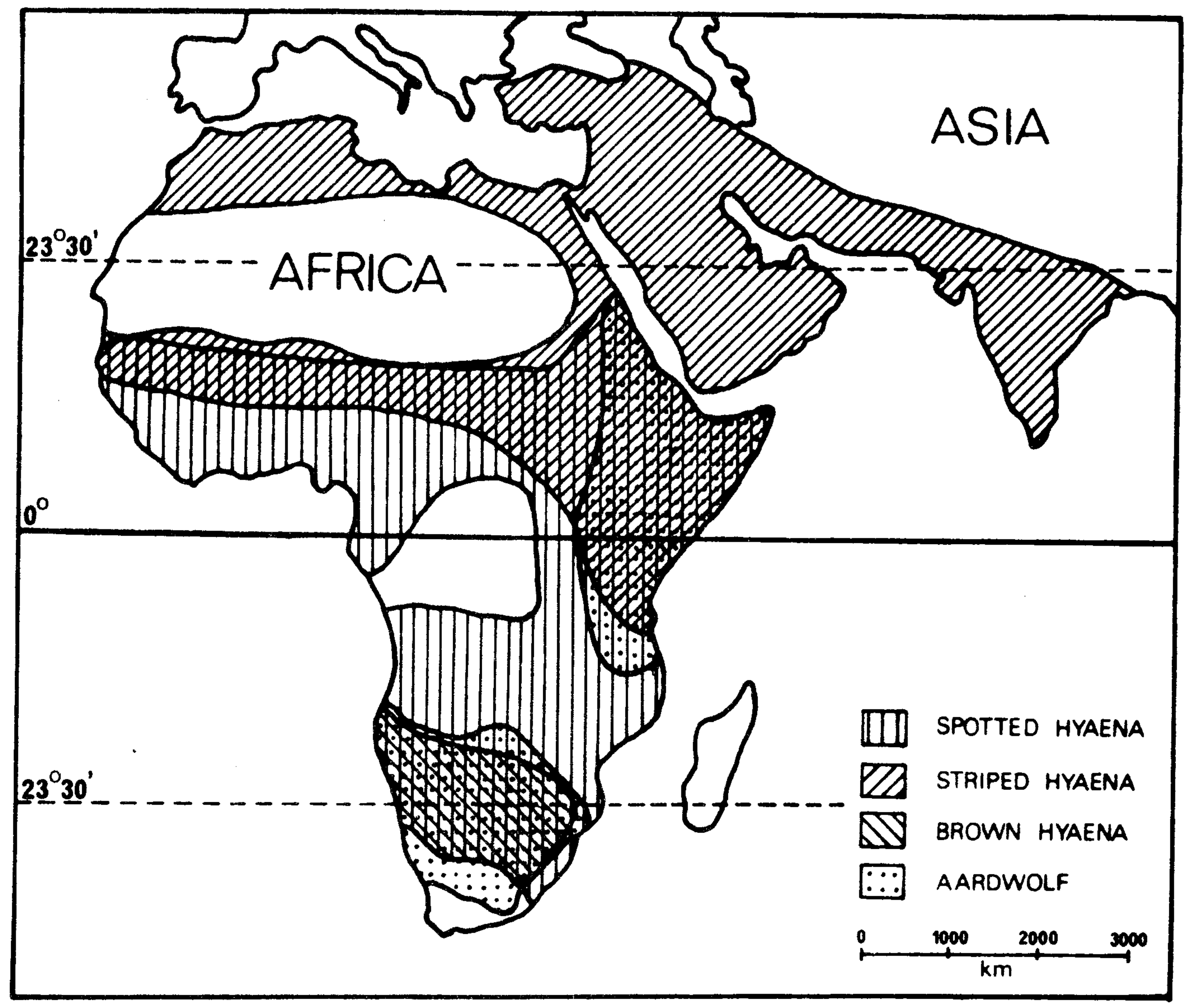

FIG. I. DISTRIBUTION OF THE HYAENIDAE

HABITAT

Spotted hyenas reach their highest densities in flat open country with few or no trees (e.g., the Serengeti), or bush country where there are large numbers of ungulates (e.g., Timbavati). Brown and striped hyenas, on the other hand, prefer drier and often rocky areas with thick bush, which do not support large ungulate biomasses (e.g., Kalahari and Negev Desert, Israel). Aardwolves are found mainly in open associations and avoid densely wooded areas (e.g., parts of the Serengeti).

DIET

Ewer (1954) has shown that the spotted hyena's dentition is the most specialized of the three hyenas', followed by the brown and then the striped. This particularly with regard to the carnassial sheer, used for cutting through hide and tendons, and to the size of one of the principle bone crushing teeth P^3. The aardwolf's dentition is greatly reduced to small peg-like structures. These morphological differences are reflected in the diets of each species as is illustrated in Table 1.

The aardwolf is the most specialized feeder, with over 90% of the food items found in feces collected in the Serengeti, being insects, the large majority of which were a single species of termite, *Trinervitermes bettonianus*. In addition, Smithers (1971) found that Isoptera occurred in all 20 stomachs of aardwolves collected in Botswana, of which the vast majority were *T. rhodesciensis*. Bothma (1971) found *T. trinervoides* to form the bulk of the stomach contents of eight aardwolves collected in the Transvaal and northern Natal, South Africa.

Ninety percent or more of the food items found in spotted hyena feces in the Serengeti and Ngorongoro were from large and medium-sized mammals. In the Timbavati, a woodland area, 90% or more were from very large, large and medium-sized mammals. Furthermore, in the southern Kalahari I have observed spotted hyenas feeding on large mammals on 23 (72%) occasions, medium-sized mammals on eight (25%), and an ostrich *(Struthio camelus)* once (3%). I have also found the seeds of wild fruits in 24 (16%) out of 149

TABLE 1. Percentage Occurrence of Various Food Categories in the Feces of Spotted (Crocuta crocuta), brown (Hyaena brunnea) and striped (Hyaena hyaena) hyenas and the aardwolf (Proteles cristatus) from different areas in Africa.

FOOD CATEGORY	SPOTTED HYENA			BROWN HYENA	STRIPED HYENA	AARDWOLF
	Serengeti[1]	Ngorongoro[1]	Timbavati[2]	Southern Kalahari[3]	Serengeti[4]	Serengeti[5]
Very large mammals (>400 kg)	0.6	0.8	38.3	0.0	0.0	0.0
Large mammals (80-400 kg)	63.0	87.5	19.1	24.7	8.9	0.0
Medium-sized mammals (12-80 kg)	35.7	10.9	39.7	3.3	19.0	0.0
Small mammals (1-12 kg)	0.2	0.0	0.7	16.5	6.8	0.0
Very small mammals (<1 kg)	0.0	0.0	0.5	1.5	1.7	0.0
Birds	0.4	0.0	0.5	4.0	12.3	0.0
Reptiles	0.0	0.0	0.1	6.0	11.1	0.0
Insects	0.0	0.0	0.0	16.8	28.5	91.8
Fruits and vegetable matter	0.0	0.0	0.0	21.0	11.7	8.2
Unidentified hair	0.2	0.8	1.1	6.0	0.0	0.0
Total number of items found	658	530	794	547	179	196
Number of feces analyzed	401	348	527	143	50	79

1 = Kruuk, 1972. 2 = Bearder, in press. 3 = Mills, 1976. 4 = Kruuk, 1976. 5 = Kruuk and Sands, 1972.

of their scats which I have examined. In the Namib Desert of South West Africa, of the few spotted hyena feces that were looked at, all contained hair of the gemsbok *(Oryx gazella)*, a large ungulate, and a few contained large insect remains (Mills and Kruuk, 1976). They, too, have been recorded eating wild fruits in this area (Stuart, 1976). Spotted hyenas, therefore, select most of their food from two or at most three of the categories in Table 1, but are capable of utilizing others when necessary.

The brown and striped hyenas have the most varied diet. The mammals that they feed on tend to be smaller than those which spotted hyenas utilize (Table 1). The mammals most frequently eaten by brown hyenas in the southern Kalahari are: gemsbok and red hartebeest *(Alcelaphus buselaphus caama)*, large herbivores; steenbok *(Rahpicerus campestris)*, a small herbivore; small canids, mainly the black-backed jackal *(Canis mesomelas)* and bat-eared fox *(Otocyon megalotis)*. It should also be mentioned that in some parts of the southern Kalahari where very few feces samples were collected, springbok *(Antidorcas marsupialis)*, a medium-sized herbivore, figured predominantly in the brown hyena's diet.

In addition, other vertebrates are also readily eaten by both species, as are insects (mainly beetles and termites) and wild fruits. Brown hyenas also readily eat birds' eggs. In the Transvaal scavenged large domestic stock, small mammals and vegetable matter make up the bulk of the brown hyena's diet (Skinner, 1976). On the coastal plain of the Dead Sea in Israel, offal, dead chickens and other abattoir waste, specially put out at a carnivore feeding site by the Nature Reserve Authority, form the bulk of the striped hyena's diet, with hyrax and fruits also being eaten (Macdonald, in press).

There is most overlap in diet, therefore, between the brown and striped hyenas, and both these species' diets overlap with the spotted hyena's and to a very small extent with that of the aardwolf. There is no overlap in the diets of the spotted hyena and the aardwolf.

An important consideration, particularly when dealing with hyenas, is how the vertebrate food was obtained. In the Serengeti 58.3% of carcasses spotted hyenas were observed feeding on were killed by the hyenas themselves, and in Ngorongoro 95.5% were. In Timbavati, where direct observations of spotted hyenas foraging were impossible, it is inferred from indirect observations that the majority of the very large mammals, which were all giraffe *(Giraffa camelopardalis)*, were scavenged and the medium-sized mammals, mainly impala *(Aepyceros melampus)*, were killed. The spotted hyena observations from the Kalahari were also mainly of an indirect nature where 28.1% of the carcasses were definitely killed by them, 37.5% were probably killed by them, 21.9% were scavenged, and 12.5% were indeterminable.

Brown hyenas in the Kalahari scavenged 95.8% of the vertebrate food items they were observed feeding on (n = 260) and striped hyenas also scavenged nearly all of their vertebrate food. Both these species direct their limited hunting behavior towards the young of medium-sized and small animals (Figure 2).

FORAGING GROUP SIZE

Foraging spotted hyenas are encountered either singly or in groups throughout their range, although the extent to which they forage solitarily or socially varies in different areas. In the Serengeti they are more likely to move about on their own than they are in Ngorongoro. Also, the size of the groups vary, with the Serengeti groups being smaller than those of the Ngorongoro Crater, 46% consisting of two individuals in the Serengeti, and 22% in Ngorongoro, where groups of up to seven individuals are almost as common as groups of two. In the Timbavati 60% of foraging hyenas encountered were solitary and in the Kalahari 49% (n = 49) were, with groups of two comprising 65 and 48% of the observations of two or more hyenas in these two areas respectively.

Striped and brown hyenas are more solitary foragers. In the Serengeti striped hyenas foraged alone on 94 out of 96 occasions and in Israel on five out of seven. On the other occasions two or three (a female with two of her cubs) individuals were seen together. Macdonald (in press) found that foraging striped hyenas sometimes came to a permanent feeding station in Israel in small groups of usually two, but up to four, individuals. In the southern Kalahari brown hyenas are almost always encountered foraging singly, very occasionally in twos, and once three large cubs were encountered moving together. In central Botswana they are also usually solitary, although unconfirmed reports of small groups do exist (Smithers, 1971), and the same is the case in the Transvaal (Skinner, 1976).

Aardwolves are also usually solitary throughout their range, although there is a record of five being seen together in northern Botswana (Smithers, 1971).

SOCIAL ORGANIZATION

In the Ngorongoro Crater spotted hyenas live in fairly closed societies called clans, numbering between 30 and 80 individuals. Each clan occupies an area of between 10 and 40 km^2, although they do not operate as a single unit and a clan member can be solitary or in a group. Each clan range has a well defined and marked boundary and members join in the defense of the area against neighboring clans. In the Serengeti, on the other hand, there are no clans with fixed membership defending a specific range, and the hyenas form temporary associations with individuals originating from different areas. In the Timbavati the spotted hyenas also form stable clans, one of which contained 12 adults and moved in an area in excess of 25 km^2 over a two-year period.

Kalahari spotted hyenas also appear to live in clans, but the density was so low while I was observing them that there were no clearly defined clan boundaries. The size of the clans were small, one consisting of about four adults and another of at least six, two of which were marked and were known to move in an area of at least 40 km^2 for three years, although the actual home range size was undoubtedly much larger than this.

Brown hyenas in the southern Kalahari live in very large, partially overlapping home ranges of anything between 340 and 540 km^2 or more, depending on the quality of the habitat which is reflected by the availability of food. Within each home range several individuals of all ages and sexes live and, although most of them are related, it is not known if all of them are. At least some of the cubs of both sexes remain in the area they were born in when they grow up. When two individuals from the same home range meet, they engage in a greeting ceremony and will feed together if the food item is big enough. When one meets up with another of the same sex from a neighboring area they are aggressive and often engage in ritualized fighting. Individuals of different sexes from different groups are apparently not aggressive towards one another, and sometimes perform the greeting ceremony when they meet.

The amount of overlap between home ranges varies, apparently being greatest in areas where food is more abundant, although sometimes the boundaries are well defined by a physical feature such as a road. Within the home ranges and particularly along the boundaries the individuals leave scent marks of various kinds.

Striped hyena social organization appears to be similar to that of the brown. Their home range size in the Serengeti was much smaller than that of the brown hyena in the Kalahari, a subadult male having a home range of 72 km^2 and a subadult female (in another part of the Serengeti) one of 44 km^2.

Aardwolves appear to hold territories maintained by a pair and covering 1.5 km^2. These territories are marked by anal gland secretions in a similar way to those of the other Hyaenidae.

Spotted hyena dens are communal where several females raise their young (Figure 3), whereas brown and striped hyenas usually raise one litter per den (Figure 4). These two also differ from spotted hyenas in that the male and female, and other family members as well, partake in raising the cubs by carrying back food for the cubs at the dens, whereas spotted hyenas do not bring food to their cubs. The denning behavior of the aardwolf is unknown.

SOCIAL BEHAVIOR

The spotted hyena has evolved numerous vocalizations and visual displays in order to maintain its complex social organization, where individuals rapidly change from being solitary to highly social. As would be expected, the other members of the family do not have this wide range and frequency of behavior patterns. For example, neither the very conspicuous whoop call nor the strange mimicry of the male's reproductive organs by the female, used in the highly developed greeting ceremony of the spotted hyena (Figure 4), are found in any of the other hyenas. When striped or brown hyenas meet they perform a greeting ceremony where sniffing is directed at the head, back and anal region (Figure 6), a more simple behavioral pattern.

The most characteristic visual display in the three smaller species is the erection of the mane which is frequently used in conflicting situations, either inter- or intra-specific, and serves to make the individual look bigger. It is probably significant that this posture is so well developed in the three smallest and least aggressive of the Hyaenidae.

DISCUSSION

The most important factor which induces social evolution among the carnivores is the food on which they specialize (Wilson, 1975).

Spotted hyenas, the most social of the Hyaenidea, feed mainly off fairly large carcasses which provide enough food for several individuals at the same time. Furthermore, by forming hunting packs they are able to overcome larger prey than they would if they were hunting alone. Within the framework of the clan system they are able to penetrate the antipredatory systems of different species of prey by varying their hunting techniques. When scavenging there is no need for spotted hyenas to move around in groups, as the chances of detecting carrion are not improved.

In the Timbavati they are believed to scavenge a large proportion of their food or to hunt impala, a medium-sized antelope which can presumably be hunted efficiently by one or two hyenas. It could be argued that a woodland habitat greatly hinders cursorial hunting by a pack with the result that they are much more likely to be encountered singly or in pairs than in the Serengeti or Kalahari, where they scavenge less and hunt larger game more often. These areas in turn have smaller foraging groups than Ngorongoro where they hardly ever scavenge and are predominantly hunters of wildebeest *(Connochaetes taurinus)* and zebra *(Equus burchelli)*.

Apart from the type of food eaten, the distribution of the food is also important in molding social organization. Thus, in the Ngorongoro and Timbavati, where a constant supply of food is available throughout the year, the clans are stable and strictly territorial. In the Serengeti, where the game is migratory, the clans are temporary associations in areas where there happens to be a concentration of herbivores.

Brown and striped hyenas utilize many smaller food items than spotted hyenas. Most of the mammals they feed on are the remains of other carnivores' kills and do not usually provide a meal for more than one individual. Thus, there is no advantage in foraging in groups; and such a strategy would in fact be a disadvantage, leading to unnecessary aggression between group members, with the stronger and more dominant animals always getting the food. In Israel, however, where the offal at a carnivore feeding site provides the bulk of the local striped hyenas' food, they are sometimes encountered in small groups.

Furthermore, when cubs are being fed, there is more chance of the adults finding food for them if they are foraging in different parts of their home range simultaneously than if they are foraging together. Neither would it be advantageous for them to den communally except perhaps in times of food abundance, as the food left at the den would be more likely to be consumed by the larger cubs.

These two species, therefore, are generally solitary foragers. They are not, however, true solitary species, which consist of mother-offspring groups and where the male only visits the female for purposes of reproduction (Wilson, 1975). There are ties between other individuals as well, which also play an active role in raising the cubs, although their contribution is not as large as the mother's.

The extended family system of brown hyenas in the southern Kalahari is seen to be a result of the distribution of their food. Large and medium-sized ungulates and many of the small mammal species are unevenly distributed in the area, being found mainly along the two dry river courses which run through the region and around pans. The same applies to wild fruits such as the tsama *(Citrullus lanatus)* and the gemsbok cucumber *(Acanthosicyos naudianus)*, which grow in unevenly distributed patches mainly in the dune areas which cover over 90% of the region. Moreover, both these food sources may become scarce in dry lands and in early summer of normal years when many of the large and medium-sized ungulates move out of the home ranges of the hyenas that I was studying (Bothma and Mills, in press). Then, too, the wild fruits are either scarce (dry years) or have been eaten by many different animal species (early summer in normal years).

Thus, a brown hyena must have a large enough home range to ensure that enough food is available over an extended period. As the fruits are mainly found in the dunes, the home range should include some dune habitat so that the hyenas can exploit these when they are available. In fact, they can survive in this habitat alone by having very large home ranges. If, however, pan and particularly river habitat is available, the home range size can be considerably smaller, as there will be much more animal food available. Thus, a female with a large stretch of river habitat in her home range lived in an area of 340 km^2, whereas another with a few pans and only some river habitat, which she did not use very much, lived in an area of 540 km^2.

Once a brown hyena has a large enough home range, it can tolerate a few other individuals, which will also contribute to the defense of the area and the feeding of the cubs, although the members do not cooperate in foraging. The indications are that the smaller home ranges near the river with the more abundant food can support more members than the larger ones in the dunes. At the den of a female that lived mainly in the dunes, for example, only this individual and the cubs that she was feeding were ever seen. At another den near a dry riverbed, however, several other individuals, in particular two of the cubs (a male and a female) from the previous litter, were regularly seen. This pattern was further expanded when the female cub grew up and had cubs at the same time and in the same den as her mother had her third litter. This occurred in 1977 after a succession of wet years when the biomass of potential brown hyena food had undergone a rapid increase (Bothma and Mills, in press; Mills, in preparation).

Home range boundaries also appear to be better defined in areas away from large concentrations of potential food, and it could be argued that here the demand on the owners to utilize the food in the home range is greater.

The fact that, in brown and striped hyenas, other group members cooperate in feeding the cubs is also seen as an adaptation to their food ecology. Cubs are not able to deal as efficiently with large food items as adults and are more likely to be brought a smaller animal than a large one. Seventy-eight percent of food remains found at brown hyena breeding dens were small or medium-sized animals and 18% were large animals (n = 246). Presumably, the female on her own cannot find enough of this type of food, and thus if another member should procure a small animal it might bring it to the den.

Thus it would seem that for brown hyenas in the southern Kalahari very large home ranges, shared and defended by a number of individuals, provide a more constant food supply for more hyenas than smaller home ranges shared by a pair could.

The aardwolf in the Serengeti apparently spaces itself out in small territories shared by a pair in a more classical territorial system in habitat where its food supply is evenly distributed and easy for one animal to procure.

There is, of course, a degree of overlap in the ecological requirements of the species in the family. This is most marked in the brown and striped hyena which are the only two species whose distributions do not overlap. The spotted hyena's distribution overlaps those of the brown and striped, but where this occurs they tend to choose different habitats. The spotted hyena is dominant to its smaller relatives and there are indications from the Kalahari that they force brown hyenas out of certain areas when they come into them; and the same probably holds true when spotted hyenas and striped hyenas meet. The aardwolf is the most aberrant member of the family, and therefore competition is least common between it and the other members.

The three genera in the family, therefore, represent three grades (Huxley, 1959 in Crook, 1970a), each with its characteristic lifestyle, although there is a measure of overlap. Within these grades each species is able to modify its lifestyle within certain limits according to the prevailing ecological conditions. This is best illustrated with the spotted hyena which has been studied in different habitats. As more studies are made on this and the other species in different areas and at different times, a more varied picture of the socio-ecology of the family will no doubt emerge, although I predict that the three grades will still be identifiable.

SUMMARY

The four extant species of the Hyaenidae have been studied to a greater or lesser extent; and they can be divided into three grades, each with its characteristic lifestyle, which can be modified within limits according to the prevailing ecological conditions.

Spotted hyenas feed mainly off very large, large or medium-sized herbivores. They are the most social species often cooperating in killing their prey, although when scavenging they are more solitary. Brown and striped hyenas feed from a wide range of food categories, including all kinds of vertebrates, insects, and fruits. They are mainly solitary scavengers. The uneven distribution of brown hyena food in the southern Kalahari has led to a social organization where several animals share a very large home range. In this home range they forage alone, but help in the defense of the area and in the feeding of cubs.

The aardwolf is the most specialized member of the family, feeding predominantly on termites and apparently spacing itself out in small territories in habitat where its food is evenly distributed.

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LITERATURE CITED

Bearder, S. K. In press. Feeding habits of spotted hyaenas in a woodland habitat. *East African Wildlife Journal.*

Bothma, J. duP. 1971. Food habits of some carnivores (Mammalia) from southern Africa. *Annals of the Transvaal Museum* 27: 15-26.

Bothma, J. duP. and M. G. L. Mills. In press. Ungulate abundance in the Nossob river valley in the south-western Kalahari Desert. *Proceedings of the XII International Congress of Game Biologists,* Atlanta.

Crook, J. H. 1965. The adaptive significance of avian social organizations. *Symposium of the Zoological Society of London* 14: 181-218.

Crook, J. H. 1970a. Social organization and the environment: Aspects of contemporary social ethology. *Animal Behavior* 18: 197-209.

Crook, J. H. 1970b. The socio-ecology of primates. Pp. 103-168, *In:* J. H. Crook (Ed.), *Social Behaviour in Birds and Mammals.* Academic Press, London and New York.

Dorst, J., and P. Dandelot. 1970. *A Field Guide to the Larger Mammals of Africa.* Collins, London.

Ewer, R. F. 1954. Some adaptive features in the dentition of hyaenas. *Annals and Magazine of Natural History* 7: 188-194.
Ewer, R. F. 1973. *The Carnivores*. Weidenfeld and Nicolson, London.
Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267.
Kruuk, H. 1972. *The Spotted Hyena*. The University of Chicago Press, Chicago and London.
Kruuk, H. 1975. Functional aspects of social hunting by carnivores. Pp. 119-141, *In:* G. Baerends, C. Beer, and A. Manning (Eds.), *Function and Evolution in Behaviour*. Clarendon Press, Oxford.
Kruuk, H. 1976. Feeding and social behaviour of the striped hyaena *(Hyaena vulgaris* Desmarest). *East African Wildlife Journal* 14: 91-111.
Kruuk, H., and W. A. Sands. 1972. The aardwolf *(Proteles cristatus* Sparrman) 1783 as predator of termites. *East African Wildlife Journal* 10: 211-227.
Macdonald, D. W. In press. Observations on the behaviour and ecology of the striped hyaena *(Hyaena hyaena)* in Israel. *Israel Journal of Zoology*.
Mills, M. G. L. 1976. Ecology and behaviour of the brown hyaena in the Kalahari with some suggestions for management. *Proceedings of the Symposium on Endangered Wildlife,* Endangered Wildlife Trust, Pretoria. July 1976: 36-42.
Mills, M. G. L. 1977. Diet and foraging behaviour of the brown hyaena *(Hyaena brunnea* Thunberg, 1820) in the southern Kalahari. M.Sc. Thesis, University of Pretoria.
Mills, M. G. L., and H. Kruuk. 1976. Report on a visit to the Namib Desert National Park. 16th-20th July, 1976. Unpublished manuscript. 3pp.
Skinner, J. D. 1976. Ecology of the brown hyaena *Hyaena brunnea* in the Transvaal with a distribution map for southern Africa. *South African Journal of Science* 72: 262-269.
Smithers, R. H. N. 1971. *The Mammals of Botswana*. Museum Memoir No. 4. National Museums of Rhodesia, Salisbury.
Stuart, C. T. 1976. Plant food in the diet of the spotted hyaena. *South African Journal of Science* 72: 148.
Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. The Belknap Press of Harvard University Press, Cambridge and London.

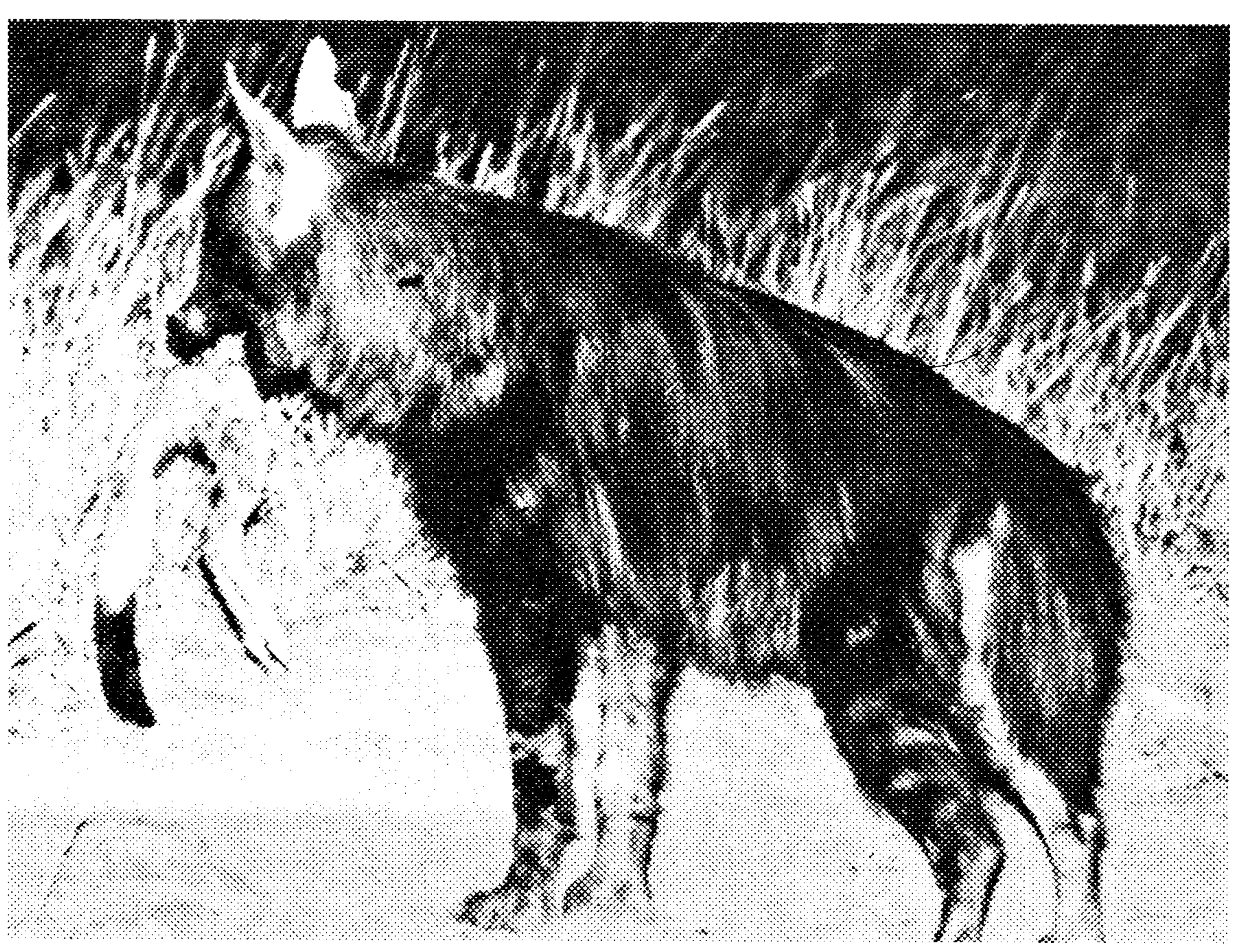

FIGURE 2. Brown hyena in the southern Kalahari with the back half of a springhare *(Pedetes capensis)* which it has killed.

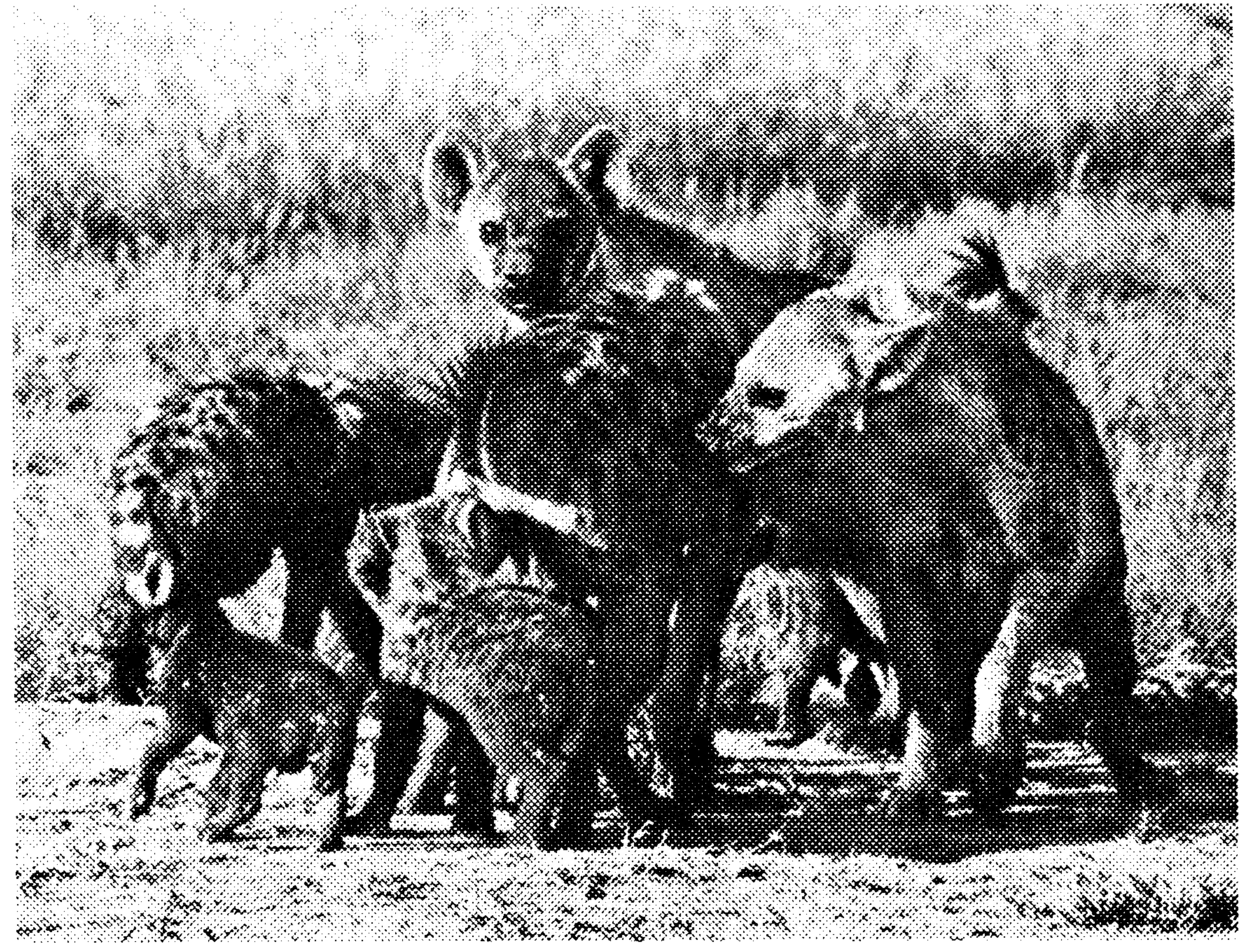

FIGURE 3. Spotted hyenas den communally. Three adults and four cubs, comprising three litters, at a den in the southern Kalahari.

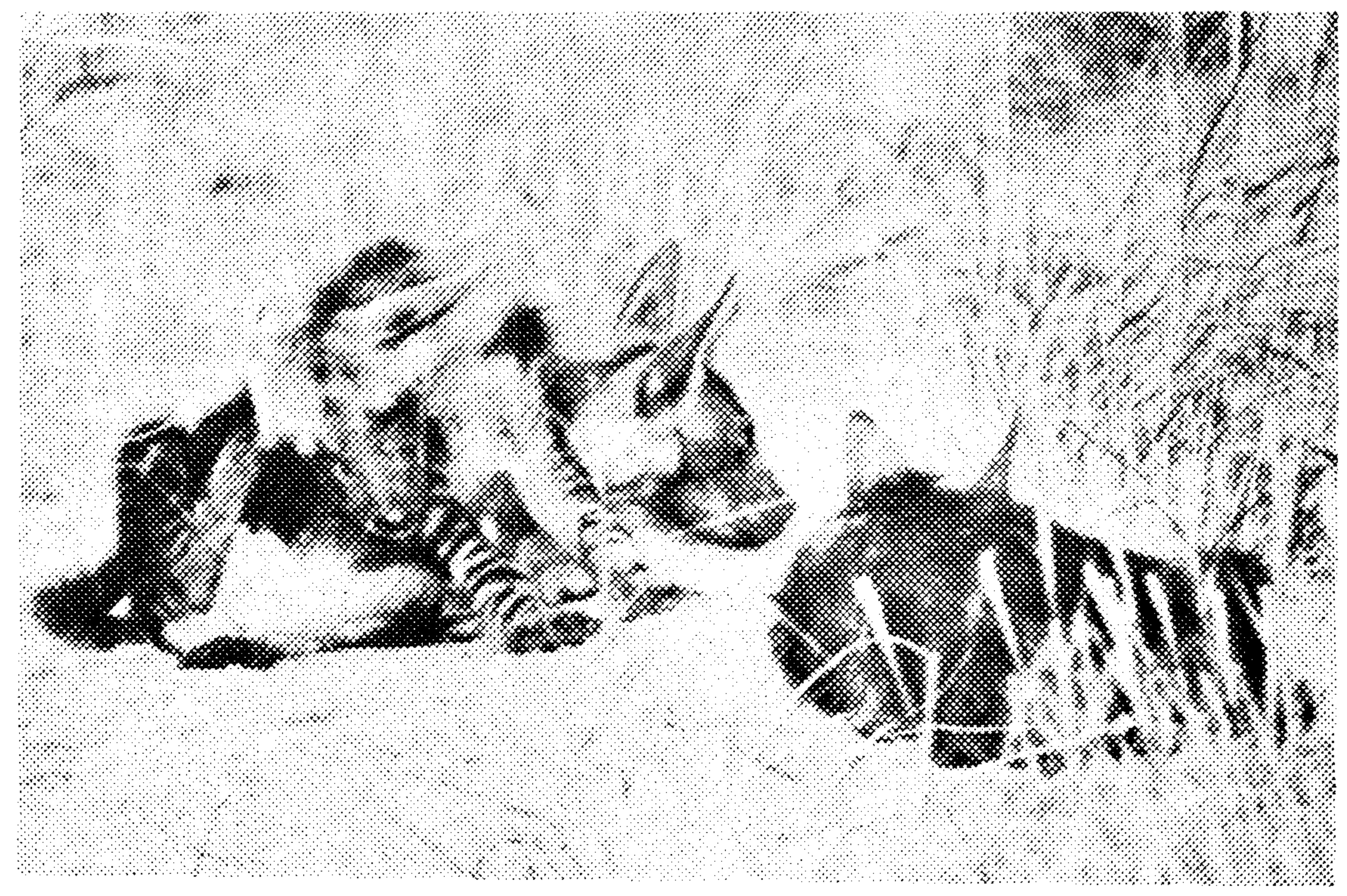

FIGURE 4. Brown hyenas only raise one litter per den. Three cubs, litter mates, at a den in the southern Kalahari.

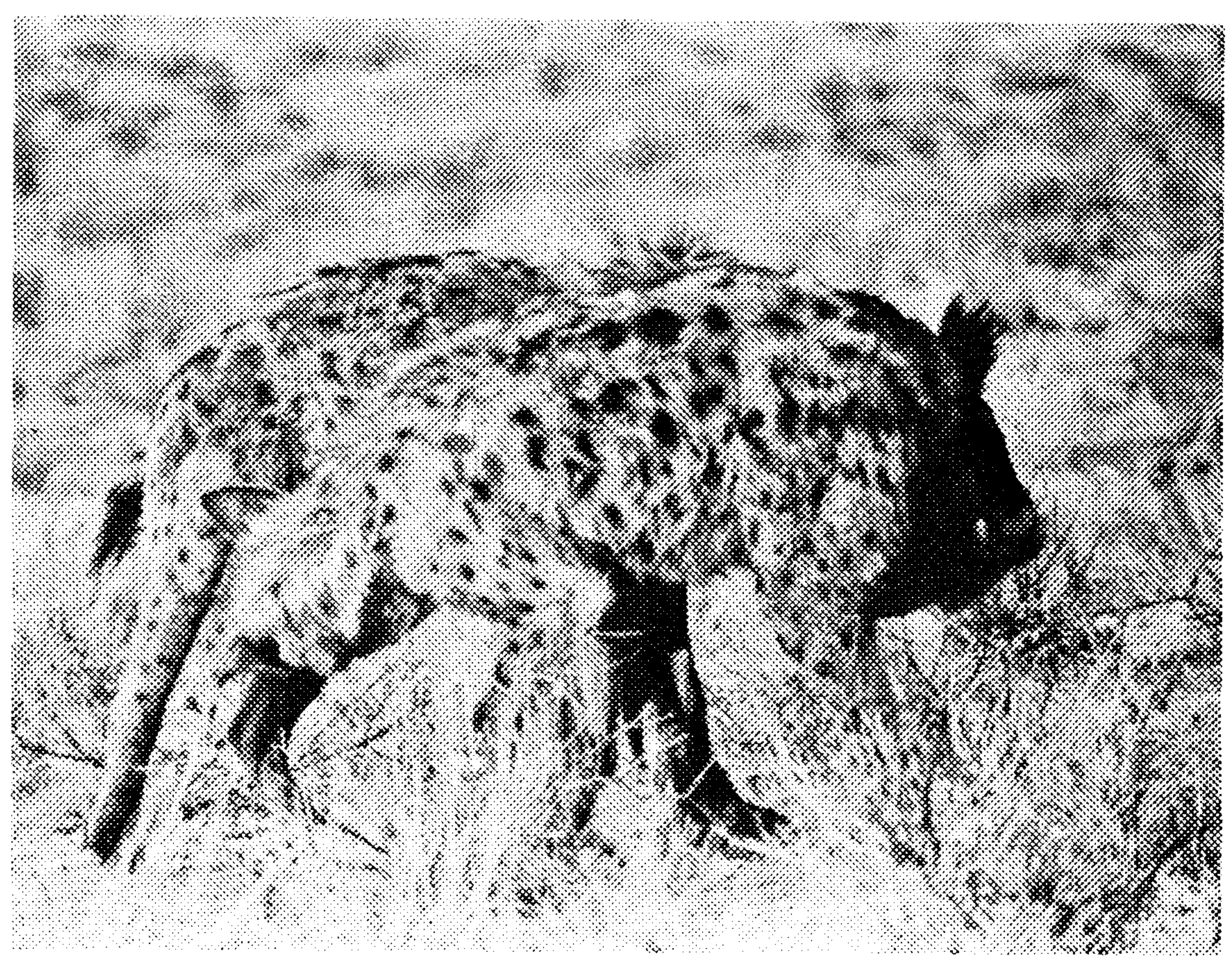

FIGURE 5. Greeting ceremony between two spotted hyenas where sniffing is directed at the genital region.

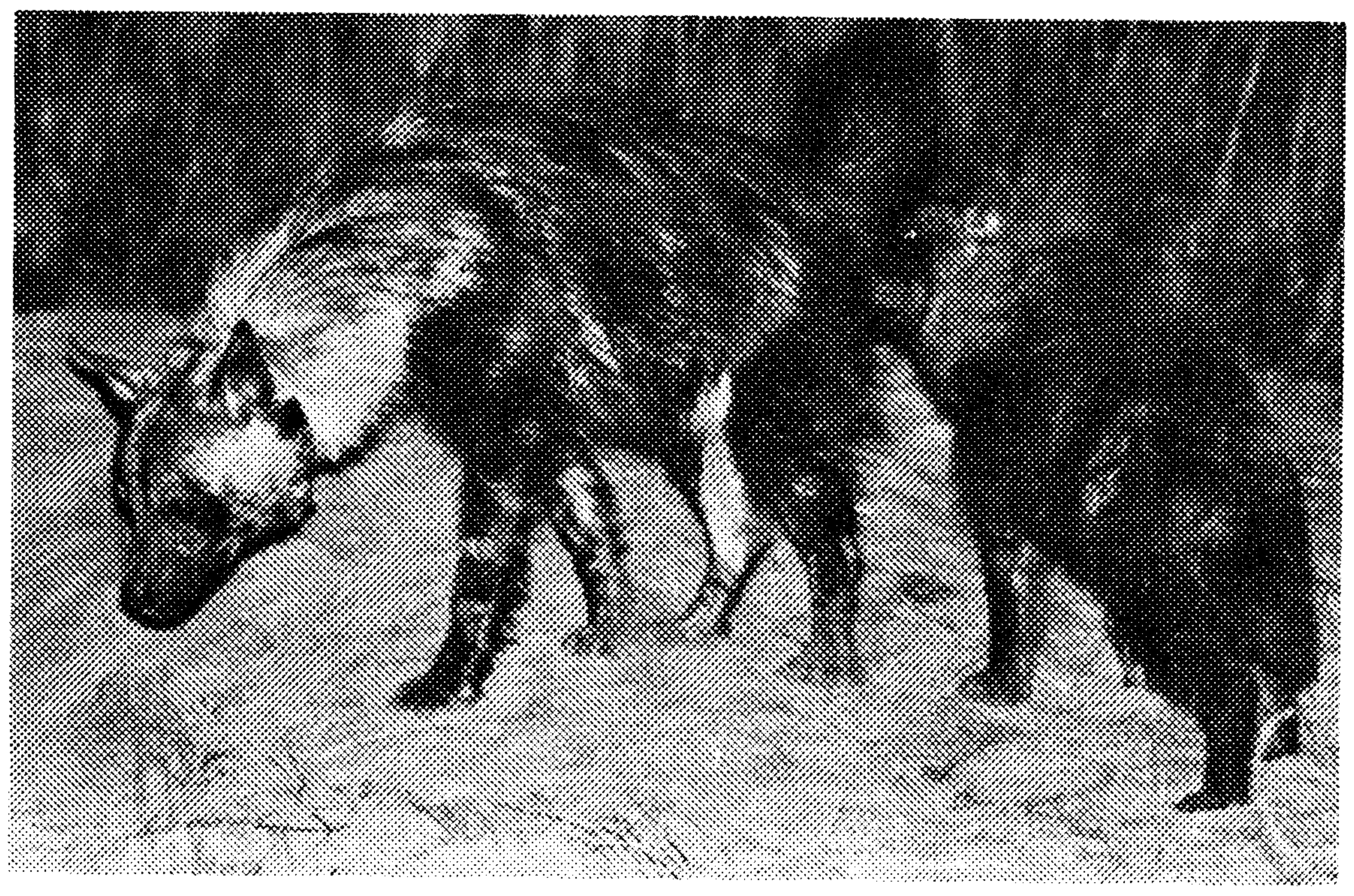

FIGURE 6. A brown hyena cub greeting its mother, where sniffing is directed at the anal region.

A COMPARISON OF SOME FEATURES OF THE EVOLUTION, ECOLOGY AND BEHAVIOR OF BLACK AND GRIZZLY/BROWN BEARS

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Abstract. Evolutionary, ecological and behavioral literature is surveyed and related to the adaptive strategy of black and brown bears. A series of hypotheses based on existing data, deduction, inference, and speculation is presented. From an evolutionary perspective black bears are more similar to ancestral forest-dwelling miacids than are brown bears. The brown bear's niche, in contrast with the black bear's, includes more exploitation of open habitat types. Various adaptations of each species to their primary habitat types are discussed. Both species are opportunistic omnivores which have relatively unspecialized guts and ingest high quality food items. When these are not available hibernation occurs. Brown bears are normally 1.5 to 2 times as large as black bears within the same biogeoclimatic zone. This is interpreted in terms of evolutionary history, and habitat preference and productivity. Reproductive rates for both species are low. The reproductive strategy for females of each species involves extended, intensive maternal investment. No paternal investment beyond the copulatory act has been identified. Individuals of both species are somewhat flexible in their use of space for foraging and reproduction, depending upon the distribution of critical resources such as food and mates.

INTRODUCTION

During the past two decades scientists have received money to study bears because of bears' cultural and economic significance to people. Prior to about 1960 much of our knowledge about bears was inferential and anecdotal. Both the black bear *(Ursus americanus* Pallas) and the brown/grizzly bear[1] *(U. arctos* Linne) seldom occur at population densities greater than one individual per square mile. Because of these relatively low population densities they are seldom seen except at concentrated food sources. Among the most common of these, at least up to a few years ago, were garbage disposal areas (Figure 1). Bears are difficult to locate in natural areas without considerable effort. Since the mid-1950's, however, the private world of bears has become increasingly public. Methods for the capture and recapture of bears have become widely known and used. The use of drugs to either capture or sedate bears has allowed the collection of data on age, weight, reproductive status, anatomy and morphology, and much more (Figure 2).

FIGURE 1. Black bears and attendant at a garbage dump, July, 1968.

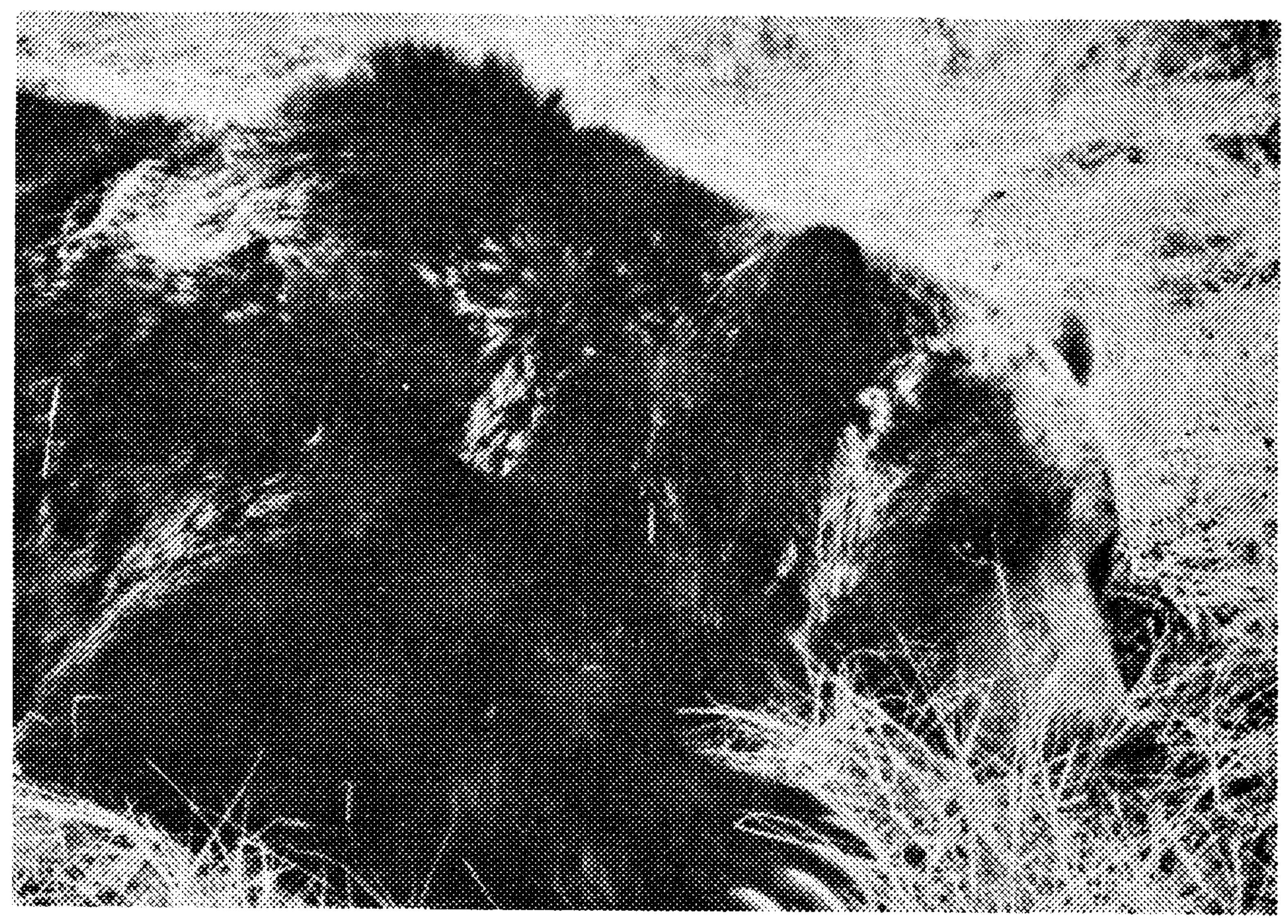

FIGURE 2. Sedated adult male grizzly bear which has been lip-tattooed and weighed and measured as part of an ecological study.

[1]Hereafter referred to as brown bear, but meant to include all North American populations of the species. Where specific reference is made to grizzly bears, this is used to be consistent with an author's original usage.

The ultimate weapon used by curious humans has been radiotelemetry. With a radio collar around a bear's neck and receivers in peoples' hands, the private world of bears vanished. Radiotelemetry has been particularly valuable in understanding the use of space by bears. In some cases individual black (Rogers, 1976) or grizzly bears (Craighead et al., 1969, 1974) have been monitored for up to seven or eight years and through several reprodutive cycles.

The avalanche of scientific research and knowledge related to bears has been documented in the published proceedings of four international conferences on the biology and management of bears (Pearson, 1968; Herrero, 1972a; Pelton et al., 1976; Martinka, in preparation). Despite tremendous advances in knowledge, the state of our understanding of bears is still mainly at the stage of collecting data. The challenge of understanding bears remains great enough at the level of geographically defined populations. For this reason most recent research has contributed towards cataloguing population characteristics within a given geographic area.

So, despite advances in knowledge, integrated theory would be premature. This is true partly because black and brown bears are long-lived species with low reproductive rates. This makes studies having durations of 10 years or more necessary in order to understand important topics such as reproductive strategies and population response to environmental variability. Only one study (Craighead et al., 1974) has thus far extended to this duration. Although data on bear populations have become considerable since 1960, these data are often fragmented and incomplete.

In this paper I summarize important literature and present a series of hypotheses related to the evolution, ecology and behavior of black and brown bears. The areas I will cover are: evolutionary history, food habits, reproductive strategy, and the use of space and its inferred relationship to reproductive strategy.

EVOLUTIONARY HISTORY

About 25 million years ago, during the early portion of the Miocene, bears appear to have diverged from the Miacidae (Colbert, 1955). The miacids were a family of small, carnivorous, tree-climbing mammals. The earliest bears were probably forest dwellers like their miacid ancestors, although the bears' diets probably included more vegetative items. Bears ultimately became opportunistic omnivores, eating meat when it was easily available and high quality vegetation when it was not. In most areas vegetative food sources are more predictable than are animal food sources. Highly digestible vegetative material came to dominate the diet. Quite late in the bears' evolutionary history species such as *Arctodus* spp., *Ursus arctos* and *U. maritimus* diverged from forest dwelling ancestors and began to utilize the productivity of more open habitat types (Herrero, 1972b). The most recently evolved of these species appear to be the polar bear *(U. maritimus maritimus)*, which not only occupies open tundra and ice-covered environments but also has redeveloped the miacid habit of being primarily carnivorous instead of following the general bear strategy of omnivory.

As I infer for their miacid ancestors, individual bears of species past and present are solitary except when females are accompanied by young, when family groups sometimes associate, when sibling groups sometimes remain together after weaning, during the breeding season, or at concentrated food sources.

Black bears and brown bears each appear in the fossil record sometime during the mid-Pleistocene. In 1970 I developed a hypothesis which explains some of the differences in adaptive strategy of the two species (Herrero, 1972b). I postulated that the brown bear evolved to exploit the seasonal productivity of non-forested periglacial environments. The productivity of periglacial environments and their influence upon many species of large mammals have been discussed by Geist (1971).

In order for brown bears to exploit the periglacial richness they had to remodel some of their forest adaptations. One of the most important redesigns involved protection of the young. Young bears of both species are sometimes killed by adult bears (Troyer and Hensel, 1962; Hornocker, 1962; Jonkel and Cowan, 1971). Historically they were probably killed by wolves and several other now extinct Pleistocene carnivores. Today in certain relatively complete ecosystems, such as exist in Mt. McKinley National Park, wolves still interact with grizzly bears. Here G. Haber (personal communication) observed wolves inflicting serious injury to a subadult grizzly bear, as well as wolves trying to get at grizzly cubs of the year while the female bear actively defended them (also see Murie, 1944, 1963). Haber says that grizzly bear-wolf encounters at ungulate kills or carrion were "common" in Mt. McKinley during his 10 years of field work.

The potential for death to young or subadults was enough to be an important selection force. The black bear female with young responds to this problem of potential predation by normally foraging in forested regions. Here the cubs receive protection from possible predation by their ability to climb trees (Figure 3). Black bears have short curved claws which appear to aid in tree climbing. This climbing ability is present early in life upon emergence from the winter den (Herrero, 1970a). The cubs climb readily when presented with unfamiliar stimuli. In this manner they protect themselves from potential predators. To protect her genetic investment, the female needs only to wait nearby or to threaten and chase off potential predators (Figure 4). She does not need to engage potential predators directly; indeed, to do so might result in injury to her and thus reduce her reproductive fitness.

The brown bear by contrast has a different strategy of cub protection. Basically it is a forest bear remodelled to exploit the seasonal productivity of periglacial edges. Today and historically, similar open habitat types are or were found in tundra, grasslands, alpine and subalpine zones, and along oceans, bays, and rivers. The brown bear has not lost its ability to forage on the forest floor, but it gained the ability to exploit open habitat types at their peaks of productivity (Figures 5 and 6). The brown bear has evolved certain characteristics in response to its periodic utilization of open habitat types. Females can defend their cubs in areas where trees do not exist. I hypothesize that they do this by being more aggressive toward conspecifics than are black bear females, especially to certain males, as well as toward other potential predators, including man. This characteristic has allowed them to exploit open habitats, but often places them in conflict with people (Herrero, 1970b, c, 1976).

FIGURE 3. Black bear cub of year climbing a tree.

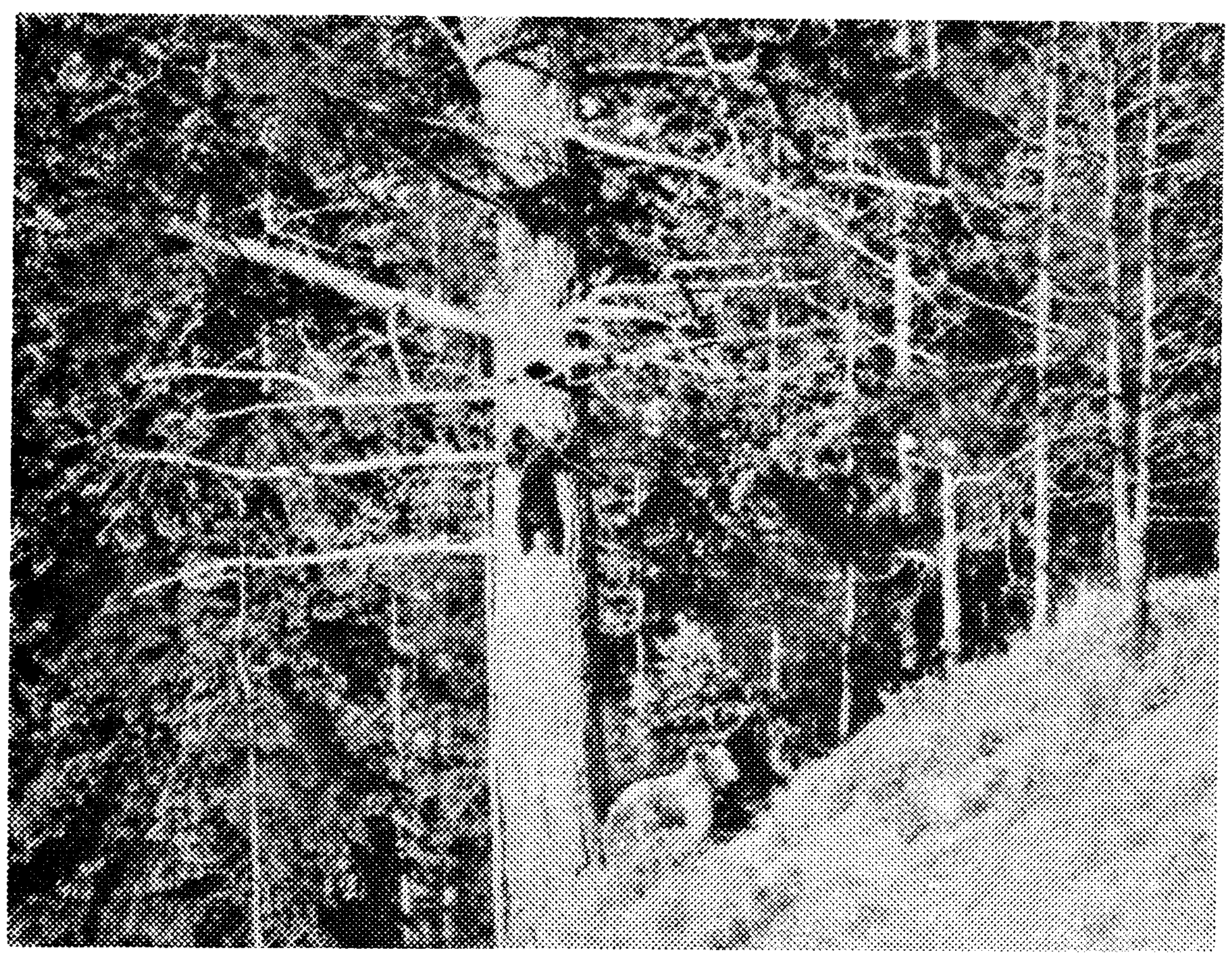

FIGURE 4. Blond color phase black bear female waits at base of tree. The female and her cub were startled by people.

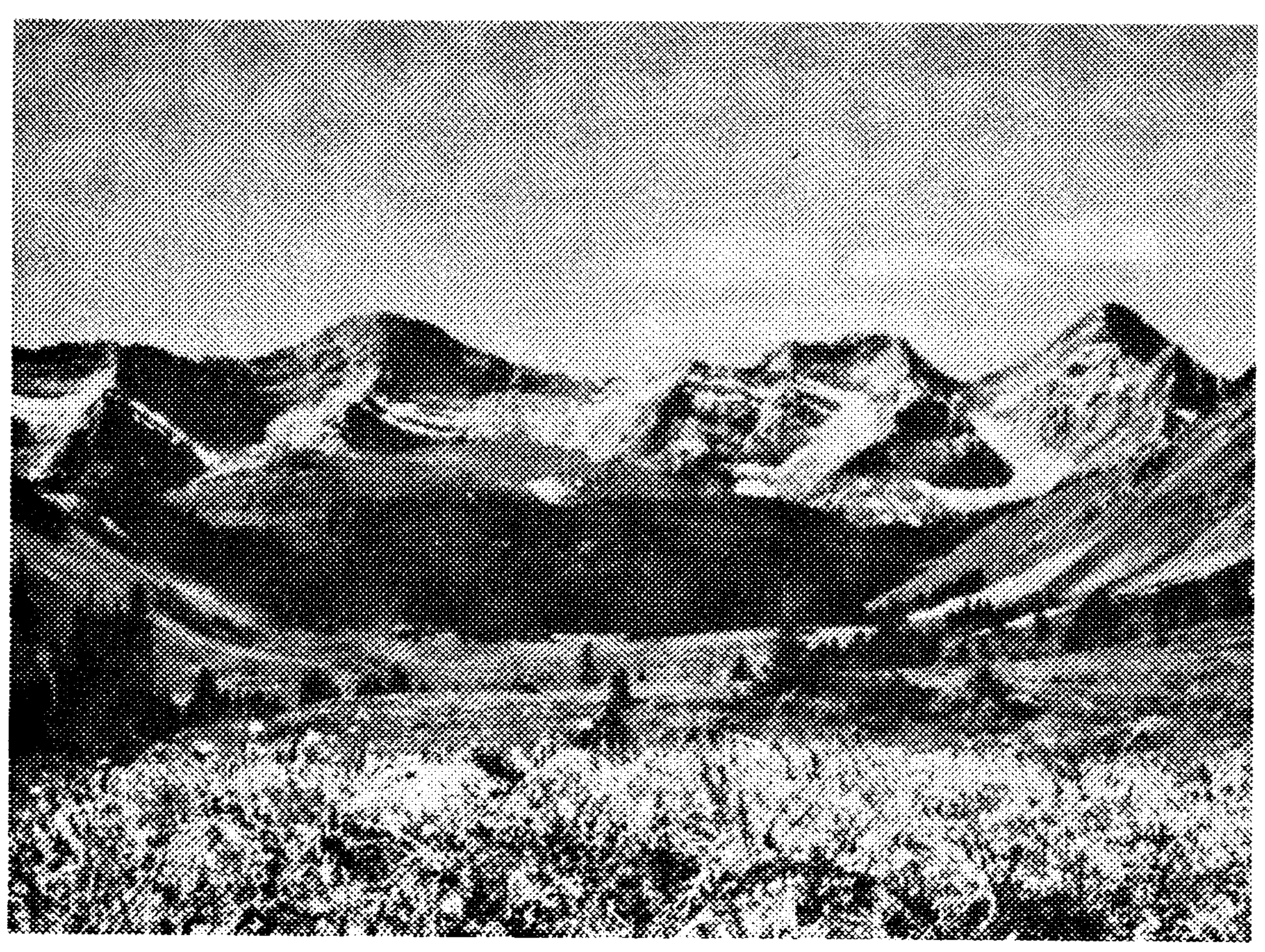

FIGURE 5. Sub-alpine meadow grizzly bear habitat in Banff National Park, Canada.

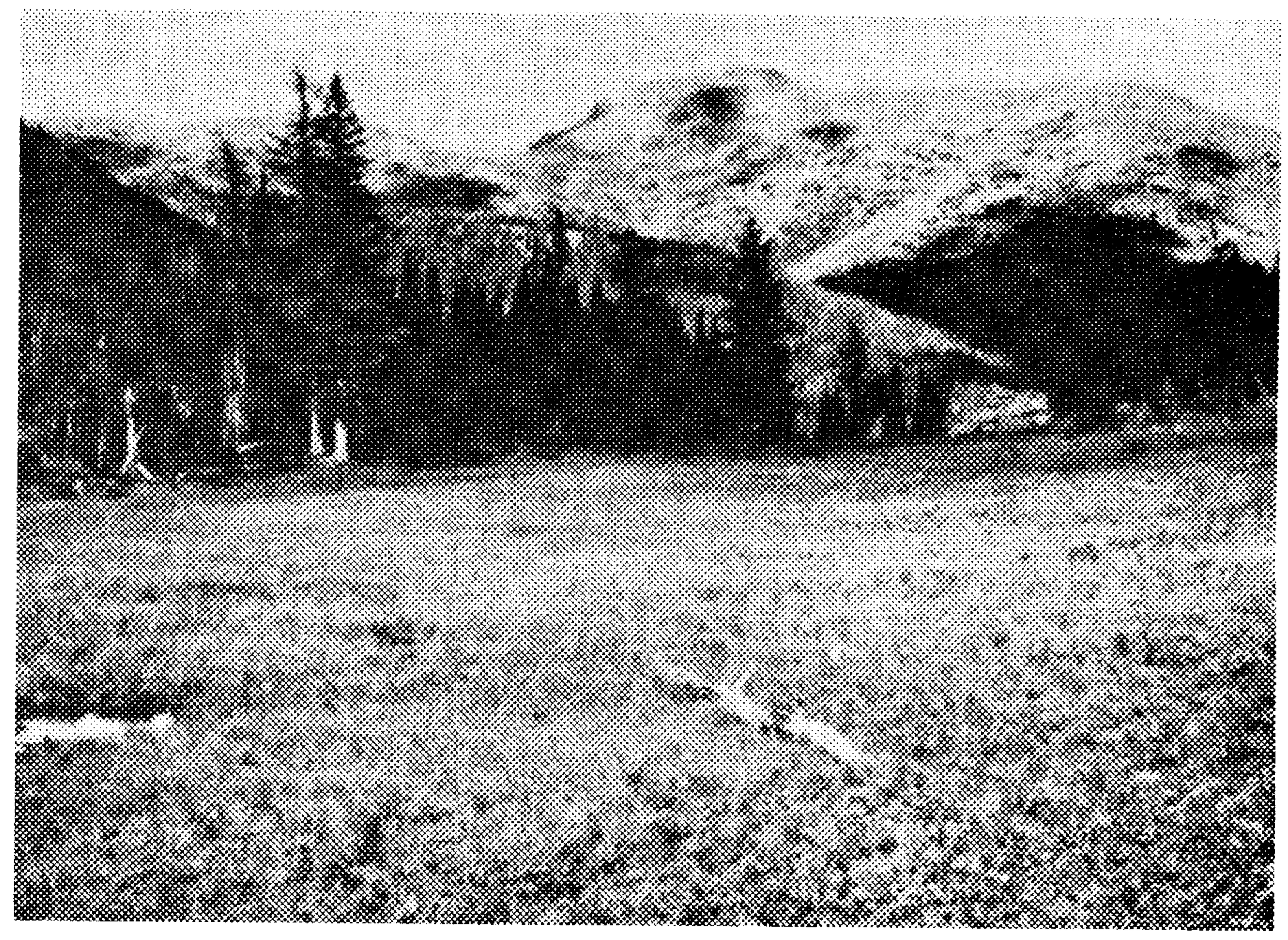

FIGURE 6. Sub-alpine wet meadow grizzly bear summer habitat in Banff National Park, Canada.

Brown bears, when compared to black bears, show other adaptations related to use of open habitat. They have longer front claws which, combined with a larger shoulder and back muscle mass, makes them rapid diggers. Perhaps these features adapted them to exploit ground dwelling rodent populations found in many types of open habitat. The distribution of brown bears was historically quite similar to that of ground squirrels (Banfield, 1964). In at least one area, the Tuktoyaktuk Peninsula in northern Canada, ground squirrels form an important component of the diet today (R. Russell, personal communication). The long claws and digging ability are also advantageous when exploiting other ground-dwelling rodents, and also roots, bulbs, corms, and tubers.

Another brown bear characteristic, when compared to black bears in the same biogeoclimatic zone, is that individuals of the same age-sex class are larger, normally by a factor of 1.5 to 2. (Data are surprisingly lacking, but I compared the data of K. Greer [personal communication] with Barnes, 1967.) Once able to exploit the productivity of open and forested areas, the evolution of brown bears was in many ways shaped by the nature of the productivity of these environments. As the glaciers retreated brown bears repeatedly moved into unexploited periglacial areas of seasonally abundant vegetative forage. Here the diet also probably contained ungulate carrion or fresh-killed ungulates, as well as ground-dwelling rodents. Under these conditions I would expect the highest possible reproduction rates, and the birth of large and vigorous young (Geist, 1971; Rogers, 1976). With abundant food the cubs could grow rapidly and attain large body sizes.

In summary the black bear is more like the typical ancestral bear—a primarily forest adapted form. Digestively it can utilize the foods of open areas, but behaviorally and anatomically it is more adapted to the forest. The North American brown bear, on the other hand, does not forage by climbing trees for mast and fruits as do black bears in some areas (Pelton and Burghardt, 1976); but otherwise it can utilize high quality plant and animal foods in the forest. Brown bears, moreso than black bears, also venture into open areas to forage.

Both species throughout all but the southernmost parts of their range face periodic food shortage during winter. They each respond to this by hibernation (Folk et al., 1972, 1977).

FOOD HABITS

The distribution and abundance of high quality food items influenced the evolutionary divergence between black and brown bears, as well as the ecology and behavior of each species. The availability of food also appears to directly control the reproductive success of black bears from year to year (Jonkel and Cowan, 1971; Rogers, 1976). It is reasonable to postulate that the same controls operate for brown bears, although this has not been demonstrated. The fact that vegetative foods do not escape, and a lack of predator pressure except on females with young, helps to explain the often solitary foraging behavior of individuals of each species. There appear to be no food resources which individual black or brown bears can better exploit cooperatively in groups. Occasionally, however, food items occur in such an abundance that many conspecifics, and sometimes bears of both species, will congregate together to feed (Hornocker, 1962; Stonorov and Stokes, 1972; Martinka, 1973; Rogers, 1977).

Food is a critical resource, sometimes in short supply because of environmental variability. A basic understanding of food habits is therefore essential to understand the ecology and behavior of each species.

Both black and brown bears are omnivorous, which does not mean that they will eat anything. They have relatively unspecialized digestive systems—essentially a carnivore's digestive system which has been lengthened (Davis, 1964), probably to allow for better digestion and absorption of vegetative matter. They have no cecum and their stomachs are too acidic to support the microflora and microfauna needed for digestion of cellulose (Rogers, 1976). Therefore, they cannot, or can only very poorly, digest the structural components of plants (Mealey, 1975). They are not ruminants, but each species of bear can survive on diets of 95% and more vegetative matter (for example, see: Mundy, 1963; Poelker and Hartwell, 1973; and Hamer, 1974). They do this by maximizing the quality of the food items ingested; for example, choosing items which can be digested by their simple guts. Given this constraint both species are digestively flexible. Starch, sugar from berries and other fruits, animal and plant protein, as well as most animal and plant storage fats, are all digested (Mealey, 1975). The proportions of each in the diet vary greatly from area to area or seasonally (Mealey, 1975, and compare Tisch, 1961, with Pelton and Burghardt, 1976, and with Poelker and Hartwell, 1973).

The digestibility of plant protein has been studied in grizzly bears by Mealey (1975). Plant protein from succulent herbs appeared to be about 43% digestible as compared to about 78% digestibility for animal protein and fat sources. Starch was about 79% digestible; sugar from berries and other fruits was assumed to be highly digestible. Digestibility of food items by black bears has not been studied but could be expected to be similar, though perhaps less efficient with regard to digestibility of plant protein. The grizzly compared to the black bear may have a longer gut (Mealey, 1975).

The ability to digest a wide range of food items is related to the omnivorous diet of each species. Individuals of each species appear to prefer the most digestible energy and nutrient-rich food items which are economically available at a given time. When plant protein is a major item in the diet its relatively low digestibility is counterbalanced by large intake.

Selection for micronutrients is as yet unstudied. With the possible exception of selection for micronutrient needs, both species of bears appear to try to maximize the intake of high quality food items such as: animal tissue, roots, bulbs, tubers, corms, berries, other fruits, mast, and certain grasses, sedges and forbs. Green plant tissue appears to be ingested by grizzly bears mainly during its phenological periods of high protein content and low presence of structural materials such as cellulose (Mealey, 1975). Other things being equal, high plant protein sources appear to be preferred over low plant protein sources. The same general model probably also applies to black bears.

Because of its claws and musculature, the brown bear is more able to exploit food items which occur in the soil and must be dug (Figures 7 and 8). The black bear being the more adept climber can more effectively forage for mast where it occurs and when it is still on trees (Pelton and Burghardt, 1976). For the most part, there appears to be a great deal of potential food item overlap between the species. In areas of sympatry brown bears appear to have a competitive advantage over black bears in open habitat types (Shaffer, 1971) (Figure 9). I relate this to the former's evolutionary history, especially their aggressive defense of young and their average larger body sizes.

FIGURE 7. A startled adult female grizzly bear. Note the long front claws.

In general, the body weights attained by individuals of each species reflect the productivity of the ecosystems where they forage. Within a given geographic area such as the so-called Yellowstone ecosystem, similar age-sex grizzly bears are roughly 1.5 to 2 times larger than black bears (compare the data of . Greer [personal communication] with Barnes, 1967). Black bears in productive food areas such as Michigan (Erickson et al., 1964) may have average weights almost equivalent to weights of grizzly bears found in food-poor areas such as the interior Yukon Territory (Pearson, 1975).

FIGURE 8. Extensive grizzly bear diggings for the roots of *Hedysarum* spp., Banff National Park, Canada.

FIGURE 9. Adult female grizzly bear with older offspring travelling through a sub-alpine glade.

Many aspects of the ecology and behavior or bears can be understood by reference to the foraging strategy of each species. I shall try to treat two topics from this perspective: firstly, reproductive strategy, and secondly, the use of space and its relationship to reproductive strategy.

REPRODUCTIVE STRATEGY

Both black and brown bears have low reproductive rates. It is commonly believed that where both species occur within the same biogeoclimatic zone black bears have a significantly higher reproductive rate. Evidence for this view is largely inferential and incomplete. Detailed population and reproductive studies have not been carried out where both species occur in the same region.

An understanding of reproductive rates is fundamental for management of a bear population. It is also essential for understanding the reproductive strategy of males and females of a species. For bears, reproductive rate can be calculated by taking the average number of cubs produced per adult female per year and dividing this by the average length of the reproductive cycle (Craighead et al., 1974). To calculate reproductive rate one has to know three parameters for a population: average age of first reproduction, average litter size, and average duration between litters. Each of these reproductive parameters has been shown to vary in response to ecosystem productivity, both from year to year and from area to area. Certain parameters would be expected to vary with hunting pressure and, in general, with the numerical status of the population. These points will subsequently be documented and discussed. They are pointed out here because they help to identify the difficulties in determining reproductive rates. What is required are detailed long-term or cross-sectional population and reproductive studies within a given area.

Only one study of one species thoroughly meets these criteria. Craighead et al. (1974) report an average reproduction rate of 0.658 and an average reproductive cycle of 3.40 years for 30 grizzly bear females in Yellowstone National Park. Reproductive rates have also been calculated for black bears in Idaho: 0.782 (Reynolds and Beecham, 1977), and Oregon: 1.07 (Lindzey, 1976). Calculation of black bear reproductive rates was based upon a small sample (5 females) in the Reynolds and Beecham study. Lindzey's work used a large cross-sectional sample (242 females collected by hunters over a three-year period). This contrasts with the Craighead et al. (1974) approach where a much smaller number of individually identified females had their reproductive histories studied longitudinally. Both the cross-sectional and longitudinal approaches should work equally well; however, a longitudinal study would better represent the influence of year-to-year environmental variability and population number variability on reproductive rate. Unfortunately, we cannot directly compare the figures of Craighead et al. (1974) with Lindzey (1976) because they were calculated in different biogeoclimatic zones; and the Lindzey population was fairly heavily hunted as compared to the Craighead et al. population which occurred mainly in an unhunted national park. The figures derived by Craighead et al. (1974) and Lindzey (1976) will help to establish the range of variability of reproductive rate after other studies are completed.

Table 1 briefly details the key reproductive parameters found by various workers throughout North America. I have only included results from major studies, and normally only those results based upon population studies of known-age individuals.

Some conclusions which seem merited from consideration of these are: 1) age of first parturition and duration of reproductive cycle are quite variable for each species; 2) the average number of offspring varies within a small range from one biogeoclimatic zone to another for a given species (although standard deviations were seldom available, sample sizes were commonly large and differences were probably significant); and, 3) productivity for black bear and brown bear populations cannot yet be validly compared.

TABLE 1. Reproductive Data From Adult Female Black and Brown Bears

BLACK BEARS

Mean litter size (#), mean placental scar rate (*), mean number of corpora lutea (+)		Hunted (X) or for the most part unhunted ( )	Studied by	Where studied
2.05 #		X	Erickson et al. (1964)	Michigan & Alaska
1.65 #		X	Jonkel & Cowan (1971)	Montana
1.88 *		X	Poelker & Hartwell (1973)	Washington
2.29 + (for females 5 yrs. & older)		X	Lindzey (1976)	Oregon
1.9 #		X (heavily hunted, at least prior to study)	Reynolds & Beecham (1977)	Idaho
Age of 1st estrus	Age of 1st reproduction			
3.5	-	X	Erickson et al. (1964)	Michigan & Alaska
4.5	1st cubs in a sample of 3 females not conceived until 6.5, 7.5 & 8.5 yrs.	X	Jonkel & Cowan (1971)	Montana
	Successful breeding by 3.5 yrs. for some individuals. Sexual maturity in 44% by their 4th summer; all by 5th summer.	X	Poelker & Hartwell (1973)	Washington
	Most, if not all, 5 yr. old females had been pregnant either as 3 or 4 yr. olds.	X	Lindzey (1976)	Oregon
	First breeding, 3.5 yrs. (N=3), 4.5 yrs. (N=5), 5.5 yrs. (N=1)	X (see prior reference)	Reynolds & Beecham (1977)	Idaho
	80% bred at 3.5 yrs.	?	Collins (1973)--as cited in Reynolds & Beecham (1977)	North Carolina
Frequency of litters				
2 females had 2 litters each within a 3 yr. period. 9 others had no litters for at least 2 consecutive years, and 2 skipped 3 yrs.		X	Jonkel & Cowan (1971)	Montana
"Corrected" lactation rate of 19% and estrus rate of 31%		X	Poelker & Hartwell (1973)	Washington
Mean litter frequency of 31% (for 3 yrs.)		X (see prior reference)	Reynolds & Beecham (1977)	Idaho
Reproductive rate				
1.07 for females 5 yrs. and older based on corpora lutea counts; however, 3 and 4 yr. old females had lower reproductive rates.		X	Lindzey (1976)	
0.782 based on 5 reproductive cycles of 4 females		X (see prior reference)	Reynolds & Beecham (1977)	

TABLE 1 (Cont.)

BROWN BEARS

Mean litter size	Hunted (X) or for the most part unhunted (0)	Studied by	Where studied
2.36	X	Troyer & Hensel (1964)	Alaska (Kodiak National National Wildlife Refuge
2.33	X	Hensel et al. (1969)	Alaska Peninsula
1.7	0	Martinka (1971)	Montana (Glacier National Park)
2.0	0	Mundy & Flook (1973)	British Columbia (Glacier National Park)
1.75-2.50	0	Craighead et al. (1974)	Wyoming (Yellowstone National Park)
1.7	0	Pearson (1975)	Yukon Territory (Kluane National Park)

Age of 1st estrus	Age of 1st reproduction			
3-6; usually at 4	3 for some females	X	Troyer & Hensel (1964)	Alaska (Kodiak National Wildlife Refuge)
4.5	7 had 1st litters at 5, 2 at 6 yrs., 4 at 7 yrs. and one each at 8 & 9	0	Craighead et al. (1969)	Wyoming (Yellowstone National Park)
6.5	3 first bred at 6.5, 3 others at 7.5, one at 8.5	0	Pearson (1975)	Yukon Territory (Kluane National Park)

Frequency of litters			
Normally bred at 3 yr. intervals	X	Hensel et al. (1969)	Alaska Peninsula
Reproductive cycle of individual females varied from 2-7 yrs. Mean reproductive cycle was 3.40 yrs.	0	Craighead et al. (1974)	Wyoming (Yellowstone National Park)
Normal interval between litters at least 3 yrs.	0	Pearson (1975)	Yukon Territory (Kluane National Park)

Reproductive rate 0.658	0	Craighead et al. (1969)	Wyoming (Yellowstone National Park)

The main environmental variable which has been identified as influencing reproductive output is the nutritional status of the female during the fall. Jonkel and Cowan (1971) were the first to convincingly correlate low reproductive output with major food crop failure for black bears. Rogers (1976), working with the same species, has convincingly documented a more general hypothesis linking reproductive output to nutritional status of the female. Rogers found that only females able to attain a certain weight in fall gave birth in spring. Postconception food crop failure appeared to induce some form of abortion in already impregnated females. Bears have delayed implantation of the fertilized embryo. This gives them what seems to me to be an opportunity for energetically inexpensive abortion. I suspect, although it has not been demonstrated, that pregnant female brown bears respond to nutritional status in the same manner. Rogers' work on black bears also showed that high calorie intakes during captivity or at rich food sites such as dumps advanced the age of sexual maturity by almost two years.

Nutrition is also suggested as a major variable influencing reproduction when productivity for the same species is compared across different biogeoclimatic zones. Several studies suggest that black bear populations have the highest productivity in the eastern United States where mast is a normal and energy-rich component of the diet (Spencer, 1955; Harlow, 1961; Stickley, 1961; Erickson et al., 1964; Collins, 1973; Rogers, 1977). Collins (1973), for example, found in North Carolina that 80% of the females first breed by 3.5 years. Generally, black bears in the eastern USA appear to have a lower minimum breeding age, higher inferred reproductive rates, and heavier body weights. Similarly, coastal areas (Poelker and Hartwell), 1973; Lindzey, 1976) appear to allow for higher inferred reproductive rates than do interior areas with continental climates (Jonkel and Cowan, 1971; Reynolds and Beecham, 1977). This last comparison, coastal versus continental area population productivity, can also be made for brown bear populations (Troyer and Hensel, 1964; Hensel et al., 1969, for coastal populations; Craighead et al., 1974; Pearson, 1975, for interior populations), and it shows the same trend.

Hunting by man probably is an important variable influencing population structure and probably influencing reproductive output via parameters such as the quality of vacant habitat and the social aspects of intraspecific competition. Intensity of hunting has not been clearly documented in any studies.

I conclude that reproductive data for black and brown bear populations have major limitations which inhibit further insight which might be gained by comparing the reproductive ability of the two species. (This contradicts Herrero [1977] who, based on more superficial examination of data, reached different conclusions.)

The conclusion that each species has a low reproductive rate is valid. Related to this, each species has a high maternal investment in care of offspring. Once the cubs are born the female attempts to maximize her reproductive fitness by intensive care and education of offspring. Defense of young has been discussed and is an important dimension of the female's maternal investment. Exactly what cubs learn from females has not been studied except anecdotally by Krott and Krott (1962). Casual observation suggests that cubs at least learn considerable information related to suitable food items and their seasonal occurrence.

Young male offspring normally disperse from the female's home range; but young females may remain, eventually being incorporated into the home range of the adult female (Jonkel and Cowan, 1971; Pearson, 1975; Rogers, 1976). Rogers (1976) implies that adult females may try to expand their own home range in order to accommodate some of their female offspring. Adult female bears thus invest heavily in their offspring.

Regarding the reproductive strategy of adult females of both species, the individual female's reproductive fitness would be maximized by choosing to mate with the "best" male (a male bear whose inclusive genetic fitness is highest). It appears, however, that males do the choosing. Grizzly bear males become especially aggressive during the breeding season and larger, more aggressive males normally dominate smaller individuals (Hornocker, 1962). Both species are sexually dimorphic and males are about 1.5 times larger than females (Jonkel and Cowan, 1971; Pearson, 1975). It is appealing to assume that larger, dominant individual males do much of the breeding, and that there is strong selection pressure for large, aggressive males. Data are lacking, but both sexes of both species can be promiscuous; therefore, it is possible for one male to mate with several females. Whether a female can be impregnated by more than one male is unknown. Poelker and Hartwell (1973) consider it unlikely that females are polyandrous, but Rogers (1977) considers to to be likely. Craighead et al. (1969) observed female grizzly bears copulating with one or two males in one day, and up to four different males in one season.

Males of both species appear to compete with one another for mates and to attempt to maximize their fitness by copulating with as many females as is possible. Spermatogenic activity in males has been shown to precede as well as exceed the period of receptivity in females (Erickson et al., 1964; Poelker and Hartwell, 1973; Pearson, 1975). The number of females which a male can mate is probably influenced by variables such as population density and distribution during the mating season. For example, the Craigheads (Craighead et al., 1969) found that adult grizzly bears of each sex were promiscuous near concentrated food sources such as dumps. By contrast, we (Herrero and Hamer, 1977) observed one male grizzly bear which isolated a single female on top of a mountain for two weeks. She copulated with the male at the end of this period. Both male and female grizzly bears therefore appear to have flexible reproductive strategies, depending perhaps upon population density and the probability of finding a mate. The area where we observed the isolation of the female was one of low population density compared to Yellowstone near the dumps. Even the most aggressive male at Yellowstone had trouble isolating and defending a female (Hornocker, 1962); it would not appear to be to the male's advantage to do so under these conditions. Whether males are able to select for female quality is unknown.

Given a flexible strategy with respect to the degree of isolation and defense of females versus the extent of promiscuity, we can still ask what makes a reproductively successful male. I speculate that, for both species, the successful male is aggressive enough, coupled with his size, to be able to dominate other males, and use his social status to gain access to reproductively ready females. He also wanders far enough during the breeding season to be able to locate females, primarily, I assume, by their scent.

A possible aspect of the male's reproductive strategy is infanticide: some males may occasionally kill cubs (Troyer and Hensel, 1962; Hornocker, 1962; Jonkel and Cowan, 1971; also, see Kemp, 1976). We do not know who kills whom, but it is consistent with evolutionary theory to assume that males will not kill their own offspring and will have evolved some means of preferentially killing the offspring of other males. This has been well documented for other species such as lions and langurs (Sugiyama, 1967; Schaller, 1972; Eisenberg et al., 1972; Bertram, 1975).

THE USE OF SPACE AND ITS INFERRED RELATIONSHIP TO REPRODUCTIVE STRATEGY

Understanding the use of space by bears is where radiotelemetry has paid the greatest dividends. I summarize what is known about the use of space and then relate information about the use of space to the concept of reproductive strategy:

1. Home range use is primarily influenced by food quality, availability, and distribution (Stickley, 1961; Hatler, 1966; Jonkel and Cowan, 1971; Amstrup and Beecham, 1976; Reynolds and Beecham, 1977; Craighead, 1977).

2. For each species, adult males have home ranges two to four or more times as large as those of adult females. Adult male home ranges overlap the home ranges of several females (Jonkel and Cowan, 1971; Poelker and Hartwell, 1973; Pearson, 1975; Amstrup and Beecham, 1976; Lindzey, 1976; Reynolds and Beecham, 1977).

3. Home ranges of adult males commonly overlap, but at least in some areas a major core portion of adult female home ranges are mutually exclusive. Some have argued that females can be territorial (Jonkel and Cowan, 1971; Pearson, 1975; Rogers, 1976). Lindzey (1976) relates spacial and temporal separation of adult female black bears to linear dominance relationships. He also postulates that cases of overlapping home range may be explained by the relatedness of individuals whose home ranges overlap. Reynolds and Beecham (1977) argue convincingly that adult female black bears are not territorial and they explain the lack of overlap of core home range areas as being due to mutual avoidance behavior at home range boundaries, which would contrast with active defense of a territory. In at least one study of grizzly bears home ranges of both males and females were shown to have significant overlap (Craighead, 1977). Despite the evidence which demonstrates significant spacial and temporal separation of female bears in most biogeoclimatic zones, there are still occasional seasonal concentrations of bears of each species and both sexes at major food sources such as salmon streams, garbage dumps, or extensive berry patches. Here heirarchical relationships appear to exist (Stonorov and Stokes, 1972; Rogers, 1977).

Both species of bears appear to be somewhat socially flexible in the use of space, the system of spacing chosen being related to relative evenness versus concentration of food and to the defendable nature of a food source. Because of their smaller home ranges, females are more apt to utilize a type of spacial and temporal isolation having little overlap.

4. The size of the home range for an individual of a given age-sex class appears to be related to how seasonally complete and productive the environment is with regard to food. This point is more clearly demonstrated for brown bears than for black bears. In interior areas such as the Yukon Territory west of the St. Elias range and in Yellowstone National Park, brown bear foods are relatively dispersed in time and space, which results in large home ranges. In coastal Alaska, however, home ranges are smaller, presumably because all brown bear forage requirements can be met within significantly smaller areas (Berns et al., 1977; Atwell et al., 1977). The degree of spacial and temporal isolation of individuals has not yet been reported for these coastal Alaska populations. Work needs to be done to quantify the food productivity of different areas for each species and its relationship to the use of space by individual age-sex classes.

5. Within a given geographic area where black bears and brown bears are sympatric, brown bears normally have significantly larger home ranges than do black bears (compare the data of Craighead, 1977, to that of Barnes, 1967, for Yellowstone). This may reflect the greater energy needs of the larger brown bear, as well as the brown bear's ability to exploit both open as well as forested areas. The brown bear moves freely from one highly productive site to another and is outcompeted only by people. In open areas the black bear normally (but not always) defers to both brown bear and man (Barnes, 1967; Shaffer, 1971).

6. Home range size and location for adult black bears can be dynamic. Alt (1977) reports changes in home range size related to reproductive status, and especially with regard to the seasonal development and distribution of food sources. Reynolds and Beecham (1977), also with black bears, found that for adult males the annual center of home range location varied significantly between years. However, others have shown stability of home range locations (Jonkel and Cowan, 1971; Amstrup and Beecham, 1976). Again, flexibility in the use of space is suggested. A similar flexibility in the use of space probably also exists for brown bears. The controlling variable appears to be the quality, distribution, and abundance of food items.

Points one through six can be interpreted as showing that the use of space is a central element in the foraging strategy of both species of bears and for both sexes. Combining this information with points previously raised, space appears to be used by bears of each species in order to gain access to at least three critical resources: food, mates, and a relatively safe area where females raise offspring. Each variable is a key component of reproductive strategy.

The female's reproductive success appears to be related to her level of nutrition. The value of a productive home range is therefore expressed in the death or life of offspring. After weaning, the reproductive success of at least the female offspring appears to sometimes be related to the mother assisting the offspring to establish a home range adjacent to and partly including that of the mother. The female's smaller home range, as compared to that of males', appears to require her to forage more intensively than do males. This is based on the assumption that, despite her smaller body size, her energy needs are high during lactation; and at other times she shares food with offspring. Her smaller home range may respond to certain needs related to cub care. It likely means that during the breeding season males must find females rather than the converse.

Pearson (1975) found that shortly after emergence from hibernation females with young will go to high altitude areas where little forage exists. He interpreted this as possibly being related to protection of the offspring from marauding males. Possible spacial isolation of females with young from adult males has not been reported for black bears or, by others, for brown bears.

The home ranges of mature males of each species normally overlap those of three or more females. This appears to allow the males access to several potential mates. Despite extensive home range overlap of adult males, they still must compete, possibly including infanticide. Kemp (1976) found that when mature adult black bear males were removed from a population, within two years the population size and density doubled. It subsequently began a decline, supposedly returning toward original carrying capacity as immature males became mature. It appears that dispersing subadult males move until they find unoccupied habitat, or habitat for which they can successfully compete.

We may now have further insight as to why bears of both species are relatively solitary. Except when engaging in courtship and copulation, or when females are with young, or when some siblings remain together after weaning (as a social unit they have increased safety and status and hence foraging ability), or when attracted to concentrated food sources, individuals of each species of bear can most effectively forage when solitary. There is no advantage conferred to larger groups either for foraging, mating, or in the protection of young. One exception may be occasional alliances of several female bears and their offspring (Murie, 1944, 1963; Craighead et al., 1969; G. Haber, personal communication), which could offer better protection against marauding male bears.

In bears, and all species, sociality and other behavior have been molded by ecological opportunity interacting with the genetic makeup of ancestral species. The manner in which individuals of a bear population exploit a given biogeoclimatic zone has been shown to be somewhat flexible and to depend primarily on spacial and temporal distribution of resources, and the constraints and patterns imposed by the evolutionary history of the species. This flexibility goes much further than I have here been able to discuss. It extends to the level of the individual bear, each of which has certain idiosyncracies in the manner in which it exploits resources and attempts to propagate its genes.

LITERATURE CITED

Alt, G. L. 1977. Dynamics of home range and movements of black bears in Northeastern Pennsylvania. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.

Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. *Journal of Wildlife Management* 40(2): 340-348.

Atwell, G., D. L. Boone, J. Gustafson, and V. D. Berns. 1977. Brown bear summer alpine habitat requirements on the Kodiak National Wildlife Refuge. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.

Banfield, A. W. F. 1964. Grizzly territory: Exact range of arctic bears is obscured by old rumors. *Natural History* 73(3): 22-27.

Barnes, V. G. 1967. Activities of black bears in Yellowstone National Park. MSc Thesis, Colorado State University, Fort Collins.

Berns, V. D., G. C. Atwell, and D. L. Boone. 1977. Fall brown bear habitat use and movements at Karluk Lake on Kodiak Island. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.

Bertram, B. C. R. 1975. The social system of lions. *Scientific American* May: 54-65.

Colbert, E. H. 1955. *Evolution of the Vertebrates*. John Wiley and Sons, New York.

Craighead, J. J. 1977. Critical habitat concept as applied to grizzly bears. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.

Craighead, J. J., M. G. Hornocker, and F. C. Craighead. 1969. Reproductive biology of young female grizzly bears. *Journal of Reproduction and Fertility* Supplement 6: 447-475.

Craighead, J. J., J. R. Varney, and F. C. Craighead. 1974. A population analysis of the Yellowstone grizzly bears. Montana Forest & Conservation Experiment Station, University of Montana, Missoula 40: 20 pp.

Davis, D. D. 1964. The giant panda, a morphological study of evolutionary mechanisms. Chicago Natural History Museum, *Fieldiana Zool. Mem.* 3: 339 pp.

Eisenberg, J. F., N. A. Muckenhirn, and R. Rudran. 1972. The relation between ecology and social structure in primates. *Science* 176: 863-874.

Erickson, A. W., J. Nellor, and G. A. Petrides. 1964. The black bear in Michigan. Agricultural Experimental Station, Michigan State University, East Lansing, *Research Bulletin* 4.

Folk, G. E., M. A. Folk, and J. J. Minor. 1972. Physiological condition of three species of bears in winter dens. Pp. 107-124, *In:* S. Herrero (Ed.), *Bears--Their Biology and Management,* New Series #23, International Union for Conservation of Nature, Morges, Switzerland.

Folk, G. E., J. M. Hunt, and M. A. Folk. 1977. Hibernating bears: Further evidence and bioenergetics. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.

Geist, V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. University of Chicago Press.

Hamer, D. 1974. Distribution, abundance, and management implications of the grizzly bear and mountain caribou in the Mountain Creek Watershed of Glacier National Park, B.C. MSc Thesis, University of Calgary.

Hensel, R. J., W. A. Troyer, and A. W. Erickson. 1969. Reproduction in the female brown bear. *Journal of Wildlife Management* 33(2): 357-365.

Herrero, S. 1970a. A black bear and her cub. *Animals* 12(10): 444-447.

Herrero, S. 1970b. Human injury inflicted by grizzly bears. *Science* 170: 593-598.

Herrero, S. 1970c. Man and the grizzly bear (past, present, but future?). *Bio Science* 20(21): 1148-1153.

Herrero, S. (Editor). 1972a. *Bears: Their Biology and Management*. New Series #23, International Union for Conservation of Nature, Morges, Switzerland.

Herrero, S. 1972b. Aspects of evolution and adaptation in American black bears *(Ursus americanus* Pallus) and brown and grizzly bears *(U. arctos* Linne) of North America. Pp. 221-231, *In:* S. Herrero (Ed.), *Bears--Their Biology and Management*. New Series #23, International

Union for Conservation of Nature, Morges, Switzerland.
Herrero, S. 1976. Conflicts between man and grizzly bears in the National Parks of North America. Pp. 121-145, *In:* M. Pelton, J. W. Lentfer, and G. E. Folk (Eds.), *Bears--Their Biology and Management,* New Series #40, International Union for Conservation of Nature, Morges, Switzerland.
Herrero, S. 1977. Black bears: The grizzlies' replacement? Paper delivered to Black Bear Workshop, sponsored by the Boone & Crockett Club, Feb. 1977, Kalispell, Montana (proceedings also in press).
Herrero, S., and D. Hamer. 1977. Courtship and copulation of a pair of grizzly bears--with comments on reproductive plasticity and strategy. *Journal of Mammalogy* 58(3): 441-444.
Hornocker, M. G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. MS Thesis, Montana State University, Missoula.
Jonkel, C., and I. McTaggart Cowan. 1971. The black bear in the spruce-fir forest. *Wildlife Monograph* 24: 57 pp.
Lindzey, F. 1976. Black bear population ecology. PhD. Thesis. Oregon State University, Corvallis.
Kemp, G. A. 1976. The dynamics and regulation of black bear, *Ursus americanus,* populations in Northern Alberta. Pp. ___-___, *In:* M. R. Pelton, J. W. Lentfer and G. E. Folk (Eds.), *Bears--Their Biology and Management,* New Series #40, International Union for Conservation of Nature, Morges, Switzerland, 467 pp.
Krott, P., and Krott, G. 1962. Zum verhalten das braun baren *(Ursus arctos* L. 1758) in den Alpen. *Zeitschrift fur Tierpsychologie* 20: 160-206.
Martinka, C. 1973. Interim report on grizzly bear research. U.S. Government memo dated Oct. 25, 1975, Glacier National Park, U.S.A.
Martinka, C. J. (Editor). *Proceedings of the Fourth International Conference on Bear Research and Management.*
Mealey, S. P. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973-1974. MSc Thesis, Montana State University, Bozeman.
Mundy, K. 1963. Ecology of the grizzly bear *(Ursus arctos)* in Glacier National Park, British Columbia. MSc Thesis, University of Alberta, Edmonton.
Murie, A. 1944. *The Wolves of Mt. McKinley.* Fauna Series #5. U.S. Dept. of the Interior, Washington, D.C.
Murie, A. 1963. *A Naturalist in Alaska.* Doubleday Anchor Books, Garden City, New York.
Pearson, A. 1975. The northern interior grizzly bear *(Ursus arctos* L.). Canadian Wildlife Service, Report Series #34: 84 pp.
Pearson, A. M. (Editor). 1968. *Proceedings of the First Bear Workshop.* Whitehorse, Yukon. Canadian Wildlife Service, Edmonton.
Pelton, M. R., and G. M. Burghardt. 1976. Black bears of the Smokies. *Natural History* 85(1): 54-63.
Pelton, M. R., J. W. Lentfer, and G. E. Folk (Editors). 1976. *Bears--Their Biology and Management.* New Series #40, International Union for Conservation of Nature, Morges, Switzerland.
Poelker, R. J., and H. D. Hartwell. 1973. *Black Bears of Washington.* Washington State Game Department Biological Bulletin 14: 149 pp.
Reynolds, D., and J. Beecham. 1977. Home range activities and reproduction of black bears in west-central Idaho. Paper delivered to Fourth International Conference on Bear Research and Management, Feb. 21-24, Kalispell, Montana.
Rogers, L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Transaction of North American Wildlife and Natural Resources Conference* 41: 431-438.
Rogers, L. 1977. Movements and social relationships of black bears in northeastern Minnesota. PhD Dissertation, University of Minnesota, St. Paul.
Schaller, G. B. 1972. *The Serengeti Lion: A Study of Predator-prey Relations.* University of Chicago Press, Chicago.
Shaffer, S. C. 1971. Some ecological relationships of grizzly bears and black bears of the Apgar Mountains in Glacier National Park, Montana. MSc Thesis, University of Montana, Missoula.
Stonorov, D., and A. W. Stokes. 1972. Social behavior of the Alaska brown bear. Pp. 232-242, *In:* S. Herrero (Ed.), *Bears--Their Biology and Management.* New Series #23, International Union for Conservation of Nature, Morges, Switzerland.
Sugiyama, Y. 1967. Social organization of hanuman langurs. Pp. 221-236, *In:* S. A. Altman (Ed.), *Social Communication Among Primates.* University of Chicago Press.
Tisch, E. L. 1961. Seasonal food habits of the black bear in the Whitefish Range of Northwestern Montana. MSc Thesis, Montana State University, Bozeman.
Troyer, W. A., and R. J. Hensel. 1962. Cannibalism in brown bear. *Animal Behaviour* 10 (3-4): 231 pp.
Troyer, W. A., and R. J. Hensel. 1964. Structure and distribution of a Kodiak bear population. *Journal of Wildlife Management* 28: 769-772.

REPRODUCTION AND SOCIAL ORGANIZATION OF LIONS FROM THE KRUGER NATIONAL PARK

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Abstract. Reproduction in male and female lions from the Kruger National Park is examined by utilizing material taken from cropped animals and observations made in the field. Subadult males emigrate from the parent group between 27 and 36 months of age while females could either remain in the parent group or emigrate as early as 24 months. All pride males (n=18) were between 5 and 9 years old (mean age = 6.5 years) and no males under 5 years of age associated sexually with adult females. All male lions under 26 months of age were sexually immature, the median age at maturity being 30 months. Female lions reached sexual maturity at between 43 and 66 months of age (mean = 48 months) and all lionesses over 5.5 years of age had previously ovulated. Twenty percent of all parous lions (n=60) were pregnant, 21.7% were lactating, i.e., had cubs <9 months old, 51.7% were non-lactating with or without offspring >24 months old, and 6.7% were sterile. At least 94.7% of all ovulations preceding pregnancy were fertile. Luteinisation of unruptured follicles was found to occur in two pregnant lions, and one pregnant lion out of 12 was found to have resorbed one of her embryos while the other embryo was normal. Lactation lasts for 8 to 9 months and the corpus luteum of pregnancy remains visible for about 1 month post partum. Corpora albicantia and ovulation scars (points) remain visible for considerable periods of time depending on the reproductive state of the female. All females with large cubs were in anestrus (limited ovarian activity). The two oldest females still capable of reproduction were 12 and 13 years old. Mean ovulation rate and litter size were both 3.08 (range = 1-5). Mean litter size for cubs <12 months old was 3.02 (range = 1-4; n = 47 litters) and for cubs 13 to 24 months was 2.71 (n = 7 litters). Most litters of lion cubs are born during the period when the major prey animals of the lion produce their young. Estrus and birth synchronization within social groups were common and some of the possible causes are discussed. No definite cases of pseudopregnancy were found during the study, and it is suggested that the high incidence of reproductive failure reported for wild lions may be due to anovulatory estrous cycles.

INTRODUCTION

Previous studies on reproduction in wild lions *(Panthera leo)* (Linnaeus, 1758) have largely been confined to populations from East Africa (Guggisberg, 1961; Schaller, 1972; Rudnai, 1973a; Bertram, 1975). Eloff (1973) provides some data on lions from the Kalahari while, for the rest, studies have been limited to groups kept in zoos or under semi-wild conditions in lion parks (Steyn, 1951; Brand, 1963; Sadleir, 1966a and b; Eaton and York, 1971; Eaton, 1972, 1974). To date there is no published account on the reproductive biology of wild lions as obtained from material collected from dead animals.

The present study was made possible when material became available from lions experimentally cropped in certain parts of the Central District of the Kruger National Park, South Africa (Smuts, 1975a and b, 1976a and b, in press), when lions were destroyed for humane reasons, or when they strayed into human settlements. Although the collection and analysis of reproductive material was not always accompanied by simultaneous detailed field observations, the social status of most of the animals was known and generally entire groups were available for examination.

In the current study those aspects of reproduction which influence the population dynamics of wild lions have received most attention. The ovaries collected from all the female lions will be subjected to more detailed histological analysis at a later date.

MATERIALS AND METHODS

Between 1974 and 1976 reproductive material was collected from 221 lions (90 males and 131 females) destroyed in the Central District of the Kruger National Park. The ages of all lions were estimated as described by Smuts et al. (in press).

Data on age and sex structure of the lion population in the Central District were taken from Smuts (1976b) where a population of 708 lions inhabit an area of 5,560 sq km. All lions were measured and weighed before rigor mortis set in and skulls collected and cleaned for later examination.

The composition (sexes and ages) of cropped groups was noted while marked animals (Smuts, 1976b; Smuts et al., 1976, 1977) helped in allocating certain individuals to their correct social groups. Known-age lions marked as cubs during 1972 and 1974 provided data on the emigration of subadults from parent groups or their recruitment to new groups. Young lions found in groups where there were no adults were regarded as being independent, i.e., had left the parent group. The following age classes are referred to: cubs (0-24 months), small cubs (0-12 months), large cubs (13-24 months), subadults (25-48 months), and adults (49 months - 16+ years).

Puberty is regarded as the interval of time when reproduction is possible but full reproductive capacity (sexual maturity) has not been reached (Emmens, 1969). It is thus a period when effective mating can occur (Fraser, 1968) and is taken to commence, for male lions, when spermatozoa first become visible in the seminiferous tubules (physiologically mature), and to end when full spermatogenesis is achieved. For females puberty commences with the first estrous cycle and ends at the first conception. In the current study the pubertal interval is the period during which the above events occurred for all male and female samples examined.

Fetal and embryonic ages were estimated by the method of Huggett and Widdas (1951). To determine "t" the conception age of any conceptus, graphically, the following data are required: gestation period (tg) = 108 days (Cooper, 1942; Asdell, 1946; Zuckerman, 1953; Sadleir, 1966a; Eaton, 1974); birth weight (w) = 1.45 kg (Crandall, 1964; Carvalho, 1968; Schaller, 1972; Rudnai, 1973b). From this $\omega^{1/3}$ = 11.32 g while $t_o \simeq 0.2 \times 108$ = 21.6 days (vide Huggett and Widdas, 1951). By plotting "t_o" of 21.6 days the first point is fixed (Figure 1), the "t_g" of 108 days and its ordinate $\omega^{1/3}$ of 11.32 g fixes the second point. By calculating $\omega^{1/3}$ for each conceptus, it is possible to estimate conception age using the graph in Figure 1. Alternatively, "t" can be calculated using the regression equation:

$$\omega^{1/3} = 0.131\ (t - 21.6)$$

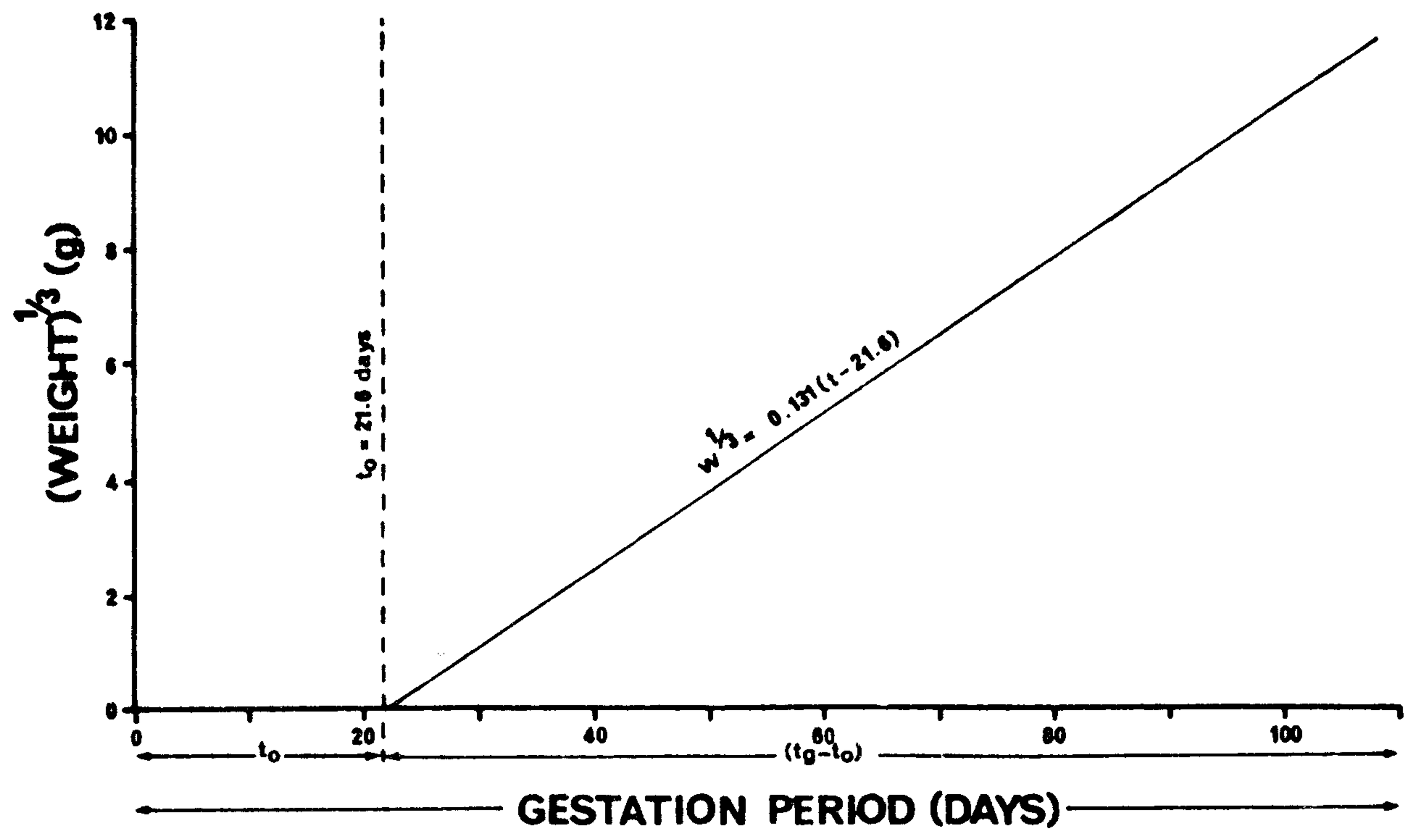

FIGURE 1. Graphical method used to determine "t", the conception age of embryos and fetuses (vide Huggett and Widdas, 1951); t_o is the period during which the conceptus is too small to weigh.

Male Lions

Testes were dissected out and weighed to the nearest 0.1 g. Specimens for histological examination were taken from one testicle and fixed in Bouin's fluid or 10% buffered formalin. The specimens were dehydrated, embedded in paraffin wax, sectioned at 5 to 10µm, and stained with Mayers haematoxylin and eosin. The stained sections of testes were examined microscopically for the presence or absence of spermatogenesis and, in all cases where autolysis did not prevent it, mean seminiferous tubule diameters were obtained using a micrometer eyepiece. Lions were classified as "immature" if the testis showed no histological signs of spermatogenesis, and "pubertal" or "mature," depending on whether partial or full spermatogenesis had been achieved.

Female Lions

Reproductive tracts, including the infra urethral part of the vagina, were removed and examined in the field. In nonpregnant lions uterine scars were counted where present, while in pregnant individuals the number and side of implantations were noted while the corresponding ovaries were marked and fixed in 10% buffered formalin. Embryos and fetuses were weighed in the fresh state and, when possible, their sex was ascertained. Females were tested to see if they had milk or colostrum and were then temporarily classified as adult or subadult, depending on the size of their nipples. Nulliparous females tend to have small nipples when compared to those that have suckled one or more litters.

Extraovarian attachments were dissected away in the laboratory where each ovary was also weighed to the nearest 0.1 g. Ovaries were then sectioned macroscopically so that follicles and corpora lutea could be counted and measured. Only the maximum length of each follicle or corpus luteum was taken by a single measurement. External characteristics such as ovulation points (scars) and shape of the ovaries were also noted. Cervical and vaginal smears were made from two estrous lions, fixed in methanol and stained with 10% Giemsa.

RESULTS

Sex Ratio and Subadult Recruitment and Emigration

The sex ratio for a number of age classes of lions from the Central District is given in Table 1.

Observations on marked lions indicated that six known-age subadult males from 24-28 months of age were still associating with their mothers in the original group. Four known-age females were still with their mothers at 27 and 28 months of age. Utilizing a larger sample (n=21 subadults) taken from groups of unknown origin, subadult males and females between 30 and 36 months and 31 and 48 months, respectively, were frequently found in the same group as adult females. In the case of the males these are assumed to be lions which had not yet emigrated from the parent group. For females, on the other hand, it is possible that some had been recruited into the groups. One known-age 4-year old (marked) female had been recruited into another group 14 km north of her original pride area, while the rest of the litter (two females) were still in the original group when five years old.

The range in ages for lions no longer in association with adults, i.e., groups of subadults cropped together, was between 27 months and 4.5 years for males, 24 and 50 months for females. These lions are assumed to have emigrated from the parent groups at some age, the earliest of which was 27 and 24 months for males and females, respectively. In summary, therefore, subadult males emigrate from the parent group between 27 and 36 months of age while females could either remain in the parent group or emigrate at as early as 24 months.

Male Reproduction

Social Organization

The youngest adult pride males (territorial males) were five years old (range = five to nine years) with a mean of 6.5 years and a modal age of six (n=18). Modal number of adult males per pride for the study area was two, the average being 2.1 (range = one to five) (n=60 prides). Only two adult males in a sample of 25 were over nine years of age, the one being 10 and the other 16 years old. The 16-year old was in a poor physical condition, and both were nomadic. Young males between four and five years of age often banded together, the largest group being seven. None of these seven lions was associating with adult females, but the lions behavior toward carcasses indicated that they were possibly on the verge of replacing three resident adult males who were estimated to be between seven and nine years old.

Puberty and Sexual Maturity

The first spermatozoa were found in the seminiferous tubules at 26 months of age, when the combined testes weight was 13 g, and mean seminiferous tubule diameter was 120 µm (Figures 2 and 3). The median age at the start of spermatogenesis was, however, 30 months and at this age the combined testes weight was approximately 20 g, and mean seminiferous tubule diameter approximately 140 µm (Figures 2 and 3). All lions over 34 months had spermatozoa in their seminiferous tubules. The relationship between total body weight and combined testes weight was exponential (Figure 4), the largest lions tending to have the largest testes. The two smallest lions which showed signs of spermatogenesis both weighed 110 kg; the largest lion showing no spermatogenesis weighed 137 kg (Figure 4). On the average, adult males (5+ years old) weigh 188.8 kg (n=22).

TABLE 1. Sex ratio of Lions from the Central District of the Kruger National Park as Obtained from Cropped Lions (Prenatal Sex Ratio) and from a Field Survey Conducted during 1974 and 1975 (Smuts, 1976b).

Age	Sample		Ratio		Chi-square value	P-value
	Males	Females	Males	Females		
Embryos & Fetuses	16	12	1	0.75	-	-
0-12 months	31	45	1	1.45	2.58	P>0.05
13-24 months	40	38	1	0.95	0.02	P>0.05
0-24 months	71	83	1	1.17	0.93	P>0.05
2-4 years	77	44	1	0.57	9.00	P<0.005
4-16 years	122	251	1	2.06	44.61	P<0.001
0-16 years	211	319	1	1.51	22.00	P<0.001

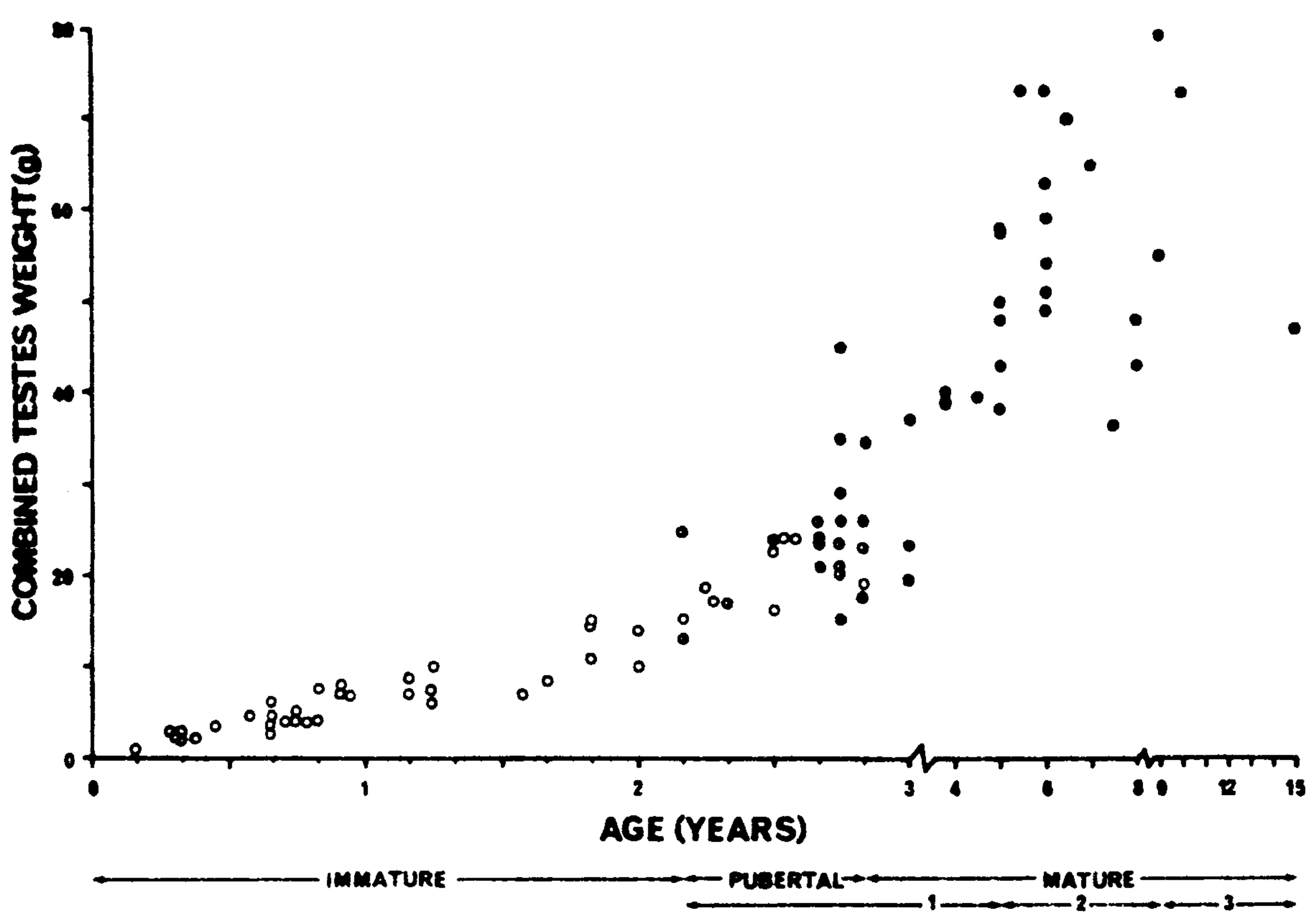

FIGURE 2. Growth in weight of testes with age. (0) No spermatogenesis; (0) slight spermatogenesis; (0) full spermatogenesis. The classes 1,2 and 3 refer to: (1) physiologically mature (26 months to 5 years); (2) psychologically mature (5 to 9 years); and, (3) past prime (9 to 16 years).

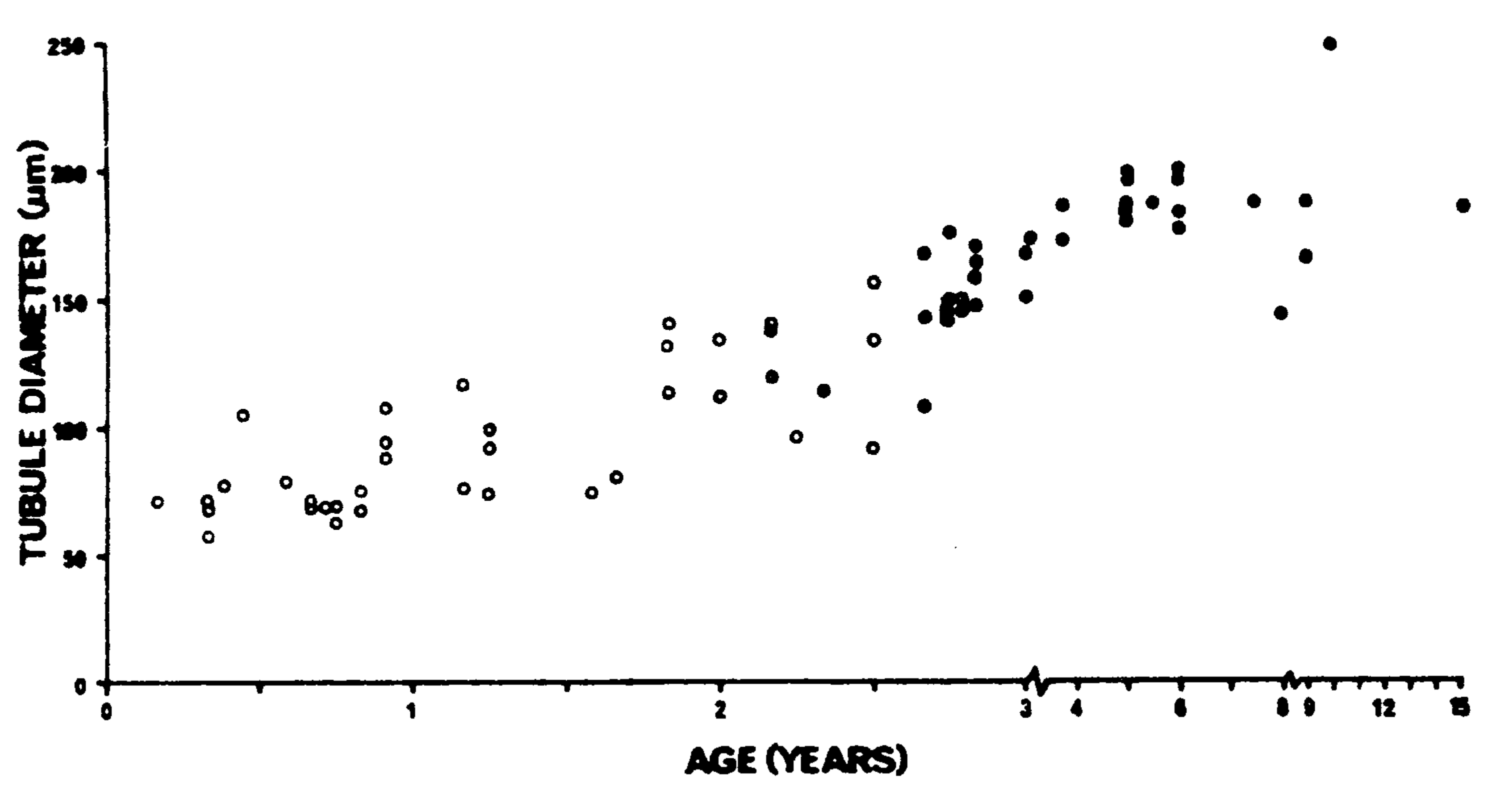

FIGURE 3. Variation in mean seminiferous tubule diameter with age. (0) no spermatogenesis; (0) slight spermatogenesis; (0) full spermatogenesis.

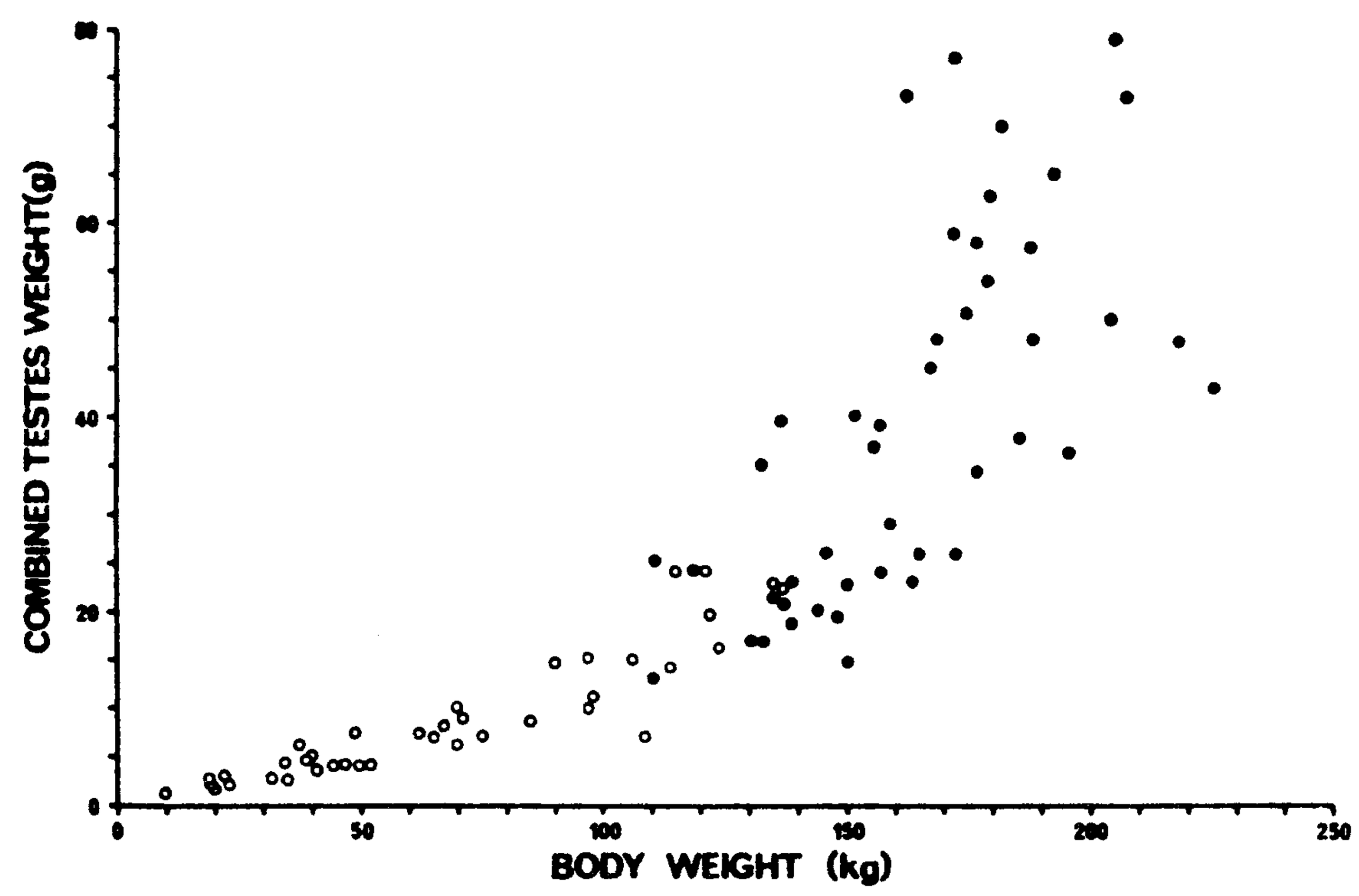

FIGURE 4. Relationship between testes weight and body weight for immature lions (0) and pubertal and sexually mature lions (0).

In summary, therefore, (Figures 2 and 3) all male lions under 26 months of age were sexually immature with the pubertal interval for the entire sample extending from 26 to 34 months of age.

Seasonal Reproductive Activity

Changes in combined testes weights and seminiferous tubule diameters could not be compared on a monthly basis due to a shortage of material from adult males. However, for the summer (wet season, October to March) mean combined testes weight and tubule diameter was 55.1 g (n=11) and 187.3 µm (n=8) respectively, while for the winter (dry season, April to September) the mean measurements were 55.0 g (n=7) and 197.2 µm (n=7), respectively. The small samples again precluded statistical analysis. Since mean tubule diameters for adult males are similar despite the season of collection and, since tubule diameter changes little after a combined testes mass of about 25 g is reached (Figure 5), it is unlikely that tubule diameter will vary seasonally in lions. Figure 5 shows that, despite the highly significant correlations (P<0.001) between tubule diameter and testes weight for preand post-pubertal lions, the latter show a considerable increase in testes weight with only a slight increase in tubule diameter.

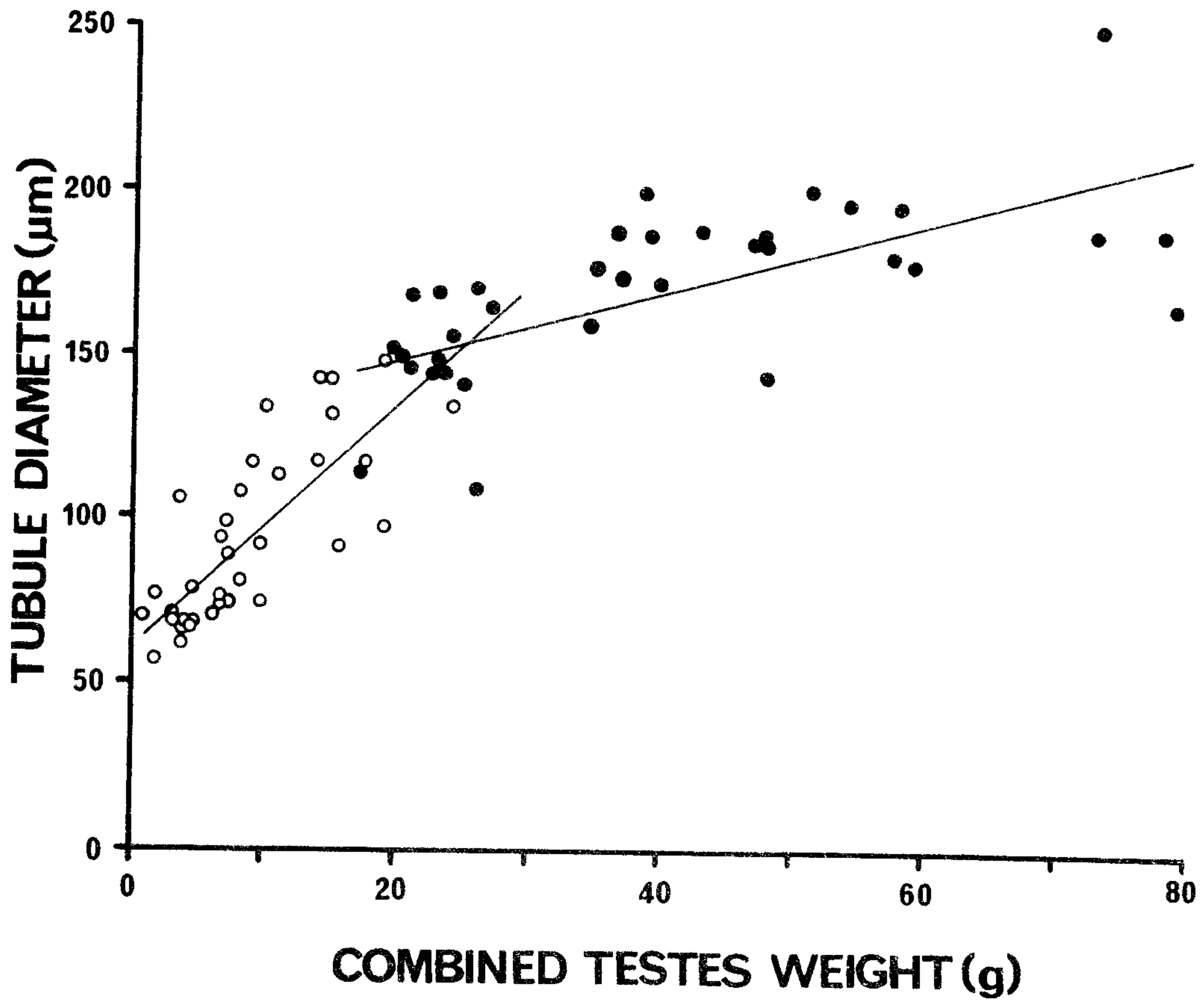

FIGURE 5. Relationship between testes weight and seminiferous tubule diameter. Immature lions (O): y = 3.7 x + 59.86, (r = 0.837); Pubertal and sexually mature lions (O): y = 1.07 x + 126.12 (r = 0.736).

Reproductive Senescence

Active spermatogenesis was found in all adult testes examined, including one emaciated specimen estimated to be 16 years old. It would thus seem that although old lions are still sexually viable they no longer contribute to reproduction of the population. No gross male reproductive abnormalities were noted during this study.

Female Reproduction

Social Organization

Once females have been recruited to a group or, should they remain in the parent group after becoming independent, they tend to remain in the group or pride until old age. In a sample of seven females from two different groups branded either as subadults or adults, all were still in their original groups and areas of activity after periods of 2.5 years (n=4) and 5 years (n=3). In both groups, however, other females had either been recruited to the group or had left at some stage.

Development of the Ovaries (Nulliparous Females)

Prior to the commencement of ovarian activity (pro-estrus), the ovaries of young lions are characteristically flattened dorso-ventrally (Figure 6). As follicles start growing the shape of the postnatal ovary becomes more laterally flattened. Figure 7 illustrates postnatal growth in weight of the ovaries for a sample of 66 immature and subadult lionesses.

The first ovarian follicles are usually visible to the unaided eye by two months of age, although no follicles could be seen in a few cubs estimated to be eight months old. Before the first estrous cycle all follicles are less than 0.5 cm in diameter. During pro-estrus they increase to between 0.6 and 1.0 cm; in two estrous females the largest follicles were between 1.0 and 1.2 cm in diameter (Figure 6). In both these females spermatozoa were located on cervical smears and they were each attended by one adult male.

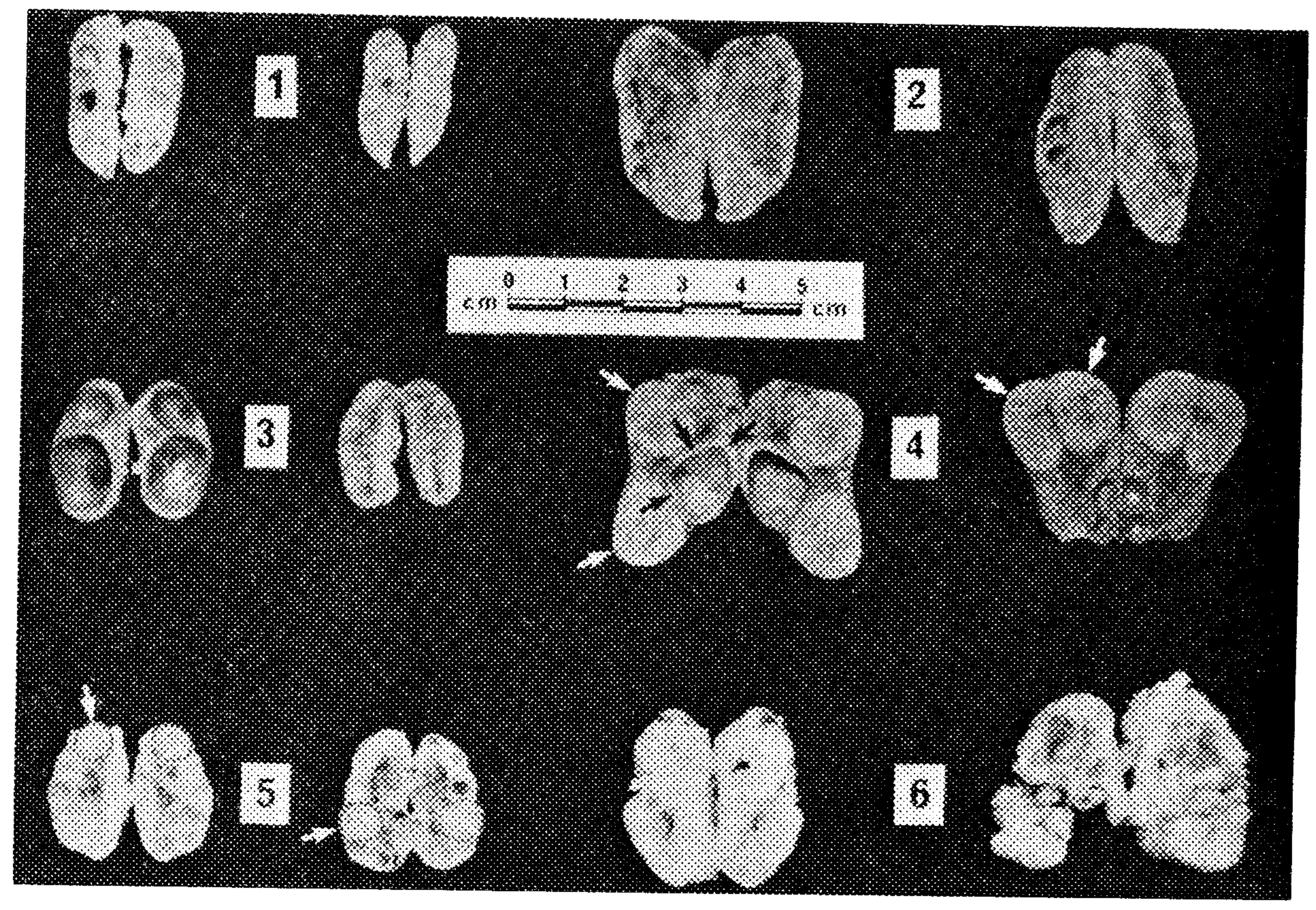

FIGURE 6. Six pairs of lion ovaries cut open from their free (ventral) to attached (dorsal) sides and showing various degrees of activity: (1) Immature female 44 months old with visible follicles between 0.1 and 0.5 cm diameter. Note characteristic dorso-ventral flattening of immature ovaries; (2) Sexually mature female 6.5 years old. Note absence of follicular activity (anestrus); (3) Pubertal female five years old undergoing first estrous cycle. Excluding the two large follicles in the one ovary, the ovaries still resemble those of an immature lion. This female had been mating prior to being collected and spermatozoa were located in the cervix; (4) Pregnant female (± day 20) five years old. Note four large corpora lutea (white arrows) and one unruptured follicle undergoing peripheral luteinisation (black arrows). The coagulated liquor foliculi has been removed from all follicles. This female had four embryos which were too small to weigh; (5) Pregnant female (+ day 90) six years old. Note that the two visible corpora lutea (white arrows and circled) have regressed considerably. The corpus luteum corresponding to the third implantation was not visible in the specific plane sectioned; (6) Sterile female 13 years old. Note irregular shape of ovaries, absence of follicles and large amount of stroma.

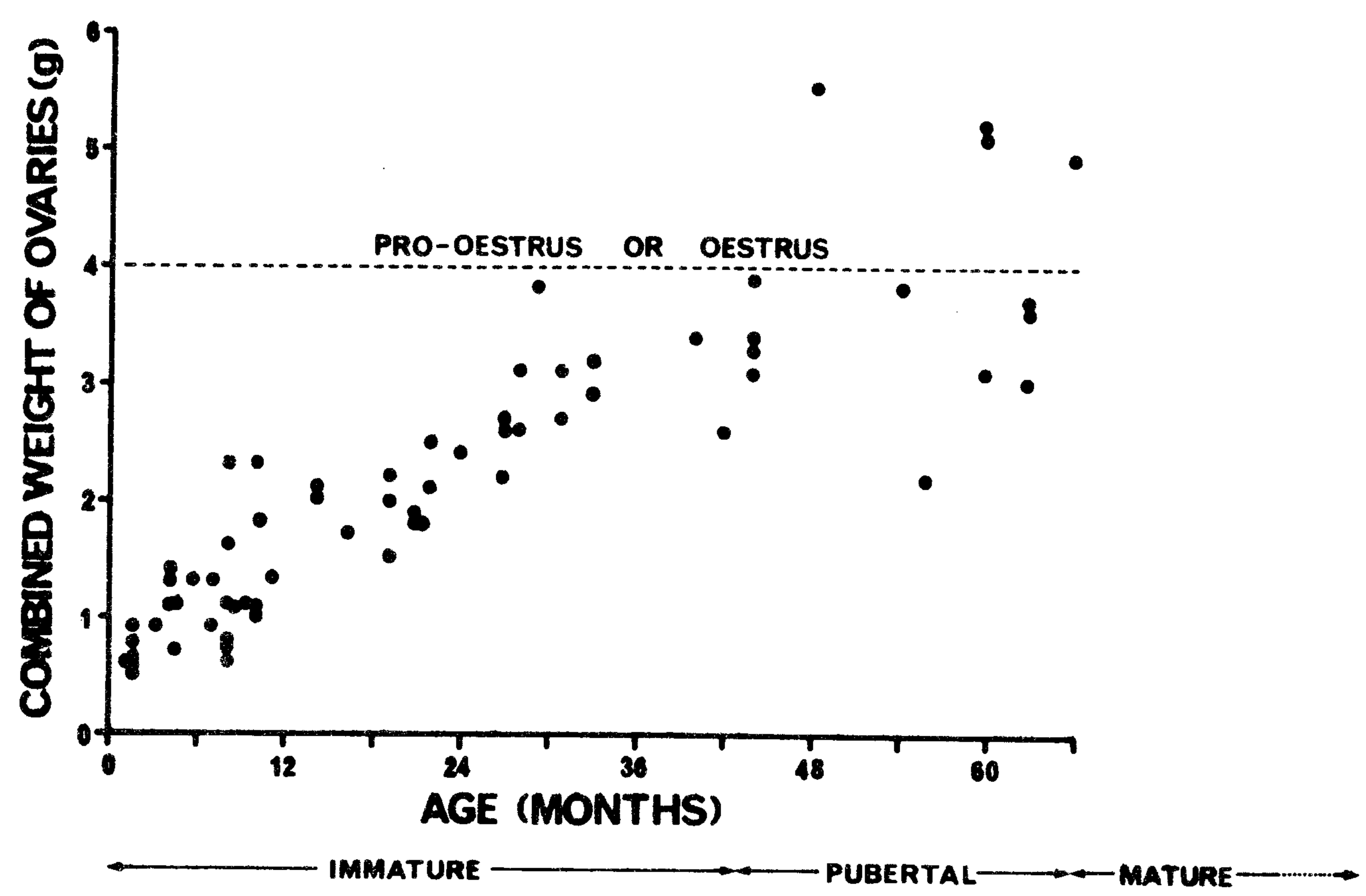

FIGURE 7. Growth in weight of the ovaries of 66 immature and subadult lions. All combined ovary weights greater than 4.0 g were of females in pro-estrus or estrus.

Puberty and Sexual Maturity

The youngest nulliparous female to show signs of increased ovarian activity (3 large 0.8 to 1.0 cm follicles) was a known-age 4-year old. In a sample of four females believed to be pregnant for the first time, on the basis that no corpora albicantia or old ovulation points could be found in their ovaries, the minimum age at first conception was 43 months (range = 43 to 54 months; mean = 49 months). Conception ages were estimated by the method of Huggett and Widdas (1951). Similarly, in a sample of 14 females which had given birth to their first litter and where the age of their cubs could be estimated, the minimum age at first conception was 43 months (range = 43 to 55 months; mean = 48 months). For these calculations the gestation period was taken to be 3.5 months. In a sample of 66 females estimated to be between 43 months and 14 years of age there were 14 which had never conceived before, the oldest being 5.5 years. Nulliparous subadults were often located in the same social group. The swo smallest females which were pregnant for the first time weighed 109 and 114 kg while the mean body weight for six females (all pregnant for the first time) was 123 kg (mean body weight for adult females [5+ years old] = 126.0 kg [n=51]).

In summary, therefore (Figure 7), all lionesses under 43 months of age were sexually immature with the pubertal interval for the entire sample extending from 43 to 66 months of age. Mean age at maturity was 48 months and all lionesses over 5.5 years were sexually mature (had ovulated before).

Reproduction in the Parous Lion

The reproductive activity for 60 cropped parous lions is summarized in Table 2. In a sample of 18 lions which were either pregnant or which had small cubs (<one month old), 54 out of 57 ovulations had been fertile (94.7%), as indicated by the presence of a viable conceptus or post-partum uterine scar. In females with small cubs uterine scars were visible for about one month post-partum after which they disappeared completely.

TABLE 2. Reproductive Activity for a Sample of 60 Parous Lions Cropped Randomly in the Central District of the Kruger National Park.

Reproductive category	n	%
Pregnant	12	20.0
Lactating (cubs <9 months old)	13	21.7
Nonlactating (cubs 9-24 months old)	15	25.0
Nonlactating (with or without offspring >24 months old)	16	26.7
Sterile	4	6.7

Ovarian characteristics of parous lions are further described for the following four reproductive categories:

1. *Pregnant lionesses.* Depending on the stage of pregnancy, the paired ovaries weigh between 12.0 g ($\pm$ 20 days post conception) and 5.0 g ($\pm$ 100 days post conception). These changes are almost entirely due to the corpora lutea of pregnancy (Figure 6) which decrease from about 1.8 cm in diameter ($\pm$ day 20) to 0.5 cm at about day 100 of pregnancy. Throughout the duration of pregnancy small follicles between 0.1 and about 0.6 cm are abundant. In 10 out of 12 instances the number of corpora lutea per female corresponded with the number of implantations. It was, however, not possible to determine whether the two exceptions, where there was a total of five implantations and seven large corpora lutea, were due to sterile ovulations or to the luteinisation of unruptured follicles. Two other pregnant females ($\pm$ 20 days pregnant) each had one large (1.0 and 1.4 cm) unruptured follicle which was partially luteinised (Figure 6). In one of these a mature corpus luteum corresponding with one of the implantations also had a small amount of coagulated liquor folliculi in its center. Although none of the pregnant lions are known to have been mating prior to being collected, one 20-day pregnant specimen had a large 1.0 cm follicle in her left ovary. The other three adult lionesses which were with her were in pro-estrus (follicles between 0.7 and 0.8 cm), the group being completed by two adult males.

Trans-uterine migration was noted in three instances out of 12, while there appeared to be no difference between the activity of opposite ovaries (23 ovulations left, 20 right) with implantations also being evenly distributed (24 left, 22 right). Observations on the ovaries (corpora lutea) and uteri (implantation scars) of females with small cubs (+1 month old) at foot were used here to augment data from pregnant females.

One 97-day pregnant female was found to have resorbed one of her two fetuses at an earlier stage of pregnancy. The other 1.03 kg fetus was normal. Colostrum could first be expressed at day 92 of pregnancy.

2. *Lactating lionesses.* The lactation period continued for eight to nine months post partum and in none of the females with cubs 10, 11, 13 and 15 months old could milk be expressed from the nipples. The corpora lutea of pregnancy are still visible shortly after parturition (0.4 to 0.6 cm in diameter), but by about one month post partum they have regressed to about 0.2 cm. After this they appear to remain visible as tiny yellow-brown corpora albicantia for an indefinite period, depending on the reproductive state of the female. Small ovulation points also remain visible on the exterior of the ovary, but for a shorter period than the corpora albicantia. In two females which raised what is believed to be their first litters at 21 and 26 months of age, corpora albicantia were still visible macroscopically when their ovaries were sectioned. Corpora albicantia do not, however, remain visible throughout the life of an individual, as none could be found in a number of relatively old pregnant and nonpregnant lions.

3. *Nonpregnant and nonlactating lionesses.* This group includes females which are in early proestrus, estrus, diestrus or anestrus and, subsequently, also includes those with cubs that were no longer suckling from them. Because of the variety of reproductive categories, combined weight of the ovaries varied between 2.4 and 9.6 g (mean = 5.2; n=21). All females with large cubs (13-24

months old) were in deep anestrus, with their ovaries containing numerous follicles between 0.1 and 0.4 cm in diameter (combined weight = 3.0 to 4.0 g). During pro-estrus there was a marked increase in the number and size of follicles and consequently in the weight of the paired ovaries (range = 4.5 to 9.6 g). No females with cubs at foot were found to be in pro-estrus or estrus.

Two females out of a sample of 23 in this reproductive category appeared either to have lost their cubs or ovulation had not been followed by pregnancy. The ovaries of one female contained three regressing corpora lutea 0.3 to 0.5 cm in diameter. Since corpora lutea of this size are usually associated with females whose cubs are less than one month old and at which stage uterine implantation scars are still visible, it would seem more likely that the corpora lutea observed were formed after sterile ovulations and that this was possibly followed by a pseudopregnant period. This female was not lactating but both the females accompanying her were and had cubs less than one month old with them. In the other female from a different group there were also three small corpora lutea (0.4 cm diameter), while a protuberance on the one uterine horn containing unidentifiable tissue indicated that embryonic death and resorption may have taken place. Two fairly large follicles (0.8 cm in diameter) indicated that this female was in pro-estrus.

Since corpora lutea quite probably regress rapidly after a sterile ovulation or a pseudopregnant period (if pseudopregnancy does occur), it is not possible to calculate the percentage of ovulations which do not end in pregnancy. The evidence available nevertheless indicates that sterile ovulations are rare.

The oldest females that were still capable of reproduction were 12 and 13 years old. The 12-year old had four cubs (± 15 months old), while the 13-year old had numerous follicles between 0.1 and 0.7 cm in diameter in her ovaries and appeared to be in pro-estrus.

4. *Sterile females.* Six females collected during the present study appeared to be sterile. Two of these were shot because they could no longer walk and were extremely emaciated. The other four were also in poor condition when compared to other adult females in the same group, and all six were between 11 and 14 years old. Their body weights ranged from 81 to 122 kg (mean = 108 kg) which is less than the average for adult females (126 kg; n=55). The combined weight of their ovaries varied considerably (2.6 to 16.5 g), with three pairs being larger and three pairs being smaller than normal involuted ovaries. Externally the texture of the larger pairs of ovaries was rough and firm to touch while internally, as for the smaller pairs, there were few or no visible follicles and corpora albicantia. Stroma was dominant in the ovaries (Figure 6), and its proliferation sometimes resulted in ovarian disfigurement. Large paraovarian cysts were found around the ovaries of two of these females.

Ovulation Rate and Litter Size

Examination of the ovaries of 25 lions (12 pregnant and 13 with young cubs) produced a total of 77 corpora lutea. This indicates a mean ovulation rate per female of 3.08 (range = 1 to 5). The 12 pregnant females carried a total of 37 embryos and fetuses (range/female = 1 to 5) to give an average litter size of 3.08. Mean litter size obtained during field counts and only including small cubs (<12 months old) gave an average of 3.02 (range = 1 to 4; n=47 litters), while the mean for cubs older than 12 months was 2.71 (n=7 litters). Modal litter size for all observations excluding cubs older than 12 cubs was 3 (63.9%) followed by those with 4 (19.4%), 2 (12.5%), 1 (2.8%), and 5 (1.3%) (n=72 litters).

Birth Season

Birth month of litters was estimated by backdating in the case of small cubs which could be aged with some degree of certainty (n=67 litters), and by projecting forward for pregnant females (n=12). These data were collected randomly over the whole study area and were not confined to a few selected groups. The monthly results obtained are given in Table 3 which also shows a total of 42 litters (53.2%) for the wet season and 37 litters (46.8%) for the dry season. These seasonal differences were nonsignificant (Chi-square = 0.3; P>0.05). Since there appeared to be a correlation between the birth season of lions and that of their prey, these were also compared as shown in Table 3. The eight prey animals selected made up over 90% of the recorded lion kills in the Central District for the period 1968 to 1975 (Smuts, 1975a).

Synchrony of Estrous Periods

Estrous synchronization among females from the same social group was noted on two occasions. In the one group of four adult females and two adult males, three of the females (two young and one old) were in pro-estrus (groups of follicles 0.6 to 1.0 cm in diameter) while the other female was about 20 days pregnant and also had a large follicle (1.0 cm diameter) in one ovary. In the other group, which consisted of two adult males and seven adult females, two of the females were sterile (old) and two of the remaining five were in pro-estrus while the other three appeared to be approaching this state--ovaries larger than usual and containing many 0.3 to 0.5 cm follicles.

Synchrony of Births

Births were regarded as synchronized if more than one litter was born or was going to be born in the same social group in the same or an adjacent month (Bertram, 1975). Using this criterion seven instances of birth synchronization were recorded during the study (Table 4). Although various degrees of birth synchronization occurred in many other groups seen during the study, it was not possible to assess the ages of cubs with sufficient accuracy unless they were captured. It was, however, clear that differences between the ages of cubs from the same social units were often more than two to three months (less-synchronized or asynchronized births). In some of these instances groups of females from the same pride could have regrouped when their cubs were a bit older, thus giving the impression that births were asynchronous for the entire group.

TABLE 3. Distribution in Births for Lions from the Central District of the Kruger National Park and its Relationship to the Birth Season of the Major Prey Animals in the Same Area.

Month	No. of litters born	%	Birth season of major prey animals in the Kruger National Park							
			Wildebeest	Zebra	Impala	Buffalo	Kudu	Waterbuck	Giraffe	Warthog
May	4	5.1				X			XX	
June	7	8.9							X	
July	4	5.1								
Aug.	5	6.3								
Sept.	6	7.6								
Oct.	4	5.1								
Nov.	9	11.4		X	XX					XXX
Dec.	6	7.6	XXX	XX	XXX					XX
Jan.	2	2.5	XXX	XXX	X	X	XX	X		X
Feb.	9	11.4	X	XXX		XX	XXX	XXX	X	
March	12	15.2		XX		XXX	X	X	XX	
April	11	13.9		X		XX			XXX	
	79	100.1								

Wildebeest	*(Connochaetes taurinus taurinus)*	- Braack (1973)
Zebra	*(Equus burchelli antiquorum)*	- Smuts (1976d)
Impala	*(Aepyceros melampus melampus)*	- Fairall (1968)
Buffalo	*(Syncerus caffer)*	- de Vos (pers. comm.)
Kudu	*(Tragelaphus strepsiceros strepsiceros)*	- Fairall (1968)
Waterbuck	*(Kobus ellipsiprymnus)*	- Fairall (1968)
Giraffe	*(Giraffa camelopardalis)*	- Hall-Martin (1975)
Warthog	*(Phacochoerus aethiopicus)*	- Fairall (1968)

DISCUSSION

Sex Ratio and Subadult Recruitment and Emigration

Captive lions show an equal sex ratio at birth (Jarvis, 1966: 67 males: 70 females; Brand, 1963: 131 males: 130 females), and this also seems to be the case for wild populations. Rudnai (1973a), for example, obtained a ratio of 23 males: 23 females for cubs under two months of age while Schaller (1972) gives a figure of 138 males: 145 females for cubs 12 months and younger. Table 1 further indicates that sex ratio is equal up to about two years of age but that some time after this age changes occur which are difficult to explain in the case of subadults where males are more abundant. All wild populations (Table 1; Schaller, 1972; Bertram, 1973; Rudnai, 1973a; van der Meulen, 1976) have considerably more adult females than males. The preponderance of subadult males mentioned above is discussed in more detail by Smuts (1976b).

Data from the Kruger National Park indicate that all subadult males had emigrated from the parent group by three years of age (range = 27-36 months). These ages are higher than those recorded by Rudnai (1973a) where the period of dependence was 21 to 24 months, but are similar to those reported by Schaller (1972), of 2 1/2 to 3 1/2 years and Bertram (1973) of three years. Subadult females also appear to leave the parent group at a later age than was found by Rudnai (1973a). Since the expulsion or recruitment of subadults is density dependent (Bertram, 1973), it follows that subadult lions from the Nairobi National Park (lion density = 26.1/100 km^2; Rudnai, 1974) would be expelled at an earlier age than those in the Central District of the Kruger National Park (lion density = 12.7/100 km^2; Smuts, 1976b).

Male Reproduction

Social Organization

Between 1974 and 1976 over 400 lions were captured and marked in the Central District of the Kruger National Park (Smuts, 1976b). Resurveys undertaken in specific areas (Smuts, 1977) have subsequently indicated that, while adult females have a reasonable life expectancy, adult males are being replaced at a greater rate. The sex ratio of adult lions (1 male: 2.1 female)

(Smuts, 1976b) also indicates that the mortality rate for adult males is higher than for females. Since numerous marked males were killed in fights with other males, it seems reasonable to assume that intraspecific competition is high and that subsequently the largest, strongest, or most dominant males would be in possession of territories and groups of females. The low mean age for territorial males (6.5 years; range - 5 to 9 years) supports these conclusions, since males attain their maximum body weight at about five years of age (Smuts, in preparation) with older lions generally being lighter. The mane is also at its largest between six and eight years of age. During part of her study period in Nairobi National Park, Rudnai (1973a) found that the three resident males were between four and five years old while Bertram (1973) mentions that in the Serengeti the males in possession of a pride change every two to three years. Since male tenure of a pride only starts at about five years of age and does not last for more than a few years after this, it is obvious that the effective reproductive life of an adult male cannot be more than about two years (maximum = four years). Since only two adult males in a random sample of 18 were over nine years, it is obvious that once ousted from a pride they probably die within a few years. All males between 3 1/2 and 4 1/2 years of age could be distinguished from prime males (five to eight years old) on the basis of their manes. It is unlikely that groups of these males would be able to compete effectively with the more dominant and experienced animals in the prime age class (which also occur in pairs or groups of up to five).

TABLE 4. Synchronization of Births in Seven Different Groups of Lions

Specimen No.	Conception Age	Age of Cubs	Month and Year of Birth
30	-	1 month	November 1974
31	-	1 month	November 1974
32	-	2 weeks	December 1974
3 adult females and 11 cubs in the group			
49	20 days	-	March 1975
50	-	1.5 months	November 1975
51	92 days	-	January 1975
52	-	1.5 months	November 1975
4 adult females and 6 cubs in the group			
76	21 days	-	February 1975
77	36 days	-	February 1975
3 adult females in the group (one not examined)			
99	-	7 months	May 1975
A1	-	8 months	April 1975
2 adult females and 6 cubs in the group			
145	-	1.5 months	June 1976
146	100 days	-	July 1976
2 adult females and 3 cubs in the group			
161	97 days	-	October 1976
162	64 days	-	November 1976
4 adult females in group (2 not examined)			
167	37 days	-	January 1977
168	38 days	-	January 1977
2 adult females in the group			

Puberty and Sexual Maturity

Although puberty in male lions commences at a relatively early age (26 months), it is unlikely that they mate effectively before five years (previous section) when psychological maturity is attained (Figure 2). No subadult males were found in association with estrous females during the present study. Schaller (1972), however, mentions an instance where one male in the Lake Manyara National Park mated for the first time at about 3 2/3 years. It is nevertheless obvious that where the opportunity presents itself, and especially in the case of captive lions, successful mating could take place before males are three years old.

Observations made during the present study indicate that adult male lions show no seasonal reproductive activity. As mentioned previously, adult male lions seldom reach an old age, while all those in possession of prides are relatively young. Sterility due to old age would subsequently be of no consequence to a lion population even if it did occur.

Female Reproduction

Puberty and Sexual Maturity

The minimum age of sexual maturity at 43 months for females from the Central District of the Kruger National Park is almost identical to that reported by Schaller (1972) for lions from the Serengeti (42 months), but considerably higher than that for the Nairobi National Park where the earliest conceptions occurred at 30 to 31 months (Rudnai, 1973a). The fact that captive female lions often mate successfully before three years of age (Rudnai, 1973a; Eaton, 1974) is most probably related to a more consistent level of nutrition. The earlier breeding age of Nairobi Park lions, which occur at higher densities than do those in the Serengeti and Kruger Park, also could be due to a low level of competition with groups outside the Park. The late breeding age of some females in the present study (maximum = 66 months) is less than that quoted by Schaller (1972) of 77 months and Bertram (1975) of 75 months for the Serengeti, but considerably more than that quoted by Rudnai (1973a) of 36 months for Nairobi National Park.

Reproduction in the Parous Lion

The lack of success of most mating periods in lions has received considerable attention during recent years. Schaller (1972), for example, found that about 80% of sexual activity did not result in births. In his study 13% of the activity could be ascribed to females which were already pregnant while another 5% included lactating females with small cubs, and 32% were brief "sexual contacts" with or without actual copulation taking place. The remaining 30% of unsuccessful sexual contacts appeared to be typical of the kind leading to conception, yet there were no births. Eaton (1976) put forward two hypotheses to explain high copulation frequency in some felids, his final conclusion (in Eaton, 1978) being that high copulation frequency evolved because of its advantages in allowing females to evaluate male vigor. Generally, the longer the same males are resident the higher is female reproductive success. Females would gain if frequent sexual rewards helped to reduce the rate of male turnover and hide conception, thus reducing infanticide by new males.

Results from the present study indicate that failure to conceive may be due to anovulatory estrus periods; i.e., follicles do enlarge during estrus, but these regress after a period of days with the result that no conception can take place. These conclusions are supported firstly by the fact that, excluding one doubtful observation (see Results section), no pseudopregnant females were collected. It is possible, however, that females which had ovulated and copulated but did not conceive were never collected. At this stage it is not known for how long the corpus luteum of a sterile ovulation would remain visible. If it remains visible for a month or more, it is unlikely that sterile ovulations were missed in the sample taken. Secondly, the high percentage of fertile ovulations preceding pregnancy (96.5%; 57 corpora lutea; 55 implantations) would tend to indicate that when ovulation and mating take place, conception can be expected. It is even possible that fertilization and implantation follow every ovulation since the above two corpora lutea in excess of the implantations could have been due to the luteinisation of two unruptured follicles. Thirdly, if ovulation is not spontaneous but of the reflex variety, as in the domestic cat (Asdell, 1955), anovulatory estrous periods would seem to be feasible. Here one would assume that ovulation would not occur when the nervous reaction initiated by coitus did not reach a certain threshold level, which could depend on copulation frequency (Eaton, 1978). Finally, it is unlikely that abortions (Bertram, 1975) rather than anovulation during estrus are resulting in the low incidence of births relative to sexual encounters. No accounts of abortion have ever been recorded in the Kruger National Park and none were observed in the material examined; however, abortion has been observed in captive lions (Eaton, 1974). The other alternative, namely embryonic resorption, could be of some importance, although only one female in the present study definitely resorbed an embryo - her other embryo was normal. In another female there were three small corpora lutea and a protuberance in one uterine horn which, as mentioned, could have resulted from the resorption of an embryo. The simplest way to prove or disprove the idea of regular anovulatory estrous periods would be to examine the ovaries of a number of females shortly after they had completed an estrous cycle. The idea that the high mating inefficiency in lions (roughly 1,500 copulations to produce one litter: Bertram, 1975) could well be an adaptation by the females serving to reduce competition among the pride males (Bertram, 1975) or perhaps sexual gratification is a means of reenforcing the social bond of males and females and their allegiance to the pride (Eaton, 1974) seem to be reasonable explanations for a pattern of behavior which in most other wild animals is very successful (Eaton, 1976). These conclusions would also provide a reason for the sexual activities, including copulations, which have been witnessed in pregnant and lactating lions (Schaller, 1972; Rudnai, 1973b; Eaton, 1974).

Ovulation Rate and Litter Size

There is a remarkably small drop between the average size of prenatal (3.08) and postnatal litters (3.02). Although all the cubs in postnatal litters were less than 12 months old, about 80% of these were also less than eight months old. Nevertheless, the results indicate that average litter size did not change much during the first year of life (assuming that prenatal litter sizes remain constant from year to year). Present postnatal litter sizes (3.02) are very similar to those in Nairobi National Park (3.05: Rudnai, 1973a), but considerably higher than those observed in the Serengeti (2.3: Schaller, 1972; 2.5: Bertram, 1975). The low values for the Serengeti could be due to elevated cub mortality related to inadequate cover (hiding places) when compared to the Central District of the Kruger National Park where cover is abundant. This is supported to some extent when studying data provided by Schaller (1972) where litter sizes for the woodlands are consistently higher than those for the plains. Rudnai's (1973a) data are also not directly comparable with that from Kruger, since only cubs two months old and younger are included.

Stevenson-Hamilton's (1937) contention that litter size in the Kruger National Park increased, as did food supply, should rather be interpreted to mean that survival and hence average observed litter size increased as did prey vulnerability. Prey vulnerability in turn has been found to be related to cover (Schaller, 1972; Smuts, 1976c); and with more food available and more cover for young cubs, one could expect an increased cub survival. No study has yet shown that average prenatal litter size in the lion increases during times of resource abundance. Well-fed captive animals always seem to have litter sizes lower than lions in wild populations (see Rudnai, 1973b). Litter size at birth for the Johannesburg Zoological Gardens, South Africa (2.78; range = 1 to 6; n=51 litters) (Laubser, pers. comm.) was also lower than that recorded in the present study. By contrast, the mean for 21 litters from the Natal Lion Park was 3.26 at birth (range = 1 to 5) these, however, being animals which are allowed to move over a fairly large natural area (B. Boswell, pers. comm.). Eaton (1974) found that in certain instances social factors such as fewer males, less competition due to fewer adults, or cohesiveness of females could result in larger litter sizes at birth. He, however, found no evidence which indicated that improved nutrition positively influenced litter size, and concluded that nutrition had its greatest effect after birth.

Birth Season

Although there was no correlation between a particular month and the number of conceptions, it is possible that a relationship exists between conception and resource abundance. However, because observations were made over a large area (5,560 km^2), it was not possible to relate monthly conceptions to food availability or the relative number of kills made per month. It should nevertheless be noted (Table 3) that 40.5% of all cubs were born during the period of February to April. These months occur roughly three months after the birth season of most of the major prey animals has commensed (gestation period for lions is 3.5 months) (Table 3), and also overlap partially with the actual months of birth of five of the major prey animals. These observations indicate that the relatively more abundant prey animals and their increased vulnerability (pregnant females and young) during the season of birth may influence the mating season and ultimately the birth season in lions. Rudnai (1973a) also found that nutrition influenced the probability of conception in lions from Nairobi National Park.

Synchrony of Estrous Periods and Births

Estrus synchronization within groups of females has been reported by Schaller (1972), Rudnai (1973a), Eaton (1974), and Bertram (1975). The present study supports these findings and indicates that when certain conditions are met for a particular group or pride, there is a communal surge of ovarian activity culminating in estrous synchronization. At this stage it is still not possible to determine whether estrous synchronization is triggered by pride mechanisms within or some characteristic of the habitat such as food supply. Since females from the two groups observed in the present study all appeared to be in pro-estrus at about the same time, it would appear that the trigger mechanism is not between females. The presence of males may, however, be of importance since both groups had two adult males with them. Eaton (1974) suggests that pheromones passed in the urine of females approaching and during estrus may affect estrous synchronization. The possible adaptive values of estrus synchronization are discussed by Bertram (1975) and Eaton (1978).

Obviously estrous synchronization must influence birth synchronization. However, since births within a group are often less synchronized than estrous cycles (Table 4), it would seem that females are still responding to the stimulus or releaser of ovarian activity, despite the fact that some may already be one month pregnant. This could again be seen to indicate that the releaser lies not within the group of females but, rather, that females are reacting to some other factor individually.

In conclusion, it may be mentioned that, although large nipples are usually an indication that a female has given birth and suckled young at some stage, this may not always be the case. During the current study nine females were classified as having had young before on the basis that they had large nipples. Subsequent examination of their ovaries indicated that they had never ovulated before since no corpora albicantia could be found in the sectioned ovaries and no ovulation scars were visible externally. Their ovaries were also similar to those of immature lions, and their ages ranged from 33 to 66 months. Since enlarged nipples could be due to normal growth in the absence of offspring, field classification without ovarian analysis should be viewed with considerable caution.

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LITERATURE CITED

Asdell, S. A. 1946. *Patterns of Mammalian Reproduction.* Comstock Publishing Company, New York.

Asdell, S. A. 1955. Endocrine organs, reproduction and growth. Pp. 849-959, *In*: H. H. Dukes (Ed.), *The Physiology of Domestic Animals.* 17th Edition. Bailliere, Tindall and Cox, London.

Bertram, B. C. R. 1973. Lion population regulation. *East African Wildlife Journal* 11: 215-225.

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology* 177: 463-482.
Braack, H. 1973. Population dynamics of the blue wildebeest, *Connochaetes taurinus taurinus* (Burchell, 1823) in the Central District of the Kruger National Park. Project report to the University of Rhodesia, Salisbury, for the certificate in field ecology.
Brand, D. J. 1963. Records of mammals bred in the National Zoological Gardens of South Africa during the period 1908 to 1960. *Proceedings of the Zoological Society of London* 140(4): 617-659.
Carvalho, C. 1968. Comparative growth rates of hand-reared big cats. *International Zoo Yearbook* 8: 56-59.
Cooper, J. 1942. An exploratory study on African lions. *Comparative Psychology Monograph* 17: 1-48.
Crandall, L. 1964. *The Management of Wild Mammals in Captivity*. University of Chicago Press, Chicago.
Eaton, R. L. 1972. Reproductive age in lions: A record. *Mammalia* 36: 158-159.
Eaton, R. L. 1974. The biology and social behaviour of reproduction in the lion. Pp. 3-58, *In:* R. L. Eaton (Ed.), *The World's Cats II*. Feline Research Group, Woodland Park Zoo, Seattle.
Eaton, R. L. 1976. Why some felids copulate so much. Pp. 73-94, *In:* R. L. Eaton (Ed.), *The World's Cats III*(2). Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Eaton, R. L. 1978. Why some felids copulate so much: A model for the evolution of copulation frequency. *Carnivore* 1(1): 43-52.
Eaton, R. L., and York, W. 1971. Reproductive biology, and preliminary observations on mating preferences, in a captive lion *Panthera leo* population. *International Zoo Yearbook* 11: 198-202.
Eloff, F. 1973. Ecology and behavior of the Kalahari lion. Pp. 90-126 , *In:* R. L. Eaton (Ed.), *The World's Cats I*. World Wildlife Safari, Winston, Oregon.
Emmens, C. W. 1969. Physiology of gonadal hormones and related synthetic compounds. Pp. 85-112, *In:* H. H. Cole and P. T. Cupps (Eds.), *Reproduction in Domestic Animals.* Academic Press, New York.
Fairall, N. 1968. The reproductive seasons of some mammals in the Kruger National Park. *Zoologica Africana* 3(2): 189-210.
Fraser, A. F. 1968. *Reproductive Behavior in Ungulates*. Academic Press, London.
Guggisberg, C. 1961. *Simba* Howard Timmins, Cape Town.
Hall-Martin, A. J. 1975. Studies on the biology and productivity of the giraffe *Giraffa camelopardalis*. DSc. Thesis, University of Pretoria, South Africa.
Hugget, A. St. G., and Widdas, W. F. 1951. The relationship between mammalian foetal weight and conception age. *Journal of Physiology* 114: 306-317.
Jarvis, C. 1966. *The International Zoo Yearbook* Vol. 6. Zoological Society of London.
Rudnai, J. 1973a. Reproductive biology of lions *(Panthera leo massaica* Neumann) in Nairobi National Park. *East African Wildlife Journal* 11: 241-253.
Rudnai, J. 1973b. *The Social Life of the lion*. The Garden City Press, Hertfordshire.
Rudnai, J. 1974. The pattern of lion predation in Nairobi Park. *East African Wildlife Journal* 12: 213-225.
Sadleir, R. M. F. S. 1966a. Notes on reproduction in the larger Felidae. *International Zoo Yearbook* 6: 184-187.
Sadleir, R. M. F. S. 1966b. Investigations into the reproduction of larger Felidae in captivity. *Journal of Reproduction and Fertility* 12: 411-412.
Schaller, G. B. 1972. *The Serengeti Lion*. The University of Chicago Press, Chicago.
Smuts, G. L. 1975a. Predator-prey relationships in the Central District of the Kruger National Park with emphasis on wildebeest and zebra populations. Memorandum. National Parks Board of Trustees.
Smuts, G. L. 1975b. Why we killed those lions. *African Wildlife* 29: 30-33.
Smuts, G. L. 1976a. A report on predator cropping experiments and related research in the Central District of the Kruger National Park (October 1975 to October 1976). Memorandum. National Parks Board of Trustees.
Smuts, G. L. 1976b. Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe* 19: 153-164.
Smuts, G. L. 1976c. Population characteristics of Burchell's zebra *(Equus burchelli antiquorum,* H. Smith, 1841) in the Kruger National Park. *South African Journal of Wildlife Research* 6 (2): 99-112.
Smuts, G. L. 1976d. Reproduction in the zebra mare *Equus burchelli antiquorum* from the Kruger National Park. *Koedoe* 19: 89-132.
Smuts, G. L. In press. Social and reproductive responses of free ranging lions to experimental cropping operations. *Carnivore*.
Smuts, G. L., Anderson, J. L., and Austin, J. C. In press. Age determination of the African lion *(Panthera leo)*. *Journal of Zoology*.
Smuts, G. L., Whyte, I. J., and Dearlove, T. W. 1976. A mass capture technique for lions. *East African Wildlife Journal* 15: 81-87.
Smuts, G. L., Whyte, I. J., and Dearlove, T. W. 1977. Advances in the mass capture of lions. XIII International Congress of Game Biologists, Atlanta, Georgia.
Stevenson-Hamilton, J. 1937. *South African Eden; from Sabi Game Reserve to Kruger National Park*. London.
Steyn, T. 1951. The breeding of lions in captivity. *Fauna and Flora* 2: 37-55.
Van der Meulen, J. H. 1976. Aspects of the lion *(Panthera leo* Linn.) population of the Matetsi Game Area. Project report to the University of Rhodesia, Salisbury, for the Certificate in Field Ecology.
Zuckerman, C. B. 1953. The breeding seasons of mammals in captivity. *Proceedings of the Zoological Society of London* 122: 827-947.

A COMPARISON OF FISHER AND WEASEL HUNTING BEHAVIOR

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The subfamily Mustelinae is characterized by small, solitary predators with long, slender bodies. The genera *Martes* and *Mustela* have holarctic distributions with two and five species respectively in North America (Hagmeier, 1956; Hall, 1951; Walker, 1968). The fossil record is poor and phylogeny of the genera difficult to determine, but the entire subfamily has retained many primitive anatomical and behavioral characteristics (Anderson, 1970; Colbert, 1969; Ewer, 1973).

All mustelines are solitary, opportunistic predators whose hunting behavior is characterized by "random search" while foraging and a neck bite for killing (Ewer, 1973). Fishers *(Martes pennanti)* hunting snowshoe hares *(Lepus americana)* utilize behavior typical of the subfamily, while fishers hunting porcupines *(Erethizon dorsatum)* utilize behavior that is unique and not previously investigated and reported in depth. Fishers and porcupines have coexisted since the Pleistocene (Anderson, 1970; Hibbard, 1970) and there is evidence that the predator-prey relationship has been long established (Barkalow, 1961; Parmalee, 1971). Hunting for porcupines has required fishers to develop a new behavior for both foraging and killing. Powell and Brander (1977) provide the only allusion to the atypical behavior of fishers foraging for porcupines. It has long been acknowledged that fishers do not use typical methods to kill porcupines. Both the scientific and popular press have unsupported references to fishers flipping porcupines over and attacking their bellies or attacking porcupines from under tree branches (Anthony, 1928; Cahalane, 1944, 1947; Coues, 1877; Pringle, 1964; Seton, 1937; Schoonmaker, 1938). Only during the last decade was it discovered that fishers kill porcupines by attacking their faces (Coulter, 1966). To give perspective to fisher hunting behavior, I discuss both typical musteline hunting behavior as examplified by weasels *(Mustela erminea, M. frenata)* and fishers hunting snowshoe hares and the unique porcupine hunting behavior of fishers.

HABITATS

The study was carried out in Ottawa National Forest (ONF), Upper Peninsula Michigan. The main study area was predominantly open, upland hardwood forest. Occasional single or small clusters of conifers (hemlock, spruce, balsam fir) were scattered within the hardwoods. The other common forest types occurred in lowland areas and were spruce-fir, spruce-aspen and alder stands. There were a few open bogs, muskegs and meadows. In addition a 25 m wide right-of-way to a buried gas pipeline (the pipeline) ran through the study area as did many overgrown logging roads.

Weasels were found in all habitats whereas fishers were found only in habitats utilized by porcupines and snowshoe hares. Porcupine habitat in winter was open, upland hardwood forest (Figure 1) where porcupines denned in large hollow trees (Figure 2) and logs (Brander, 1973; Powell and Brander, 1977) and ate the cambium of hemlocks, yellow birch, elm, sugar maple and basswood (Brander, 1973). Porcupines usually spend daylight hours in their dens and night time hours in their feeding trees (Brander, 1973). Dens which have been used for several years have an accumulation of porcupine excrement at their entrances which can be smelled from a considerable distance by humans (Figure 2). Hare habitat was lowland spruce-fir (Figure 3), spruce-aspen and alder stands. Open bogs, muskegs, meadows, the pipeline and large logging roads were not utilized by porcupines, hares or fishers.

FIGURE 1. Porcupine habitat: open hardwood forest providing hollow trees and logs for dens. Porcupines eat hemlock, yellow birch, elm, sugar maple and basswood during winter.

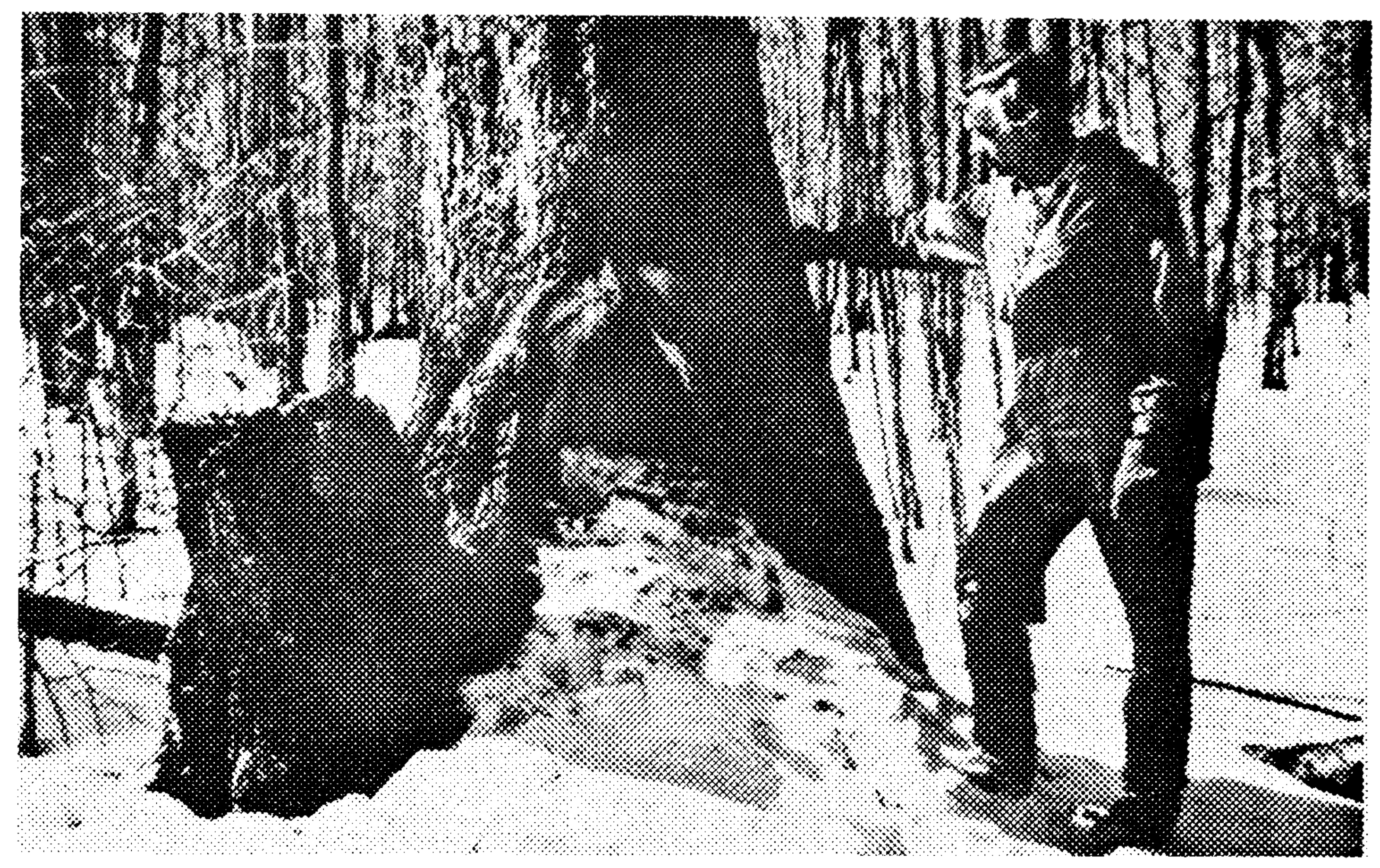

FIGURE 2. Porcupine den: porcupines den in large hollow trees and logs during winter. The debris spreading from the hole is a large pile of porcupine dung.

FIGURE 3. Hare habitat illustrated by dense spruce-fir. Alder stands and spruce-aspen also provide sufficient cover or food to constitute hare habitat.

METHODS

Thirty-three weasel tracks and 33 fisher tracks were followed to note foraging patterns. For some of these tracks the ratio of actual distance the animal travelled to the distance along the general line of travel was determined to quantify the direction changes of hunting weasels and fishers. Frequent changes indicate lack of systematic, directioned foraging methods.

Weasel hunting behavior was studied from track and sign in the snow and from observations of four captive long-tailed weasels (One, a male captured in Gunnison National Forest, Colorado; 3 females captured in ONF) from 1972 to 1974. Weasels were housed singly in various cages and in two rooms. They were fed mice, road-killed mammals and birds, and a hamburger-egg-oatmeal-vegetable mixture. Live mice (deer mice, *Peromyscus maniculatus;* voles, *Microtus* spp.; house mice, *Mus musculus)* and chipmunks *(Eutamias minimus)* were released into the weasels' cages or rooms and the methods of capture and killing observed.

Fisher hunting behavior was studied using track and sign in the snow, two handleable fishers (one male, one female, captive born), and six wild-caught fishers (two males, four females, captured in ONF) from 1973 to 1976. Captive fishers were maintained singly in cages allowing separate access to a covered 6x12 m pen. They were fed road-killed and live-trapped mammals and birds. Twenty-one snowshoe hares and three porcupines were released into the pen and killing behavior of the fishers observed or reconstructed from sign in the snow. Twelve observations were made of porcupine carcasses eaten by fishers.

Fisher scats were collected while tracking fishers. Scats were washed and bones and hair identified from comparison to samples of bones and hair of prey species.

RESULTS

Tracking Observations and Foraging Behavior

Track measurement results are shown in Table 1. The foraging pattern of fishers in porcupine habitat is significantly different from the foraging pattern of fishers in hare habitat and from weasel foraging patterns.

Weasel foraging behavior was characterized by frequent direction changes. The distance a weasel travelled was often considerably greater than the distance along its general line of travel and the ratio of these was highly variable (Table 1). Weasels also foraged beneath the snow (Klimov, 1940; Kraft, 1966; Nyholm, 1959; Seton, 1929; Teplov, 1948) so that the line of travel was changed in both the horizontal and vertical planes. Prey captured on the snow surface were taken after breaking from cover. The longest chase observed in the snow was 5 m. The frequency at which mice eluded weasels could not be determined because the temporal relationship between mouse and weasel tracks was unknown.

Fishers were tracked a total of 105 km: 77 km in porcupine habitat and 28 km in hare habitat. These are equivalent to 123 km, 79 km and 44 km respectively when adjusted by the ratios shown in Table 1. Twenty-one tracks utilized both porcupine and hare habitats and there were 75 incidences of habitat change. Eight tracks stayed in porcupine habitat and four in hare habitat for the entire tracked distance. Fishers avoided habitats with no overhead cover: the pipeline, large logging roads, muskegs, meadows. Track patterns showed that fishers always run across open spaces, frequently minimizing the open distance to be crossed.

Fisher foraging behavior in hare habitat is also characterized by frequent changes in direction (Table 1). Foraging fishers inspected likely coverts and forms and ran along hare runs (Powell and Brander, 1977). Hares were captured after breaking from cover; no long chases were reconstructed from tracks. As with weasels, the frequency with which hares eluded fishers could not be determined. The three hare kills found were preceded by short rush attacks.

In contrast, fisher foraging in porcupine habitat was characterized by long distances (up to 5 km) travelled with infrequent direction changes (Table 1). These long upland travels often passed within a meter or one or more porcupine dens (Figure 4). Sometimes a fisher would abruptly change direction before going directly to a porcupine den, as if the fisher had smelled the den. Some porcupine dens were visited every winter of this study, even when they were inactive.

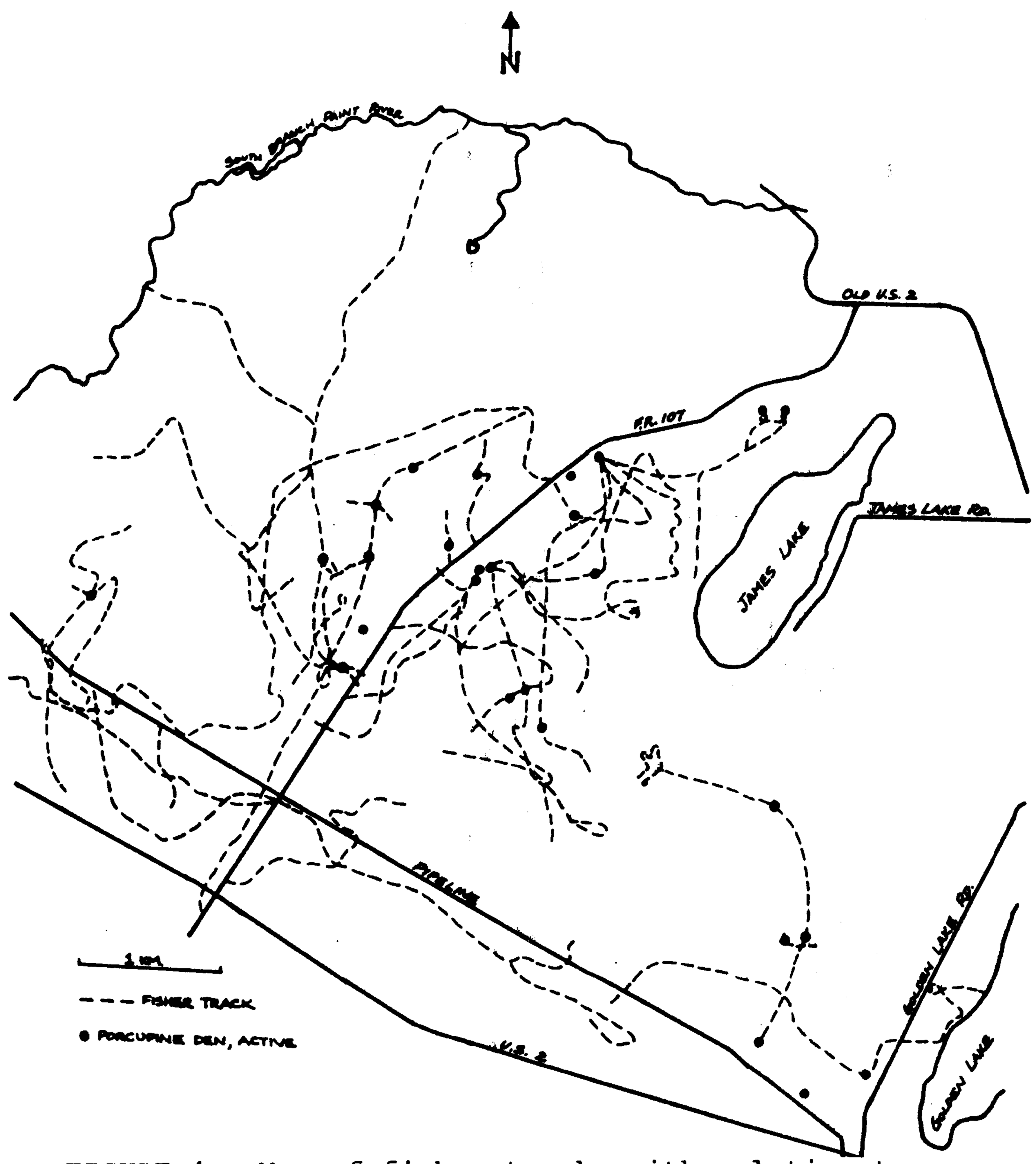

FIGURE 4. Map of fisher tracks with relation to 27 known active porcupine dens.

Twenty-seven porcupine dens were known to be active at least one of the three winters (Figure 4). Table 2 summarizes the numerical relationships between dens and fisher tracks visiting them. To see if fishers hunting porcupines had a tendency to inspect several porcupine dens before going back to hunting hares, the right-hand column in Table 2 was compared to a Poisson distribution. The number of dens visited by a fisher was significantly different from a Poisson distribution ($p<0.02$), indicating that fishers visit several dens while foraging in porcupine habitat.

TABLE 1. Mean Ratios (+SD) of Distance Run (R) to Straight-line Distance Along the Direction of Travel (T).

	(R/T) ± SD	Range	T (km)	Number of Observations
Weasel[a]	1.48 ± 0.68	1.04 - 3.52	0.3	20
Fisher in hare habitat[b]	1.55 ± 0.24	1.26 - 1.90	2.8	5
Fisher in porcupine habitat[ab]	1.03 ± 0.03	1.00 - 1.11	20.4	18

a) difference significant ($p<0.01$, Student's T test)
b) difference significant ($p<<0.01$, Student's T test)

TABLE 2. Summary of Fisher Track Visitations to Porcupine dens.

N	Number of dens visited by N tracks	Number of tracks visiting N dens
0	3	13
1	14	7
2	4	3
3	2	4
4	4	3

Tracking Observations and Hunting Success

Five porcupines killed by fishers were found within 24 hours of the kill so that reconstruction of the kill was possible. Track and sign indicated that all porcupines were found on the ground by the fishers and that the porcupines were killed by repeated wounds on the face. Each porcupine appeared to have tried to keep its face against a tree while the fisher circled and attacked the porcupine's face when possible. Bark scrapings in the snow indicated that the fishers climbed the trees in order to force the porcupines back and into the open (see captive animal observations).

On two occasions fisher tracks I followed showed that the fisher climbed a tree in which there was a porcupine but did not kill the porcupine. In both cases the porcupines were facing out from the trunk when I came by several hours after the fisher. Out of 12 observations of porcupines in trees for which the direction the porcupine faced was noted, the porcupine faced the trunk of the tree in only one case ($p<0.01$, Chi-square).

Table 3 shows the results of the analysis of 35 scats. Snowshoe hares, porcupines, deer carrion *(Odocoileus virginianus)*, mice and squirrels *(Sciurus carolinensis, Tamiasciurus hudsonicus, Glaucomys sabrinus)* were the prey items most often found in scats. Many scats contained remains of more than one prey type. For example, one scat had both hare and porcupine remains.

TABLE 3. Percent occurrence of different prey types in 35 fisher scats.

Prey type	% occurrence
snowshoe hare	31
porcupine	20
dead deer	20
mice	20
squirrels	14
shrews	8
vegetation	6
unidentified	14

A total of 14 kills and scavenges were found along tracks: one porcupine kill, one hare kill, two squirrel kills, two mouse kills, seven scavenges of small pieces of hide or bone and one deer more than half gone when the fisher found it. The porcupine and hare kills were made by the same fisher. I also found one completely consumed deer and two completely consumed porcopines which had been utilized by fishers. Live-trapped fishers showed further evidence of predation on porcupines: 9 of 15 had quills in their necks and shoulders.

Captive Animal Observations

Weasel killing behavior was characterized by a neck bite (Allen, 1938; Ewer, 1973; Glover, 1943; Hamilton, 1933; Llewellyn, 1942). A weasel first attempted to bite its intended prey at any place available. If this initial hold were not the prey's neck, the weasel would wrap itself around the prey (Figure 5), grasping with all four feet while releasing its bite and finding the back of the prey's neck (Heidt, 1970; Miller, 1931). Once the weasel had a firm hold with its teeth on the back of the prey's neck it would release its hold with its feet and wait for the prey to be immobilized. Prey were not always killed by the neck bite. Twice mice which had been immobilized but not immediately eaten escaped after 5 to 10 minutes of apparent death. Eating commenced at the head and the entire mouse was consumed, excluding sometimes the feet, tail and intestines. Weasels given more mice than they could eat would kill all mice (Erlinge et al., 1974; Ewer, 1973), but cache uneaten mice in their nest boxes.

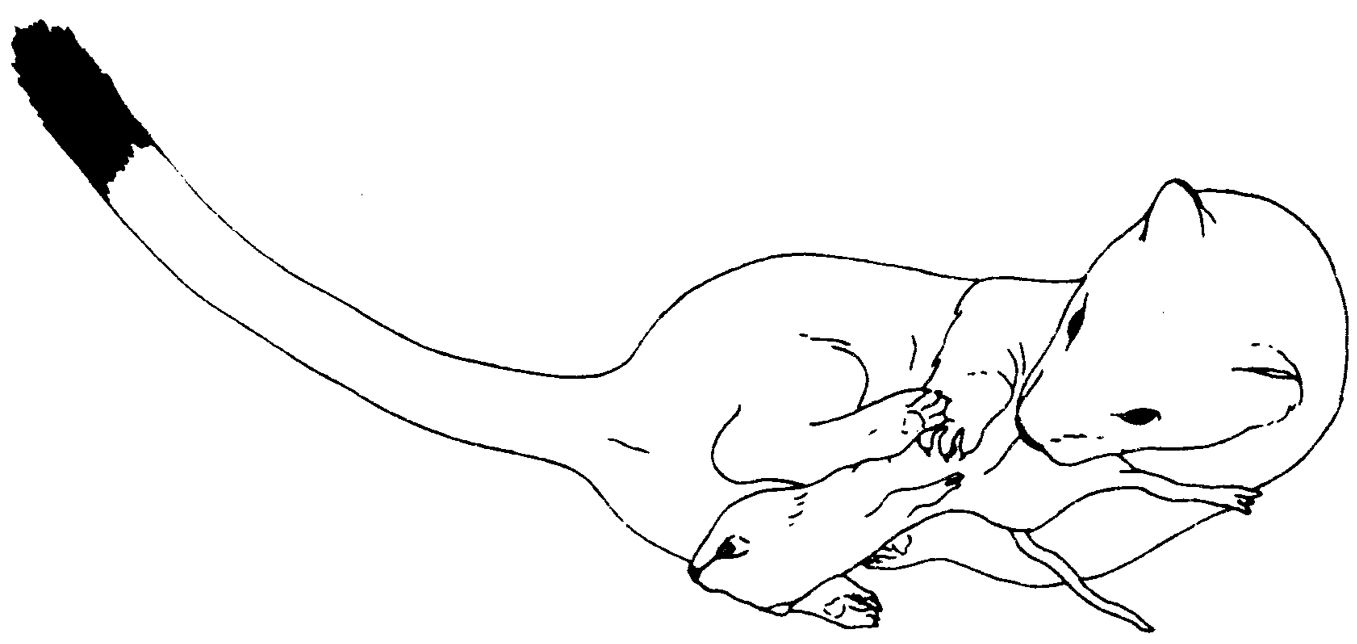

FIGURE 5. A long-tailed weasel exhibiting the wrap-around assist in killing a deer mouse. Fishers use the wrap-around assist in killing snowshoe hares. Drawing taken from a photograph.

Fishers killed hares by biting the back of the neck or head (Coulter, 1966). In all observations, the behavior of fishers killing hares was the same as that of weasels killing mice. One kill took 15 seconds from the time the fisher first bit the hare until the hare stopped breathing; the fisher did not utilize the wrap-around assist. On three occasions hares which were immobilized but not eaten attempted escape after five minutes of apparent death, but their equilibria were faulty and running abilities impaired. These hares were killed immediately after the fisher noted the attempted escape. Eating did not commence from any particular body region, but was often preceded by licking the bloody eyes, nose and mouth of the hare. Fishers took dead hares into their nest boxes when satiated.

Fishers killed porcupines on the ground with repeated attacks on the porcupines' faces, the only exposed part of porcupines not protected by quills. An attacked porcupine attempted to keep its back towards the fisher and would face the pen fence and fence posts, standing as close as possible to protect its face. It would swipe upward or upward and slightly to the side with its tail and rump in defense. An attacking fisher repeatedly circled a porcupine, attempting to bite its face. One fisher climbed the fence and came down head first toward the porcupine, forcing it away from the fence. That fisher was acutely aware of the porcupine's tail and jumped back and away if the porcupine gave its tail a slight twitch. A fisher would suddenly begin to attack excitedly when I scared the porcupine from its relatively immobile position against the fence. Facial wounds weakened a porcupine so that it could no longer defend itself. It was impossible to obtain killing times, but Coulter (1966) obtained three times of one-half hour. Eating commenced on the ventral surface of the porcupine and heart, liver and lungs were usually eaten first. Fishers minimized contact with quills while eating, skinning porcupines neatly and leaving only a few large bones, feet, intestines (sometimes), and skin with quills.

Two hand-raised fishers killed hares and porcupines as described above without parental instruction.

DISCUSSION

With the generally primitive characteristics of the Mustelinae and similar body shapes, it is not surprising that foraging and killing behavior of weasels and fishers hunting snowshoe hares are essentially identical. Frequent direction changes has the added advantage to weasels of predator avoidance (Powell, 1973, 1975, in press). Weasels are preyed upon by raptors (Craighead and Craighead, 1956; Errington, 1967; Mendall, 1944; Selwyn, 1966), martens (Weckwerth and Hawley, 1962), foxes (Latham, 1952), and cats (Gaughran, 1950). An avian predator unable to predict a weasel's movements may be more likely to miss when striking.

Although weasels and fishers use sound and sight to locate prey (Seton, 1929; R. Willey, 1970, personal communication); abrupt changes in direction followed by direct approach to a porcupine den strongly suggest that fishers use olfactory cues to locate porcupine dens.

Both weasels and fishers respond to prey movement as a stimulus for attack. That both lost interest in and allowed immobilized prey to recover indicates that lack of movement is a stimulus for prey release. The high metabolic rate of weasels (Brown and Lasiewski, 1972; Moors, 1975, 1977) puts strong demands on weasels to find sufficient food. Repeated killing and caching of prey items is one method of insuring future food (Ewer, 1973; Hall, 1951; Kruuk, 1972; Moors, 1975, 1977). Movement as a stimulus for attack may be important to fishers because when a porcupine moves quickly it is more likely to expose its face than when cautiously keeping its back to the fisher and face towards a tree.

Both weasels and fishers use their body and feet to handle prey. This behavior is not characteristic of other canoids, undoubtedly because of body shape, but is used by genets (*Genetta* spp.: Ewer, 1973) which are not dissimilar in shape from fishers. The wrap-around assist is not used by mongooses (Ewer, 1973), indicating that the behavior is not a direct corollate to body shape.

Fishers in ONF appear to hunt mainly for porcupines and snowshoe hares. Deer carrion was rare and scats containing remains of deer were found only from tracks around dead deer. Mice, squirrels, and other small mammals are overrepresented in the scats of carnivores relative to the weight of them eaten (Floyd et al., in preparation) because of their high proportion of fur and bones. Consequently, deer, mice, and squirrels should be of less importance to fishers than indicated by scat analysis.

Interpretation of tracks supports the above. Fishers never used the open habitats which were frequently used by foxes and coyotes to hunt mice. One fox travelling less than one km on a logging road killed four mice, while fishers killed only two mice on 105 km of tracks. The fishers approached the two squirrels killed without changing stride and killed them without a chase. No difference was ever noticed in track patterns in areas with little or much squirrel activity.

Track, scats and kills suggest that all fishers in ONF hunt both hares and porcupines. The three captive fishers which killed porcupines also killed hares and neither hare killing nor porcupine killing require parental instruction. This evidence does not preclude a subpopulation of fishers which kills both porcupines and hares and another which kills only hares, but it strongly supports there being one population which hunts for and kills both prey species.

Fisher tracks indicated that fisher hunting in porcupine habitat is directed towards porcupine dens. Nine known active porcupine dens were visited by more than one fisher track and 10 fisher tracks visited more than one den (Table 3, Figure 4). That the right-hand column of Table 3 differs from a Poisson distribution indicates that fishers tend to visit several dens while foraging in porcupine habitat. This can be interpreted that fishers specifically search for porcupine dens and do not simply pass dens on the way from one patch of hare habitat to another.

Fishers hunting porcupines exhibit behavior not used by weasels. Porcupine dens are located far apart in habitat offering little else as prey for a fisher. Typical musteline foraging behavior would be highly unproductive in porcupine habitat. Also, because of its odor, a porcupine den can be located by smell further away than by direct inspection. Porcupine den locations can be learned and foraging directed towards them. There is an obvious selective advantage for fishers which minimize energy expenditure and quickly locate food sources. Consequently, the typical musteline foraging pattern has been replaced by directional travel to porcupine dens.

Fishers have evolved a unique technique to kill porcupines. Repeated facial attacks have not been reported for other mustelids, but in long-tailed weasels and blackfooted ferrets *(Mustela nigripes)*, "If prey is relatively large, a few preliminary bites delivered anywhere convenient may precede a definitive attack" (Allen, 1938; Progulske, 1969, respectively: quoted from Ewer, 1973: 177). If fishers also display preliminary bites "anywhere convenient" when attacking large prey, such behavior could easily have developed into repeated facial attacks on porcupines. Adaptations of fishers for killing porcupines have been discussed by Powell and Brander (1977). Body shape and size uniquely characterize fishers as highly successful predators on porcupines. The evolution of a successful and relatively safe technique for killing porcupines opened a new source of food to fishers for which they had little competition.

Porcupines can reduce the danger of fisher attack by limiting access to their faces. Before the fisher was reintroduced to ONF in the early 1960's, porcupines sometimes used hollow log dens with holes at both ends (R. B. Brander, personal communication). Since the reestablishment of fishers in ONF, use of such dens has ceased, possibly because porcupines have learned that such dens are not safe from fisher attack or all porcupines which used such dens have been killed, favoring only those porcupines which utilize dens with one entrance. Porcupines in trees appear to avoid predators by facing away from the trunk. If a porcupine were to face towards the trunk a fisher could either attack its face or force it backwards until it fell from the tree. Then the fisher could make a normal attack.

SUMMARY

Hunting behavior of fishers and weasels is generally very similar, probably because of close evolutionary relationship and similarities in body shape. Typical foraging is characterized by frequent direction changes and killing is characterized by a neck bite. Fisher foraging for porcupines, however, is characterized by infrequent direction changes and foraging directed towards porcupine dens. Fishers kill porcupines by attacking their faces. This hunting behavior is unique among the mustelines and enables fishers to utilize a food source for which there is little competition.

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LITERATURE CITED

Allen, D. L. 1938. Notes on the killing technique of the New York weasel. *Journal of Mammalogy* 19: 225-229.

Anderson, E. 1970. Quaternary evolution of the Genus *Martes* (Carnivora, Mustelidae). *Acta Zoologica Fennica* No. 130: 132 pp.

Anthony, H. E. 1928. *Field Book of North American Mammals.* G. P. Putnam's Sons, New York.

Barkalow, F. S. Jr. 1961. The porcupine and fisher in Alabama archaeological sites. *Journal of Mammalogy* 42: 544-545.

Brander, R. B. 1973. Life-history notes on the porcupine in a hardwood-hemlock forest in Upper Michigan. *Michigan Academician* 5(4): 425-433.

Brown, J. H., and R. C. Lasiewski. 1972. Metabolic rate of weasels: The cost of being long and thin. *Ecology* 53: 939-943.

Cahalane, V. H. 1944. *Meeting the Mammals.* Macmillan Co., New York.

Cahalane, V. H. 1947. *Mammals of North America.* Macmillan Co., New York.

Colbert, E. H. 1969. *Evolution of the Vertebrates.* 2nd Edition. John Wiley and Sons, New York.

Coues, E. 1877. *Fur-bearing Mammals: A Monograph of North American Mustelidae.* USDI Miscellaneous Publication No. 8: 348 pp.

Coulter, M. W. 1966. Ecology and management of fishers in Maine. Unpublished PhD thesis,

State University College of Forestry at Syracuse University, Syracuse, New York.
Craighead, J. J., and F. C. Craighead, Jr. 1956. *Hawks, Owls and Wildlife.* Stackpole, Harrisburg, Pennsylvania and Wildlife Management Institute, Washington, D.C.
Erlinge, S., B. Bergsten, and A. Kristiansson. 1974. Hermelinin och des byte -- Jaktbeteende och flykreaktioner. *Fauna och Flora* 69(6): 203-211.
Errington, P. L. 1967. *Of Predation and Life.* Iowa State University Press, Ames.
Ewer, R. F. 1973. *The Carnivores.* Cornell University Press, Ithaca, New York.
Floyd, T. J., L. D. Mech, and P. A. Jordan. In preparation. Relating wolf scat content to prey consumed.
Gaughran, G. R. L. 1950. Domestic cat predation on short-tailed weasel. *Journal of Mammalogy* 31: 356.
Glover, F. A. 1943. Killing techniques of the New York weasel. *Pennsylvania Game News* (10): 11.
Hagmeier, E. M. 1956. Distribution of marten and fisher in North America. *Canadian Field-Naturalist* 70: 149-168.
Hall, E. R. 1951. *American Weasels.* University of Kansas Publications, Museum of Natural History, Vol. 4: 466 pp.
Hamilton, W. J., Jr. 1933. The weasels of New York. *American Midland Naturalist* 14: 289-344.
Heidt, G. A. 1970. The least weasel, *Mustela nivalis* Linnaeus: Developmental biology in comparison with other North American *Mustela. Publications of the Museum,* Michigan State University, Biological Series 4(7): 227-283.
Hibbard, C. W. 1970. Pleistocene mammalian local faunas from the Great Plains and Central Lowland Provinces of the United States. Pp. 395-433, *In:* W. Dort, Jr. and J. K. Jones, Jr. (Eds.), *Pleistocene and Recent Environments of the Central Great Plains.* University of Kansas Department of Geology Special Publication No. 3. Lawrence.
Klimov, Yu.N. 1940. [Data on the biology of the ermine.] *Trudy Biologischeskogo Instituta* 7: 80-88.
Kraft, V. A. 1966. [Influence of temperature on the activity of the ermine in winter.] *Zool. Zhur.* 45: 567-570.
Kruuk, H. 1972. Surplus killing by carnivores. *Journal of Zoology* 166: 233-244.
Latham, R. M. 1952. The fox as a factor in the control of weasel populations. *Journal of Wildlife Management* 16: 516-517.
Llewellyn, L. M. 1942. Notes on the Alleghenian least weasel in Virginia. *Journal of Mammalogy* 23: 439-441.
Mendall, H. L. 1944. Food of hawks and owls in Maine. *Journal of Wildlife Management* 8: 198-208.
Miller, F. W. 1931. A feeding habit of the long-tailed weasel. *Journal of Mammalogy* 12: 164.
Moors, P. J. 175. The annual energy budget of a weasel *(Mustela nivalis* L.) population in farmland. Unpublished PhD thesis, University of Aberdeen, Scotland.
Moors, P. J. 1977. Studies of the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel *(Mustela nivalis). Oecologia* 27: 185-202.
Nyholm, E. S. 1959. [Stoats and weasels in their winter habitats.] *Suomen Riista* 13: 106-116.

Parmalee, R. W. 1971. Fisher and porcupine remains in cave deposits in Missouri. *Transactions of Illinois Academy of Science* 64: 225-229.
Powell, R. A. 1973. A model for raptor predation on weasel. *Journal of Mammalogy* 54: 259-263.
Powell, R. A. 1975. The misunderstood weasels. *Defenders* 50: 440-441.
Powell, R. A. In press. (about weasels). *Animal Kingdom.*
Powell, R. A., and R. B. Brander. 1977. Adaptations of fishers and porcupines to their predator prey system. Pp. 45-53, *In:* R. L. Phillips and C. Jonkel (Eds.), *Proceedings of the 1975 Predator Symposium.* Montana Forest and Conservation Experiment Station, University of Montana, Missoula.
Pringle, L. 1964. Killer with a future -- The Fisher. *Animal Kingdom* 67(4): 82-87.
Progulske, D. R. 1969. Observations of a penned, wild-captured black-footed ferret. *Journal of Mammalogy* 50: 619-620.
Schoonmaker, W. J. 1938. The fisher as a foe of the porcupine in New York state. *Journal of Mammalogy* 19: 373-374.
Selwyn, S. 1966. Kestrel catching weasel. *British Birds* 59: 39.
Seton, E. T. 1929. *Lives of Game Animals.* Doubleday, Doran and Co., New York.
Seton, E. T. 1937. *Animals.* Doubleday, Doran and Co., New York.
Teplov, V. P. 1948. [The problem of sex ratio in ermine.] *Zool. Zhur.* 27: 567-570.
Walker, E. P. 1968. *Mammals of the World.* 2nd Edition. Johns Hopkins Press, Baltimore.
Weckwerth, R. P., and V. D. Hawley. 1962. Marten food habits and population fluctuations in Montana. *Journal of Wildlife Management* 26: 55-74.
Willey, R. L. 1970. Sound location of insects by the dwarf weasel. *American Midland Naturalist* 84: 563-564.

OPTIMIZATION OF TIME AND ENERGY CONSTRAINTS IN THE FEEDING BEHAVIOR OF CATS: A LABORATORY SIMULATION[1]

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Most hypotheses about the feeding behavior of domestic cats arise from the interaction between what the owner thinks the cat should eat and what the cat thinks it should eat. There are very few data on the spontaneous feeding patterns of the domestic cat. The present paper describes the pattern and amount of food typically consumed by the freely feeding cat and examines the influence of food availability on the pattern of feeding and amount consumed.

Feeding behavior has long provided the central data for psychological theories of motivation and learning, physiological theories of regulation and brain mechanisms, and ecological theories of niche structure and optimal behavior; and for this reason it occupies a position of unique significance in these areas. However, psychological and physiological research in feeding has focused almost exclusively on the laboratory behavior of the white rat, giving almost no consideration to the naturalistic observations (e.g., Schaller, 1972; Kruuk, 1972; Mech, 1970) of feeding behaviors of other species. Similarly, psychological and physiological research has focused on consumption of items provided by the experimenter and has considered, neither empirically nor theoretically, the series of foraging behaviors by means of which animals acquire their food. Behaviors involved in feeding can be conveniently resolved into five elements, i.e., *search, identification, procurement* (or pursuit), *handling,* and *consumption* (Figure 1; see Schoener, 1971). The first four of these constitute the general class of foraging activity which have, for the most part, been only studied in the field. However, it seems possible that all elements of the chain can be simulated and studied in the laboratory, possibly gaining some precision but potentially losing some relevance. The present research is concerned with the manner in which one element of foraging, i.e., procurement, is exhibited by the freely feeding cat. Procurement is used here in the sense of that part of foraging behavior which follows identification of a food item and precedes contact with the item. It includes behaviors as diverse as reaching for a particular leaf or clump of grass by a herbivore and the pursuit of a prey item by a carnivore. In the present case the instrumental behavior studied was the operation of a lever required to gain access to food. It was assumed that at least in some aspects this behavior simulated the procurement portion of the feeding chain.

In our experimental situation, individually caged cats were free to initiate and terminate feeding at will. To gain access to a meal, the cat was required to execute a specified number of instrumental lever presses. Having accomplished this, the cat was free to determine the size and duration of its own meal. This differs from the usual paradigm in psychological research in that the total meal rather than a portion of a meal was made contingent upon the instrumental response. Food availability, defined in terms of cost rather than scarcity, was manipulated by varying the effort (and indirectly the time) required to execute the instrumental response.

Data was obtained daily over a two-year period from two female cats *(Felis domestica)* which averaged 2,050 g and 2,060 g during the study. Each was confined to a Hoeltge, (Cincinnati, OH), HB-101-1 dog metabolism cage, 71 x 86 x 71 cm with a 20 x 45 x 28 cm plexiglass tunnel attached to one end. At the distal end of the tunnel was a 22 x 10 x 14 cm feeding dish filled daily with approximately 300 g of Purina cat chow.

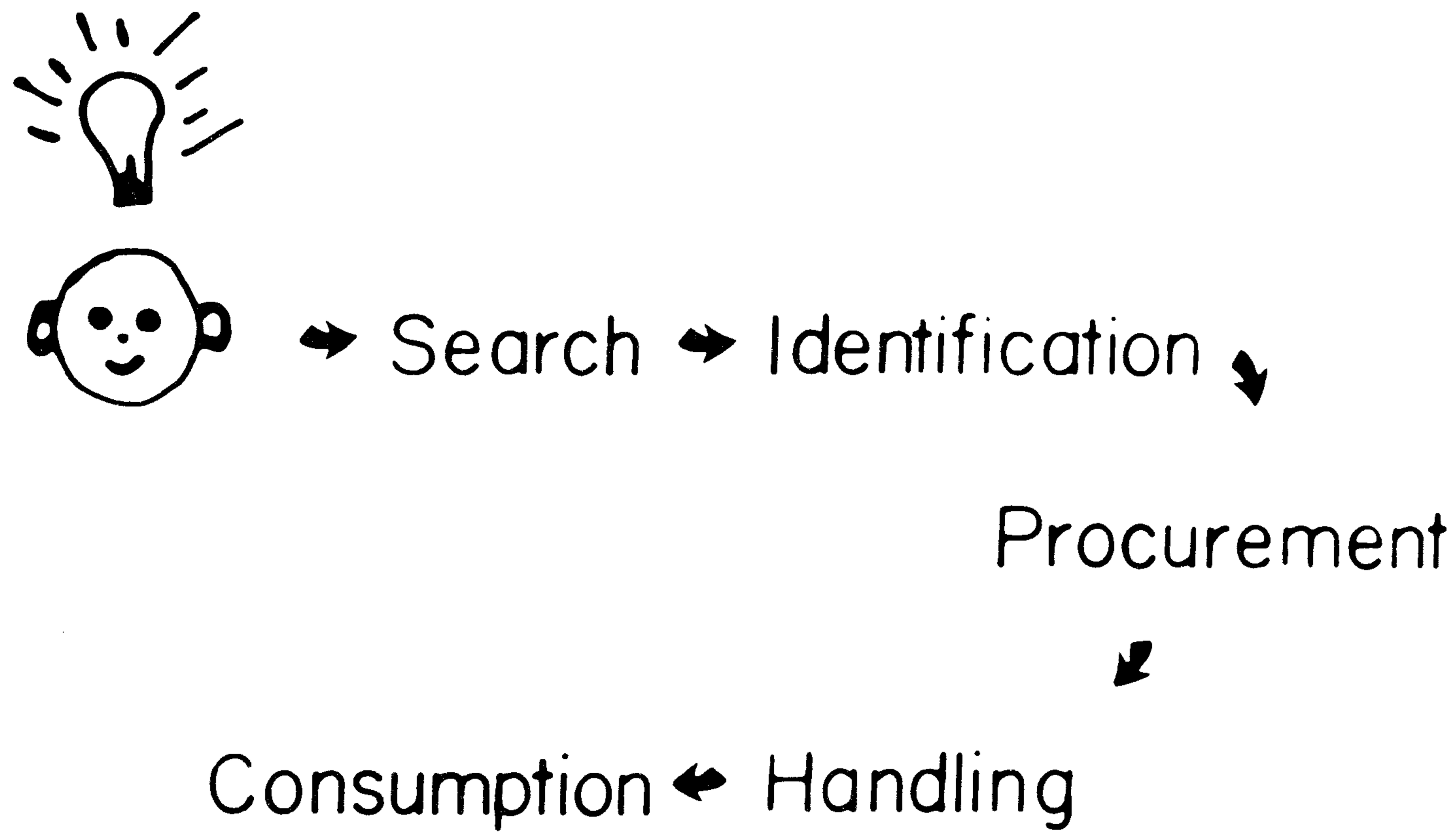

FIGURE 1. The sequence of behaviors leading to a meal in a freely feeding animal.

Access to the food was controlled by a sliding door made of clear plexiglass. Feeding was monitered by a pair of photocells mounted above the food dish. A T-shaped bar (BCS, South Plainfield, N.J.) requiring a force of 35 g through a throw of 2.8 cm for operation, was located on the left wall of the tunnel, 10 cm in front of the door. Figure 2 shows one of the cats in the process of pressing the bar.

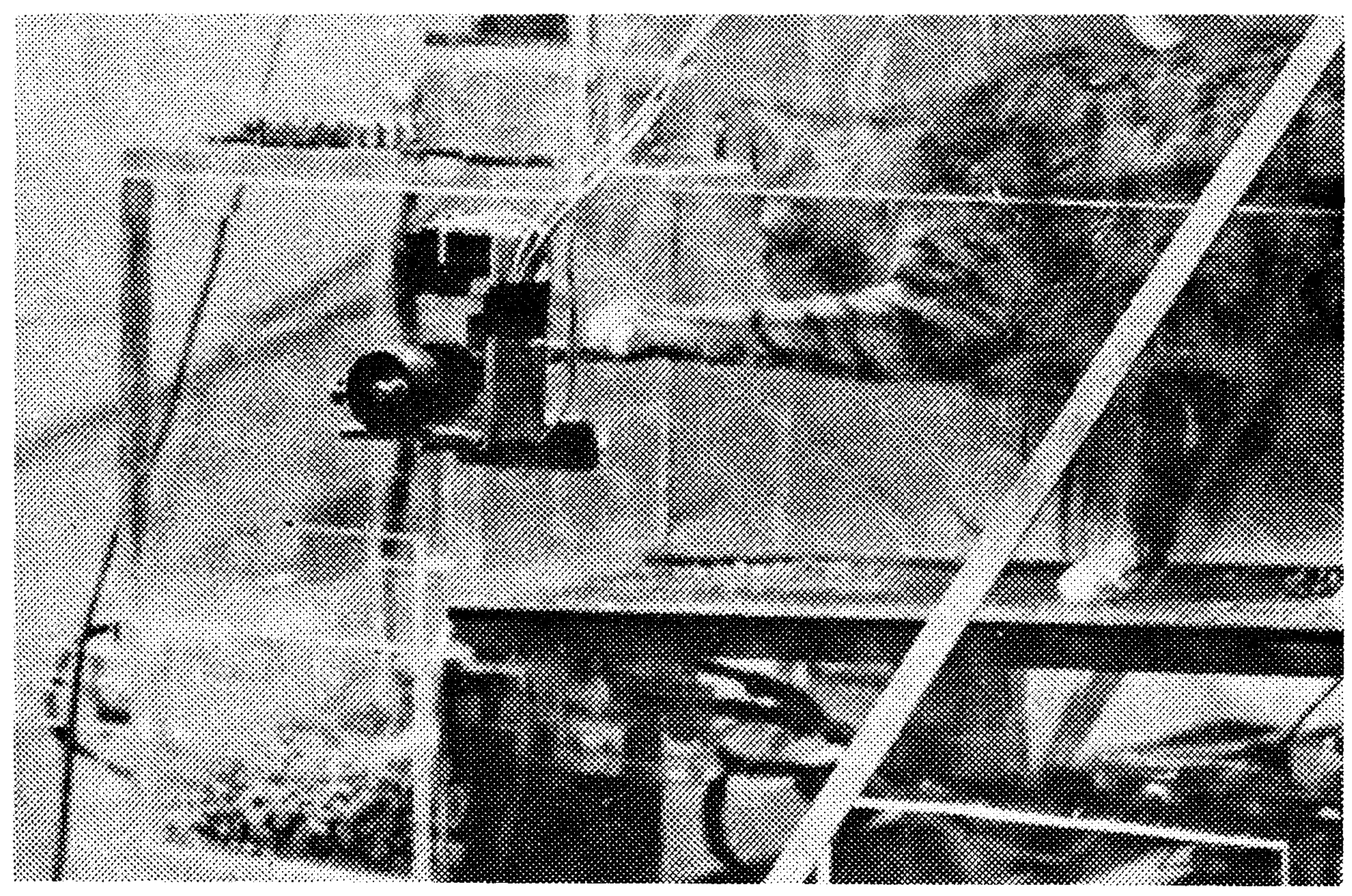

FIGURE 2. Cat 2 pressing the bar. The cat is standing in the feeder tunnel with the weighted lever mounted in the foreground. The food container is in the lower corner of the figure.

Water was available ad libitum. The animals were maintained on a 12-hour photoperiod, with light onset at 0700 hour, and given a one-hour exercise period outside of their cages nine hours after light onset.

During the course of the experiment, access to food for a meal was made contingent upon completion of a fixed number of bar presses. Completion of this requirement opened the door to the food dish, which closed again if the cats did not begin feeding within 10 seconds. Once feeding had begun, the door remained open until 10 minutes had elapsed without a photocell break. Preliminary observations showed that when a cat withdrew from the feeder, without reentry for at least 10 minutes, the probability of reentry within the next hour was virtually nil.

As the experiment progressed the fixed ratio (FR) requirement of bar presses was periodically increased through an ascending series of 1, 10, 20, 40, 80, 160, 320, 640, 1,280, 2,560, 5,120, and 10,240. (FR 20 meaning that 20 bar presses were required for access to a meal.) Following completion of the ascending sequence, the ratios were presented to the cats again in either a random (Cat 1) or descending (Cat 2) order. For a more complete description of the procedure see Kanarek (1975).

The pattern of free feeding without the imposition of an instrumental response for access is shown in the top line of Figure 3 for each cat. These data show that freely feeding cats eat 9-10 meals per day with an average intake of 5.6 g/meal. Although approximately 70% of their meals occurred during the dark phase of the light-dark cycle, the single largest meal invariably occurred during the light phase, immediately following the handling and exercise period. These laboratory findings have since been corroborated using two free-ranging male cats, one living as a family pet and one living on the roof of the psychology building at Rutgers University, both of which received all sustenance (Purina chow) from automated feeders (unpublished data). Neither cat was confined and for both a wide variety of activities were available; yet their daily feeding frequency was also 9-10 meals per day, with the majority of them occurring during the night.

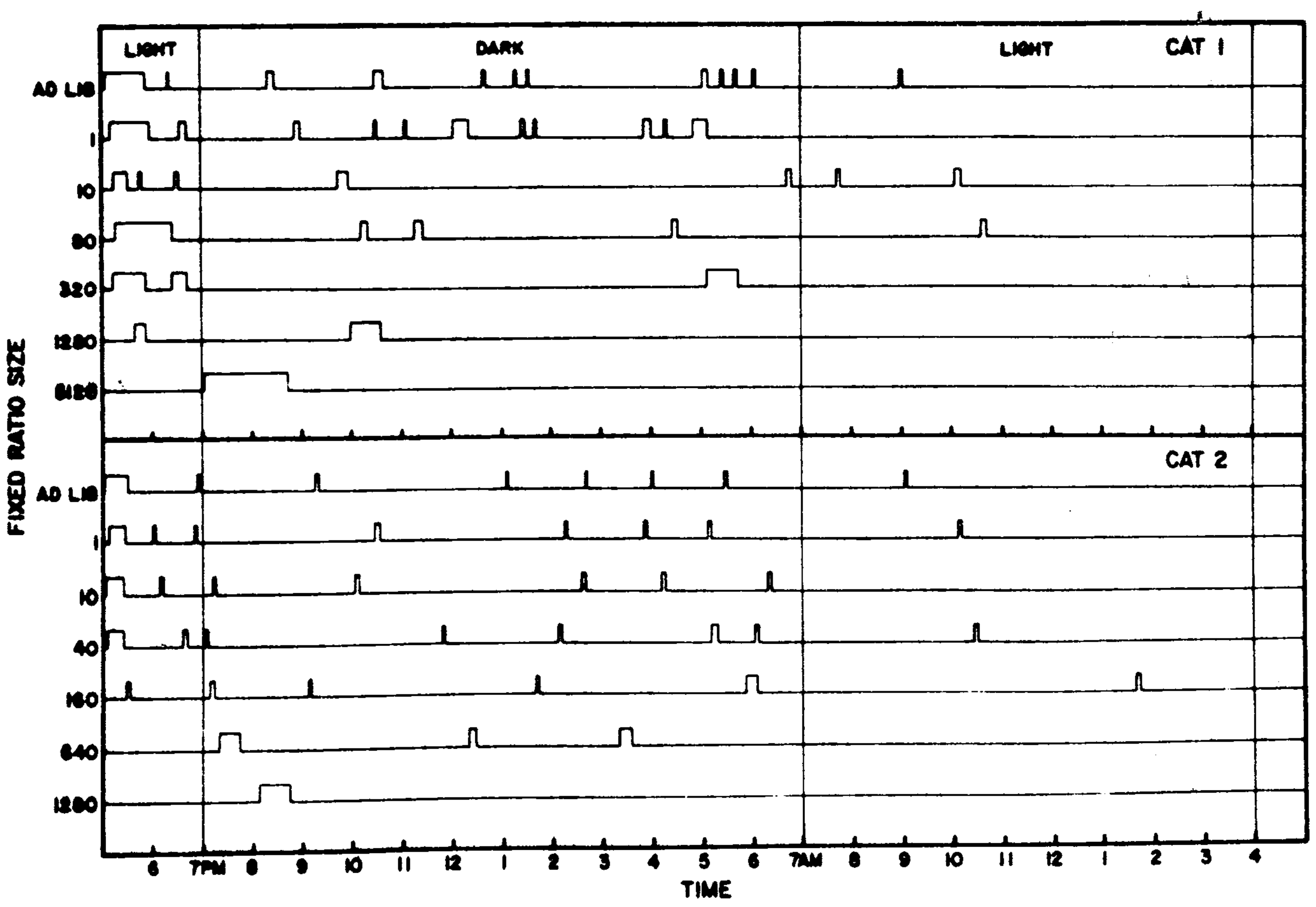

FIGURE 3. The temporal sequence of meals and intermeal intervals at selected fixed ratio sizes for each cat. The width of the pen deflections indicates meal duration. The cats were maintained on a 12/12 light/dark cycle. The lights came on at 7 A.M. and maintenance occurred at 4 P.M. The size of the ratio was the number of bar-presses the animal was required to make to gain access to a meal.

The effects on meal frequency of increasing the cost of feeder access by requiring an increased number of bar presses, thus functionally decreasing food availability, is also shown in Figure 4. As the number of bar presses required to produce a meal increased, the number of daily meals decreased. On FR 1 both cats were still feeding approximately 10 times per day. As the requirement increased both cats eventually reduced their meals to one every 3-4 days. Meal frequency as a function of FR size was completely recoverable with no significant differences in meal frequencies between the original ascending series of FR requirements and the retested values (Figure 4).

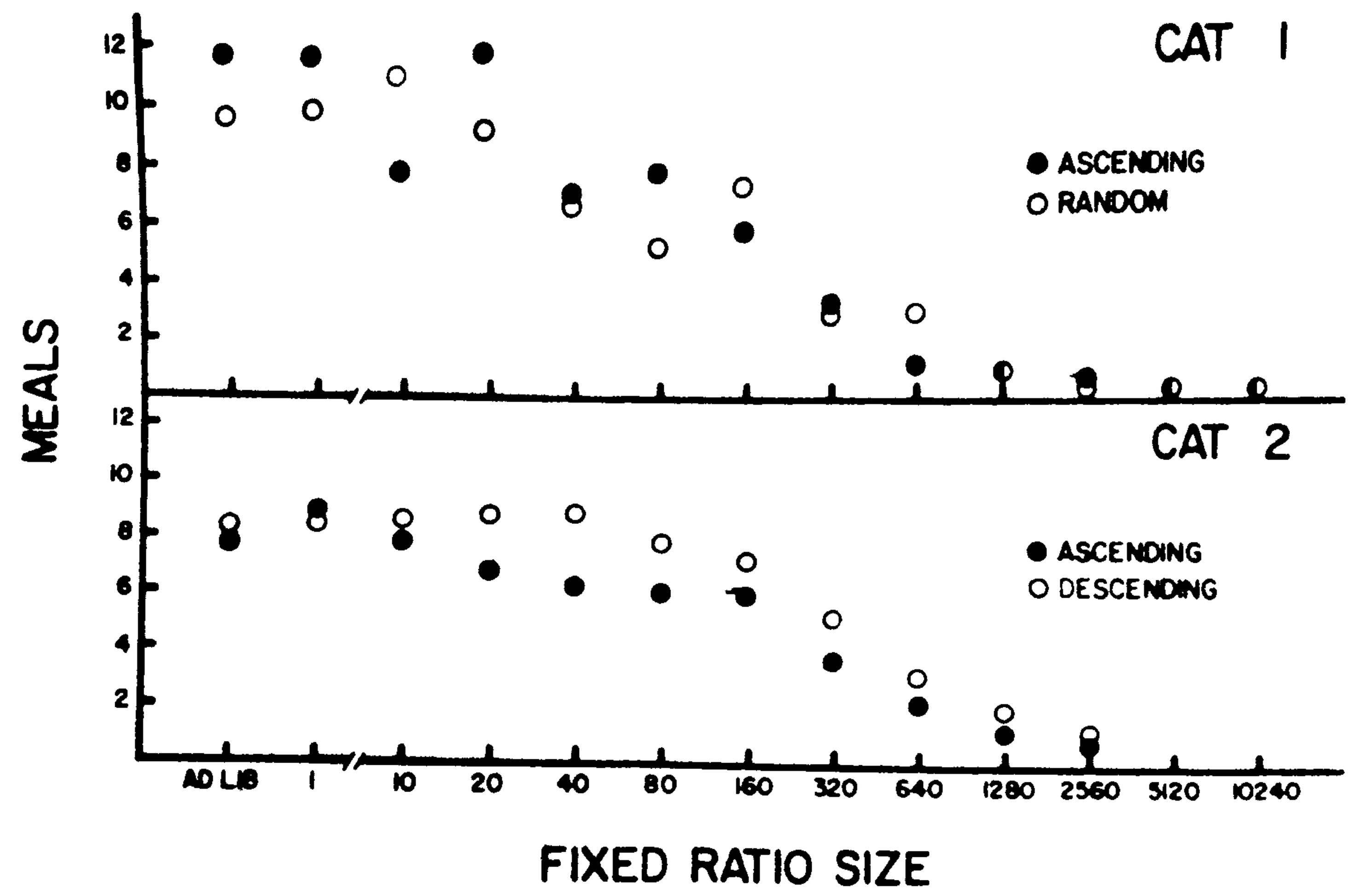

FIGURE 4. Mean daily meal frequency as a function of fixed ratio size for each cat (reprinted from Kanarek, 1975).

Once a cat had initiated bar pressing, it seldom interrupted the train of presses until access to the food had been obtained (see Figures 15 and 16). The FR 10,240 requirement took Cat 1 3-4 hours to complete. The rate of bar pressing did not change significantly as the ratio requirement (or meal cost) increased. Rather, as the meal frequency declined, meal duration (Figure 4) and meal size (Figure 6) increased. This strategy can be seen more clearly by returning to Figure 3 which shows both meal frequency and meal duration at different cost requirements to the animals. By this strategy the cats conserved total intake (Figure 7), except at the most extreme ratios, and maintained a relatively constant body weight (Figure 8).

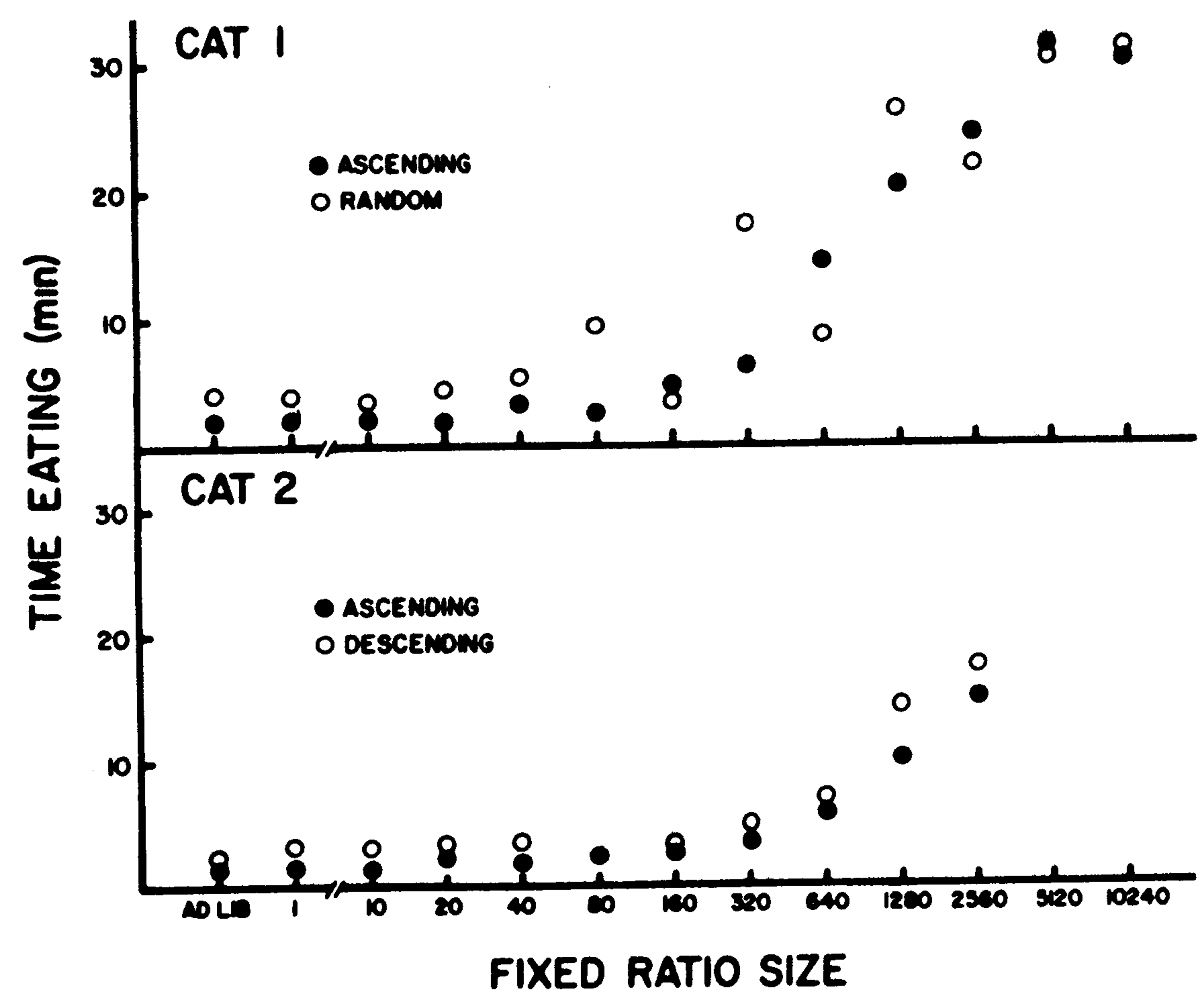

FIGURE 5. Mean time eating per meal as a function of fixed ratio size for each cat (reprinted from Kanarek, 1975).

The results show that when the cost of procurring a meal increases, a cat will compensate by decreasing the frequency of meals and increasing meal size. This strategy is similar to those exhibited by rats (Collier et al., 1972), guinea pigs (Hirsch, 1973; Hirsch and Collier, 1974a,b), and chickens (unpublished data). This inverse correlation between meal frequency and meal size had the effect of conserving total intake and thus body weight. At the most extreme values of cost, however, intake and body weight dropped with the cats then defending lower, but stable, values of these parameters. Thus, there also appears to be a trade-off between cost and body weight.

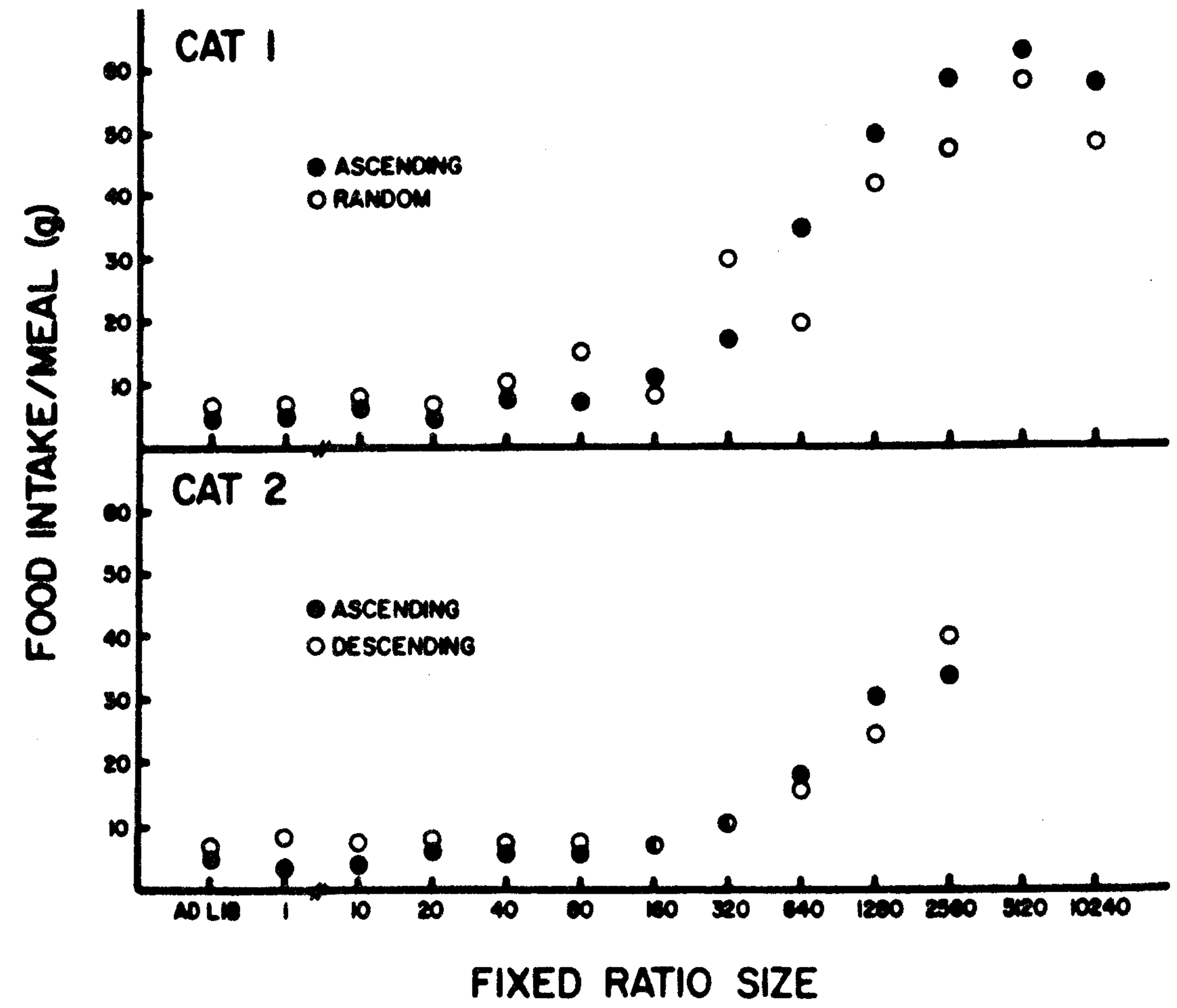

FIGURE 6. Mean food intake per meal as a function of fixed ratio size for each cat (reprinted from Kanarek, 1975).

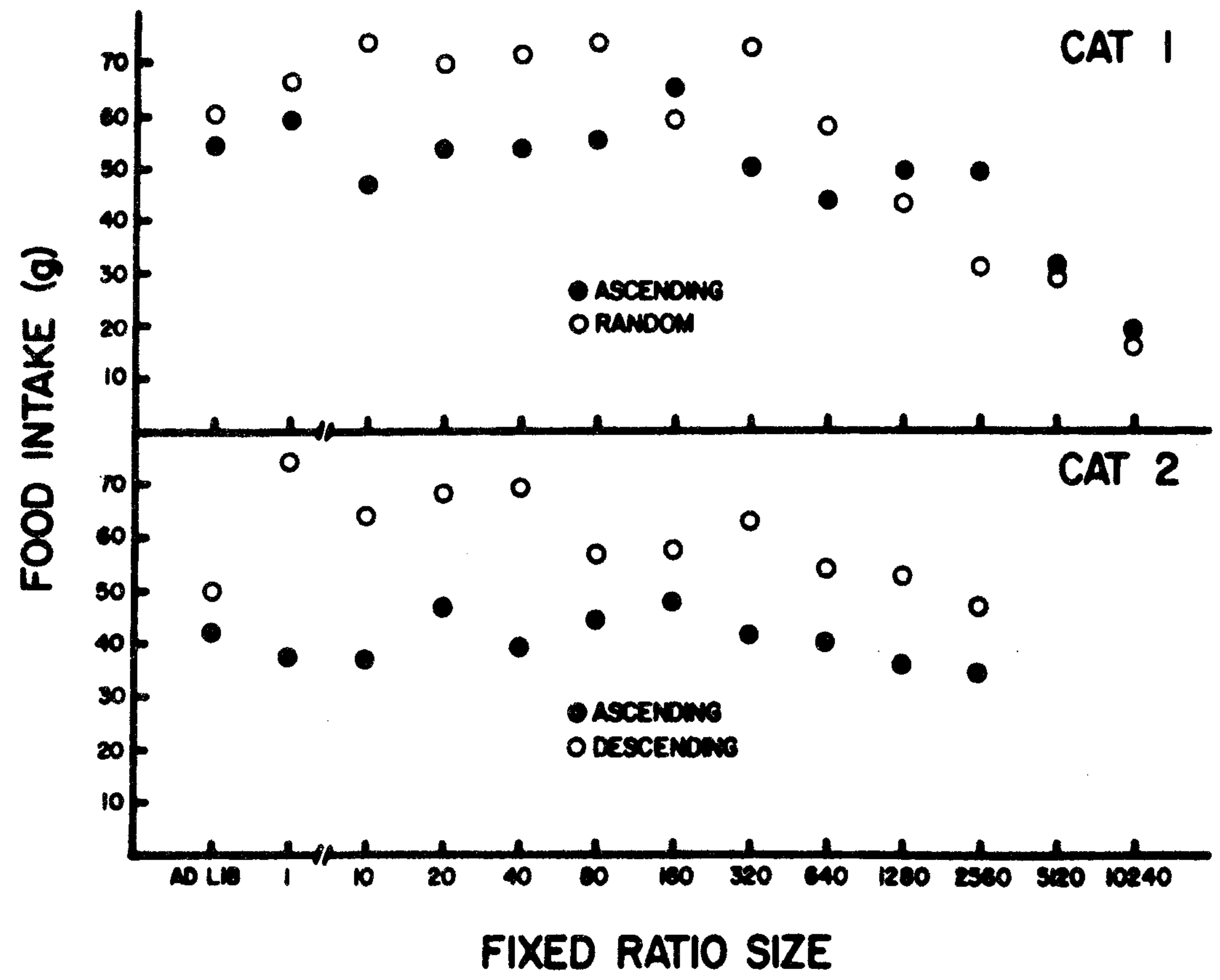

FIGURE 7. Mean total food intake per day as a function of fixed ratio size for each cat (reprinted from Kanarek, 1975).

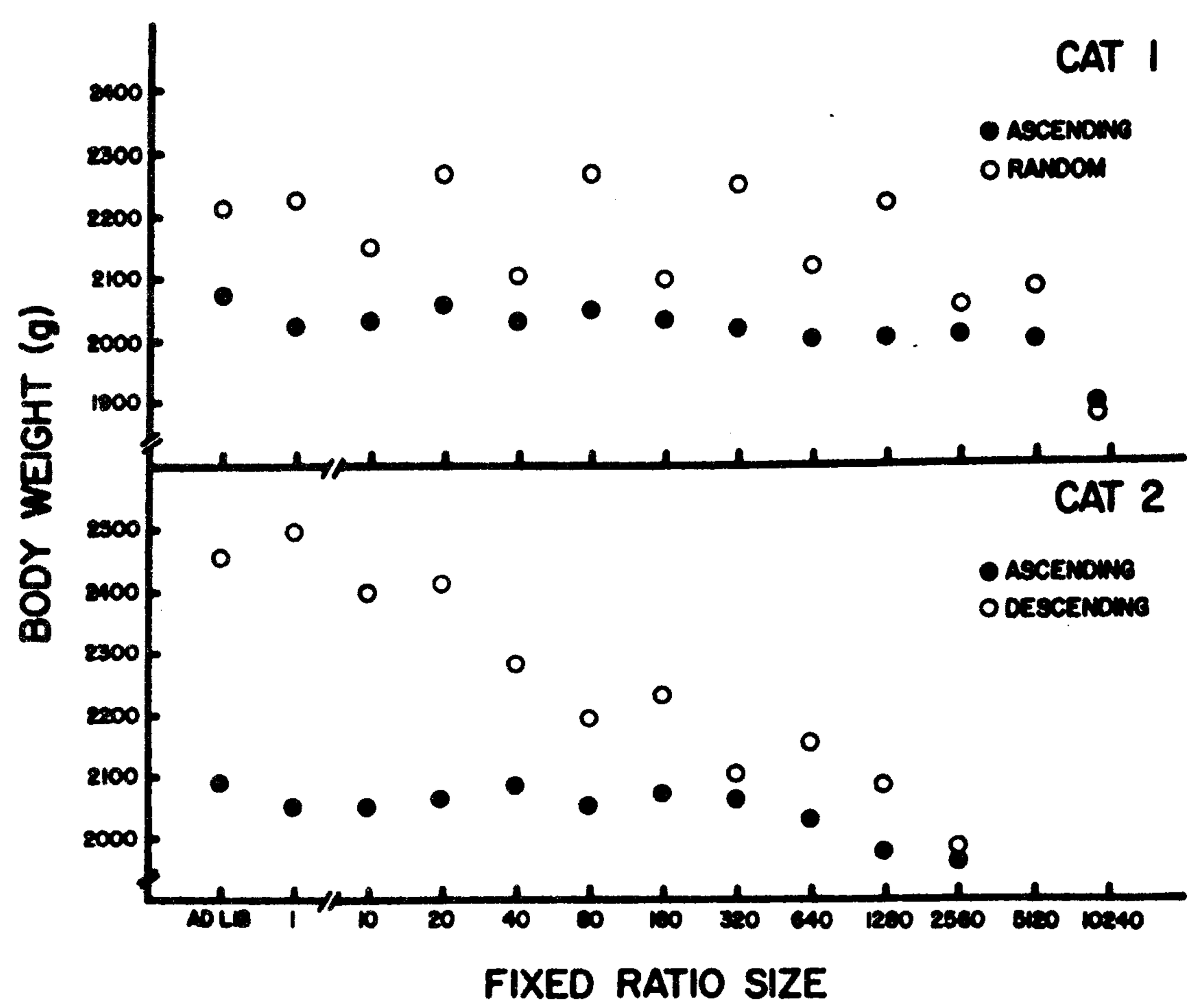

FIGURE 8. Mean body weight as a function of fixed ratio size for each cat (reprinted from Kanarek, 1975).

It should be noted that as the cost to obtain a meal increased the total number of bar presses to obtain a given unit of food also increased, but not as rapidly, because of the decrease in meal frequency and increase in food intake per meal. That is, the strategy of decreasing meal frequency and increasing meal size as a function of cost operated by limiting the total number of bar presses required to maintain daily intake. This constraint on the total number of bar presses had two consequences: (1) it reduced the time spent obtaining meals at a given cost, and (2) it reduced the work required to obtain a meal at a given cost. Two additional strategies were available to the cat which could have affected procurement time. First, if the cat increased the rate of bar pressing as the ratio size increased, time spent procuring a meal at a given cost would be reduced. Second, if the cat ate faster once a meal was obtained, then the total time spent eating would be reduced. Neither of these rates varied under the present conditions. (See Kanarek, 1975, and below for conditions which do affect these rates.)

Recent theories of optimal feeding (Emlem, 1973; MacArthur, 1972; Rapport and Turner, 1977; Schoener, 1971) have argued that animals either minimize the time or energy required to obtain food, or both. These two parameters were confounded in the results of the previous experiment since increasing the number of responses required to obtain a meal increased both the time and work required. In an attempt to partial out these two factors, a second experiment was performed in which effort required to operate the bar was varied.

In this experiment the same subjects and apparatus were used as in the previous experiment. The procedure used in this experiment was similar to that of the first experiment with the exception that the effort required to operate the bar, as well as the number of bar presses required to obtain a meal, was varied. This was done by loading the distal end of the bar with weights (see Figure 2). The bar weights employed ranged from 100 to 1300 g in 100 g steps. Ascending and descending sequences of weights were used at four different fixed ratios (10, 40, 160 and 640) for Cat 1 and three different fixed ratios (40, 160, and 640) for Cat 2. The only other alterations in procedure were in the times of light onset (0500 hour) and exercise period (4 hours after light onset).

Many of the FR x Weight combinations were replicated more than once and since the variability of these points was small, all the following figures represent the data obtained on the initial ascending sequence.

Meal frequency as a function of combination of bar weight and ratio size is shown in Figure 9. Increases in the magnitude of either of these variables decreased meal frequency. It is clear that these two variables interact, each variable having its maximum effect when the other variable is small. The expected compensatory increase in meal size and duration occurred, as shown in Figures 10 and 11 respectively, resulting in a relatively constant daily intake except at the terminal weight-ratio combination in each FR series. One exception was shown by Cat 1 on FR 10. Her meal size did not increase at the lower ratios, producing a fall in intake, but strangely no fall in body weight. Consummatory rate did not vary as a function of either variable (Figure 12). Fluctuations in body weight (Figure 13) appear to be the result of extraneous, unmeasured factors (e.g., estrus), except at the most extreme values of the ratio-weight combinations. The maximum weight losses, with one exception, were 10% or less.

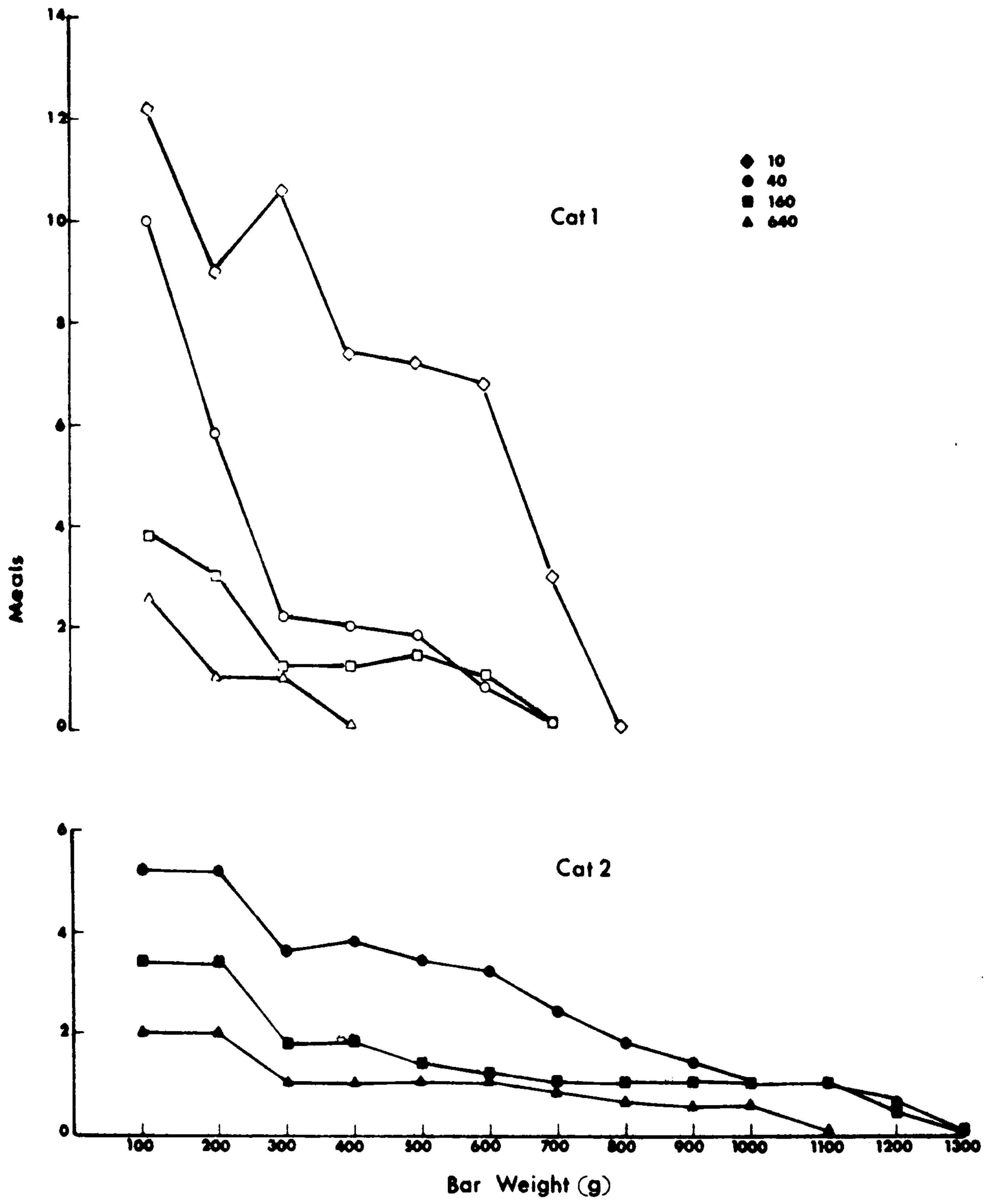

FIGURE 9. Mean daily meal frequency as a function of fixed daily ratio size and bar weight for each cat.

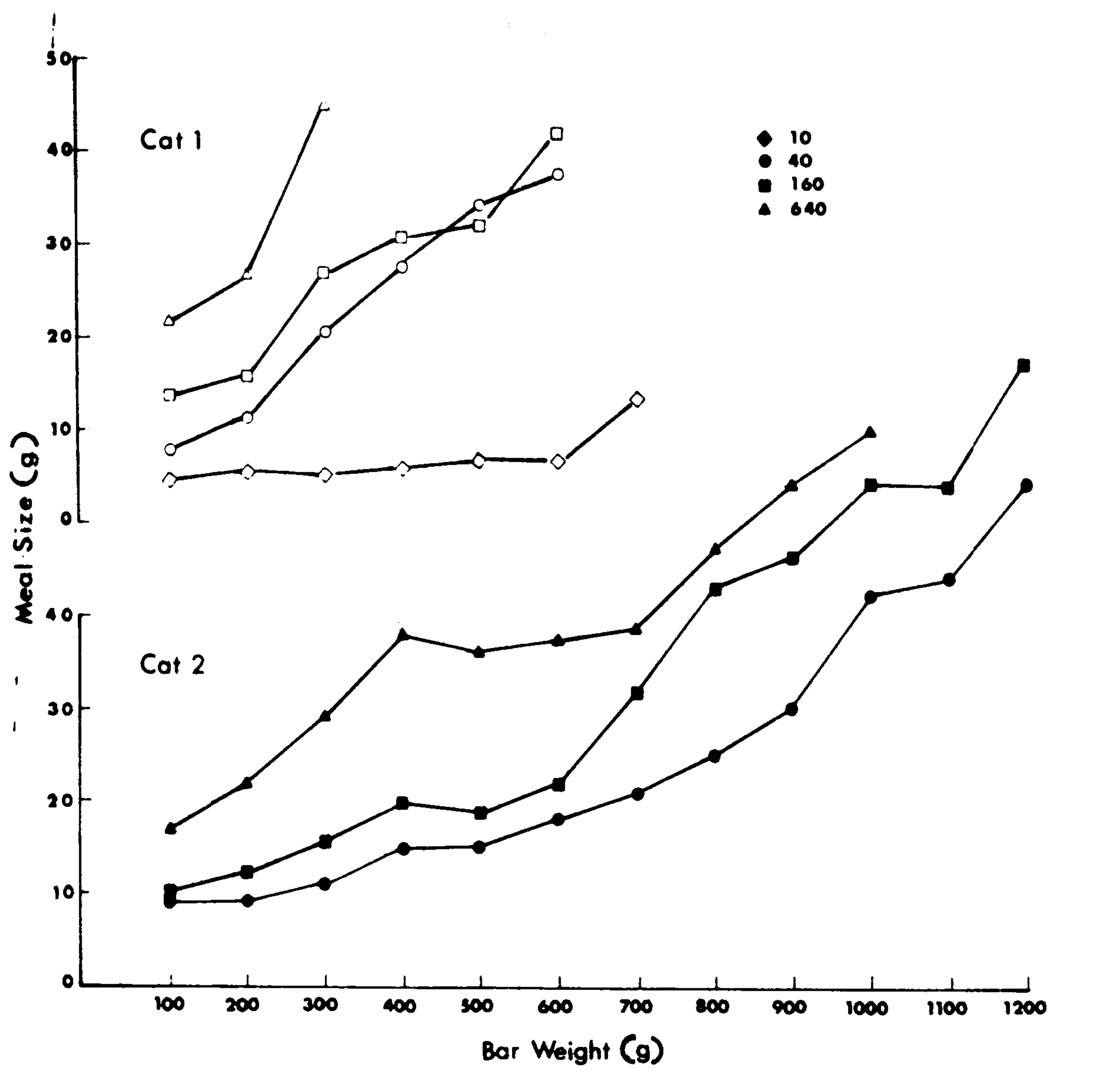

FIGURE 10. Mean food intake per meal as a function of fixed ratio size and bar weight for each cat.

As previously pointed out, there were two ways in which an animal could minimize time spent gaining food in this type of situation: (1) he could eat less frequently and/or (2) he could increase his rate of instrumental responding, reducing the time required to complete a given ratio, as the number of responses required per meal increased. For the cat, increasing the rate of instrumental responding would be analogous to increasing the rate at which a hunt takes place, and does not seem to be a biologically reasonable strategy for animals which stalk game. (It may, however, be an appropriate strategy for animals such as the guinea pig, a monogastric herbivore competing with his conspecifics within a patch. See Collier et al., 1977; Hirsch and Collier, 1974a). It is clear from the previous experiment and the present one that increasing ratio size decreases meal frequency, but does not affect rate of responding (Figure 14), with the exception that Cat 1 appears to respond faster on FR 10 than the other ratio requirements. On the other hand, increasing bar effort substantially *reduces* rate of responding, increasing the amount of time required to complete any given ratio (Figure 14). There is no apparent interaction between these variables. Appreciation of this relationship can be gained from the representative individual cumulative records shown in Figures 15 and 16.

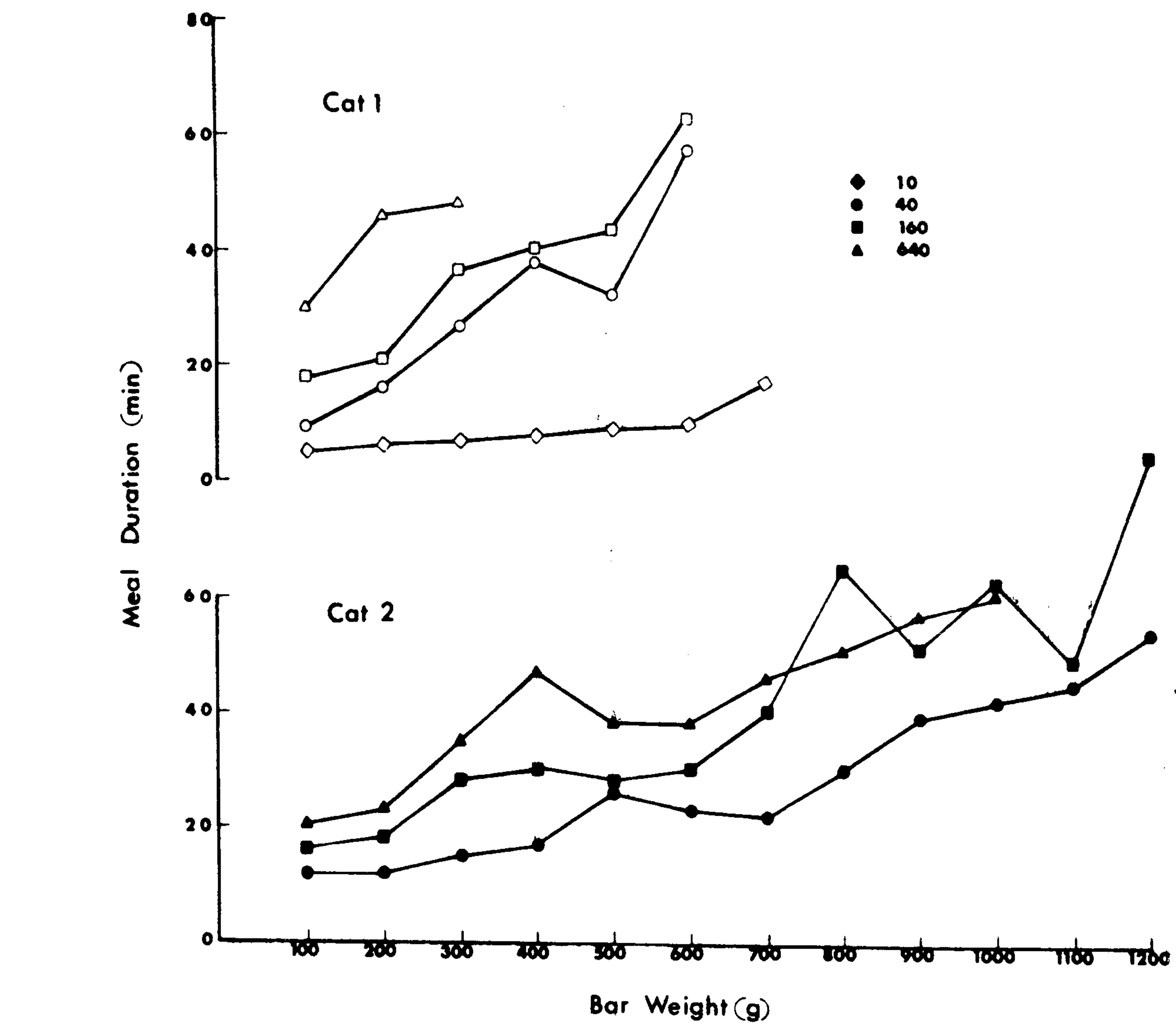

FIGURE 11. Mean time eating per meal as a function of fixed ratio size and bar weight for each cat.

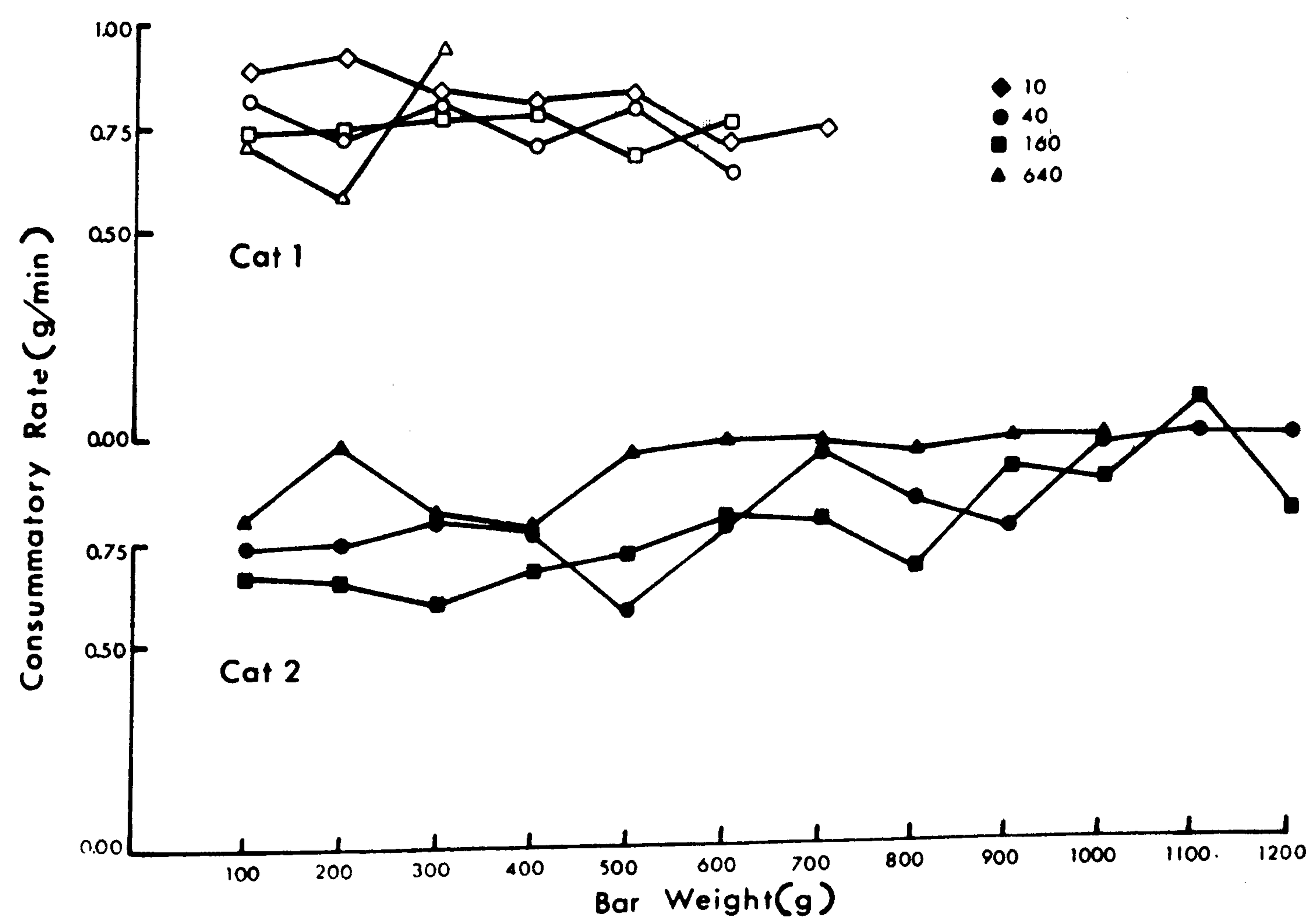

FIGURE 12. Mean rate of eating as a function of fixed ratio size and bar weight for each cat.

The chart on which the information in these figures is recorded moves by the recorder pen at a fixed rate (15 cm/hr in this case). Each bar press displaces the pen a small distance across the page from its previous position, producing a time-based cumulative record of bar presses for a given meal.

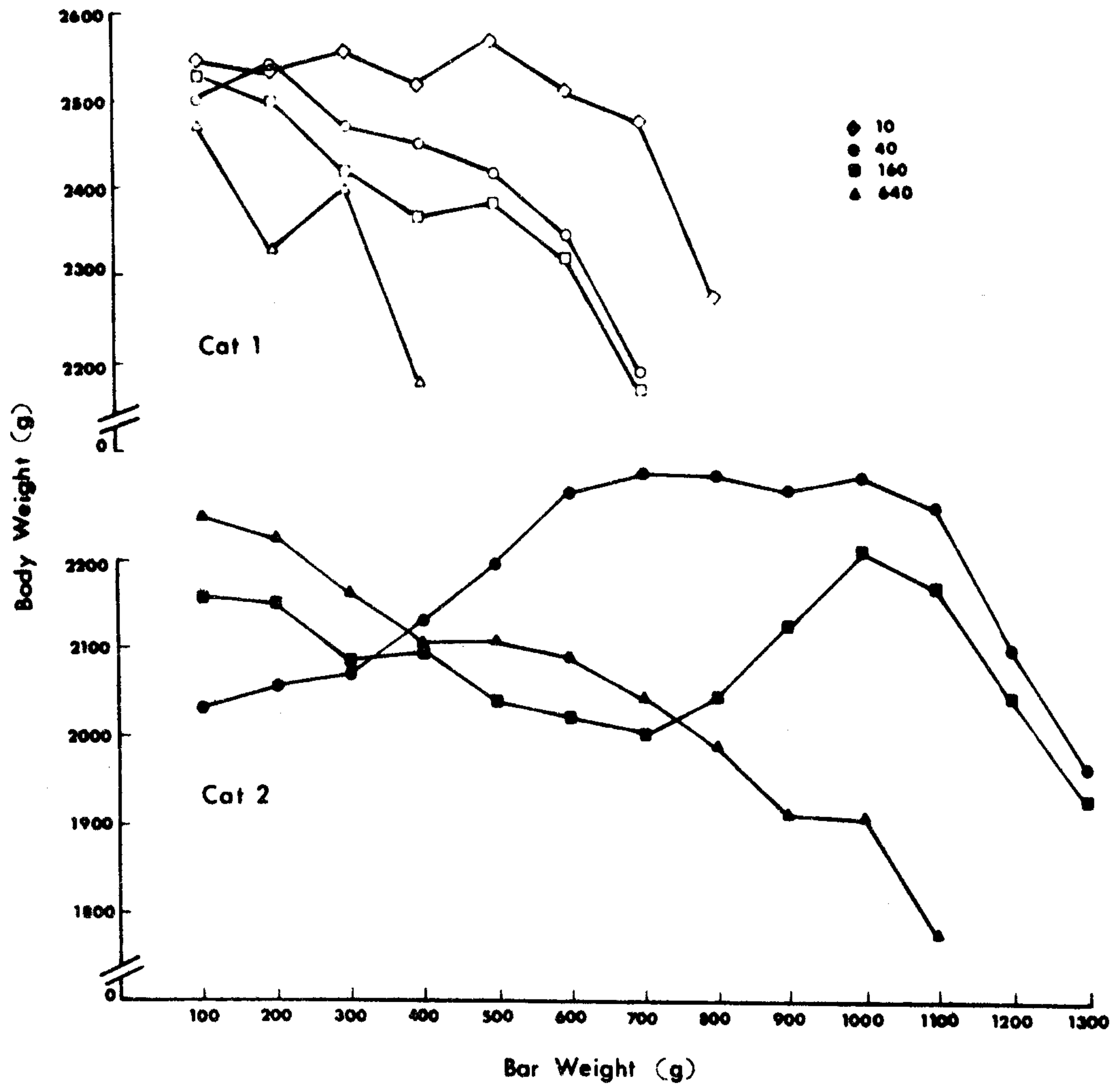

FIGURE 13. Mean body weight as a function of fixed ratio size and bar weight for each cat.

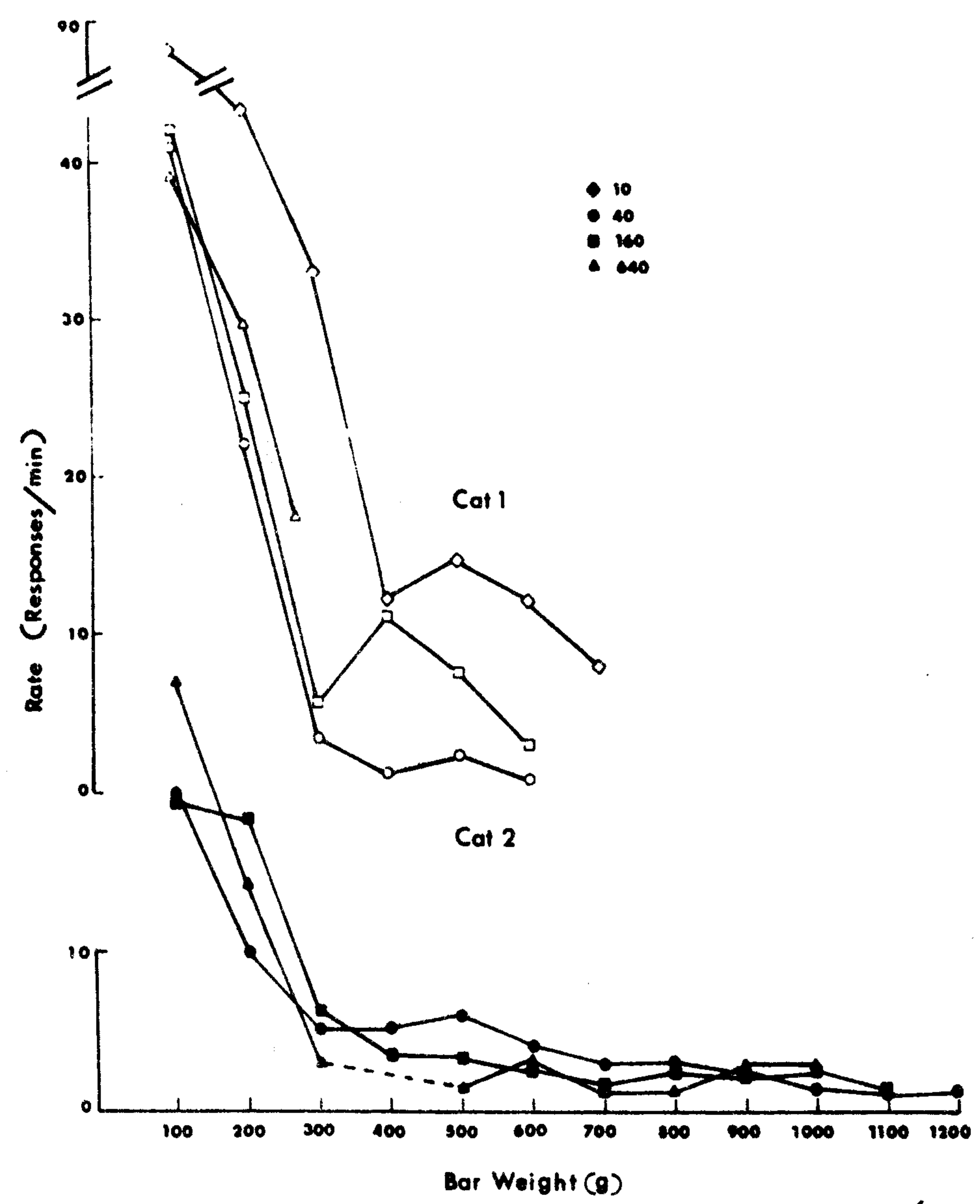

FIGURE 14. Mean rate of bar pressing as a function of fixed ratio size and bar weight for each cat.

Both quantitative and topographic changes in the bar-pressing response account for the form of these records. The pattern of responding in the cat in this situation consists of bar pressing and interpolated activities. The latter consist of bar touching without activation, scratching of the magazine door, and stereotyped circling movements of the cage accompanied by vocalizations. A description of the typical pattern of responding for Cat 2 on a FR 40 schedule with a bar weight of 800 g taken from a video tape is as follows: The cat spends several minutes circling the cage and walking in and out of the feeder tunnel, vocalizing occasionally. Each time the cat enters the tunnel it looks at the bar and into the food dish. Finally the cat crouches in the tunnel, facing the food dish, and spends most of the next 8-12 minutes looking at the bar and the food dish. The cat then stands and bats the bar several times with its left paw without depressing the bar enough to register a bar press (although they can at lower weights), and finally it places both paws on the bar and depresses it. The cat then looks at the feeder, turns, leaves the feeder tunnel, vocalizes, walks around the cage, may use the litter box or scratching post, returns to the tunnel, bats the bar, completes a bar press, and continues in this manner until the required number of bar presses have been made. As the schedule nears completion the amount of time spent in the cage between bar presses decreases (e.g., the cat quickly walks out of the feeder tunnel, turns around and returns), while the intensity of the behavior directed toward the feeder increases and may include scratching on the feeder door. The whole sequence occupies approximately 20 minutes from the first bar press until the schedule is completed. Small ratios and lower bar weights result in less interpolated behavior, while as ratios and bar weights increase, the amount of interpolated behavior, particularly during the initial segment of the ratio run, increases. Thus, part of the difference in rate resulting from increased bar effort can be accounted for by the increased amount of interpolated behavior. But, as can be seen from Figures 15 and 16, the rate in the final segment of the ratio run, which is relatively less affected by interpolated behavior, is lower for larger efforts. Thus, there is also a quantitative as well as a topographical change in rate. A second topographical change was shown by Cat 2, who shifted from a single paw bar press to a two-paw bar press at the heavier bar weights. It seems likely that this response strategy accounts for the ability of Cat 2 to respond at the higher response efforts.

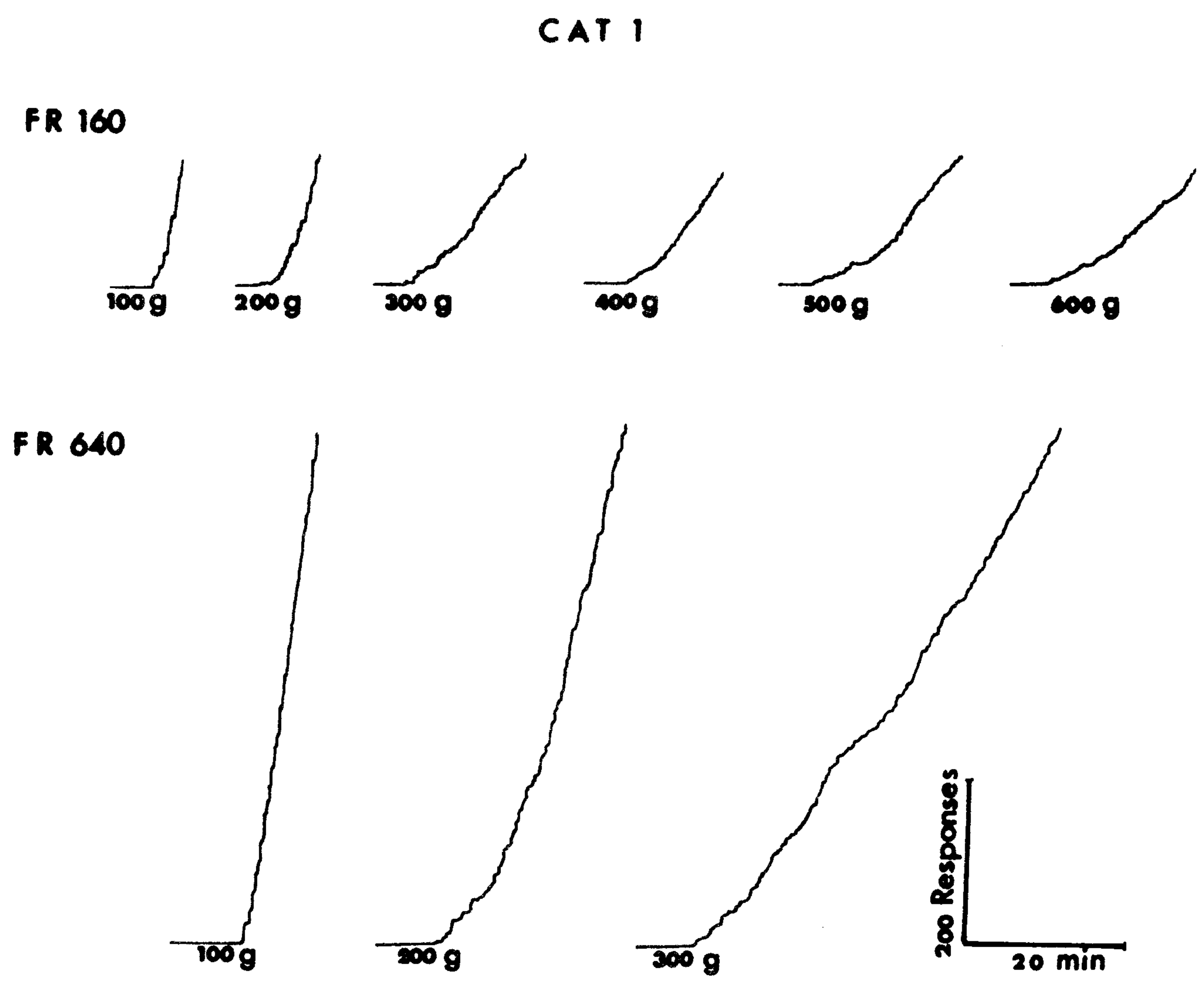

FIGURE 15. Cumulative record of bar pressing responses at representative fixed ratios and bar weights for Cat 1. Each bar-press resulted in an upward increment of the pen on the chart which was moving at 15 cm/min. Each sample record shows the rate and pattern of bar-pressing to obtain access to a meal for different combinations of FR size and bar weight.

Returning to the question of time-minimization, increasing the number of responses required to obtain a meal did not change the rate of responding. Therefore, the time it takes to acquire a meal increases with an increase in ratio size, since an increasing number of responses are required. Increasing the effort of each response required to obtain a meal decreases the rate of instrumental responding and therefore also results in an increase in the time to acquire a meal. Each variable, then, should produce a decrease in the frequency of feeding if the cat is to defend the time spent feeding. Since both variables result in longer times to gain access to a meal, no direct decision between time minimization and energy minimization can be made. If the cat is an energy minimizer, meal frequency should be a decreasing function of work (bar weight x bar excursion x number of responses) per meal. The results of considering meal frequency as a function of work are shown in Figure 17. It is clear that there is ratio-effort interaction for this variable, since equivalent amounts of work on different ratio schedules do not result in equivalent meal frequencies. However, the differences are small relative to the major trend of the relation between work and meal frequency, supporting the notion that energy dimension of foraging cost is an important determinant of the pattern of feeding in the domestic cat.

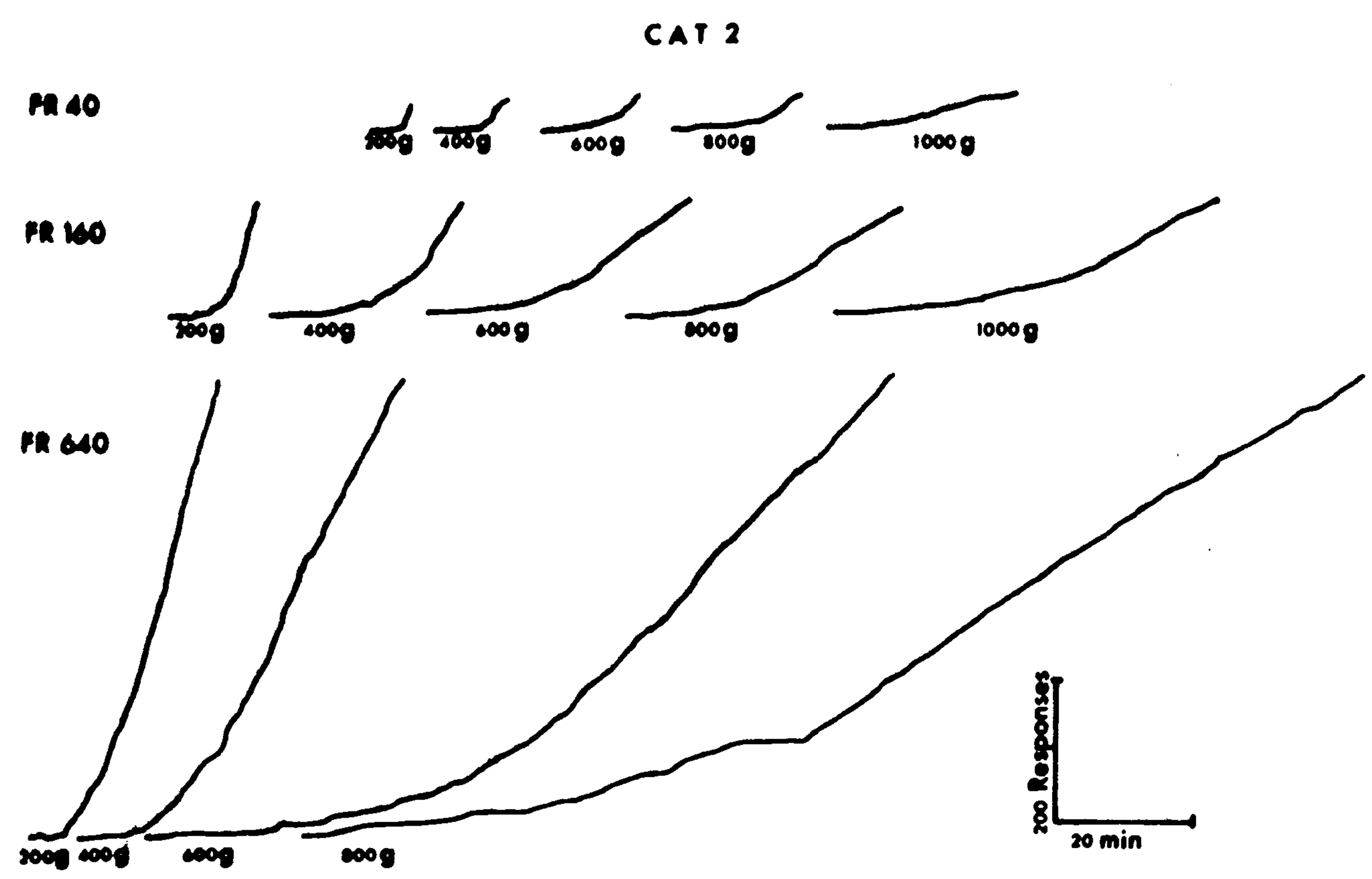

FIGURE 16. Cumulative record of bar press responses at representative fixed ratios and bar weights for Cat 2.

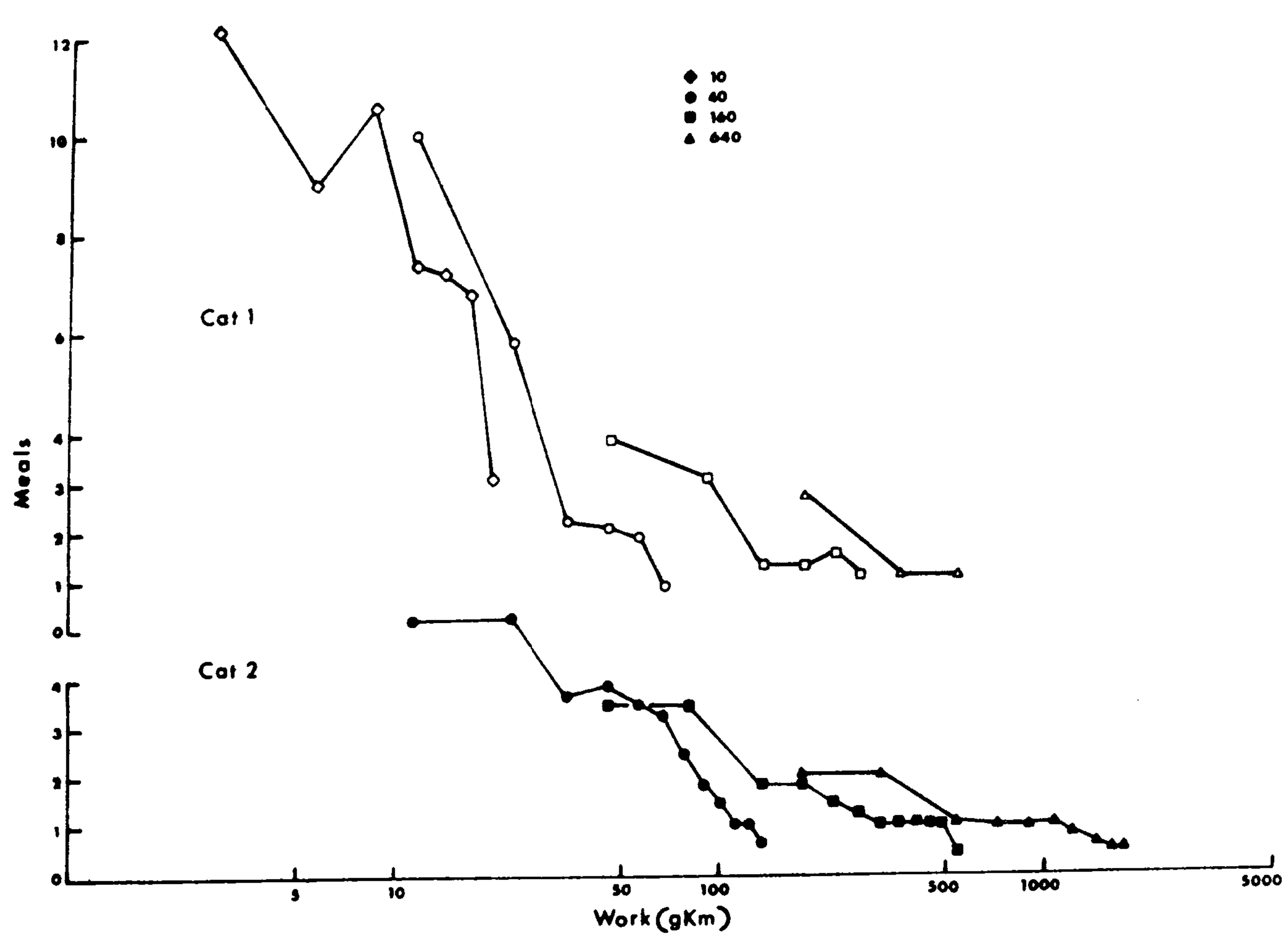

FIGURE 17. Mean daily meal frequency as a function of work (bar weight x bar excursion x number of responses) for each cat.

Another problem facing the foraging animal is the selection of dietary items. Food items vary not only in cost, but also in nutritional quality and caloric density. The problems of regulation of caloric intake and selection of a nutritionally balanced diet differ at different trophic levels. Herbivores eat diets which, in general, are of low caloric density, poor nutritional quality and containing varying degrees of secondary compounds. To meet these problems, different digestive mechanisms such as fermentation and rumination have evolved along with some specialization on and selection of dietary components. Carnivores, on the other hand, eat diets of constant high caloric density and nutritional quality. Therefore, herbivores and carnivores should experience less selection pressure with respect to detecting caloric density and nutritional quality when compared to omnivores, who eat opportunistically and consume food of *varying* caloric density and nutritional quality.

For example, rats fed diets varying in caloric density adjust their bulk intake in such a fashion as to conserve caloric intake (Adolph, 1947; Collier and Hirsch, 1977; Kanarek, 1976). On these grounds it was hypothesized that cats should have little or no tendency to show the caloric compensation characteristic of omnivores. To test this hypothesis, celluflour was added to powdered Purina cat chow and the effect of this diet tested within the availability paradigm (Kanarek, 1975). Cats did not compensate for caloric dilution, eating a constant amount and losing weight. In this respect, they differed from rats (Kanarek, 1976) and resembled guinea pigs (Hirsch, 1973). The results obtained with the cats have been replicated by Hirsch (unpublished data), using a large number of cats and several dilutions. In these studies, cats maintained different body weights on diets of different dilutions for long periods of time (six months or longer in Hirsch's experiments), but at each dilution their body weights were constant. These results suggest that one of the major factors, if not the sole factor, in the regulation of caloric intake by cats is the bulk of the food which they consume.

Again, we are dealing with an effort variable, in this case, consummatory effort. The greater the caloric dilution, the larger the amount of food the animal must eat in order to defend caloric intake, resulting in a larger number of calories spent per calories gained. In this case, however, consummatory effort did not affect meal frequency (Kanarek, 1975)—a not unexpected result since changes in meal frequency as a function of a consummatory effort cannot affect total effort (Collier et al., 1977). This result points out an important feature of the foraging chain: the effect of the same variables on different components of the chain may be different.

What do these data suggest about cat feeding behavior? When allowed to feed *ad lib* on easily available foods, cats eat small, frequent meals. In this they resemble a number of (domesticated) species, e.g., chickens, guinea pigs, rats, etc. There appears to be some advantage to this pattern of feeding insofar as animals seem to revert to it whenever conditions allow. Each of the species we have studied has a characteristic meal frequency associated with a given food (e.g., guinea pigs eat approximately 22 meals per day, rats eat 15, chickens eat 30-40, etc.), and each individual animal appears to have a characteristic meal frequency over its lifetime (Collier et al., 1977; Hirsch, 1973).

Past studies of feeding behavior by psychologists and physiologists have focussed entirely on the consummatory component of the feeding chain while ecologists have focussed for the most part on the foraging components. Studies (e.g., Collier, 1969) have shown relations between the rate and amount of consumption and the physiological state (i.e., hunger) of the animal. In fact, these relations are the basis for homeostatic theories of feeding. The present results, looking at the procurement component of the feeding chain, lead to a somewhat different conclusion. It is clear from these results that initiation and termination of a meal by the cat is determined not only by the time since it last ate (deprivation), but also by the structure of its habitat (e.g., availability). Meal size, meal frequency, rate of eating, the body weight, and size defended (Katz, 1976; Moen, 1973) are strategies which the animal uses to cope (optimize), and not just consequences of its state of depletion. It appears that a complete analysis of the feeding patterns of animals, in terms of amount, distribution, and selection must consider the niche within which the animal operates and the current state of its habitat, of which food availability appears to be one major dimension. The concept of "availability" can have many meanings. Among them, are density of prey and time and/or energy required to forage for prey. When confronted with changes in food availability which altered their pattern of foraging, cats responded in an economic way, shifting their characteristic pattern of feeding in such a fashion as to minimize the time and effort spent obtaining food. The lower limit on meal frequency for different species appears to be determined by their digestive systems. Of the animals studied, guinea pigs, who are monogastric herbivores, were most limited (i.e., maintained relatively frequent meals), whereas cats were the least limited. Schaller (1972) reported that lions, during periods of low availability, can consume 25% of their body weight in single meals obtained at intervals of a week or longer. It is an interesting question as to why animals eat small, frequent meals when circumstances allow. The answer may be physiological, for example, increased efficiency of utilization or lower digestive effort; or behavioral, for example, optimum allocation of time between various activities.

The current formulations of the optimization problem in feeding strategies have treated time as the major dimension of cost, the energy cost being absorbed in the difference between calories gained and calories spent (Schoener, 1971). However, the present results suggest that optimal feeding behavior cannot be predicted by consideration of time-cost alone. Rather, effort, which appears to have a stimulus as well as an energy dimension, influences feeding strategies in a manner similar to that of time. The effects of effort cannot be explained simply in terms of an indirect effect of time on the cat. Although increasing effort slows the average rate of responding and increases the time to obtain food, it does not do so in a reciprocal fashion. Combinations of different efforts and ratios which consume equal amounts of time do not necessarily lead to equal meal frequencies.

The domestic cat, when freed of the constraints of its owner's "pet" theories and allowed to obtain free access to a variety of foods, may be the best judge, at least of its caloric, if not its nutritional requirements. It would appear that a domestic cat has retained sufficient of its heritage to feed in an optimal fashion in the domestic jungle.

LITERATURE CITED

Adolph, E. F. 1947. Urges to eat and drink in rats. *American Journal of Physiology* 151: 110-125.

Collier, G. 1969. Body weight as a measure of motivation in hunger and thirst. *Annals of the New York Academy of Sciences* 157: 589-609.

Collier, G., and E. Hirsch. 1977. Nutrient factors as determinants of sucrose ingestion. Pp. - , *In*: J. M. Weiffenbach (Ed.), *Taste and Development: The Genesis of Sweet Preference*. U.S. Dept. of Health, Education and Welfare, Bethesda, Maryland.

Collier, G., E. Hirsch, and P. Hamlin. 1972. The ecological determinants of reinforcement in the rat. *Physiology and Behavior* 9: 705-716.

Collier, G., E. Hirsch, and R. Kanarek. 1977. The operant revisited. Pp. - , *In*: W. K. Honig and J. E. R. Staddon (Eds.), *Handbook of Operant Behavior*. Prentice-Hall, New York.

Emlen, J. M. 1973. *Ecology: An Evolutionary Approach*. Addison-Wesley, Reading, Massachusetts.

Hirsch, E. 1973. Some determinants of intake and pattern of feeding in the guinea pig. *Physiology and Behavior* 11: 687-704.

Hirsch, E., and G. Collier. 1974a. The ecological determinants of reinforcement in the guinea pig. *Physiology and Behavior* 12: 239-249.

Hirsch, E., and G. Collier. 1974b. Effort as a determinant of intake and pattern of drinking in the guinea pig. *Physiology and Behavior* 12: 647-655.

Kanarek, R. B. 1975. Availability and caloric density of the diet as determinants of meal patterns in cats. *Physiology and Behavior* 15: 611-618.

Kanarek, R. B. 1976. Energetics of meal patterns in rats. *Physiology and Behavior* 17: 395-399.

Katz, P. L. 1976. Dynamic optimization in animal feeding strategies with application to African weaver birds. *Journal of Optimization Theory and Applications* 18: 395-423.

Kruuk, H. 1972. *The Spotted Hyena*. University of Chicago Press, Chicago.

MacArthur, R. H. 1972. *Geographical Ecology*. Harper and Row, New York.

Mech, L. D. 1970. *The Wolf*. Natural History Press, New York.

Moen, A. N. 1973. *Wildlife Ecology*. W. H. Freeman, San Francisco.

Rapport, D. J., and J. E. Turner. 1970. Determination of predator food preferences. *Journal of Theoretical Biology* 26: 365-372.

Schaller, G. B. 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago.

Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*. 2: 369-404.

WHY SOME FELIDS COPULATE SO MUCH:

A MODEL FOR THE EVOLUTION OF COPULATION FREQUENCY[1]

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In most species a healthy male fertilizes a healthy female in a small number of copulations, and probability of conception is high. Copulation takes time and energy that otherwise could be spent to enhance fitness and, probably more important, copulating individuals may be at risk. Thus, natural selection generally favors low copulation rates. Among cats *(Felidae)*, however, several species copulate frequently and conception rate is low in relation to number of copulations and of estrous periods.

Some felids copulate frequently for periods of several days (Table 1). The social lion *(Panthera leo)* copulates frequently, as much as several asocial congenitors and the asocial puma *(Puma concolor)*, whereas the social cheetah *(Acinonyx jubatus)*, the asocial bobcat *(Lynx rufus)*, ocelot *(Leopardus pardalis)*, snow leopard *(Panthera onca)* and black-footed cat *(Felis nigripes)* have low copulation rates. Copulation rates are not clearly related to sociality, nor to taxonomic affinity: four of five *Panthera* felids and the monogeneric, distantly related *Puma* have a high frequency; one of five *Panthera* felids and six other species of four genera have a low frequency of copulation.

A symposium on reproduction in felids offered no substantive explanations for high copulation frequency, although Eaton (1974a) speculated that sexual gratification in lions is an evolved mechanism that achieves bonds of males to females in social groups. Possibly, physiological or anatomical peculiarities are responsible for excess mating. However valid these suggestions, no plausible evolutionary theory has been proposed.

The fact that most *Panthera* cats copulate frequently may be related to their large size and the consequent low risk of being attacked by predators and possibly conspecifics while mating. The *Puma* is also large and copulates a lot, yet the snow leopard does not.

Among the high-rate copulators, the puma is either the socially dominant carnivore throughout much of its range, or able to escape (including arboreally) from potential aggressors, such as bears. In Africa, the leopard is socially subordinate to the lion and to grouped hyenas *(Crocuta)* and wild dogs *(Lycaon)* (Schaller, 1972; Eaton, 1975), but leopards rarely confront these groups. Moreover, leopards prefer to mate in dense vegetation (with ready escape available in trees) where lions seldom occur (N. Myers, unpublished manuscript; Hamilton, 1974). The tiger, jaguar and lion are dominant species (except to man) in their respective ranges. Contrarily, among the low-rate copulators, the cheetah, ocelot, bobcat, black-footed cat and Geoffroy's cat rank low in their respective guilds and probably are often the prey of larger, sympatric carnivores (Young and Goldman, 1946; Eaton, 1974b; J. Visser, 1976, personal communication). Unlike most smaller felids, the sand cat appears to have no enemies, and it has a high copulation rate (Hemmer, 1977). Except for the snow leopard, also a high-ranking species, there appears to be an inverse correlation between copulation frequency and the risks of interspecific aggression in mating.

Whatever the advantages of a high copulation frequency, they appear to apply only to larger species or species that are relatively secure from interspecific aggression. As species that do not conform with an expected low frequency of copulation appear to be relatively free from risks of attack, low risks to copulating individuals should be a necessary but not a sufficient condition for evolution of high copulation frequency.

THE HYPOTHESES

Two hypotheses to explain high copulation frequency are advanced; these are not necessarily mutually exclusive:

1) *High copulation frequency allows females to assess male vigor.* If more than one male competes for an estrous female or if several males are likely to mate with the same female during one estrus, a high copulation frequency would serve the female's interest by increasing the probability that she is fertilized by a vigorous male.

If ovulation is induced by frequent copulation, then the male must copulate a lot to achieve fertilization. Because of inevitable uncertainties surrounding ovulation and hence fertilization, males are trapped. If a male contributes to the survivorship of his offspring, a female may improve her fitness by ovulating only when a male copulates with her at a high rate. If he reduces his copulation rate he may signal a lower vigor, thus a higher probability of male turnover and infanticide. The female may defer conception rather than risk investment in his offspring. If a male has copulated with a female, he would probably not attack her young because he has no way of knowing if the offspring are his.

With the exception of the lion and cheetah, felid social organization generally consists of a number of females who exhibit territoriality toward other females, and a single male who mates with two or more females who live within his larger, inclusive territory. There is little association between adults except for mating and periodic attempts by floaters to get territory. The social systems of the lion and cheetah are elaborations of this basic pattern (Eaton, 1976, in press a). In the cheetah, individual females are territorial and several females may be defended by either individual or grouped males. In the lion, groups of females are mated by smaller groups of males or single males who defend breeding territories.

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[1] An earlier but significantly different version of this paper appeared in *The World's Cats* III(2), 1976.

TABLE 1. Copulation Rates of Several Felids (Small = 5 pounds or less)

	Copulation Frequency/ day	Average Estrous Period (Days)	Probability of Conception/	Dimorphic	Social	Average Size	Source
Puma *Puma concolor*	50-70	7-8	0.67	Yes	No	100 lbs.	Eaton and Velander, 1977
Leopard *Panthera pardus*	70-100	7	0.65	Yes	No	100	Eaton, 1977b
Tiger *Panthera tigris*	50	7	?	Yes	No	400	Kleiman, 1974; Sahkhala, 1967
Jaguar *Panthera onca*	100	7	?	Yes	No	200	Eaton, unpublished observation
Snow leopard *Panthera uncia*	5-15	3-8	0.50	No	No	100	Freeman, 1977, personal communication; Eaton, unpublished observation; Lanier and Dewsbury, 1976
Lion *Panthera leo*	100	6-7	0.20-0.25	Yes	Yes	375	Schaller, 1972; Rudnai, 1973; Bertram, 1973, 1975; Eaton, 1974a
Cheetah *Acinonyx jubatus*	1-3	5-14	?	Yes	Yes	100	Eaton and Craig, 1973; Eaton, 1974b; Frame and Frame, 1976, 1977
Bobcat *Lynx rufus*	5	?	?	Yes	No	25	McCord, 1974; Provost et al., 1973
Black-footed cat *Felis nigripes*	(low)	1.5	?	No	No	small	Armstrong, 1977; Eaton, unpublished observation; Leyhausen and Tonkin, 1965
Ocelot *Leopardus weidii*	5-10	5	0.60	Yes	No	20	Eaton, 1977a
Sand cat *Felis margarita*	(high)	?	?	Yes	?	small	Hemmer et al., 1976; Hemmer, 1977
Geoffroy's cat *L. geoffroyi*	1-2	1	1.00	?	No	small	Kachuba, 1977

The following arguments generally apply to both asocial and social species. Expelled offspring either wait passively or compete for breeding status. The particular strategy chosen should depend upon local circumstances, but the risks and gains of either choice differ for males and females. Among breeding populations, the sex-ratio is biased in favor of females, probably an average of about 2.5 per male for all dimorphic species. The turnover rate of breeding males is probably higher than for females because males have more to gain by assuming high risks in competition for females (Lesowski, 1963; Young and Goldman, 1946; Erickson, 1955; Schaller, 1972; McGregor, 1976; Dewar and Dewar, unpublished manuscript; Rudnai, in press; Koford, 1978).

Normally, most mating males have a territory, which in itself is an indication of their vigor. However, if the male is a poor sexual performer, he is likely to be displaced by a more vigorous competitor. If a female were to conceive with a male who stood to lose his status soon, she would risk losing considerable reproductive investment, because a new male might kill the previous male's offspring.

In lions, new males kill or contribute to starvation of offspring of the previous males (Schaller, 1972; Rudnai, 1973; Bertram, 1977), thus serving their genetic interests. Observation of adult males killing offspring, juveniles or young adults (puma: Young and Goldman, 1946; Lesowski, 1963; Seidensticker et al., 1973; Dewar and Dewar, 1976; tiger: Schaller, 1967; housecats: Ewer, 1973) suggests the same pattern in asocial species.

For most of the species with high copulation frequency, high turnover rate can be inferred from observation of severe combat and killing by males, which for lions is well documented (Schaller, 1972; Bertram, 1973; Smuts, 1978). If male turnover rate were not high, the incidence of infanticide by floating males might be sufficient to favor excessive mating. In the polygynous species, it is common for younger adult males to move through breeding territories. They tend to behave submissively and avoid the larger, resident males; but they also prey on offspring when encountered (Erickson, 1955;

Hornocker, 1970; Robinette et al., 1973; Young and Goldman, 1946), and may mate with resident females (Seidensticker et al., 1973).

As adult males of the polygynous species tend to be from 15 to 40% larger than adult females, and since females spend much time away from offspring, defense of smaller young by the female is impractical. By mating with subordinate males (e.g., Hornocker, 1971), females would reduce infanticide, assuming that copulation by a male would thereafter inhibit his predation on offspring in that female's area. The predictions could be further tested in captive environments, possibly with existing data on the behavioral and breeding relationships of adults correlated with rates of infanticide by males.

All species with high copulation frequencies are fundamentally polygynous, and competition between males is intense. The first hypothesis would be further supported if monogamous, high-ranking species copulated at low frequency. Competition among males in these species would be relatively low and females would have less to gain by evaluating male vigor via high copulation frequency. A relevant example is the snow leopard, which appears to be socially dominant--at least in pairs--in the range it occupies during mating (Schaller, 1972b, 1977). It is sexually monomorphic, which suggests relatively low intrasexual competition among males, and the behavior of males suggests greater parental care than exists in other felids. As the snow leopard's habitat is harsh and dictates an extremely low density (Schaller, 1972b, 1977) and breeding is fixed to a brief period annually (Freeman, 1977), the only effective strategy would be monogamy. The occurrence of a low copulation frequency in this species supports the first hypothesis.

2) *High copulation frequency is a means by which females compete with one another for reproductive success.* Potentially competing females should gain by delaying starts of litters of other females; exhausting males may accomplish this delay. Simply attracting males for sterile sexual activity may be advantageous by reducing the fitnesses of other females.

For larger felids, the primary prey resources are highly mobile and seasonally abundant (Eaton, 1974b; Hornocker, 1970; Schaller, 1972). Females in an area may compete indirectly for a surplus of more vulnerable individuals of mobile herds of large prey species. The female who can most closely correlate conception, pregnancy and lactation with food abundance is most likely to have more success, everything else being equal. Therefore, females who mate with the same male are competitors for the male's attention at the optimal time to conceive. Selection should not only favor females whose behavior results in optimal timing of reproduction, but it should also favor any characteristics that reduce competition for reproductive success with other females. Surviving offspring leave voluntarily or are expelled: subadult and young adult males by territorial males, females by their mothers. The female whose offspring occupy a breeding area sooner should have higher fitness. The female whose expelled young incur greater risks in competition with other aspiring females or males should tend to have lower fitness. Those females should be favored whose dispersed offspring face the least competition for available food resources or vacant territories. Females can only effectively influence the fitness of other females who breed with the same male. Sexual deceit is a potential means of reducing competition.

A female's interest should be best served by attracting and holding the attention of the male (if possible, sexually exhausting him), so that "his" other females either are not fertilized, or are not fertilized for a period long enough to reduce competition. If a female can *sexually* occupy the male to increase her fitness at the expense of other females, then not all potential breeding females should reproduce at the same time within a male's territory.

Several studies substantiate the fact that, whereas all the species with high copulation frequency tend toward reproductive seasonality, breeding does occur year-round (references in Table 1). Even strictly tropical populations respond to unpredictable increases in food abundance by sudden surges in mating activity. In the lion, the surge may be followed by synchronous reproduction *within* groups (Rudnai, 1973), an adaption that favors individual females in groups by allowing them to divide reproductive labor and enhance their fitnesses (Bertram, 1977; Eaton, 1974a, 1976).

If the male cannot achieve regular, frequent copulation, it is likely that an adjacent female has just conceived; therefore, the next female should defer ovulation long enough to reduce competition. Low probability of conception per estrus may indicate, among other things (such as the resorption of embryos in response to insufficient resources), that selection has favored females who sometimes mate with males *without* becoming pregnant, or who merely occupy males in pursuit and courtship activities without coitus, as a means of reducing competition with other females.

Females attract males for mating primarily with olfactory stimuli. As breeding-status females occupy relatively large territories and a male is intermittently present, competition among females might be indicated in communicatory behavior that attracts males. A solitary female patrolling the boundaries of her territory could collect olfactory information on the breeding status of adjacent females. When an adjacent female advertises breeding condition to attract a male, the first female might gain by attracting the male to her instead. By exhibiting estrus, a female would gain by attracting a male to herself for mating while other females are receptive, even if the female did not conceive.

There are numerous observations of synchrony and overlap of estrus in felids (e.g., Burke, 1975; Eaton, 1974a, 1977a, 1977b; Eaton and Velander, 1977; Kleiman, 1974). The onset of estrus in the tiger, jaguar, leopard or puma will trigger estrus in other females kept with her or in olfactory (and possibly auditory) communication. False or anovulatory estrus could account for probabilities of conception of 40 to 60% or lower (Table 1). The fact that female cats exhibit estrous periods during pregnancy (Asdell, 1964; Catchpole, 1969; Eaton, 1974a; Eaton and Velander, 1977; Kleiman, 1974) supports the hypothesis that competition among females could be intense enough to cause evolution of high copulation frequency in dominant species.

Most larger felids mate for about one week which is probably too short a period to be significant in terms of gains to a competing female. The period could suffice to exhaust the male sexually. Even if the male mates with another female relatively soon, he may not be able to achieve fertilization. The estrous cycle is variable but usually averages at least four weeks or longer in the larger species. If females exhibit synchrony of estrus, the minimum period between their parturitions would be about five weeks.

A test of the second hypothesis would involve demonstration of 1) asynchronous reproduction in dominant, asocial felids, and 2) higher fitness in the first female of a group of females who mate the same male. (These predictions are expected if there is a valid relationship between the fitness of females and their time of conception relative to optimal seasons or favorable fluctuations in resources.)

If the female competition hypothesis is true, then within a polygynous breeding population the distribution of births in time should never be unimodal. Females of the low copulatory polygynous species should gain by staggering births, although females of dominant species should gain even more by employing high copulatory rates. This prediction should be true for both seasonal and year-round breeders. The distribution of births may not precisely correspond with the average number of females established in male territories; for example, the puma who often breeds every other year, compared with the bobcat who usually breeds annually. Fluctuating rates of litter mortality and other factors will alter frequency and timing of births. Overall, however, the breeding sex-ratio (male:female) should correlate inversely with the distribution of births. If births are staggered within populations, the second hypothesis would be supported.

Breeding data from the field and captivity indicate staggering of births within populations of polygynous felids. Female bobcats in the same area have staggered births, with peaks in each of four consecutive months; moreover, female bobcats ovulate only once per year (Erickson, 1955). Males patrol much larger areas than females. Trapping offtake of males relative to females should indicate increased male mobility during periods of mating activity. As females come into estrus, males should become relatively more active per unit of time; thus males should be taken more frequently in traps. Erickson (1955) found that male bobcats prevailed in trapping harvest during February and April--a third peak in July was accounted for by the expelling of subadult males, probably by resident males. Since most resident females of this population reproduced annually, these data suggest that the average breeding sex-ratio is 1:2, and that females stagger ovulation by an average of 1.5 months. On the other hand, the distribution of projected fertilizations indicates a higher sex-ratio, possibly as great as 1:4. In any event, births are staggered, and indirect behavioral data further support the prediction that within breeding territories, fertilizations are staggered.

In a study of puma reproduction in Utah and Nevada, there was a bimodal distribution of pregnancies with peaks in January-February and June-July (Robinette et al., 1961). Reproductive data collected over several years from adjacent females in Idaho reveal nearly the maximum possible asynchrony of births within the major breeding season. At least some of these females appeared to reside within the same male's territory (see Seidensticker et al., 1973). California pumas exhibited four birth peaks from 1.5 to 5.0 months apart according to Bruce (1922), but a single peak in April according to Grinnel et al. (1937).

A bimodal distribution of births was found in two large populations of captive pumas in Washington (Eaton and Velander, 1977) and for a large population of captive leopards (Eaton, 1977b). Most of the captive female pumas and leopards were either kept two to a male or held adjacently in all but tactile communication. Synchrony of estrus was common, but synchrony of birth was rare.

These findings support the hypothesis that females compete with one another to become fertilized at the optimal period or otherwise act to stagger fertilization to minimize competition.

If excessive sexual contact evolved because of competition among females, then socially dominant species that copulated at low frequencies should be monogamous. The snow leopard appears to be such a species.

While high mating frequency may have evolved because it serves the female's interest in mate selection, the hypothesis that females compete with one another by sexually attracting males is also plausible.

RESOLUTION OF THE HYPOTHESES

It was postulated that high copulation frequency, including anovulatory estrus, could favor females because of advantages in evaluation of male vigor, including reduction of infanticide by males, or reproductive competition with females. Several considerations lend further support to the male-vigor hypothesis and discount the female-competition hypothesis.

Females might gain by cooperating to evaluate the vigor of males. Synchrony of estrus would increase the probability that females would become informed about the competitive status (vigor) of males. Synchronous estrus is more likely to attract floaters and allow females to copulate with most or all males likely to inhabit their territories in the future, which should reduce infanticide. Synchronous estrus entices intermale competition and maximizes the probability that the most vigorous male in the area is or quickly becomes resident. If the resident male is vigorous, floating males will be expelled. If the resident male is weak, a new, more vigorous male should emerge as dominant and establish residency. Thus, probability of infanticide by floaters or probability of male turnover following synchronous estrous periods should be minimized. The probability of conception per estrus (about 50%) could reflect a strategy of using synchronous or anovulatory estrous periods to resolve uncertainties about the male environment.

Because male turnover is unpredictable by females, in either case--continuation or replacement of the male--females should gain by synchronous estrus. The benefits of cooperation may exceed any costs to females from not achieving fertilization at the optimal time. Moreover, the difference in time of parturition, only about 5 weeks, is probably too small to be significant in such species.

Although females need not be related to gain by cooperating to evaluate male vigor, related females should gain more by inclusive fitness. Thus, selection would favor female behavior that tends to increase relatedness of females in an area. The existing information suggests that adjacent females of asocial, polygynous felids are often closely related.

If females were competitors, then mothers would be expected to expell daughters so that they settled in territories surrounded by unrelated females. If females were not competitors, there would be advantages in female offspring settling near their mothers; maternal behavior would result in female offspring settling close by. In the puma, which is probably representative, resident females may be one requisite, as indicator of suitability of habitat, for females to settle (Seidensticker et al., 1973). Pumas are site-tenacious, persisting in certain localities despite long-term disturbance by man. Most felids may exist in metapopulations, more of less disjunct breeding populations composed of kinship groups with unpopulated spaces between them (C. Koford, personal communication, 1978). Relatedness in an area is probably much higher for females than males.

Cats are highly specialized predators in which individually acquired experience is especially important to survival and reproductive success. Early learning about prey selection, foraging tactics and interspecific competition would tend to favor females who settled in or as close as possible to the area in which they matured. Closely related females could gain by cooperating directly, such as in sharing of food or adoption of offspring; this has been observed in cheetahs (Graham and Parker, 1965; Frame and Frame, 1976; J. Rudnai, personal communication) believed to be mother and daughter, in related female lions who otherwise consorted little (Rudnai, 1973), and possibly among related female tigers (Schaller, 1967). Daughters might even gain inclusively by avoiding reproduction in favor of mothers--"helper at the breeding territory."

Synchrony of estrus appears to maximize the ultimate interests of adjacent females in that it provides maximum information about vigor of males and achieves a sufficient degree of synchrony of births such that cooperation, such as adoption of offspring and sharing and defense of large food items is possible. The former advantage would hold for related or unrelated females; the latter would be expected only between relatives, and both benefits should be greater for relatives.

The hypothesis that females utilize copulation frequently for intrasexual competition does not appear to be valid, particularly if the typical social organization of females is governed by kin selection. It is conceivable that females in one male territory cooperate so as to compete with females in territories of adjacent males. The more vigorous a male is, the higher the reproductive success of females is likely to be. If relatedness of females is higher within than it is between male territories, kin selection might favor females which attract more vigorous males away from other groups of breeding females. High copulation rate and synchrony of estrus could achieve this. Competition among groups of females for the most vigorous males in an area is a prediction of the first hypothesis.

All polygynous felids, whether low or high copulators, appear to employ anovulatory estrus and synchrony of estrus, apparently to evaluate male vigor. High copulation frequency achieves additional benefit for females of high-ranking species as it provides additional information about vigor of males. High copulation rate can be expected to evolve in polygynous species of high interspecific rank because females gain by evaluating vigor of males.

THE LION

Bertram (1975, 1977) considers the mating of lions to be inefficient because the probability of births is so low relative to number of copulations or estruses. He says that lions are under much less selection pressure than other animals to breed efficiently because lions do not have a breeding season and they incur no risk of predation. There is considerable risk from predation, both interspecific and intraspecific, although the former may especially be lacking in areas protected from humans, and lions respond reproductively to fluctuations in resources (Rudnai, 1973). Besides constituting a group selection argument, if, as Bertram says, each copulation meant little to a male, would males copulate so vigorously: up to 100 times per day, often for several days? Certainly such investment could be well spent in other ways which could enhance fitness. Lions employ numerous adaptive strategies to maximize their fitnesses.

The hypothesis fully applies to the lion. The extremely high copulation rate, the often low probability of conception per estrus and the occurrence of synchronous estrus are expected for groups of related females having to contend with risks of male turnover.

It is probably common for males to be ousted from prides and their offspring to incur high mortality (Schaller, 1972; Bertram, 1973). In some populations grouping by males, often but not always close relatives (Smuts et al., 1978), is favored because of advantages to individuals in intrasexual competition (Eaton, 1976, in press a). The loss of vigor in one male of a group should correlate with a higher probability of replacement by other males and lower fitnesses of resident females. Thus, females could enhance their fitnesses by regularly evaluating the vigor of *all* the males of their pride, which high copulation frequency would achieve.

It is fairly common for a female to mate with more than one male--sometimes all and as many as five--in an estrus (Eaton, 1974a; Schaller, 1972). Females either sexually exhaust males in succession or exchange mates throughout the estrus (although the former is more characteristic when males are unrelated and the latter when males are closely related). A female who mates with more than one male should be able to make better decisions about whether or not to ovulate.

Groups of males are sometimes composed of unrelated males (Eaton, 1976, in press a), and such males may be more prone to competition and, thus, splintering, a risk to females. Females could evaluate the vigor of the *group* by copulating with several or all of them. If males compete, this could indicate to females a high probability of male turnover, in which case females might gain by deferring conception while also stimulating splintering and subsequent takeover by a more vigorous group of males.

Because groups of females (prides) are composed almost exclusively of closely related individuals, inclusive fitness of females in groups varies as a function of the entire group's reproductive success. A pride's reproductive success is a function of the number of males that a pride is able to attract and support and the rate of male turnover. Males affect pride territory size (and thus resources) and protect offspring from attack by foreign lions and competing species which, in large enough groups, dominate or kill female lions (but usually not males: Eaton, in press b), steal food and kill offspring. Generally, the longer the same males are resident, the higher should be female reproductive success. If males could maximize their fitnesses by leaving one pride and locating in another with more females, then females should behave in such a way as to prevent otherwise suitable males from leaving. Departure of males occurs voluntarily and can be costly to females (Schaller, 1972). As female groups probably compete with one another for the most vigorous males, females should gain by sexually rewarding males as much as possible, which would favor high copulation rate.

Among felids deception has reached its peak in the lion. Pregnant females and mothers consistently exhibit anovulatory estrus; apparently this reduces the mortality of offspring sired by departed or expelled males. A new male recognizes existing offspring as other than his or his associates, and gains by killing them or in some way contributing to their death. But once a male has copulated with a female (or any female if sharing of offspring care deceives males about which female is actually the mother), he risks filial cannibalism if he kills any offspring born after the mating. The invitation by estrous females to copulate with strange males encountered in their territory (Schaller, 1972) is expected, as such a male is more likely to become resident there in the future and, if so, would be inhibited about infanticide. I once introduced a male into a captive group of six closely related females. Several of the females were pregnant at the time from a former male who had been removed. Initially the females were aggressive to the new male, but within 6 weeks every female had mated with the male, who lost 75 pounds (Eaton, 1973, 1974a). The male's behavior toward offspring born later was the same as for males who actually sired offspring.

Females rearing offspring also mate with males but have a low rate of conception (Eaton, 1974a). Such behavior appears to contribute maximally to the reduction of male sexual motivation, a male's predictor of fitness, thereby reducing the probability of loss or turnover of males. Sexually gratified males should be most prone to assume risks in defense of their status and generally should tend to remain longest with prides.

Given that the ancestral lion was asocial and polygynous and as such would have exhibited synchrony of estrus for reasons discussed above, synchrony of reproduction would have become advantageous to group-living females (Eaton, 1976, in press a). While synchrony of estrus is common in lions, it does not seem to be fully accounted for by the benefits of synchronous reproduction. At least in seminaturally contained prides, synchronous mating periods also occur without large increases in food, and the probability of conception is lower than for asynchronous matings (Eaton, 1974 a). Synchronous estrus with low probability of conception could be favored for several reasons. It would tend to reduce, for example, male turnover, resulting from hoarding of mating by one male, which could stimulate intragroup strife or splintering. When several females are simultaneously in estrus or have overlapping estruses, a single male cannot possibly achieve all copulations (the maximum number of females a male can service on a normal schedule of female readiness is two), either because of simple space and time limitations or sexual exhaustion. Synchrony tends to gratify sexually *all* males of a pride, which should not only reduce male turnover (the "turnon/turnover" ratio), but also increase the investment by males in ways that benefit females. Often such investment involves cooperation and risks; gratified males should be most conducive to female fitness.

Anovulatory estrus is effective in preventing infanticide by new males only if the female is already pregnant or if she has offspring not yet integrated into the pride. Schaller (1972) suggests that infant cubs are kept away from prides until they are several weeks (6-8) old because they are not able to move with the adults. Females with secluded infants periodically visit and associate with pride members, supposedly to use food provided by other lions (Schaller, 1972; Rudnai, 1973). Infants should be more susceptible to predation away from the pride and its immediate area of intense use, than in it, where adults and even subadults could protect them. Closer location would also benefit the mother if the major reason she visits the pride is to procure food. An alternative hypothesis is that the probability of infanticide by new males is a greater threat to a female's success than predation on offspring. Females should parturate away from the pride so that, if a turnover occurs, her offspring are not killed. By visiting the pride the female could monitor the male environment and mate with new males, thus preventing infanticide when offspring are later introduced and first encountered by males. Also, a female could enter the pride with a related female who had already mated with new males, and she could thus confuse the males as to their relatedness to the offspring.

Males can successfully influence infant death indirectly by keeping kittens away from food (Schaller, 1972). Females appear to have adapted to this possibility with prolonged lactation; lions suckle their offspring 8-10 months (Adamson, 1960; Eaton, 1973), several months longer than similar felids (Ewer, 1973). The so-called "weaning heat" occurs in lions, but they often continue to suckle offspring for several weeks or months afterward. In many felids, a weaning heat occurs, but it does not seem to be physiologically necessary for the cessation of lactation. Rather, it may reduce the probability of infanticide. By mating just prior to the time that offspring become mobile and active away from a den, and thus more vulnerable, a female may successfully inhibit infanticide by males, including floaters. If the female's litter is so small when the weaning heat occurs that the female stands to gain by starting over, she can conceive, as in the lion and leopard (Rudnai, 1973; Eaton, 1973, 1977b).

The weaning heat offers options to females and one of these appears to be use of copulation to evaluate male vigor. It is also possible that anovulatory weaning heat benefits the female by attracting males who reduce the risk of interspecific predation and competition for resources or provide and share large food items at a time when the physiological condition of the female is relatively poor (Scott, 1976).

High copulation frequency appears to be adaptive in lions for the same reasons as in other felids: females can evaluate vigor of males. Cooperation by female lions employing frequent copulation to deceive and gratify males appears to be a simple extension of the system of related females sharing a male territory. In both the asocial and social condition, related females may cooperate so as to compete with unrelated groups of females for the most vigorous males.

THE HOUSECAT

The housecat is the most intensively studied felid; it provides a model object for much investigation by numerous disciplines. Oddly, the fundamental types of data being rapidly accumulated about many feral species do not exist for the housecat, including copulation rates. Based on my own observations, housecats copulate more often than most smaller felids, but less often than the high copulators in Table 1.

Although the housecat has relatively high copulation rate compared to similar-sized felids who live with numerous dominant species, it may be adapted to lower interspecific risks than its nondomesticated ancestors (but see Todd, 1978). Copulating housecats face risks of attack primarily by dogs. Cats seem quite well adapted to avoid such risks, their adaptations including, in my opinion, knowledge about the location and activity patterns of dogs in their area, as well as careful selection of habitats with escape cover.

Regardless of whether or not housecats incur lower risks during copulation, their densities are so high in civilized habitats that intermale competition must be very intense. Floaters are common and turnover rate is probably high (judging by the number of veterinarians supported primarily by treating disease resulting from intermale combat). Selection should favor high copulation rates for its advantages to females in evaluating male vigor and reducing infanticide.

A major support of new sociobiological constructs is widespread observation, not at all new, of infanticide by males. The housecat has presented such data for decades (and centuries!) but without deduction from sociobiology such data are paradoxical. For example, some males kill kittens, others do not, or the same male will kill some kittens but not others, and females enter estrus while pregnant (Catchpole, 1969). We may now view such patterns as neither pathological nor physiological accidents, but as predictable and adaptive. The hypothesis has relevance for veterinary medicine and zoo biology.

DISCUSSION

In a relatively short-term study involving usually one pair of a felid species mating in one or part of one estrus, Lanier and Dewsbury (1976) recorded lower rates of copulation than summarized for some species in Table 1. There are a range of factors that appear to influence copulation rate in any pair of felids and many other species. Fundamentally high copulators seem more prone to variation in copulation rate, and if not rate, then duration or plasticity in structure of copulation. My impression from over 3,000 hours of observation of courting felids of ten species and six genera is that there are striking differences within and among individuals and in pairs regarding rate or duration of copulation. Such variation does not alter the general conclusions about species-typical patterns and the classification of species as relatively high or low copulators.

Mere quantitative description is not only subject to inherent biases, the radical patterns themselves are not open to understanding without deductively derived models based on natural selection. Within the evolutionary model of cost and benefit, the hypothesis for copulation frequency offers prediction about social organization and interspecific rank of species. The hypothesis can encompass equivalent aspects of mating behavior, such as investment in courtship, duration of copulation or anatomy of reproductive organs.

Bears: How Often or How Long?

High-ranking polygynous species should tend either to high copulation rate or overall high investment in achieving conception. An example is the Ursidae, which do not copulate very frequently, but which do invest greatly in courtship and have durable copulations (Herrero, 1978). The defensiveness of females plus the risk they present force males to persist for many taxing hours or days to achieve copulation. The copulation is prolonged, up to 20 minutes, which must be demanding for these large animals and may further evaluate a male's vigor (Eaton and Carey, in preparation).

Bears tend to have an exceptionally prolonged estrus, up to about 4 weeks, during which they may copulate (at low rates) with several males. As the risk of infanticide by males is probably high, acceptance of several males may reduce infanticide, including in subsequent breeding seasons.

Canids: Is the Female Locked In?

Canids tend to be monogamous and competition for mates is usually annual. Canids typically have a low copulation rate: if a canid copulates it usually does so only once or twice annually. In some species (also of mustelids), individuals lock for long periods, from a few minutes up to about two hours. The locking mechanism, an enlargement of the penis following intromission, is widely believed to be a case of adaptation to sperm competition. Since once locking occurs neither the male nor female has a choice as to sexual partners, the duration of locking would not seem to be an indicator of male vigor.

Males increase their vulnerability to attack by other males when locked, but a male could be killed while locked and still reproduce. If there were risks from other species during locking, both male and female would be equally vulnerable. If the costs to females of locking exceeded the gains of mate selection, locking could not evolve. Thus, duration of copulation in canids should inversely reflect the risks of interspecific aggression to copulating individuals.

The wolf should lock longest among canids because of its high interspecific rank, and it does, while lower-ranking canids should lock less or not at all. The coyote locks for about 15 minutes and the wild dog, which may not lock at all, copulates for about 5 minutes (Ewer, 1973). Sociality in the wild dog may imply a relatively high rank, and expectation of higher investment in copulation; however, the wild dog ranks lower in its guilds than does the wolf. The wild dog is susceptible to attack by several high-ranking species (codominants or dominants--spotted hyena, lion, man), especially as it prefers relatively open habitats and is diurnal. To dominate or escape from competing species, the wild dog often requires extreme cooperation by all group members. For two wild dogs of a pack to be competitively immobilized very long could be disastrous.

Anatomy of Penises

The anatomy of penises offers predictions about the biology of species. This especially applies in mammals to the shape and structure of erect penises, which have become observable with the development of techniques in semen collection (Seager, 1977). Penis shape should be an important correlational factor permitting increased accuracy of prediction about the social behavior and interspecific ecology of species.

Relevance to Human Evolution

In general, carnivory is probably the single most important niche dimension in human evolution. The convergence of man with such species as the lion, high-ranking, social predators, would suggest parallel evolution in reproductive strategies. Other primates may employ copulation to deceive males and reduce infanticide (Hrdy and Hrdy, 1976). For example, the rhesus monkey has anovulatory estrus (Conaway and Koford, 1965). But primates other than man have a relatively low copulation rate and copulation duration is brief. Man has a relatively high copulatory rate and longer duration of copulation than other primates. Both would be expected in a primate in which interspecific rank were relatively high and the mating system were polygynous, such that intermale competition were intense.

The hypothesis that high copulation frequency evolves in high-ranking polygynous species because of advantages to females in evaluating male vigor appears applicable to man. In humans, as in felids, a high copulation rate deprives a male of information about when fertilization occurs. Thus, a female can solicit a male's investment in offspring when he is not the actual father.

The problem of floating males exists for the female felid as well as for the female human. In both, dominant or resident breeding males are often not with their female mates, and floaters represent risks in terms of mating with (or stealing) females, infanticide and so on. However, unlike the formidable female felid, the human female cannot defend herself or offspring against floating males. Still, the female felid can gain by copulating with floating males as they could kill offspring in her absence or they might become resident. If the female human is raped, copulation can gratify her actual mate (lack of copulation by females is grounds for divorce in primitive and civilized societies), reinforce mating bonds and encourage provisioning by the male whether or not he is the father. It is "conceivable" that frequent copulation provides information to the female about the male's vigor: his emotional attachment and phenotypic fitness, both of which are critical to the female's success. Vigorless copulating by a male could inhibit conception or encourage a female to seek another mate.

Under primitive conditions, copulation rate is lower, possibly two to four times per month (e.g., Thomas, 1958), than in large societies. Duration of copulation is typically short, about 2 minutes, in small societies compared to contemporary large societies. However, the fundamentally innate pattern of about 2 minutes exists in modern males; prolongation of copulation is normally learned with considerable investment and difficulty.

Unstable mating environment exists less in primitive societies and more in larger societies in which women interact or are exposed continually to strange males who might rape them. Males encounter a multitude of females, and being basically polygynous, are attracted to other women than their mates. These conditions, which have more or less accelerated over the past several thousand years, should favor higher copulation rates and prolonged copulation as evaluators of mating interest.

Copulation frequency in humans is probably regulated by a drive system which is trophic. Trophicity of copulation would evolve under primitive settings due to uncertainty about male turnover and as a mechanism of attracting or holding males. The modern social environment would stimulate the system so as to produce steadily higher copulation rates. Under the extremely uncertain conditions of civilized life, other indicators of male vigor would provide additional information to females; these probably include prolongation of copulation by the male, which in turn can deceive females about his intentions, because it is ordinarily behavior indicative of strong emotional attachment. Prolongation probably developed independently in many cultures after the appearance of civilization. But it is likely to have genetic feedback on sexual learning mechanisms.

Menstruation involves physiological loss. Many species are capable of resorbing such material. To offset such loss, there must be a selective gain to menstruation. If it is adaptive for females to establish synchronous menstrual cycles because this achieves synchronous reproduction, as in the lion, then selection should maximize any means of communication between females that would achieve synchrony. Relatively, humans are poorly adapted for scent-communication although, largely at the unconscious level, they may be quite responsive to sexual pheromones. By passing fluids carrying reproductive hormones, females could communicate about their reproductive cycles. A copious flow of fluids high in pheromones could achieve synchrony. As menstruating females move around camps or forage, they would deposit pheromones and thereby maximize communication with interdependent females.

If the menstrual cycle has evolved to achieve synchronous reproduction, then ovulation should occur at the greatest interval between deposition of pheromones, as this would permit maximum period for adjustment or initiation of cycles among females. Normally, ovulation in humans occurs at the midpoint of the menstrual cycle.

Apparently, cohabiting females quickly achieve synchrony of cycles, which implies that one of the females may set a group's cycle. This raises intriguing sociobiological questions about the role of status among women in groups; I suspect that female lions offer a model.

The hypothesis that high copulation frequency is primarily a means for females to evaluate male vigor would appear to apply universally to man. It seems important to give higher priority to the understanding of carnivores as models for human evolution.

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LITERATURE CITED

Adamson, J. 1960. *Born Free*. Collins, London.

Armstrong, J. 1977. The development and hand-rearing of black-footed cats. Pp. 71-80, *In*: R. L. Eaton (Ed.), *The World's Cats III*(3). Carnivore Research Institute, Burke Museum, University of Washington, Seattle.

Asdell, S. A. 1964. *Patterns of Mammalian Reproduction*. Second Edition. Cornell University Press, Ithaca, New York.

Bertram, B. C. R. 1977. Kin selection in lions and in evolution. Pp. 281-301, *In*: R. P. G. Bateson and R. A. Hinde (Eds.), *Growing Points in Ethology*. Cambridge University Press, London.

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology* 177: 463-482.

Bertram, B. C. R. 1973. Lion population regulation. *East African Wildlife Journal* 11: 215-225.

Bruce, J. 1922. The why and how of mountain lion hunting in California. *California Fish and Game* 8: 108-114.

Burke, T. J. 1975. Feline reproduction. *Feline Practice* 5(6): 16-19.

Catchpole, H. R. 1969. Hormonal mechanisms during pregnancy and parturition. Pp. 415-440, *In*: H. H. Cole and P. T. Cupps (Eds.), *Reproduction in Domestic Animals*. Academic Press, New York.

Conaway, C. H., and C. B. Koford. 1965. Estrous cycles and mating behavior in a free-ranging band of rhesus monkeys. *Journal of Mammalogy* 45(4): 577-588.

Dewar, P., and P. Dewar. 1976. Northwest Bay cougar study progress report. Unpublished manuscript. Mimeo.

Eaton, R. L., and B. Carey. In preparation. *Mating Behavior in Kodiak Bears*.

Eaton, R. L., and S. J. Craig. 1973. Captive management and behavior of the cheetah. Pp. 217-254, *In*: R. L. Eaton (Ed.), *The World's Cats I*. World Wildlife Safari, Winston, Oregon.

Eaton, R. L., and K. Velander. 1977. Reproduction in the puma: biology, behavior and ontogeny. Pp. 45-70, *In*: R. L. Eaton (Ed.), *The World's Cats III(3)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.

Eaton, R. L. In press a. Evolution of sociality in the Felidae. *In* : R. L. Eaton (Ed.), *The World's Cats III(2)*. Second Edition.

Eaton, R. L. In press b. Interspecific competition among African carnivores and its relationship to sociality. *Carnivore* 1(2).

Eaton, R. L. 1977a. Breeding biology and propagation of the ocelot. *Der Zoologische Garten* 47(1): 9-23.

Eaton, R. L. 1977b. Reproductive biology and behavior of the leopard. *Der Zoologische Garten* 47(4):

Eaton, R. L. 1976. Evolution of sociality in the Felidae. Pp. 95-142, In: R. L. Eaton (Ed.), The World's Cats III(2). Carnivore Research Institute, Burke Museum, University of Washington, Seattle.

Eaton, R. L. 1975. Interspecific competition, social dominance and sociality in African carnivore guilds. Abstract published by American Society of Mammalogists, Annual Meeting, June 1975, Missoula, Montana.

Eaton, R. L. 1974a. The biology and social behavior of reproduction in the lion. Pp. 3-55, *In*: R. L. Eaton (Ed.), *The World's Cats II*. Feline Research Group, Woodland Park Zoo, Seattle.

Eaton, R. L. 1974b. *The Cheetah*. Van Nostrand Reinhold Co., New York.

Eaton, R. L. 1973. Aggressive behavior in the lion. Ph.D. Thesis, Purdue University Library, West Lafayette, Indiana.

Erickson, A. 1955. Ecology of bobcats in Michigan. M.S. Thesis, Michigan State University, East Lansing.

Ewer, R. F. 1973. *The Carnivores*. Cornell University Press, Ithaca.

Frame, G., and L. H. Frame. 1977. Our three years with cheetahs. *International Wildlife* 7(1): 4-10.

Frame, G., and L. H. Frame. 1976. Interim cheetah report. *Serengeti Research Institute Annual Report 1975-76*. Via Arusha, Tanzania. 27 pp.
Freeman, H. 1977. Breeding and behavior of the snow leopard. Pp. 36-44, *In*: R. L. Eaton (Ed.), *The World's Cats III(3)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Grinnel, J., J. S. Dixon, and J. M. Linsdale. 1937. *Fur-bearing Mammals of California* Vol. II. University of California Press, Berkeley.
Hamilton, P. 1974. The Tsavo leopard project. *African Wildlife Leadership Foundation News* 9: 2.
Hemmer, H., P. Grubb, and C. P. Groves. 1976. Notes on the sand cat, *Felis margarita*. *Zeitschrift fur Saeugetierkunde* 41(5): 286-303.
Hemmer, H. 1977. Biology and breeding of the sand cat. Pp. 13-21, *In*: R. L. Eaton (Ed.), *The World's Cats III(3)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Hornocker, M. 1971. Suggestions for the management of mountain lion as trophy-species in the Intermountain Region. Pp. 399-402, *In*: *51st Annual Proceedings Western Association of State Game and Fish Commissioners*.
Hornocker, M. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* 21.
Hrdy, S. B., and D. B. Hrdy. 1976. Hierarchical relations among female Hanuman langurs. *Science* 193: 913-915.
Kachuba, M. 1977. Sexual behavior and reproduction in captive geoffrey's cats. *Der Zoologische Garten* 47(1): 54-56.
Kleiman, D. G. 1974. The estrous cycle in the tiger. Pp. 60-75, *In*: R. L. Eaton (Ed.), *The World's Cats II*. Feline Research Group, Woodland Park Zoo, Seattle.
Koford, C. 1978. Welfare of the puma in California. *Carnivore* 1(1): 93-97.
Lanier, D. L., and D. A. Dewsbury. 1976. A quantitative study of copulatory behaviour of large Felidae. *Behavioural Processes* 1: 327-333.
Lesowski, J. 1963. Two observations of cougar cannibalism. *Journal of Mammalogy* 44(4): 586.
Leyhausen, P., and B. Tonkin. 1966. Breeding the black-footed cat, *Felis nigripes*, in captivity. *International Zoo Yearbook* 6: 178-182.
Macgregor, W. G. 1976. The status of the puma in California. Pp. 28-35, *In*: R. L. Eaton (Ed.), *The World's Cats III(1)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
McCord, C. M. 1974. Courtship behavior in free-ranging bobcats. Pp. 76-87, *In*: R. L. Eaton (Ed.), *The World's Cats II*. Feline Research Group, Woodland Park Zoo, Seattle.
Provost, E. E., C. A. Nelson, and A. D. Marshall. 1973. Population dynamics and behavior in the bobcat. Pp. 42-67, *In*: R. L. Eaton (Ed.), *The World's Cats I*. World Wildlife Safari, Winston, Oregon.
Robinette, W., J. Gashwiler, and O. Morris. 1961. Notes on cougar productivity and life history. *Journal of Mammalogy* 42(2): 204-217.
Rudnai, J. In press. The ecology of lions in the Nairobi Park-Kitengala area. *Carnivore*.
Rudnai, J. 1973. Reproductive biology of lions in Nairobi National Park. *East African Wildlife Journal* 11: 241-253.
Sankhala, K. S. 1967. Breeding behavior of the tiger, *Panthera tigris*, in Rajasthan. *International Zoo Yearbook* 7: 133-147.
Schaller, G. B. 1972. *The Serengeti Lion*. University of Chicago Press, Chicago.
Schaller, G. B. 1967. *The Deer and the Tiger*. University of Chicago Press, Chicago.
Schaller, G. B. 1977. *Mountain Monarchs*. University of Chicago Press, Chicago.
Scott, P. P. 1976. Diet and other factors affecting the development of young felids. Pp. 166-179, *In*: R. L. Eaton (Ed.), *The World's Cats III(2)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Seager, S. W. 1977. Collection and freezing of semen of captive wild Felidae. Pp. 112-119, *In*: R. L. Eaton (Ed.), *The World's Cats III (3)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Seidensticker, J., M. Hornocker, W. Wiles, and J. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* 35.
Smuts, G. L., J. Hanks, and I. J. Whyte. 1978. Reproduction and social organization of lions from the Kruger National Park. *Carnivore* 1 (1): 18-29.
Thomas, E. M. 1958. *The Harmless People*. Vintage Books, New York.
Todd, N. B. 1978. An ecological, behavioral genetic model for the domestication of the cat. *Carnivore* 1(1): 53-61.
Visser, J. 1976. The status of southern Africa's smaller cats. *In*: R. L. Eaton (Ed.), *The World's Cats III(1)*. Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Young, S. P., and E. A. Goldman. 1946. *The Puma*. Dover, New York.

AN ECOLOGICAL, BEHAVIORAL GENETIC MODEL FOR THE DOMESTICATION OF THE CAT

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Abstract: It is postulated that the process of domestication of *Felis catus* was essentially initiated by cats to exploit the opportunities afforded by human settled communities. Thereafter, cats tracked the development and elaboration of the urban niche. In so doing, the cat was forced to shift from a feeding strategy based primarily on solitary predation through a derived phase of scavenging to an ultimate stage of interspecific soliciting and provisioning. The initial impetus to embark on this sequence of changes was probably triggered by the natural prey of cats being attracted to and concentrated around human habitations. As human populations grew and prospered, a reliable scavenging base was created which permitted further expansion of the cat population.

Throughout the transition from wild to domesticated, selection would favor behavior that reduced territorial requirements and attenuated inter- and intraspecific agonistic responses. One mechanism for achieving this result depends upon modification of endocrine metabolism, with concomitant pliotropic alterations of pigmentation. The present frequencies and clinal distributions of pigment polymorphisms in domestic cat populations are hypothesized to relate to the cumulative intensity of the selection pressures favoring domestication. These clines should, therefore, correspond to major events in the history of urbanization and commerce of man, thereby providing a test of the model here presented.

INTRODUCTION

Archeological and cultural records are entirely inadequate for the purpose of reconstructing the history of the domestication of the cat. It is the intent of this paper to present a model for the domestication of this species based on the integration of ecological observations and the findings of population and behavioral genetics. It will be argued that the domestication of the cat is the result of a natural evolutionary transition to the exploitation of a new niche created by the development of settled human communities. In contrast to the contrived domestication of many other species, the cat became a domesticant in the absence of any human effort designed to bring about this end. In contrast, Baldwim (1975) has hypothesized that a requisite interplay of ecological and religious forces developed only in Ancient Egypt. While this review and summary is quite successful in harmonizing the interaction of biological and cultural conditions for a given time and place, it still skirts the question of basic mechanisms and proposes a very restricted venue for the process.

Over the last two and a half decades the population genetics of the domestic cat has been studied with increasing intensity. Today knowledge of cat population genetics is much greater, if less publicized, than that of most mammals. Most studies may be found by referring to the literature citations accompanying this paper. The work to date has clearly shown that the cat is a convenient and useful species for such research. In Europe, North Africa, and the Middle East, those areas where domestication largely commenced, very interesting clines exist for a number of coat color mutants (Dreux and Todd, 1974; Todd and Todd, 1976; Todd and Kunz, 1977; and many recent findings that extend and modify the maps as previously published). Furthermore, almost all populations studied appear to conform to Hardy-Weinberg equilibrium or where they depart an explanation not too far-fetched is available. In addition, evidence is accumulating that human preference (at least as expressed in opinion polls) plays little or no role in influencing mutant frequencies (Clark, 1975). In fact, some mutant frequencies may rise in the face of preferences against them, and others that seem much preferred fail to rise (Dyte, 1974).

The populations that have been investigated range from household pets to strays and cut across extremes of climate and ecology. However, none of the mutant clines that have been defined suggests any relationship to those ecological circumstances that are broadly determined by geophysical or climatological factors. The only hypothesis proposed to date holds that the frequencies of several mutant alleles are modified by a factor or factors highly correlated with urbanization. It seems that a variety of loci carry alternative alleles of differential sensitivity to some unknown selection pressure generated by the urban environment. It has been argued, in particular, that the major changes presently occurring result in darker phenotypes (Moffatt, 1968; Dreux, 1968; Todd, 1969; Clark, 1975). In spite of continued findings that are consistent with this general proposition, specific evidence that relates this phenomenon to the overall pattern of mutant clines has yet to be uncovered. Of course, at the base of any explanation must be the long-term trend of replacement of a relatively homogeneous wild type population with a highly polymorphic domesticated population. Whether this is leading ultimately toward a new homogeneity cannot as yet be specified but at least two mutants, nonagouti (a) and blotched tabby (t^b), may be moving to fixation in certain areas.

At the moment the populations most closely approaching the presumptive ancestral condition, i.e., having the lowest frequencies of mutant alleles, have been found in Eastern Turkey (Todd and Todd, 1976) and remote areas of the Highlands of Scotland (Clark, in press). But even these populations have most mutants well above "trace" levels. While it is obvious that most of the mutations arose at different times and places, extensive overlap occurs in all populations that have been studied. In other words, the cline maps for each mutant, when taken together, fail to point to a particular area that might still contain a primitive population or, conversely, to a place that might have represented an initial seat of domestication.

What is now required is some new insight into the nature of the selection pressures that shape and modify genetic profiles of cat populations. This will necessitate asking some very basic questions about the genetic biology, behavior, ecology and history of the cat. Many of the existing assumptions about the nature of cats and cat populations have become highly suspect in the process of sifting the data collected in recent studies. Since the question of population genetics has not been explored in the past, taxonomists, ecologists, archaeologists and historians, to the extent that they have dealt with the problem at all, have largely gone their own respective ways. None of this individual effort has brought about a synthesis of ideas, let alone contributed to any kind of precise understanding of the issues now arising in the form of various mutant clines. In order to begin to clarify the picture, certain basic information needs to be recited. This may be divided, for convenience, into four topics: 1) the relationship of the domestic cat to certain wild cats; 2) the population density and dynamics of cats; 3) the ecology of wild and domestic cats; and 4) the history of the domestication of the cat.

THE RELATIONSHIP OF THE DOMESTIC CAT TO CERTAIN WILD CATS

There can no longer be any doubt about the fact that the domestic cat, *Felis catus,* is a conspecific of one species of Old World small cats that include, in particular, such wild forms as so-called "Felis silvestris" and "Felis lybica." Whether or not other nominal species *(F. bieti, F. margarita,* etc.) can be brought into this assemblage is still uncertain but not improbable. Pocock's (1951) taxonomic justification for recognizing three distinct species, *F. catus, F. silvestris* and *F. lybica,* can be viewed with a certain sympathy but not with any conviction. The lack of evidence for intergradation of *silvestris* and *lybica* (with the possible exception of some untraced information for Italy) seems to rest entirely on geographic isolation. It proves nothing about hybridization of either form with domestic cats. The seeming lack of typical domestic mutants in either wild race may be attributed in part to bias and in part to biology. In the first place, such animals that display these mutants are consigned, sometimes uncritically, to the feral domestic category when, in fact, they might be either F_1 hybrids (in the case of certain dominant or sex-linked mutants), or the result of alleles that have introgressed and recombined in essentially wild populations. It is even possible that one "domestic" mutant, nonagouti-(a) was present at high levels in predomestic populations (Saliternik and Todd, unpublished). The list of "feral" skins discussed by Pocock (1951) may contain many such cases. In the second place, behavioral traits of cats would preponderately favor a flow of alleles from wild to domestic populations. This situation arises in the following way: Tomcats generally operate in their own domains. Thus it is likely that a domestic or even a feral male would face a disadvantage in seeking a mate among wild females, for this would normally place him in confrontation with wild toms. Between wild and domestic populations there probably often exists a buffer population of feral[1] animals. Wild males might well recruit mates from this feral pool. In turn, the hybrid wild/feral male progeny might occasionally acquire a domestic mate. Hence, the usual flow of alleles will be from wild (via feral) to domestic populations because this route is predetermined by the mating prerogatives of males. This phenomenon was noted by St. Hilaire (cited in Hamilton, 1896) for hybridization between domestic cats and wild cats in Africa. Because the numbers of domestic (and even feral) cats are, at least at present, vastly greater than those of wild cats, the impact of the flow of wild alleles to domestic populations is inconspicuous. Finally, some evidence suggests that certain mutants may be at a selective disadvantage in feral populations (Dartnall, 1975) and, therefore, probably in wild populations as well. Even if a trickle of domestic mutants moves into wild populations, these will tend to be purged en route or soon afterward.

While the direct evidence of interfertility of domestic cats with "sylvestris" and "lybica" is largely anecdotal (but no doubt admissable as valid) (see, for example, Hamilton, 1896), at least one well-documented, intentional attempt to hybridize a wild male from Scotland with a domestic female has been recorded by Pitt (summarized by Robinson, 1972). This led to the subsequent breeding of the F_1, establishing beyond question the fertility of the hybrids. The evidence for the interfertility, and hence genetic introgression between domestic cats and "lybica," rests on the fact that the wild-type phenotypes of domestic cats in Morocco (Rabat) conform to that of "lybica" rather than to that of European domestic and wild cats (Genermont, 1974).

THE POPULATION DENSITY AND DYNAMICS OF CATS

The question of population densities of cats becomes crucial in the interpretation of gene frequency data. The numbers of wild, feral or rural domestic cats on the one hand, and those of urban areas on the other, will affect the rate of allele spread over space and time as a function of the relative densities of populations. The available information on populations at large is sketchy and difficult to quantify, especially for wild, feral and rural cats, but at least some order of magnitude values may be proposed. Lindemann and Riek (1953, cited in Leyhausen, 1960: 59, but not discovered in the cited text) give the territory of the Carpathian wild cat as 50 hectares. This suggests a density (assuming total utilization of a given geographic area) of slightly more than five cats per sq. mi.

Forbush (1916) discussed the occurrence of feral cats in rural New England. Unfortunately, most of these data cannot be translated into any precise standing population values. One figure, coupled with an area, "in seven months, twenty-eight cats have been shot . . . on twenty acres," can be used to derive a minimum estimate of density. Assuming 100% efficiency in killing, 100% of the habitat suitable for occupation and utilization and the ability of the surrounding environment to "donate" replacement animals at the rate equivalent to killing (approximately one cat per week), then as few as four cats at a given time, foraging at random within the square mile encompassing the 20-acre ($1/32$ mi^2) killing site, could account for the observation. Hence, a minimum density of four cats per sq mi is indicated. Marshall (1961) notes that for an insular area of 11.76 sq mi, up to 40 feral cats per year have been killed,

[1]The term "feral" will be used throughout this paper in a restricted, and strictly speaking incorrect, way to distinguish wild cats with domestic progenitors from wild cats with no such ancestry.

apparently without decimating the population. Hence, the standing density must approach a minimum of four cats per sq mi. These two crude estimates indicate minimal feral densities under what are probably, aside from the persecution, quite favorable circumstances. Anderson and Condy (1974) give a minimum estimate of the cat population on Marion Island as 500 animals, but suggest it might be as high as 2000. The corresponding densities would be 4.3 to 17.2 cats per sq mi. To hazard a guess, wild populations under average conditions would be considerably more sparse.

Pearson (1964, 1966, 1971, personal communication) has studied carnivore activities in a parkland adjacent to urban areas of Berkeley, California. Some observations indicate that cat densities may rise to nearly 150 per sq mi, although they are not sustained at these levels.

The question of information on *owned* urban cat populations has been summarized, with additional findings, for essentially northwest European and derivative societies (Todd, 1977). The impact of socioeconomic and ecological factors is very complex, but densities between 200 and more than 1000 cats per sq mi are indicated without taking stray animals into account.

For many cities of the world, especially those of the Mediterranean, conditions would appear to be conducive to the development of cat populations much larger than those found in British and American cities. While cat ownership may well be low in the Mediterranean and Middle East, indifference to and indulgence of stray cats is enormous. This difference in human attitudes is not trivial and dictates the strategies used for conducting surveys in such contrasting situations. Only an insignificant number of cats can be spotted in many British and similar cities by a careful search of gardens, alleys, and so on. On the other hand, many Mediterranean cities will routinely yield between 20 and 25 sightings per hour in what seem to be more or less equivalent ecological settings. Some of this is certainly due to the presence of uncontrolled strays, but it appears inconceivable that absolute numbers are not also very much larger. More important is the fact that more than 100 sightings can be made in an area of less than 1 sq mi (in one case in about one hour) without duplication of observation and nothing approaching saturation coverage. If, optimistically, it is assumed that 10% of all resident animals were seen, then a working estimate of densities becomes more than 1000 cats per sq mi *as a minimum*. Of course, these densities will not characterize an entire urban area, for cats can hardly be expected to be distributed evenly over a city.

Although no effort will be made to model mathematically the genetic changes to be discussed in the present paper, it may be suggested that when such projects are undertaken, the relative densities of wild, feral and rural populations to suburban and urban populations may be taken provisionally as more than 1:100. Even without a mathematical treatment, any interpretation of allele flow or increase must be done with an awareness of the magnitude of these differences.

Before leaving the topic of population size and density, at least some mention must be made of further complexities introduced by trying to estimate these factors in ancient cities. Perhaps the least distressing concern is with regard to ecological differences between modern and ancient conditions. While the differences may be conspicuous, they should not be overemphasized. Many of the modern features of cities are not more than a few decades old. Even today, large areas of many great cities probably offer few significant distinctions to times past so far as cats are concerned. This would seem to be especially true for many eastern Mediterranean and North African cities (Mumford, 1961: 73-76) and for the sprawling slums of many urban complexes, whether these are peripheral accretions due to rapid urbanization or, latterly, central decay due to rapid suburbanization. But the problem is not solved by rationalization of the similarity of modern and ancient cities. The primary difficulty arises when an effort is made to determine human population size for ancient cities (Chandler and Fox, 1974). However, this issue need not be belabored at this juncture.

In addition to densities a very important facet of cat population dynamics concerns the migratory abilities and propensities of the species. Wild, feral and rural domesticated cats may wander extensively, up to several miles, in the course of their daily activities (Leyhausen and Wolff, 1959; Leyhausen, 1965a, 1965b), but so far as is known (and this is certainly too little) they confine themselves to a relatively set area that might be loosely termed a territory or home range. These cats probably live their entire lives not far from their place of birth.

Water, desert and high mountain ranges are either impassable or only rarely traversed barriers. All cats are constrained by these limitations with one significant exception, viz, domestic cats and water barriers. Rivers, lakes, seas and oceans actually come to facilitate the dispersal of domestic cats because of the common practice of transporting them in vessels. But land barriers are seldom breached as cats do not constitute normal baggage of overland trade and commerce. An appreciation of these factors is indispensable in the process of making sense out of mutant clines.

THE ECOLOGY OF WILD AND DOMESTIC CATS

In the wild *F. catus* preys on a variety of small mammals. Most of these are rodents and rabbits but occasionally may include bats, insectivores and probably any other creature that can be overcome. Lindemann and Rieck (1953) found that over 80% (by weight) of prey species consisted of mammals. The extent to which birds are taken appears to vary according to circumstances (Anderson and Condy, 1974; Marshall, 1961; McBride, Parer and Foenander, 1969). From all evidence, both feral and domestic cats exploit virtually the same fare (Forbush, 1916; Marshall, 1961). Reptiles and amphibians do not seem to be an important constituent of the diet although ingestion of insects may sometimes be substantial (McMurray and Sperry, 1941).

Hence, while *F. catus* is essentially adapted as a predator, it has by no means a limited prey preference. This lack of specialization no doubt preadapts the species for penetration into the urban niche provided by man. The cat as a domesticant acquires food in three fundamentally distinct ways: active predation, scavenging, and inter-specific soliciting (begging). Only the last is really novel and is shared by the dog and a few other animals. The three strategies have one important thing in common. The opportunities for each are enhanced by (or depend upon) the proximity and penetration of human communities. Nor, of course, are the three mutually exclusive; but each represents a stage in a sequence requiring quite different behavioral and presumably genetic adaptations. If the three are treated as phases, then it is possible to discuss some of the conditions and consequences surrounding each.

Phase I is initiated by human settled existence wherein food storage and waste disposal sites attract vermin. This concentration of potential prey provides the cat with a "supernatural" niche, if in fact cats are able to accommodate to the inevitable concomitant inter- and intraspecific competition. At the same time conditions are established for the opening of an alternative niche, that of scavenging.

Phase 2 begins as soon as human prosperity is translated into larger urban settlements that increase the volume of garbage to the point that a significant number of cats can be largely or wholly sustained as urban scavengers (McMurray and Sperry, 1941). "Field" observations suggest that cats (and dogs) may be as great a threat to rodent (specifically rat) populations through competition in scavenging as by direct predation. In Baltimore, Maryland Jackson (1951) found that only 3.5% of the diet of alley cats consisted of rats. In any case some of the huge urban cat populations that exist could not be maintained by predation alone, so at some point scavenging becomes a necessity rather than an option. An interesting and complex human response further extends the scavenging phase and undoubtedly contributes to the realization of the last phase, begging. Either from mistaken notions of pest control or for what might be called "humanitarian" reasons, humans consciously provision and otherwise encourage cats and cat populations. To the cat, food placed in the environment for its consumption is initially just one more opportunity to scavenge. But, at some point the connection is made between the provider and the food, and only a stupid cat would fail to take advantage of a situation that is nothing more than operant conditioning.

Phase 3 is the logical endpoint in the overall sequence. It arises when cats are largely or totally dependent on handouts. Such conditions have only been recently realized and may represent at last effective human control over the species. While it may be very important for the future of the cat, it has probably had little influence in the past.

Obviously the sequence just outlined as taking place over time will be reflected over space. The present studies of population genetics have been conducted in areas that approximate each of these phases in at least a general way. In considering mutant allele frequencies it will undoubtedly be necessary to take into account the status of each population according to where it falls in the sequence. There is no ready formula for the characterization of a given population. It will ordinarily be composed of varying proportions of animals all along the spectrum. Hence, each case must be appraised individually and justified by comprehensive description and discussion. In the final analysis, one hopes, it may be the genetic profile itself that will provide a quantitative measure. But even this will have to be reckoned against the overall geographical and historical patterns.

THE HISTORY OF DOMESTICATION

The origin of the domestication of any species, plant or animal raises a host of questions, including where, when, why, and how? (Reed, 1971). It has often been taken for granted that domestication results from peculiar circumstances of time and place combined with some human innovation. Thereafter the domesticant is spread by human agency either as the diffusion of the appropriate technology or the exportation of the finished product as an item of trade. While the relative merits of this explanation will vary from species to species, for cats it is especially unattractive. The domestication of this species requires no special technology. Cats need not be corralled or penned to foster affiliation with man. Nor, aside from their real or presumed rodent-controlling abilities, are cats of any vital use to human economy or progress. All that seems required to begin the process is an attractive environment, perhaps nothing more than a settled village community, with its garbage and rodents. Isaac (1971) notes that "even today there is a symbiotic relationship between the wild cat and man in Southern Nubia, but despite the long history of this relationship no development toward domesticity has taken place." Unfortunately, the statement stands essentially alone and the full implications are not self-evident. The wild cat is *F. catus lybica*. The nature of the symbiotic relationship is little more than the congregation of these animals about human habitations where presumably they are tolerated for reasons of rodent control (E. Isaac, personal communication). The status of the community of men, the Azande in the south of the Sudan, is somewhat peculiar. This is an agricultural tribal group living in well dispersed settlements comprised of not much more than the huts of extended family groups. Hence, rather than emphasize the negative implication that "no development toward domesticity has taken place," perhaps the attraction of cats to settlements hardly qualifying as villages should be stressed.

Domesticity need not, or should not, be equated with a relationship of affection. Epstein (1971: 120) records the relationship of certain cats to a human community.

> In the towns and villages of the Near East large numbers of cats may be observed that have . . . turned pariah. A group of dustbins which they defend against all newcomers usually forms the center of a family group of such pariah cats. Like pariah dogs they have no master and no home; they are not fed nor bred or protected by anyone. They do not get accustomed to a home, remaining wild and ferocious unless taken in at a very tender age. Although resembling pariah dogs in their mode of life and state of domestication, these cats have never been claimed to constitute a transitional stage from wild *Felis lybica* to the properly domesticated cat, so obvious is their derivation from domestic stock.

Despite the clear disclaimer that these cats are historically transitional in the process of domestication, it is clear that they are *de facto* intermediate in the sequence. The extent to which their ancestors were "lap-cats" is a moot point.

Epstein (1971: 125) comments on the appearance of animals in the wake of the development of a physically new community.

> It has been observed in Palestine that wherever a new human settlement is established, a border zone for the pariah is automatically called into existence; 'the pariah dogs arrive at once, as if *it* [sic] were out of nothingness' (Menzel and Menzel, 1948). In the same country pariah cats and wild jackals have shown a rapid increase in number with an increase in human habitations.

Most domesticated species are recognized by signs of genetic modification as judged by osteological remains or more complex evidence such as proportional age representation of remains suggesting cropping. For the cat no such signals have come to light, although opinions vary enormously on the question of the ability to distinguish wild from domestic on the basis of skeletal remains. Isaac (1971) asserts that the record of mummified cats from Egtpt shows "a sequence of development from the ancestral Lybian wild cat (Felis catus Lybia [sic]) to the domestic cat." However, the proposition is not expanded to indicate what developmental changes are noticeable. Bokonyi (1974), referring to the mummies, concluded only "that they represented a fairly homogeneous population . . ."

Although often misinterpreted, Zeuner (1963: 388-390) quite clearly stipulates by summarizing many studies that there are no skeletal features that permit an unambiguous separation of wild and domestic cats, especially when only fragmentary remains are available for study. This was again recently confirmed in comparisons of adequate samples of wild and domestic cats from Czechoslovakia (Kratochvil, 1973). Therefore, only cultural indications can essentially provide unequivocal indications of domestication. While this may be something of a disappointment, it should not be a surprise. Other species were selectively bred to emphasize or exploit some incipient attribute of the wild form or to tailor it to some perceived human need. If the cat was only an uninvited but not unwelcome guest in the human community, there is no reason to expect it to be modified in any dramatic way. In fact, since tolerance of its presence was based on its continuing to function in a manner virtually identical to its wild progenitors (i.e., active predation), modification might have interfered with its acceptance. Also, as previously noted, genetic introgression with wild races still takes place. This would have the effect of suppressing any effort to alter the species, particularly in early stages when domestic populations were relatively smaller than they were to become and wild reservoirs were more accessible to urban settlements. Hence, a lack of any osteological clues to the origin of domestication of the cat can be taken only to indicate a lack of any effective selection pressures that would bring about skeletal changes. On the other hand, if the adjustments requisite for exploitation of the domestic niche relate to characteristics (especially behavioral), not likely to be preserved in the archeological record, then there is no reason to dismiss the possibility that cats have lived in intimate association with men ever since there was any advantage to them in doing so.

The usual explanation of the domestication of the cat in ancient Egypt for the purpose of protecting grain stores from rodent depredations is simply naive. While there is no disputing that improperly stored grain draws rodents, and these in turn attract cats, this equation as the *sine qua non* has been greatly oversimplified and exaggerated in importance. One study, for instance, has shown that while cats may retard rodent infestation, they cannot prevent it, nor are they very effective in the presence of an overload (Elton, 1953). Anyway, grain storage predates the earliest cultural evidence of the domestication of cats by thousands of years (Wendorf et al., 1970) and it seems unlikely that cats would have been chosen at this relatively late date to deal with what must have been an age-old problem. Furthermore, there is simultaneous evidence of the domestication, or at least encouragement, of the Egyptian mongoose *(Herpestes ichneuman)* (Zeuner, 1963). Both cats and mongooses ultimately became venerated and associated with cults, and it is probably to this religious interest that any cultural evidence of their presence at an early time is available. Subsequent to this spectacular demonstration, the historical record, while not entirely mute, is incredibly thin with regard to cats. Hence, under normal circumstances, the undoubted presence of domestic cats leaves no conspicuous record. Thus, in much earlier times no more should be expected. But the interlude of cultism can be construed to have been based on a long-standing, if undocumented, familiarity with the cat.

In summary, there would appear to be no compelling reason to expect indisputable archeological evidence for the time and place of domestication of the cat. Probably the association began, as it continues, with the cat exploiting the opportunities provided, whenever and wherever men adopted a settled village existence. The cat then becomes a standard fixture in the urban environment simply by being present from the earliest phases of urbanization. It only required a tolerance on the part of people and an ability on the part of cats to make the appropriate genetic adjustments to the new and developing niches. According to this model the history of the domestic cat becomes the history of this adaptation; and in the absence of other kinds of evidence, the only record will be preserved in the mutant alleles representing this adjustment, and the subsequent factors controlling their dispersal.

GENETIC MECHANISMS IN THE ADAPTATION TO DOMESTICITY

Several allusions have been made to the genetic adjustments that must accompany the transition from wild to domestic status. The most noticeable difference between the two extremes is the homogeneity of pelage phenotype in wild populations and the extensive polymorphisms for coat color, pattern and texture in domesticated forms. This does not imply a lack of variation in wild forms but the diversity that does exist is confined to more or less subtle modifications within a basic phenotypic pattern. A second distinction between the two extremes is behavioral although a good deal of caution needs to be carried into any comparison. The "fierce," "savage," temperament of the wild cat is notorious, and that notoriety is undoubtedly deserved. From numerous accounts it appears that it can only be partially suppressed even when wild kittens are taken into a domestic situation at an early age (Lindemann and Riek, 1953). But in fairness, success in taming feral or domestic kittens is hardly greater. There would appear to be a crucial phase during which cats can be conditioned to a satisfactory (from an anthropocentric viewpoint) affiliation with man. Perhaps the single most important difference between wild and domestic cats is the kind of early exposure and experience they encounter, but even this does not close the behavioral gap. The precise role of heredity in this process can only be surmised, although it undoubtedly works in ways similar to those demonstrated in other animals.

In the transition from wild to domestic, one of the most obvious changes that occur as one phase follows another is the increase in population density. This may amount to a difference between fewer than five cats per sq mi to over 1000 cats per sq mi. Hence, one of the most significant variables in the accommodation to the urban niche is that which cats must make to one another. The literature is full of studies on the effects of increases in population density. The "classic" examples are based on rodents. In any event these investigations have shown clearly that crowding leads either to regulation through feedback mechanisms (Christian, 1961, 1963a, 1970) or to "social pathology" (Christian, 1963b). It must be accepted that domestic cats have evolved a modified behavioral repertoire that permits considerable crowding vis-a-vis wild optima. The thresholds of ancestral feedback mechanisms must have been raised so as not to be triggered at present densities. Furthermore, sensitivity to stimuli that would generate social disorder must also have been elevated. More explicitly, territorial prerequisites must have been greatly eroded, suppressed or displaced and aggression and hostility replaced with tolerance or indifference. These latter adjustments must be extended to apply not only to conspecifics, but also to other domesticants and man. Domestic cats must not only become tolerant of the presence of man, cattle, pigs, etc., but they must also not prey upon poultry and the young of other species. A very dramatic demonstration of this is provided by the example of abandoned cats and chickens living in a feral state on islands of the Great Barrier Reef, Australia (McBride et al., 1969). Although many generations have elapsed since either species was kept in a domestic context the cats still fail to prey on the chickens.

Many studies have revealed that behavioral traits such as fear and aggression are susceptible to modification through selective breeding. The breeds of dogs provide myriad examples of genetically determined temperament and behavioral patterns (Scott, 1954; Scott and Fuller, 1965) and recently experimental selection in foxes has been studied (Belyaev and Trut, 1975). Strains of mice and rats are readily produced with consistent differences in fear and aggression (Keeler, 1942, 1947; Weimer and Fuller, 1966).

Usually hereditary variations in behavior are attributed to polygenic determinants and effects far removed from primary gene action. However, there are examples of single or few mutant changes that produce remarkable behavioral alterations. One such group of mutants are those that simultaneously control coat color polymorphisms. Also, upon examination it is found that the distance between primary gene action and behavioral modification is not very great.

Keeler et al. (1968) and Keller (1970, 1975), working with the red fox *(Vulpes vulpes)*, have revealed a correlation and a cause and effect relationship between three coat color mutants and reduced fear and aggression. The mutants not only change pelage phenotype, but also modify pituitary, thyroid and adrenal functions. With respect to the thyroid the effects of each mutant appear to be cumulative and interfere with thyroxin production by altering the breakdown of a precursor substance. The behavioral manifestation of this is hypothyroidism, although not to the extent that it would be labeled a pathology.

The data on the pituitary gland is least developed at the present time, but a significant reduction in gland to body weight has been demonstrated in foxes homozygous recessive for various coat color mutants.

In the case of adrenal functions the mutants not only cause some difference in adrenal/body weight ratio, but also appear to alter a common precursor in the synthesis of adrenalin and malanin. Again the effects of each single mutant seem to be additive.

The behavioral results of these hormonal modifications can be measured in a variety of ways—in the present case by "startle tests." Not only does each mutant individually reduce the startle and flight distance, but also the more mutants present simultaneously, the more pronounced the behavioral modification.

The three mutants studied in the fox are nonagouti *(a)* blue *(b)* and chocolate *(c)*. Nonagouti in the fox appears to be strictly homologous to that in the cat. Blue, likewise, seems homologous to blue or dilute *(d)* of the cat, in that the pelage phenotype is brought about by clumping of melanin pigment granules in both species rather than by other mechanisms that give a similar visual effect. Chocolate in the fox is probably homologous to brown *(b)* in the cat, but this mutant in the latter species is very rare in all populations thus far studied. Finally, two mutants of special interest in the cat that appear to have no homologue in the fox are sex-linked orange *(O)* and blotched tabby (t^b). However, blotched tabby has some nonagouti-like phenotypic effects and Robinson (personal communication) has shown that *a* and t^b have a highly correlated distribution in European populations ($\chi^2 = 57$ for 47 d.f.). On both accounts it seems reasonable to propose that t^b confers much of the selective advantage of *a*. And the effects may be additive for t^b is visually hypostatic to *a*.

Behavioral modification associated with coat color mutants seems sufficiently widespread and common in rats, mice, and mink (Keeler and Moore, 1961), as well as in foxes, to assume that similar phenomena operate in cats. Hence, despite a lack of direct testing, it is reasonable to develop a model which assumes that the primary advantage of many coat color mutants in cats derives from pliotropic behavioral alterations that facilitate, in one way or another, the adjustment to the exploitation of the urban niche and to domestication. There is, of course, the possibility that some mutants are basically involved in conspecific adaptations while others primarily benefit the association with man. If this be so, then those mutants basically modulating conspecific adjustments (tolerance) should be highest where cat density is highest, irrespective of degree of affiliation with humans. Such conditions may exist in large, stray, urban populations. In contrast, the frequencies of those mutants that may be involved in the cat-man accommodation (tameness) should be high where the affiliation is high, irrespective of cat density. The pet populations of suburban and rural areas may serve to evaluate this possibility. Of course, a single mutant may subserve both functions, thereby making the correlation more difficult to assess. The fact that cat and human density are correlated may tend to confound these distinctions as well.

In several species the nonagouti mutant has already been implicated as being especially sensitive to selection favoring both reduced aggression and fear. No direct testing has been conducted on cats, but the clinal distribution of this mutant (Figure 1) may be interpreted in a manner that is consistent with the advantages such behavioral modifications would confer. The pattern strongly suggests a dispersal particularly dependent upon maritime activities. Under such circumstances cats would be highly susceptible to selection for fitness as shipmates. If that premise is true, then each time cats were introduced to a new area selection would tend to raise the frequency of nonagouti above that of the donor population. Thus, so long as the spread is a step-wise process, the further domestic cats are distributed, the higher the expected frequency of nonagouti.

Wherever very high frequencies of *a* are found above .70, evidence can be deduced for an intimate relationship between cats and men, either as an ongoing phenomenon or at least as a precondition for the inception of the population. Some extraordinary examples may be noted: Van, in Eastern Turkey, where cats at present enjoy a special relationship based on a strong local tradition (Todd, Sawyer and Todd, unpublished); Khartoum in The Sudan, where cats in the main must have been introduced by Nile commerce (Todd and Todd, unpublished); Denver, Colorado, where cats only entered in close association with man (Morrill, personal communication); Curacao, Netherland Antilles, and Caracas, Venezuela, where cats clearly were introduced by man (Todd et al., 1974). But, while all cases of high *a* seem amenable to an interpretation of human influence, not all places where this influence must have occurred show a high incidence of *a*. Iceland and the North Atlantic islands would appear to be conspicuous exceptions (Todd et al., 1975). In these latter cases either other forces were operative at the time of inception, or subsequent events have obliterated the original profile. That nonagouti levels may fall when the cat-man affiliation is attenuated or terminated is implied by a significantly lower frequency of *a* in feral cats of Tasmania than in the domestic populations from which they must be derived (Dartnell, 1975). Hence, the exceptions do not negate the "rule," they only obscure it.

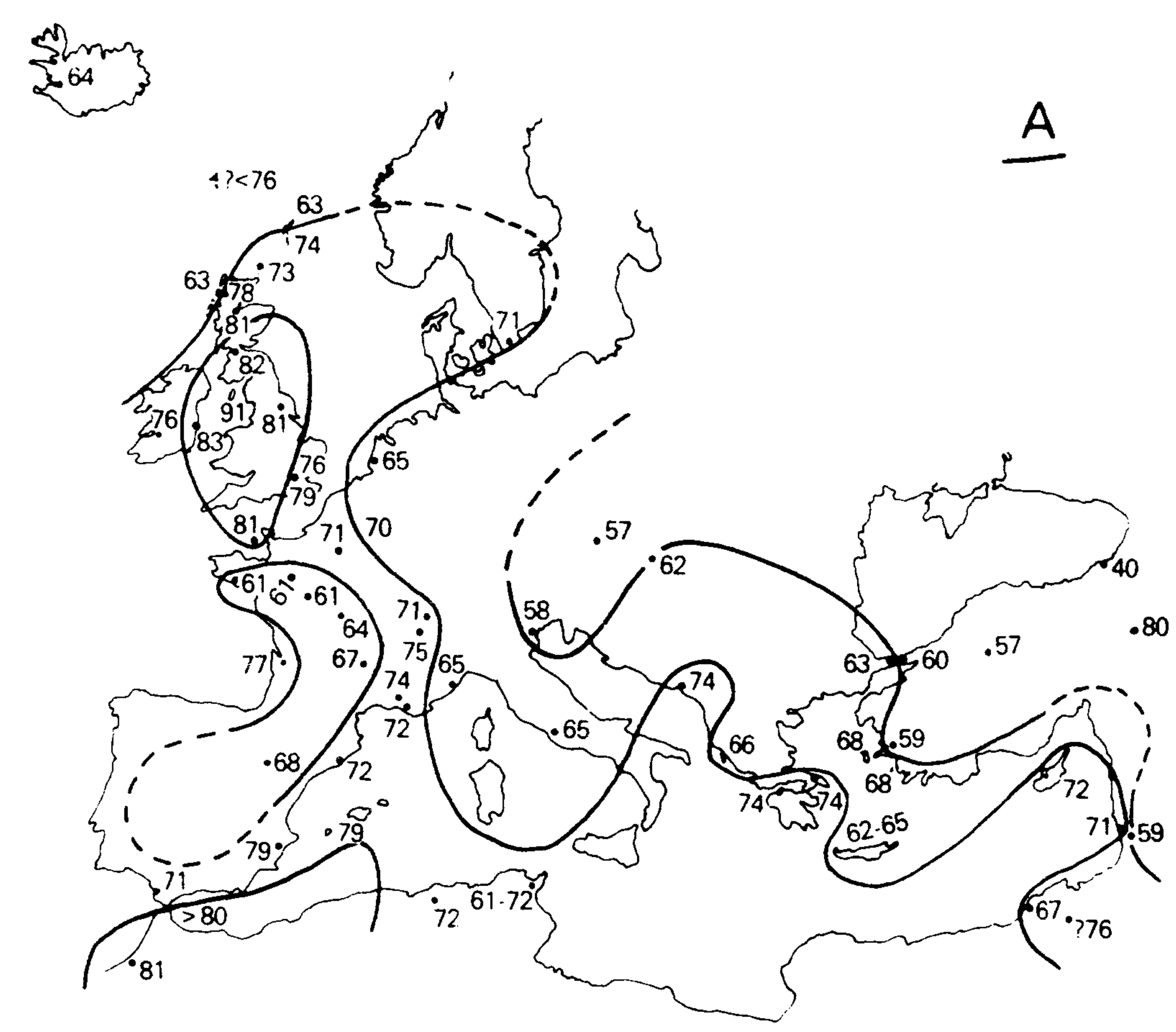

FIGURE 1. Clinal distribution of the mutant allele nonagouti *(a)* in cats of Europe, North Africa, and The Middle East. Frequencies in the 0.5-0.6 range are suggested to be close to equilibrium established by heterozygous advantage. Higher frequencies are taken to indicate disruption of this equilibrium by selection favoring the homozygous recessive condition. Probable clinal fronts are indicated by solid lines, possible fronts by dashed lines. See text for further discussion.

It is consistent with the present distributions to propose that as the Western Mediterranean was opened to the civilizing influences of Greeks (Massalia) and Phoenicians (Carthage), both carried a fortified population of nonagouti cats from their homelands to their new-found colonies. When these colonies, notably Carthage, became colonizing forces in their own right, further sampling bias in the transportation of cats would again increase the proportion of nonagouti. Some very high levels of nonagouti characterize the Western Mediterranean to the Straits of Gibraltar and, judging from Rabat, at least to the Atlantic Coast of North Africa. The Balearics, Alicante, Algeceras, Tangier and even Rabat are all areas once dominated by Carthage. The mother city itself, having been destroyed and depopulated, no longer bears the hallmark. The one area of lower incidence in the Mediterranean is clearly in the region of early Roman hegemony. Even this is compatible with the present interpretation, for the populations of Rome were not founded by maritime activity; and the Romans were generally content to leave maritime commerce to others.

Finally, when cats entered the British Isles, where frequencies are among the highest in the world, the propagules must have been preselected on several occasions for those genotypes most suited to accompany men in close quarters. That this last "migration" passed through central France, along the Seine-Rhone valleys, is attested to by the fairly homogeneous and elevated nonagouti frequencies in this corridor when compared to the hinterlands. Historically this route has been a traditional alternative to transport via the Straits for centuries.

Finally, one intriguing question may be asked, viz. are the presumed pliotropic effects (endocrine and color/pattern) entirely coincidental, or has there been selection for both a visual manifestation and perception of behavioral changes? In other words, do non-wild type pelage phenotypes fail to elicit innate aggressive responses from conspecifics and have these same non-wild type phenotypes been associated with potential tameness by man?

LITERATURE CITED

Anderson, G. D., and P. R. Condy. 1974. A note on the feral house cat and house mouse on Marion Island. *South African Journal of Antarctic Research* No. 4: 58-61.

Baldwin, J. A. 1975. Notes and speculations on the domestication of the cat in Egypt. *Anthropos* 70: 428-448.

Belyaev, D. K., and L. N. Trut. 1975. Some genetic and endocrine effects of selection for domestication in silver foxes. Pp. 416-426, *In:* M. W. Fox (Ed.), *The Wild Canids*. Van Nostrand Reinhold, New York.

Bokonyi, S. 1974. *History of Domestic Mammals in Central and Eastern Europe*. Akademiai Kiado, Budapest.

Chandler, T., and G. Fox. 1974. *3000 Years of Urban Growth*. Academic Press, New York.

Christian, J. J. 1961. Phenomena associated with population density. *Proceedings of the National Academy of Sciences, U.S.* 47: 428-449.

______________. 1963a. The pathology of overpopulation. *Military Medicine* 128: 571-

______________. 1963b. Endocrine adaptive mechanisms and physiologic regulation of population growth. Pp. - , *In:* W. W. Mayer and R. Van Gelder (Eds.), *Physiological Mammalogy*. Academic Press, New York.

______________. 1970. Social subordination, population density and mammalian evolution. *Science* 168: 84-90.

Clark, J. M. 1975. The effects of selection and human preference on coat colour gene frequencies in urban cats. *Heredity* 35: 195-210.

Clark, J. M. 1976. Variation in coat colour gene frequencies and selection in the cats of Scotland. *Genetica* 46: in press.

Dartnall, J. A. 1975. Gene frequencies of feral domestic cats of Tasmania. *Carnivore Genetics Newsletter* 2: 248-250.

Dreux, Ph. 1968. Gene frequencies in the cat population of a French rural district. *Journal of Heredity* 59: 37-39.

Dreux, Ph., and N. B. Todd. 1974. Clinal distribution of the t^b and *O* alleles in European domestic cats. *Carnivore Genetics Newsletter* 2: 177-180.

Dyte, C. E. 1974. An aspect of human selection affecting coat variation in the domestic cat. *Carnivore Genetics Newsletter* 2: 219-224.

Elton, C. S. 1953. The use of cats in farm rat control. *British Journal of Animal Behavior* 1: 151-155.

Epstein, H. 1971. *The Origin of the Domestic Animals of Africa*. Africana Publishing Corp., New York.

Forbush, E. H. 1916. *The Domestic Cat*. Economic Biology Bulletin 2. Massachusetts State Board of Agriculture.

Genermont, J. 1974. Estimation des frequences de quelques genes determinant la coleur du pelage dans la population de chats domestiques de Rabat (Moroc). *Carnivore Genetics Newsletter* 2: 181-182.

Hamilton, E. 1896. *The Wildcat of Europe*. Porter, London.

Isaac, E. 1971. On the domestication of cattle. Pp. - , *In:* S. Struever (Ed.), *Prehistoric Agriculture*. American Museum of Natural History, Garden City, New York.

Jackson, W. B. 1951. Food habits of Baltimore, Maryland cats in relation to rat populations. *Journal of Mammalogy* 32: 458-461.

Keeler, C. E. 1942. The association of the black (nonagouti) gene with behavior. *Journal of Heredity* 33: 371-384.

____________. 1947. Modification of brain and endocrine glands, as an explanation of altered behavior trends, in coat-character mutant strains of the Norway rat. *Journal of the Tennessee Academy of Science:* 202-209.

____________. 1975. Genetics of behavior variations in color phases of the red fox. Pp. 399-413, *In:* M. W. Fox (Ed.), *The Wild Canids*. Van Nostrand Reinhold, New York.

____________, and L. Moore. 1961. Psychosomatic synthesis of behavioral trends in the taming of mink. *Bulletin of Georgia Academy of Science* 24: 125-130.

____________, T. Mellinger, E. From, and L. Wade. 1970. Melanin, adrenalin and the legacy of fear. *Journal of Heredity* 61: 81-88.

Kratochvil, Z. 1973. Schadelkriterien der Wild- und Hauskatze *(Felis silvestris silvestris* Schreb. 1777 und *F. s. f. catus* L. 1758). Acta Sc. Nat. Brno. 7: 1-50.

Leyhausen, P. 1965a. A sane community - a density problem? *Discovery* Sept.: 27-33.

____________. 1965b. The communal organization of solitary mammals. *Symposium of the Zoological Society of London* 14: 249-263; reprinted 1970 in P. Prohansky (Ed.), *Environmental Psychology*. Holt, Rinehart and Winston, New York.

____________, and R. Wolff. 1959. Das revier einer Hauskatz. *Zeitschrift fur Tierpsychologie* 16: 666-670.

Lindemann, W., and W. Riek. 1953. Beobachtungen bei der Aufzucht von Wildkatzen. *Zeitschrift fur Tierpsychologie* 10: 92-119.

Marshall, W. H. 1961. A note on the food habits of feral cats on Little Barrier Island, New Zealand. *New Zealand Journal of Science* 4: 822-824.

McBride, G., I. P. Parer, and F. Foenander. 1969. The social organization and behaviour of the feral domestic fowl. *Animal Behaviour Monographs* 2: Part 3:

McMurray, F. B., and C. C. Sperry. 1941. Food of feral house cats in Oklahoma, a progressive report. *Journal of Mammalogy* 22: 185-190.

Moffatt, B. 1968. Cat gene frequencies in two Australian cities. *Journal of Heredity* 59: 209-211.

Mumford, L. 1961. *The City in History*. Harcourt, Brace and World, New York.

Pearson, O. P. 1964. Carnivore-mouse predation: An example of its intensity and bioenergetics. *Journal of Mammalogy* 45: 177-188.

____________. 1966. The prey of carnivores during one cycle of mouse abundance. *Journal of Animal Ecology* 35: 217-233.

____________. 1971. Additional measurements of the impact of carnivores on California voles *(Microtus californicus)*. *Journal of Mammalogy* 52: 41-49.

Pocock, R. I. 1951. *Catalogue of the Genus Felis*. British Museum, London.

Reed. C. A. 1971. Animal domestication in the prehistoric near east. Pp. - , *In:* S. Struever (Ed.), *Prehistoric Agriculture*. American Museum of National History, Garden

City, New York.
Robinson, R. 1972. Hybrids of wild and domestic cats. *Carnivore Genetics Newsletter* 2: 93-94.
Scott, J. P. 1954. The effects of selection and domestication upon the behavior of the dog. *Journal of the National Cancer Institute* 15: 739-758.
__________, and J. L. Fuller. 1965. *Genetics and the Social Behavior of the Dog.* University of Chicago Press, Chicago.
Todd, N. B. 1969. Cat gene frequencies in Chicago and other populations of the United States. *Journal of Heredity* 60: 273-277.
__________. 1977. The dynamics of owned domestic cat populations. *Carnivore Genetics Newsletter* 3(3): In press.
__________, G. E. Glass, and I. McLure. 1974. Gene frequencies in some cats of South America: Caracas, Venezeula; Willemstad, Curacao. *Carnivore Genetics Newsletter* 2: 230-235.
__________, R. M. Fagen, and K. Fagen. 1975. Gene frequencies in Icelandic cats. *Heredity* 35: 172-183.
__________, and L. M. Todd. 1976. Mutant allele frequencies in the domestic cats of Turkey and Greece. *Genetica* 46: 183-192.
__________, and T. H. Kunz. 1977. Mutant allele frequencies in domestic cat populations of Greece. *Biologia Gallo-Hellenica* 6: 289-310.
Weimer, R. E., and J. L. Fuller. 1966. Patterns of behavior. Pp. 629-654, *In:* E. L. Green (Ed.), *Biology of the Laboratory Mouse (2nd Edition)*. McGraw-Hill, New York.
Wendorf, F., R. Said, and R. Schild. 1970. Egyptian prehistory: Some new concepts. *Science* 169: 1161-1171.
Zeuner, F. E. 1963. *A History of Domesticated Animals*. Harper and Row, New York.

DOMESTIC CAT DEMOGRAPHY AND POPULATION GENETICS IN A MIDWESTERN U.S.A. METROPOLITAN AREA

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The study of domestic cat *(Felis catus)* demography and population genetics potentially offers novel information on gene flow (seldom measurable in the wild) and on the biology of domestication. Such data are of veterinary and public-health interest as well. Over the past two years I made separate demographic and gene-frequency surveys of domestic cats in Champaign and Urbana, U.S.A., two contiguous cities located in a rural area of east central Illinois, about 80 km south of Chicago.

Basic research on feline genetics, behavior, ecology and epidemiology requires accurate data on cat population density and on components of the cat-human relationship affecting reproductive fitness, such as neutering and access to veterinary care. For this reason a number of investigators (Dorn et al., 1967; Dorn et al., 1968; Griffiths and Silverberg, 1975; Todd, in preparation) have conducted surveys of cat ownership in Britain and the United States using various methods. For the demographic survey I selected a rectangular region of 281 ha (1.08 sq mi) located adjacent to the University of Illinois campus. This area contained three distinct neighborhoods identified by consulting a zoning map. This classification was verified by direct visual inspection and by analysis of housing costs. The first neighborhood (168 ha, 0.65 sq mi) is zoned for multiple-family housing and contains numerous apartment buildings and rooming houses with some single-family dwellings. Many University students live in this area. The second neighborhood (79 ha, 0.30 sq mi) is zoned for 1- and 2-family housing, and it is inhabited by married students, faculty and others. The third neighborhood (34 ha, 0.13 sq mi), by far the most affluent, is zoned exclusively for single-family residences. It was of interest to determine whether these obvious differences between neighborhoods corresponded with differences in cat ownership.

Cats of Champaign were investigated in a separate survey designed to elicit information about population genetics for purposes of comparison with gene frequency data obtained in surveys at other localities in North America and worldwide. The two surveys did not overlap in time or in space. However, contiguity and homogeneity of the two cities and frequent human migration between them suggest the hypothesis that few if any differences in cat gene frequencies between the cities should be expected.

Domestic cat coat phenotypes, including color, hair length, and striping pattern have a simple genetic basis that makes population gene frequency surveys possible. All required data can be gathered in the course of simple visual inspection of each cat. Most relevant phenotypic characteristics are obvious and can be correctly assessed even when the animal is some distance away. For this reason the population genetics of the domestic cat are now quite well known worldwide, although many intriguing geographical distribution patterns still await explanation.

Cat coat phenotypes and their genetic determinants are reviewed by Robinson (1977) and by Todd (1971). The following brief description mentions loci discussed in this report.

Sex-linked orange is a locus on the X-chromosome. A male cat may have at most one copy of the orange allele, and if so he is an orange cat. A female homozygous for this allele is likewise orange, but the heterozygous condition produces the so-called tortoiseshell phenotype, in which patches of black or orange hair appear, or orange and black hairs are intermixed giving the coat a characteristic brindled appearance.

All other known coat loci in cats are autosomal. The agouti-nonagouti locus determines whether a cat will be striped or alternatively will show solid color (black or grey). A nonagouti *(aa)* cat is solid color. The nonagouti allele is recessive to the agouti alternative. Nonagouti and sex-linked orange interact epistatically; thus an orange cat will exhibit the striping pattern whether it has agouti or nonagouti alleles.

Two different types of tabby striping patterns occur frequently in North American and western European cats. The striped or mackerel tabby has thin, dark markings on a greyish-yellow background, while the blotched tabby, a much darker phenotype, exhibits light curved or lyre-shaped markings on a dark background. Blotched tabby cats $(t^b t^b)$ are homozygous for the recessive allele.

Maltese dilution, when present in homozygous form *(dd)*, results in a grey cat (or a cream-colored cat if orange alleles are present). Various shades may occur, but the coat color never approaches the deep black or rich orange of the non-dilute phenotype.

Many cats have piebald white spotting on their legs or sides, and in some animals these white patches are so extensive that the tabby or solid color is reduced to a few spots on the head or on the back. The dominant piebald allele *(S)* produces these varying degrees of white spotting. Genetic modifiers appear to influence the extent of white spotting in piebald cats.

A different locus, dominant white, also produces a white phenotype, but in this case the dominant *(W)* allele results in an all-white cat. Dominant white is generally a rare allele in cat populations in comparison with the other mutant alleles described above.

METHODS

Demographic Survey

I wished to survey not less than 1,000 households in the given area. A sample of roughly 1,000 names was obtained from the Urbana-Champaign telephone book as follows. Preliminary calculations indicated that in order to obtain a sample of the required size, 63 listings should be selected from each page of the book. These 63 listings included a sufficient number of addresses actually in the survey area to produce a total sample of 1,000 names. Addresses given in the listings were then checked on a city map, and a pencil mark made next to each residential listing for which the address fell within the designated geographical survey area.

Volunteers conducted the survey by telephone using a standard form (Appendix). Respondents' answers were recorded on this form by the caller.

Data were tabulated and analyzed using a computer program written by David J. Moriarty. Tests for significance of differences between ownership distributions in the different neighborhoods were performed by analyzing the corresponding two-way contingency tables (χ^2 statistic). A significance level of $\alpha = 0.05$ was used for all tests.

Population Genetics Survey

I walked or bicycled through all residential districts of the city, spending roughly equal amounts of time in each area. The neighborhoods visited consisted of many single-family dwellings with yards, a few apartment buildings, and some student housing. Almost all cats seen in the course of the survey appeared well-fed and well cared-for, and their degree of affiliation with humans seemed quite high. (Most animals were seen in yards, on porches, or in the windows of houses).

Each cat seen was scored for the following pairs of alleles: black (O^+) versus orange (O); agouti (a^+) versus nonagouti (a); striped tabby (t^+) versus blotched tabby (t^b); intense (d^+) versus dilute (d); piebald spotting (S) versus non-piebald (s^+); and dominant white (W) versus pigmented (W^+). Sex of animals seen was not scored, and maximum-likelihood estimation (Robinson, 1972) was used to calculate frequency of O. An effort was made to avoid including closely-related animals in that when mother-kitten groups or groups of sibs were encountered, one member of each group was randomly selected for analysis. Siamese $(C^s C^s)$ cats and Abyssinian tabbies (t^a-) were not included in the gene frequency calculations. (In addition to the sample of 228 cats used in these calculations I saw about 20 cats, mostly mongrels, and one mongrel Abyssinian tabby. The latter animal was calico [+/O, S_].)

The location of each cat observed was recorded in order to prevent inclusion of the same cat in the survey more than once. This information was also used to analyze the spatial distribution of the various phenotypes and to test whether particular phenotypes tended to be concentrated in particular areas of Champaign. To test for non-random distributions of cats having specified phenotypic traits, I divided the city in half and performed chisquare tests of association between phenotypes and locality; both north-south and east-west comparisons were made.

RESULTS

Demographic Survey

In all, 836 households responded (i.e., were reached by telephone and agreed to participate in the survey). This figure represents a 20% sample of the area. Of these households, 124 (14.8%) owned one or more cats. Cat population density was 4.5 cats/ha (1160 cats/sq mi). The average number of cats per cat-owning household was 2.02. Table 1 presents the frequency distribution of cats per household. Somewhat less than half (43.4%) of all cats had been neutered (Table 2). Females were more likely to be neutered than males. Cats owned by respondents were almost all mixed-breed (90%) with a few Siamese and Persian (Table 3). Most animals had been obtained from a friend or as gifts, were the offspring of another cat in the household, or had been adopted as strays (Table 4). A total of 72.6% of all cat-owning households surveyed used veterinary services. There had been 20 cat deaths during the period June 1974-May 1975 in the households surveyed, or a crude mortality rate of 8%. Many cats who died were hit by cars, and this was by far the most frequent cause of death (Table 5).

Cat ownership in the student neighborhood was significantly less than in either of the other two neighborhoods surveyed (Table 6): $\chi^2 = 6.7$ (2 d.f.), $P<0.05$. A total of 12.8% of respondents in the student neighborhood owned one or more cats, compared with 20.0% in the intermediate neighborhood zoned for 1- and 2-family housing and 19.2% in the third (most affluent) neighborhood. Estimated population densities were 4.6/ha (1180/sq mi), 4.8/ha (1250/sq mi), and 3.1/ha (800/sq mi) for the three neighborhoods respectively. Thus, while the lowest ownership rate occurred in the student neighnorhood, cat population density was nearly as high as in the intermediate neighborhood and higher than in the affluent neighborhood. The frequency distribution (and therefore the average number) of cats per cat-owning neighborhood, frequency of neutering, sex of cat, and veterinary usage did not differ significantly among the neighborhoods surveyed.

TABLE 1. Frequency Distribution of Cats Per Household (Aggregate Data).

Cats/household	0	1	2	3	4	5	6	7	8	9-13	14	15	16	>16
Households	712	70	27	15	3	4	2	0	1	0	1	0	1	0

TABLE 2. Sex and Neutering (aggregate Data).

	Male	Female		Total
Neutered	46	63	=	109
Whole	72	44	=	116
Total	118	107		225

(Sex and/or neutering of 26 cats was not reported)

TABLE 3. Breeds of Cats Surveyed (Aggregate Data).

Breed	Number
Mixed	225
Fancy	25
Siamese	17
Persian	7
Abyssinian	1
Not reported	1
TOTAL	251

TABLE 4. Sources of Cats Surveyed (Aggregate Data).

Source	Number
Friend	70
Bought	16
Gift	45
Humane Society	7
Offspring of other cat in household	53
Stray	43
Brought from out of state	8
Unknown	9

TABLE 5. Causes of Death (aggregate Data).

Cause	Deaths
Hit by car	7
Intestinal infection	2
Poisoning	2
Old age	2
Feline leukemia	2
Broken neck	1
Birth defects	1
Heart attack	1
Diabetes or kidney failure	1
Unknown	1

Population Genetics Survey

Allele frequency estimates obtained were qO = 0.32, qa = 0.78, qt^b = 0.32, qd = 0.45, ql = 0.35, pS = 0.27, and pW = 0.022 (Table 7). Most cats seen exhibited low to medium grade piebald spotting (Table 8). Champaign allele frequencies were in general agreement with those obtained for other Midwest U.S.A. populations (Table 9); of particular interest is the high frequency of sex-linked orange, which is also found elsewhere in the American Midwest but not in the rest of North America. Phenotypes were randomly associated, with the possible exception of orange-piebald (Table 10). Phenotype was randomly associated with locality within the city except that a highly significant excess of orange cats was found in south Champaign (Tables 11, 12).

Chisquare analyses of association between pairs of traits (Table 10) yielded no significant results. Significant associations would be expected either if a cat's phenotype were determined by nonrandom assortment of the component alleles or if particular combinations of alleles were favored by selection. That no such associations were found suggests that neither of these hypotheses is likely to hold for Champaign cats.

Chisquare tests of association between phenotype and locality (Table 11) revealed a significant concentration ($P<0.005$) of orange cats in south Champaign. No other significant north-south differences and no significant east-west differences in phenotype distribution within the city were found. Table 12 displays the observed phenotype distribution at this locus in north and south Champaign, with maximum likelihood estimates of qO and the fraction of males for individual and pooled samples. In south Champaign, an excess of orange animals appears to be present, with the estimated fraction of males nearly 0.7.

TABLE 6. Cat Ownership by Neighborhood.

	Neighborhood				
	1 (student)	2 (intermediate)	3 (affluent)		Total
Households owning at least one cat	77	37	10	=	124
Households owning no cats	522	148	42	=	712
Total	599	185	52		836

TABLE 7. Phenotype Data and Estimated Allele Frequencies for Cats of Champaign, Illinois.

Sex-linked orange

Black	Tortoiseshell	Orange	ML estimate of qO
130	35	52	0.32

Nonagouti

Agouti	Nonagouti	Est. qa
61	95	0.78

Tabby

Striped tabby	Blotched tabby	Est. qt^b
107	12	0.32

Maltese dilution

Intense	Dilute	Est. qd
171	44	0.45

Long hair

Short hair	Long hair	Est. ql
201	27	0.35

Piebald

Spotting absent or restricted	Piebald	Est. pS
116	101	0.27

Dominant white

Pigmented	White	Est. pW
217	11	0.022

TABLE 8. Distribution of Extent of Piebald Spotting in Cats in Champaign, Illinois. Scoring Method According to Dreux (1968).

Grade	1	2	3	4	5	6	7	8	9
Number of cats	13	16	20	18	11	7	8	4	4

TABLE 9. Comparison of Allele Frequencies in Champaign With Those in Other North American Cities.

City	qO	qa	qt^b	qd	ql	pS	qW	*Source*
Midwest U.S.A. populations:								
Champaign, Illinois	0.32	0.78	0.32	0.45	0.35	0.27	0.022	This paper
Chicago, Illinois	0.23	0.72	0.34	0.46	0.37	0.31	0.020	Todd 1969
St. Louis, Missouri	0.30	0.79	0.51	0.43	0.48	0.39	0.016	Dorn 1973
Columbus, Ohio	0.29	0.64	0.31	0.50	0.39	----	0.007	Tinney and Griesemer 1968
Crocker, Missouri	0.43	0.64	0.49	0.47	0.21	0.28	0.036	Todd (pers. comm.)
Other North American populations:								
Boston, Mass.	0.19	0.64	0.44	0.43	0.32	0.44	0.022	Todd 1964
Atlanta, Georgia	0.23	0.65	0.46	0.43	0.31	0.29	0.032	Todd 1969
Dallas, Texas	0.25	0.67	0.28	0.32	0.44	0.18	0.000	Gerdes and Sorenson 1971
Houston, Texas	0.25	0.69	0.29	0.29	0.35	0.24	0.005	Gerdes 1973
Mexico, D. F.	0.14	0.65	0.23	0.29	0.73	0.28	0.015	Todd (pers. comm.)

TABLE 10. Analysis of Two-way Interactions Between Phenotypes.

Phenotypes	χ^2	d.f.	p
Orange-dilute	0.04	2	$p > .05$
Orange-long hair	3.0	2	$p > .05$
Orange-piebald	6.5	2	$.05 > p > .025$
Nonagouti-dilute	0.03	1	$p > .05$
Nonagouti-long hair	0.2	1	$p > .05$
Nonagouti-piebald	0.2	2	$p > .05$
Tabby-piebald	0.2	1	$p > .05$
Dilute-long hair	0.1	1	$p > .05$
Dilute-piebald	0.7	2	$p > .05$
Long hair-piebald	2.9	1	$p > .05$

TABLE 11. Analysis of Two-way Interactions Between Phenotype and Within-city Geographical Location in Cats of Champaign.

Phenotype	Dimension	χ^2	d.f.	p
Orange	North-south	13.4*	2	$p<.005$
Orange	East-west	0.6	2	$p>.05$
Nonagouti	North-south	2.6	1	$p>.05$
Nonagouti	East-west	1.0	1	$p>.05$
Dilute	North-south	2.0	1	$p>.05$
Dilute	East-west	0.1	1	$p>.05$
Long hair	North-south	0.4	1	$p>.05$
Long hair	East-west	1.8	1	$p>.05$
Piebald	North-south	4.0	2	$p>.05$
Piebald	East-west	3.1	2	$p>.05$
Dominant white	North-south	0.1	1	$p>.05$
Dominant white	East-west	1.0	1	$p>.05$

TABLE 12. Phenotype Distribution at Sex-linked Orange Locus in North and South Champaign.

	Black	Tortoiseshell	Orange	ML est. of q0	ML est. of fraction male
North	66	16	11	0.20	0.47
South	64	19	41	0.40	0.68
Total	130	35	52	0.32	0.63

DISCUSSION

Demographic Survey

The student population in Urbana is a transient one, and while (as this survey indicates) students do frequently keep cats, it is often the case that landlords forbid pet ownership. Dormitory regulations and many apartment leases do not permit renters to keep cats and dogs. In addition, students may be unwilling to commit themselves to care for an animal for a variety of reasons. The ownership figure of 20% obtained from the (primarily) non-student districts should be used for comparison of Urbana with other residential localities.

Although fewer households in the student neighborhood own cats, cat density is almost as high in this neighborhood (4.6/ha) as in the intermediate neighborhood (4.8/ha) and greater than that is the affluent neighborhood (3.1/ha). Because the frequency distribution of cats per cat-owning household did not differ significantly among neighborhoods, the greater housing density in the student neighborhood is likely to be the factor that compensates for the lower rate of ownership.

Data of Table 4 suggest an immigration rate from out of state of at least 3.2% (8/251) per year. This figure is a lower bound because the categories "from friend," "gift" and "unknown" could also include some immigrants. In future surveys that gather both demographic and genetic data simultaneously, data like these could be used to calculate estimates of gene flow, a factor seldom measurable in the wild. Are observed allele frequency differences between populations consistent with various hypothetical amounts of gene flow? What is the maximum amount of gene flow that would allow observed gradients to maintain themselves? Answers to this question might result from future cat surveys, although effective population size would also need to be calculated in such analyses.

Another interesting question is the possible correlation of mortality with phenotype (controlling for sex). Respondents were not asked to specify the coat color phenotype of their cat, as it was felt that reports would often be imprecise. Therefore, the surveys reported here cannot shed light on this question, although it could be answered in future surveys in which known cats were followed for a period of time and recensused periodically.

Population Genetics Survey

Champaign cats, like other cats in the American

Midwest, exhibit high frequencies of sex-linked orange, suggesting a North American epicenter in southern Illinois, Missouri, or perhaps Arkansas. World cat populations, except those in the Far East, seldom exhibit such high frequencies of sex-linked orange. Champaign cats, like those found in other areas of the midwestern United States, appear to exhibit relatively high frequencies of the orange *(O)*, striped tabby *(t^+)*, and dilute *(d)* alleles compared to European values (Table 3; see Todd et al., 1975, for European data).

As mentioned above, cats seen in my survey appeared to be pets rather than strays or unwanted animals. Previous Midwestern surveys (Crocker, Chicago, Columbus and St. Louis) all dealt with "unwanted" individuals. My results are consistent with the results of these other surveys, suggesting that major regional trends in cat gene frequencies will be manifest whether pet or stray populations are studied.

A significant excess of orange cats in south Champaign and an apparent preponderance of male cats in this district (nearly 70%, if the maximum likelihood analysis is correct) may be interpreted in light of the fact that orange is sex-linked, meaning that since males are hemizygous a greater proportion of them exhibit the trait. Parallels to this situation may exist in other localities. Dreux and Legel (1973), for example, studying cats brought to a veterinary clinic in the Hague, Netherlands, found qO = 0.21 and fraction male = 0.64. Since a steep cline in qO is present in Western Europe (Dreux and Todd, 1974), this qO value, while relatively high for continental European populations, is not necessarily surprising. But in light of the high fraction of male cats in the sample and, since the data for south Champaign appear to exhibit a similar combination of high qO and high male fraction, possible relationships between these two parameters may be worth considering. A possible explanation is that orange cats, whatever their sex, might be naturally counterselected in the absence of human intervention, producing an excess of black animals and an excess of females in the adult stray population. According to this hypothesis, human intervention would reverse this trend, producing an excess of orange animals and an excess of males in the adult pet population. Metcalfe and Turner (1970), for instance, found that stray males in York, England tended to be black while males brought in by their owners tended to be orange. Although north and south Champaign appeared equivalent to me, unrecorded differences in, for example, the age structure or stability of the human populations could produce a between-neighborhood difference in the extent to which humans care for their cats.

A lack of association between phenotypes is not surprising; the single exception may simply reflect statistical variation expected when performing multiple chisquare analyses. On the other hand, the significant geographical concentration of orange cats could result from a temporary aggregation of males and from differential reproduction and/or survivorship. Human activity, including human selection, could affect all of these processes, especially the latter two.

SUMMARY

A survey of cat ownership and management in 836 households in three neighborhoods in Urbana, Illinois (U.S.A.) showed that neighborhoods differed significantly in cat ownership rate per household, but not in cat population density per hectare. Cat ownership in a student neighborhood was significantly less than in either of the other two neighborhoods. Almost three-quarters of all cat-owning households used veterinary services, and somewhat less than half of all cats had been neutered. Rates of birth, death and immigration were estimated.

Cats of Champaign, Illinois (U.S.A.) were surveyed in order to estimate frequencies of seven coat color or pattern alleles in this population. The Champaign frequencies found are similar to those reported from other localities in the midwestern United States. The high frequency of sex-linked orange at this locality confirms a trend suggested by these earlier surveys. Observed frequencies of particular combinations of phenotypic traits did not deviate significantly from expectations based on the population frequencies of individual traits. Traits were not only distributed randomly with respect to one another, but were also (with one exception) distributed randomly over different neighborhoods of the city. The sole exception to random geographical distribution occurred at the *orange* locus.

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LITERATURE CITED

Dorn, C. R. 1973. Cat gene frequencies in St. Louis. *Carnivore Genetic Newsletter* 2(5): 106-112.

Dorn, C. R., D. O. N. Taylor, and H. A. Hibbard. 1967. Epizootiologic characteristics of canine and feline leukemia and lymphoma. *American Journal of Veterinary Research* 28: 93-101.

Dorn, C. R., D. O. N. Taylor, R. Schneider, H. A. Hibbard, and M. R. Klauber. 1968. Survey of animal neoplasms in Alameda and Contra Costa counties, California. II. Cancer morbidity in dogs and cats from Alameda County. *Journal of the National Cancer Institute* 40: 307-318.

Dreux, Ph. 1968. Panachure chez le chat. *Carnivore Genetics Newsletter* 1(4): 64-65.

Dreux, Ph., and J. C. Legel. 1973. Gene frequencies in the cat population of the Hague (The Netherlands). *Journal of Heredity* 64: 337-339.

Dreux, Ph., and N. B. Todd. 1974. Clinal distribution of t^b and *O* alleles in European domestic cats. *Carnivore Genetics Newsletter* 2(7): 177-180.

Gerdes, R. A. 1973. Cat gene frequencies in five Texas communities. *Journal of Heredity* 64: 129-132.

Gerdes, R. A., and K. J. Sorenson. 1971. Cat gene frequencies in north Texas. *Carnivore Genetics Newsletter* 3(1): 26-28.

Griffiths, A. O., and A. Silverberg. 1975. Stray animals: Their impact on a community. *Modern Veterinary Practice* 56: 255-256.

Metcalfe, J. A., and J. R. G. Turner. 1971. Gene frequencies in the domestic cats of York: Evidence of selection. *Heredity* 26: 259-269.

Robinson, R. 1972. Mutant gene frequencies in cats of Cyprus. *Theoretical and Applied Genetics* 42: 293-296.

Robinson, R. 1977. *Genetics for Cat Breeders*. 2nd Edition. Pergamon Press, London.

Tinney, L. M., and R. A. Griesemer. 1968. Gene frequencies in the cats of Columbus, Ohio, U.S.A., and a comparison of northeast U.S. populations. *Carnivore Genetics Newsletter* 5: 96-99.

Todd, N. B. 1971. Gene frequencies in world cat populations and their relevance to research. Pp. 250-262, *In: Defining the Laboratory Animal*, National Research Council, Washington, D.C.

Todd, N. B., R. M. Fagen, and K. Fagen. 1975. Gene frequencies in Icelandic cats. *Heredity* 35: 172-183.

APPENDIX. CAT SURVEY QUESTIONNAIRE

By ______________________ Date ______________________

1. Name ______________________
2. Address ______________________
3. Any cats housed here during last 12 months? ______________
4. Number of cats in household during last 12 mo. (include deaths) ________
5. Number of people in household ______________________
6. For each cat (alive now or formerly alive) please indicate:

	CAT #1	CAT #2	CAT #3	CAT #4
Living now or died (L,D)				
Sex (M,F)				
Age (at death if D)				
Neutered (yes or no)				
Where spends time (mostly indoors, mostly outdoors, or some of each)				
How long at this address (mo.)				
Breed				
Where obtained				
(If dead or now ill): Cause of death or sacrifice, and/or nature of illness				
(If dead or now ill): Were tests for feline leukemia performed?				
Result of test (if known)				
(If patient at U of I): Cat's name and clinic ID				

IF MORE THAN 4 CATS, CONTINUE ON ANOTHER SHEET

7. Do/did your cat(s) receive veterinary checkups & care? ________

   if so, name of clinic or veterinarian ______________________
8. Food for cat(s) comes from: ______________________
9. Do the cat(s)' owner or owners spend more than two hours of the day in any particular building or buildings other than this residence? If so, where?

   ____

HOMOLOGOUS COAT COLOR VARIATION IN FELIS

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Among the more esoteric information on the various felid species has been the steady flow of reports of novel coat color variants. Although there are several notable exceptions, few of the reports are of great significance considered alone. Nevertheless, a systematic collation has revealed a pattern which conforms well with mammalian pigmentary genetics based upon experiments with laboratory rodents. That is, there is good reason for thinking that phenotypically similar color forms in both rodents and felids are genetic homologues.

HOMOLOGIZING COLOR MUTANTS

The concept of gene homology has long ceased to be mere speculation (Searle, 1968). The criteria for homology have been outlined elsewhere (Robinson, 1970, 1976) and need not be repeated here. However, the main gene loci and the mutants which may arise from them need to be detailed. The coat of most mammals is an agouti, commonly drab in color but sometimes pale or richly hued. A feature of agouti fur is that the hairs are sub-apically banded with yellow (the tip is black, followed by yellow, then black paling rapidly to pale blue as the pigment granules become progressively sparse).

The agouti coloration results from the backward slope of the hair exposing part of the agouti band, thus causing an intermingling of yellow and black tipping. Much of the variation is produced by the width of the band and the intensity of the yellow pigment. Many sandy agouti animals have a wide band without necessarily having an increase in the intensity of yellow. The felids are remarkable in possessing typical patterns of stripes, rosettes or spots superimposed upon the agouti. This characteristic felid melanoid pattern is independent of agouti.

Basically, six loci are responsible for the majority of mutant colors. In summary, these are agouti *(A)*, black pigmentation *(B)*, full expression of color *(C)*, dense pigmentation *(D)*, extension of black *(E)*, and dark-eyed *(P)*. The most frequently recurring mutant alleles arising at these loci will be described.

A. This locus produces the non-agouti gene *a* where the yellow agouti band is absent. Individual hairs are black tipped, paling rapidly to "blue" towards the skin. Phenotypically, non-agouti animals are self-black.

B. The locus for black pigmentation may mutate to an allele *b* producing brown or chocolate pigmentation. The self-chocolate phenotype is produced in combination with non-agouti (i.e., *aabb)*. The agouti form *(A-bb)* is usually a sandy agouti because of replacement of black ticking by brown. The eye may remain dark but the iris may be a lighter shade of brown and the pupil may glow a dull red in bright illumination.

C. It is possible for the *C* locus to produce three distinct forms of alleles. These are chinchilla (c^{ch}), acromelanic albinism (c^{h}), and complete albinism *(c)*. The locus is fundamental in the physiology of pigment production. The three forms represent progressive steps in the loss of pigmentation. Chinchilla animals typically lack yellow pigment or have it reduced to pale cream. The Rewa "white" tiger is a good example. Acromelanic animals usually have a white or light body with pigmented extremities. The Siamese cat is a fine example. Complete albinism is devoid of all pigment, the coat is white and the eyes are pink because the blood vessels are no longer obscured by pigment. The eyes of chinchillas may be light brown or blue and those of acromelanic albinism may be blue or red.

D. This locus frequently produces an allele *d* which results in a pale bluish phenotype. The eye color is normally unaffected, but the black of the coat is bluish while the yellow becomes cream. The dilution is due to a defect of the melanoblasts, so that the pigment is not fed smoothly into the growing hair shaft. The outcome is that the pigment is laid down in clumps with pigmentless sections. Light rays are consequently not absorbed as efficiently as normally and are more greatly scattered (as in "white" hairs). The optical effect is to dilute the intensity of the coat color.

E. The extension of black locus is so-named because a frequent mutant *e* produces a yellow phenotype, as if the black pigment "non-extended" throughout the coat. This mutant is commonly regarded as responsible for the yellow, red, or erythritic variants. The variation of intensity of yellow is due to independent polygenes.

P. This locus gives rise to a recurring allele *p* which produces a pink-eyed diluted phenotype. The eye color may vary from pink to dull red while the coat may vary from bluish-cream to yellowish with light ticking. The coat color is variable because the gene may dilute both black and yellow pigment differentially, usually the former more strongly than the latter.

Two other loci may be noted. An incompletely dominant gene *S* for white spotting is known in the domestic cat. The expression is variable, ranging from white noses and front paws to white areas on the body in the heterozygote *Ss*. The homozygote *(SS)* is more extensively marked with white. A similar gene has been reported for the lion and possibly for two other species (Table 1).

T. The domestic cat possesses another locus of particular interest. This locus has three alleles, each largely responsible for a different form of tabby. The first is Abyssinian tabby (T^{a}) where the melanoid pattern is restricted to the head, limbs, tail and lower flanks, *silvestris* or mackerel-type tabby *(T)*, with curving vertical stripes on the body, and blotched tabby (t^{b}), with whorls or spirals and some coalescence of pattern (extensive on occasion). The order of dominance is T^a to T to t^b. The mackerel pattern is taken as the genetic "wild type"; hence one mutant allele is dominant and the other recessive to type (Robinson, 1971).

The interesting aspect is that the three very different patterns are produced by alleles of a single locus. All three patterns vary so that polygenes are involved in determining the expression. The mackerel pattern varies in two directions: from a well-defined pattern to one which is diffuse or composed of fine stripes, or to one which is breaking up into short bars or spots; this is similar in general terms to the variation exhibited by the *silvestris-libyca* species complex (Weigel, 1961). The blotched pattern is especially variable, mainly in the direction of heavy bars or coalescence of markings.

It is noteworthy that a semi-inbred stock of laboratory cats has been observed in which the coalescence is extensive, producing large blotches or "slabs" of black pigmentation interspersed with agouti. Yet the mackerel allele assorting against this same genetic background produces a typical mackerel-type phenotype. The T alleles, therefore, appear to behave as switch genes, bringing into action different groups of modifying polygenes determining the expression of a particular melanoid pattern.

The Abyssinian allele T^a shows the least variation of tabby pattern, yet even here there is variation. Domestic cat fanciers have selected for minimal pattern, suppressing the vestigial markings on the stomach and lower flanks. The juvenile coat of the Abyssinian shows some spots on the stomach, and these fade or become less obvious as the cat matures. This is an interesting parallel with color changes shown by certain species which have a very restricted felid pattern as adults but are spotted as juveniles. It may be speculated that similar genes to T^a might exist in the jungle cat, puma or even the lion. However, the results of crosses between the species (see later) suggest that the presence of stripes or spots appear to be dominant to their absence. This is contrary to the dominant heredity of T^a in the domestic cat and must be regarded as grounds for caution. On the other hand, if T^a type genes are involved, there is no reason for these to necessarily behave as dominants. Different genes may be involved, apart from the fact that they would be manifested against a different (species) genetic background.

HYBRIDIZATION

Most felids seem capable of producing viable hybrids, although these may be partially or fully sterile (Gray, 1972; Robinson, 1976). However, the phenotypes of the hybrids are intriguing. The stripes of the tiger are a distinctive pattern among the larger felids since rosettes or spots appear to be the rule. The available data, although meager, imply that the tiger striping is "dominant" to the leopard-type spotting and to absence of pattern as found in the lion. Obvious stripes are present in the hybrids, although they may be less extensive, less well-formed, or broken up into spots for certain regions of the body. The fact that the striping is poorly expressed in the hybrids indicates that the tiger has a background for full expression while the leopard and lion do not.

The progeny from crosses of leopards and lions showed the spotted pattern of the former although attenuated. Similar results emerged from crosses between the leopard and puma. Both the lion and puma display a spotted pattern as cubs but not as adults. The ability to produce the pattern is evidently not absent, but is largely suppressed in the adult coat. The leopard may have introduced genes which counteracted the effects of the suppressors.

It is impossible to estimate how many genes are involved in the interspecies differences (striped versus spotted pattern, striped versus absence, or spotted versus absence). Because of the virtual lack of F_2 data, it is difficult to judge whether the effects are due to major genes, or simply polygenes. The few second generation young which have been produced indicate a sort of segregation of a relatively few genes.

DISCUSSION

Table 1 summarizes the variant colors reported in the literature. Full details, with supporting documentation, have been presented by Robinson (1976). The domestic cat has all but one of the colors and, where it has been possible to conduct breeding experiments, these have conformed with the generalized heredity discussed earlier.

The more recurrent variant is full black or melanism. The majority of cases are likely to be of the recessive non-agouti form, although it must be mentioned that dominant genes producing a black phenotype are known. In the domestic cat and leopard, the general hypothesis of recessive heredity of the black color is confirmed by breeding data. It is reasonable to posit that all solidly black variants are genetically non-agouti until proven otherwise.

The next most frequent mutant type is yellow, red or erythrism. The coat color is bright, distinctive, and not likely to be overlooked. Recessive heredity is likely to be the rule. It is interesting that those instances of coat color polymorphs among the felids have involved melanistic and erythritic morphs (Huxley, 1955).

It is remarkable that a mutant gene of this type is unknown in the domestic cat. The yellow cat is due to a sex-linked gene and the heterozygous female is characteristically parti-colored (tortoiseshell). It is worth stressing that should a phenotype be observed which is comparable to the tortoiseshell and occurring only in the female, then it is reasonable to conclude that a sex-linked gene is involved. This is legitimate even without recourse to breeding experiments, although it would be desirable to have such confirmatory evidence.

A fair number of chinchilla-type variants have been described and it is probable that the majority do represent this mutant. It is possible for the phenotype to vary between variants and between species, yet by within the general category. On the other hand, mutants at other loci can mimic chinchilla-type mutants; hence, there are grounds for caution. The "white" tigers of

Rewa are almost certainly chinchilla mutants by virtue of phenotype and recessive inheritance (Robinson, 1969).

TABLE 1. Probability of Homology of Mutant Phenotypes in Felis Species.

Species	Mutant gene									
	a	*b*	c^{ch}	c^{h}	*c*	*d*	*e*	*p*	*S*	*T*
Acynonyx jubatum (cheetah)	.	.	+	.	.	.	.	.	.	C
Felis bengalensis (leopard cat)	+	.	.	.	.	.	.	.	.	.
Felis canadensis (Canadian lynx)	.	.	.	.	.	+	+	.	.	C
Felis caracul (caracul)	+	.	.	.	.	.	?	.	.	.
Felis chaus (jungle cat)	+	.	.	.	.	.	.	.	?	.
Felis colocolo (pampas cat)	+	.	.	.	.	.	.	.	.	.
Felis concolor (puma)	+	.	.	.	+	.	+	.	.	.
Felis domesticus (domestic cat)	++	++	++	++	+	++	.	+	++	C
Felis geoffroyi (Geoffroy's cat)	+	.	.	.	.	.	.	.	.	.
Felis jagouaroundi (jaquarondi)	.	.	+	.	.	.	+	.	.	.
Felis pardalis (ocelot)	.	.	.	.	.	.	+	.	.	.
Felis rufus (bobcat)	+	.	?	.	+	+	+	.	?	.
Felis serval (serval)	+	.	.	.		.	.	.	.	C
Felis silvestris (European wild cat)	.	.	+	.	.	.	.	.	.	.
Felis temmincki (Temminck's cat)	+	.	.	.	.	.	.	.	.	.
Panthera leo (lion)	.	.	+	.	.	.	+	.	+	.
Panthera onca (jaguar)	+	.	.	.	.	.	.	.	.	.
Panthera pardus (leopard)	++	.	+	.	+	.	+	.	.	C
Panthera tigris (tiger)	+	.	++	.	+	.	+	.	.	.

KEY: Degree of homology is indicated as follows:

++ almost certain, + probable, and ? possible.
C under *T* means a major change of the typical Felid spotted pattern.
See text for details.

Complete albinism (pink or red eyes, white coat) has been reported for several species. This is a distinctive form and is inherited as a recessive in every species for which breeding data are forthcoming. It is not legitimate to call any white-coated animal an albino unless the eyes are unpigmented. Blue or brown-eyed white mutants are known. These are not albinos and may be inherited as recessive or dominant, often the latter.

Any variants with drab, pale or faded coats may be referred to as dilute forms. If the eyes are dark, they could well be *d*-type mutants; if the eyes are red or ruby, they could be *p*-type mutants. Unlike the variant forms described earlier, it is difficult to be as confident of the genetic homology of pale forms.

The Felid melanoid pattern is reported to vary for a few species. The most well-known situation is that of the domestic cat. However, there is also the almost equally well-known case of the striped and blotched cheetah. This variant was given species status (*A. rex*) before it was appreciated that the form was probably nothing more than genetic variation. Marked increases in amount of melanoid pattern has been noted for the leopard, with fusion of spots and "nigrescent" forms. In the serval (*F. serval*) there is the variation between the so-called serval and servaline grades of pattern. Little appears to be known regarding the amount of variation, but if it is saltational it could be monogenically determined.

Although it is appreciated that it is impossible to tackle the question experimentally at this time, it is proposed that the felid melanoid pattern is primarily governed by a single locus. This concept is prompted by the situation for the domestic cat where alleles of a single locus control three distinctly different patterns. It is supported by the basic unity of the pattern between all members of the felid group of species (Weigel, 1961). The implication is that the pattern is primordial, being subtly modified to suit the evolutionary needs of different species. The single locus concept has the merit of being simple, for it is difficult to conceive that such stability could result from the heredity of more than a few major genes. The fewer, the better, from an evolutionary standpoint (Robinson, 1976).

It may be noted that the felid melanoid pattern, or a counterpart thereof, is expressed in a number of fairly closely related groups, namely, in certain hyenids (particularly) and viverrids, and even procyonids (if the characteristic banded tail is taken either as a nascent or vestigial pattern). This could mean either parallel or convergent evolution or that the pattern is even more primordial, stemming from an ancestor remote but common to these groups of mammals. The interesting point may be made that the melanoid pattern appears to have attained its highest expression and diversity among the felids. This aspect has been exhaustively treated by Weigel (1961). It would be satisfactory to be able to say that the pattern (obviously complementary in these species to the ubiquitous agouti coloration; Robinson, 1970b) is due to a single complex locus which behaves as a switch gene. Admittedly, firm genetic evidence for the proposition is not available at this moment, and very probably will not be forthcoming for some time; but the expression and genetic behavior of the pattern (tabby) in the domestic cat is certainly relevant and is a strong pointer in this direction. From a heuristic viewpoint, it is proposed that the melanoid pattern is primordial, functioning as concealment or camouflage for cubs or adults as befitting predatory species. This does not necessarily imply that all such species must possess the pattern. Some may have lost the pertinent alleles or have gained suppressor genes as indicated by the results of interspecies hybridization.

LITERATURE CITED

Gray, A. P. 1972. *Mammalian Hybrids*. Commonwealth Agricultural Bureaux, Farnham Royal.

Huxley, J. S. 1955. Morphism and evolution. *Heredity* 9: 1-52.

Robinson, R. 1969. The white tigers of Rewa and gene homology in the Felidae. *Genetica* 40: 198-200.

__________. 1970a. Inheritance of the black form of the leopard. *Genetica* 41: 190-197.

__________. 1970b. Homologous mutants in mammalian coat colour variation. *Proceedings of the Symposium of the Zoological Society of London* 26: 251-269.

__________. 1971. *Genetics for Cat Breeders*. Pergamon Press, London.

__________. 1976. Homologous genetic variation in the Felidae. *Genetica* 46: 1-31.

Searle, A. G. 1968. *Comparative Genetics of Coat Colour in Mammals*. Logos Press, London.

Weigel, I. 1961. Das Fellmuster der Wildebenden Katzenarten und der Hauskatze in vergleichender und stammesgeschichtlicher Hinsicht. *Saugetierkundliche Mitteilungen* (Supplement) 9: 120 pp.

THE EVOLUTIONARY SYSTEMATICS OF LIVING FELIDAE: PRESENT STATUS AND CURRENT PROBLEMS

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Present knowledge of the fossil history of the living cat species was outlined in the Third International Cat Conference in 1974 (Hemmer, 1976a). Since then enough new material has accumulated to attempt a new synopsis on the evolutionary systematics of the living Felidae.

The history of modern felid classification in the first half of this century is mainly the work of one man, the English mammalogist Pocock. His many papers published between 1907 and 1951 provided the basis for all later systematic and taxonomic investigations of this carnivore family. Pocock's studies employed such diverse characters as skin color and pattern, morphology of the ears, rhinarium and feet, and osteology (mainly of the skull). On the whole his statements on cat systematics are purely morphological.

Other mammalogists have made important contributions on morphology. In 1923 Sonntag studied the comparative anatomy of the tongue in several species. Lonnberg (1926) partially grouped recent cats according to the structure of the anterior portion of the zygomatic arch, using some cats from eastern Asia. Both Cabrera (1940) and Schwanger (1936, 1941) contributed further substantial considerations. The era of pure morphologic research in cat systematics ended with the studies of Haltenorth on cranial characters of large cats (1936, 1937) and on the evolutionary systematics of some species commonly assigned to the genus *Felis* in the proper sense (1953). Weigel's (1961) later work on skin pattern and color of the Felidae has been the only one based entirely on morphological characters and was of great significance for the knowledge of the evolution of living cat species.

The use of ethological characters began in 1950 with the first publication of Leyhausen. Further work by Leyhausen and others show the advantages and limits of behavioral work for classification in felids. At the beginning of this new era, Leyhausen as well as the author of this synopsis promoted the integrative application of character complexes from morphology, ethology and physiology. The chromosomal studies of Wurster-Hill (1973) and others has opened a new field in the last decade. While biochemical research does not yet play an important role for felids, physiologically relevant differences were found by the author between species groups concerning the gestation period and postnatal development, and reported at the 1974 cat conference (Hemmer, 1976a).

Besides the research into cat evolutionary systematics, most of the zoologists and paleontologists studying felid relationships have discussed taxonomic problems. In this connection it has to be stressed that only systematics deals with the evolutionary events, phylogenetical radiations, or relationships between two or more forms compared with each other. Taxonomy, on the other hand, arises from man's drive to classify everything he observes in nature into fixed categories, i.e., to arrange the results of dynamic processes, such as evolution, into static units which is impossible when complete consistency is the aim.

The best example for this in the case of cats is the basic question: What has to be called a cat? While zoologists usually classified the Madagassian fossa *Cryptoprocta ferox* not in the cat family, but in the viverrids, the paleontologists De Beaumont (1964) and Thenius (1967) placed this species as the most conservative member of recent cats. De Beaumont showed that *Cryptoprocta ferox* is a descendant of the Early Tertiary proailurines which were the basic group in the evolution of the more modern cats. This group which unites felid and viverrid characters could be classified with the Viverridae by common symplesiomorphic characters as well as with the Felidae by synapomorphic, typical felid characters; it could also claim to be ranked as a separate family, an intermediate group between the other two. All three possibilities have been realized by different discussants in recent decades. Therefore, the position of *Cryptoprocta* concerning evolutionary systematics is quite clear, while concerning the much less important and man-made taxonomy it is not. For this reason only species names are used in the following to avoid disputable generic names.

The cheetah *(jubatus)* has hitherto been assigned by all zoologists and paleontologists to an isolated position with regard to the other modern cats (e.g., Pocock, 1917c; Haltenorth, 1937; Weigel, 1961; De Beaumont, 1964; Hemmer, 1966; Thenius, 1967). This species has a puzzling combination of primitive, plesiomorphic and highly specialized, apomorphic characters mainly related to its special adaptations as a high-speed sprinter (Pocock, 1916d; Hemmer, 1966). Therefore, its systematic relationship with other species must consider its less or nonadaptive characters. The cheetah has the same karyotypic pattern as the puma *(concolor)*, the leopard cat *(bengalensis)*, and the fishing cat *(Viverrinus)* (Wurster-Hill, 1973). Unfortunately we do not have information given by banding patterns for all these species. The relatively long gestation period of the cheetah corresponds to that of all other large cats and most of the South American species, whereas the leopard cat and the fishing cat share a relatively short gestation with the wild cat, the domestic cat and their relatives, and the lynxes (Hemmer, 1976b). The cheetah's threatening posture is the same as in the pantherines (Leyhausen, 1973); but the situation of the puma is not known well enough in this respect to be fully comparable. Plucking intensity is less than in the pantherines and puma and resembles that shown by most of the smaller Old World species (Leyhausen, 1973). The combination of other ethological characters similarly shows no close relationship to one species or species group (Leyhausen, 1956; Hemmer, 1966). The tongue has its own type of papillae combination and forms (Sonntag, 1923). All the information now available indicates that the cheetah may have originated closer to other recent cat groups than previously thought, coming from some early radiation which gave rise to other modern cat lines. The longitudinal grooves on the canines typical for most modern cats may be completely lacking in the cheetah (Schmid, 1940). They are usually faintly indicated on the upper or lower canines alone or even on only one of the four canines. They are seldom marked on all teeth. A similar variability exists in the plump canines of pumas, where in some cases the grooves are lacking and in others are only weakly developed. The situation in golden cats *(temmincki)* is similar. As the lack of these grooves is a character found in most Tertiary felid groups as well as the *Pseudailurus* group (as a forerunner of the modern cats), the radiation leading to the cheetah, puma and golden cat lines obviously took place at least as early as in the Miocene (unless this lack has not redeveloped independently in all these lines).

The systematic position of the puma *(concolor)* has been much disputed in the past. Pocock (1917c) showed its closer relationship to the small cat species than to the pantherines by the anatomy of the hyoidean apparatus. According to him the feet resemble more those of Geoffroy's cat *(geoffroyi)*, jaguarundi *(yagouaroundi)*, fishing cat *(viverrinus)* and wildcat *(silvestris)* and do not conform to the type found in the pantherines. The same is true for the morphology of the rhinarium. Lonnberg (1926) pointed out a great craniologic resemblance between the golden cats and the puma. On the other hand, Haltenorth (1937) saw the puma as closely related to the pantherines *(leo, pardus, onca, tigris, uncia)* through its cranial morphology. Leyhausen (1950, 1956) described behavioral characters which distinguish this species from the pantherines just as did the morphological characters found by Pocock. Weigel (1961) held that the skin pattern of young pumas was very near the basic pattern type of modern cats and arranged the puma phylogenetically between the pantherine line and a line leading to the southeast Asian and South American cats. Hemmer (1966) emphasized that the puma is distinct from the pantherines by summarizing the different characters known to date, but mentioned a resemblance in vocalization to the tiger *(tigris)* and the snow leopard *(uncia)* on one hand and to the cheetah on the other. Wurster-Hill (1973) listed the karyotypic conformity with the cheetah, leopard cat and fishing cat and dissimilarity to the pantherines. Finally Leyhausen (1973) classified the puma without any substantiation in a common genus with the golden cats *(temmincki, tristis, aurata)* and the caracal *(caracal)* but at the same time pointed out the different plucking intensity which ranks the puma in a different species group than the golden cats and the caracal. Compared with primitive canine morphology suggesting a branching off of the puma line at an early stage of cat evolution, as is the case for the cheetah and the golden cat lines, the similarities between the puma and the golden cat seems to be merely common primitive, symplesiomorphic characters. This may also be true for the resemblance of the undifferentiated os penis of the puma and the pantherines (Kratochvil, 1976). To answer the question of whether the puma came from the same evolutionary branch as the golden cats and cheetahs or whether the cheetah or the golden cats separately branched off later on, a knowledge of the homology or parallelism of the karyotypic situation in the puma and cheetah as well as the derivative possibilities between puma and golden cat karyotypes must be gained.

In view of the interpretation of characters connecting golden cats and puma as symplesiomorphic, the question now arises whether the characters connecting the golden cat species themselves are not also merely common primitive ones which indicate nothing about a nearer relationship with one another than with other modern cat lines. It seems to be quite clear from a biogeographical viewpoint that the separation of the African species *aurata* and the Asian species *temmincki,* both of which inhabit tropical forested areas, took place at a time when there was a connection between the rain forests of the two continents, which from the end of the Miocene was broken down by steppe and savannah regions. The phylogenetic splitting of the golden cat has to be dated back into the Miocene and the *Pseudailurus* evolutionary level (Thenius, 1967). This result has already been derived above for the golden cat-puma-cheetah radiation on the basis of the canine morphology. It is noteworthy in this respect that Weigel (1961) argued that the pattern of one of the golden cat species cannot be derived from the other clearly and convincingly.

The Chinese *tristis* cat has a spotted skin resembling the ocelot pattern, while the normal *temmincki* cat is more uniformly colored. Pocock (1932) held that the only known skins and mandible belonging to the golden cat are a patterned form. Weigel (1961) disputed this and classified the *tristis* cat nearer to the leopard cat *bengalensis*. Leyhausen (1973) placed it without argument as a separate species within the golden cat group. Information now available points more to the relationship with the Asian golden cat than with the leopard cat, but whether it is a separate species or not cannot be said with certainty at present.

Another question concerns the Bornean red cat *badia*. Pocock (1917, 1932) published the only facts on this species and described the skull and external morphology. Externally this cat looks exactly like a small Asian golden cat in its color and skin pattern as well as in the morphology of the feet, whereas cranial characters seem to be more like those of the marbled cat *marmorata*. Thus Pocock (1917c) first classified this species with the marbled cat into one genus, then created a separate genus for it. Later studies pointed to the fact that alterations in cranial proportions between *temmincki* and *badia* may be due only to allometric-size relations and not to real differences in skull construction, and therefore united this species with the golden cats (e.g., Weigel, 1961). Finally, Leyhausen (1973) classified the Bornean red cat anew with the marbled cat, but gave no new reasons for doing so. Some research on the skull allometries has yet to be done. Nothing is at present known about this cat apart from morphological characters.

When discussing the problem of the Bornean red cat, Haltenorth (1953) proposed to unite this species with the golden cats and the marbled cat *(marmorata)* in one genus by their common type of skull structure. Weigel (1961), on the other hand, related the marbled cat to the leopard cat *(bengalensis)* and Petzsch (1968) joined it with the clouded leopard *(nebulosa)*. Recently Wurster-Hill and Meritt (1974) published the banding pattern of the marbled cat's chromosomes. They found a pattern identical to that of the tiger *(tigris)*. The latter species has a distinctive B 4 chromosome in common with the lion which can be "envisioned as a pericentric inversion of the B 4 chromosome that occurs in all the other species" hitherto studied (Wursterhill and Gray, 1973). Therefore, the marbled cat clearly belongs to the pantherine line. According to Pocock (1932), its feet also closely resemble those of the pantherines and especially those of the clouded leopard. Studies on gestation period and behavior by Rosenthal and Hemmer (in preparation) also relate the marbled cat to a primitive level of pantherine evolution.

The evolutionary line of the pantherines themselves is the best known in the felids up to date (Hemmer, 1966, 1968, 1974b). The last radiation in this group led to the three closely related species of lion *(leo)*, leopard *(pardus)* and jaguar *(onca)* in the early Pleistocene era some two million years ago (Hemmer, 1971, 1974b, 1976a). The lines to the predecessor of these species, to the tiger and perhaps to the snow-leopard *(uncia)*, too, obviously came from another and earlier branch of this stem. The snow leopard may have split off even earlier, in a branch giving rise to its line and the line of the clouded leopard. Summing up all morphological, ethological and physiological characters, the snow leopard mediates between the clouded leopard and the tiger

(Hemmer, 1966, 1968). Another possible interpretation is that one geographical radiation led to the clouded leopard line in southeast Asia, to the snow leopard line in the central Asian mountain regions, and to the tiger line in northern Asia, where the basic population of the jaguar-leopard-lion line may have split away to North America. Further paleontological studies should help to clarify the real succession of radiations and the evolutionary and primary dispersal centers of the individual species. New knowledge on the marbled cat suggests the origin of this species is in the first radiation within the pantherine stem that separates it from the clouded leopard line or from the basic line to all later radiations within this group.

The pantherine line originally seemed to be related at least to the line leading to Temminck's golden cat, since both have a F 3 chromosome (Wurster-Hill and Gray, 1973). Both African and Asian golden cats apparently have something in common with the ocelot line, too. Van Mensch and Van Bree (1969) discuss in detail the relation pointed out by Pocock (1907) in skull and skin characters. These authors found *temmincki* in some respects intermediate to *aurata* and *pardalis,* while in others *temmincki* more related to *aurata* but clearly distinct from *pardalis, pardalis* closer to *aurata* in two cranial characters than to *temmincki* and in one such feature *pardalis* intermediate to *aurata* and *temmincki.* Blonk (1963) mentioned the smell of *aurata* to be quite like that of *pardalis.* With a reduction of chromosome number to 36, the karyotypic pattern divides the ocelot line from both the African and Asian golden cats. On the whole, this line and the golden cats seem to have originated in one geographic radiation, possibly the same one which gave rise to the pantherine line in a fourth region of Eurasia. The ocelot line itself later split into two very closely related species, the ocelot itself *(pardalis)* and the margay *(wiedi).* These two forms have many common characters in morphology as well as the synapomorphic karyotypic pattern separating them from all other cats (Pocock, 1917; Schwangart, 1941; Weigel, 1961; Wurster-Hill, 1973; Robinson, 1976).

Leyhausen (1963, 1973) and Geisler, Gropp, Leyhausen and Tonkin (1968) classified another small South American cat variously called little spotted cat, ocelot cat or oncilla *(tigrinus)* with the ocelot and the margay. At the same time, on the basis of a comprehensive discussion of former mistakes in the classification of South American spotted cats, Leyhausen posed the question whether there may be several partially sympatric species concealed under the name *tigrinus.* Extensive studies on populational variability and breeding experiments with the three types of little spotted cats separated by Leyhausen will be necessary to throw light on this question. In any case, these cats show a high variability including specimens looking like leopard cats as well as ones looking like margays. Nevertheless, Leyhausen's conclusion of a close relationship existing between this form and the margay and ocelot cannot be maintained in light of the information available on different characters either for all little spotted cats if they are only one species or at least for one of them if it may really prove that more than one species exists. *Tigrinus* certainly shares the derived chromosomal number with *pardalis* and *wiedi* - 36 against 38 in other felid species. But the same number by no means implies the same karyotypic pattern (e.g., Wurster-Hill, 1973). While the ocelot and the margay have one pair of acrocentric F group chromosomes and three pairs of D group chromosomes, the little spotted cat as well as Geoffroy's cat *(geoffroyi)* and the pampas cat *(pajeros)* have no F chromosomes, but possess four pairs of D chromosomes (Wurster, 1969). In comparison with other cats both lines have three pairs of C chromosomes in common. According to Wurster-Hill and Gray (1973), the C 3 chromosome "can be considered to be the product of a tandem fusion" of an F 2 and an F 3 chromosome, as present in the Asian golden cat and the pantherines. So either the karyotypic pattern of the *pardalis* group evolved independently of the *tigrinus* group pattern by "fusion of one pair of acrocentrics with one pair of D group chromosomes," as indicated by Wurster (1969), or a D group chromosome in the ocelot line changed in some way to an acrocentric chromosome on the basis of the little spotted cat's karyotype. Perhaps banding pattern studies could help to clarify this problem.

Pocock (1917b) showed that the ocelot-margay-group on the one hand and the little spotted cat-Geoffroy's cat-kodkod group on the other are markedly different in their morphological characters. Schwangart (1941) and other authors also pointed out differences in the neck hair, but doubted their systematic value. The species *tigrinus, geoffroyi* and *guigna* seem to be an example of geographical speciation with allopatric distributions if they have full species character at all. The skin pattern of the northern races of Geoffroy's cat is similar to the pattern of the little spotted cat living in the forested parts of northern South America, and the Chilenian kodkod has the same dotted pattern found in the *salinarum* subspecies of Geoffroy's cat. In all three forms melanism occurs very frequently. The phylogenetic origin of this group, which has the same relative length of gestation period as the species of the ocelot group, the pantherines, the puma and the cheetah (Hemmer, 1976b) and the same intensity of plucking behavior as the pantherines and the puma (Leyhausen, 1973), appears to be near the root of the pantherines and Timminck's golden cat. Originally they shared the F2 and F3 chromosomes which fused to the C 3 chromosome (Wurster-Hill and Gray, 1973).

The identical karyotypic pattern shows that the pampas cat *(pajeros)* also belongs to the *tigrinus* line (Wurster-Hill and Gray, 1973). Pocock (1917b) supposed its affinities with this group, Allen (1919) pointed to some cranial similarity with *geoffroyi,* Weigel (1961) placed it near the leopard, the ocelot, and little spotted cat group by its skin pattern. Presumably *pajeros* originated in an earlier branch of the *tigrinus* line, because it occurs sympatrically with forms of the later *tigrinus-geoffroyi-guigna* radiation. The mountain race of the pampas cat was sometimes confused with another species, the Andean cat *(jacobita).* The relationships of this form are obscure and nothing seems to be known of living specimens. Schwangart (1941) classified it with the pampas cat, and the skin pattern induced Weigel (1961) to relate it in some way to a pattern group with the leopard cat line, the little spotted cat line, and the ocelot lines. Faunal relationships between the Puna center as the distributional area of *jacobita* and the Patagonian, Monte, Pampa, Uruguay and Chaco dispersal centers of terrestrial vertebrates (Muller, 1973) may also possibly point to *pajeros* relations of this species.

Compared with other felids the jaguarundi *(yagouaroundi)*, as the last South American small cat, is aberrant in many characters. Pocock (1917b, 1941) classified it with the *tigrinus* line of South American cats and found the skull to some degree comparable with that of the pampas cat; Schwangart (1941) also mentioned a similar palatal bone to other small South American cat species and even discussed the possibility of viverrid relations to the jaguarundi. A similarity to viverrids in the hair, i.e., a strong banding in the brownish color type of this color-polymorphous species, may be due to convergent evolution. Weigel (1961) found no possibility of relating the jaguarundi by its fully reduced skin pattern to any other cat group. The anatomy of the tongue shows close resemblance to the situation in the puma (Sonntag, 1923). In the karyotypic pattern *yagouaroundi* is also quite isolated, being the only species having no F group chromosomes, but five pairs of E group chromosomes. Its E 4 chromosome is similar to that of *bengalensis* and *viverrinus* (Wurster-Hill and Gray, 1973). The puma and the cheetah correspond in their karyotype to the two latter species (Wurster-Hill, 1973). The length of the gestation period does not link the jaguarundi with the other small South American cats of the *pardalis* and *tigrinus* lines, in which it lasts about one week longer at the same body weight level, but rather mediates the leopard cat group and other Old World felids with even shorter gestations (Hemmer, 1976b). Schneider (1932) observed a jaguarundi performance of the gesture of Flehmen with a somewhat hanging tongue as in the puma and the tiger. Observations made by the author showed the same variability of this gesture found in the puma. Leyhausen (1956, 1973) described similarities to the puma in some behavioral characters as group-specific in felids, and some resemblance to the puma's staccato, chuckle-like (not "Prusten") vocalization suggest affinities. The available information indicates some relationship of the jaguarundi with the puma by either originating in the same basic radiation (if the common characters are symplesiomorphic ones), or a later branching off from the puma line (if the common characters are synapomorphic).

Chromosomal studies (Wurster-Hill, 1973) point to some basic relationship between the puma, cheetah, and leopard cat lines. In the last, characterized by a sum of external and cranial characters, the three species of leopard cat *(bengalensis)*, rusty-spotted cat *(rubiginosus)* and fishing cat *(viverrinus)* seem to be closely related (e.g., Pocock, 1939). The same anatomical characters of the tongue (Sonntag, 1923) and the same karyotype (Wurster-Hill and Gray, 1973) were found for *bengalensis* and *viverrinus*, although these features have not yet been studied for *rubiginosus*. In addition, all three species have the same type of skin pattern (Weigel, 1961). Obviously, they originated in one radiation.

According to Pocock (1932), the flat-headed cat *(planiceps)* is closely related to these three species, judging from the structure of its skull. Its teeth are well differentiated from those of all other cats by the extreme development of the P_3, which seems to correlate to its habit of eating fish and other marine animals. The morphology of the feet closely resembles that of the Bornean red cat *(badia)* (Pocock, 1932). Its strongly contrasted white and colored face markings resemble to some extent the markings of the Asian golden cats, but otherwise the head pattern is like that of the rusty-spotted cat. It is nearer to the pattern of the *bengalensis* group in detail while the golden cat's face markings place the latter species between the *bengalensis'* group on one side and the pantherine line and the South American spotted cats on the other. Weigel (1961) found no other characters of the skin pattern in common between the flat-headed cat and the leopard cat group. On the whole, the information hitherto available points to some relationship of *planiceps* to the *bengalensis-rubiginosus-viverrinus* line, indicating a branching off in an earlier radiation of this phylogenetic line.

The same could be true for the Iriomote cat *(iriomotensis)* described 10 years ago by Imaizumi (1967), who held this species to be related to the common ancestor of the Old and New World cats. Petzsch (1970) disputed any close relationship to South American species and arranged the Iriomote cat with the leopard cat line, as clearly supported by the facial markings. Leyhausen (1973) classified this species with the latter group also, but suggested that it might be an intermediate form between the leopard cat group (with which it has most characters in common), the marbled cat, and the golden cats. As the leopard cat line seems to be related in an early radiation of modern cat groups to the golden cats, especially by common ethological characters (Leyhausen, 1973), such a situation would locate the origin of the Iriomote cat in an older radiation than that which gave way to the species *bengalensis, rubiginosis* and *viverrinus* (perhaps in the same radiation leading to the flat-headed cat). Glass and Todd (1977), however, discussed the possibility of *iriomotensis* being merely a small island population of *bengalensis* "subjected to extreme selective pressures with the attendant possibility of genetic drift."

The last group to be discussed is the line ultimately leading to the domestic cat. It is characterized by a karyotypic pattern having an F 1 and an F 2 chromosome in common (Wurster-Hill and Gray, 1973). The relatively short gestation period relates it to the leopard cat group (Hemmer, 1976b). Central representatives of this line are the European, African and Asian wild cats and the domestic cat on the one hand and the lynxes on the other. The situation in the wild cat group was reviewed by the author when discussing the classification of the sand cat *(margarita)* (Hemmer, 1974a; Hemmer et al., 1976). One geographical radiation seems to have given rise to the species *chaus, bieti, margarita* and to the *silvestris* line which ultimately radiated into the three form groups of the European wild cat *(silvestris)*, the Asian steppe cat *(ornata)* and the African wild cat *(lybica)* (which have subspecific or semispecific status).[1] The sand cat *(margarita)* seems to mediate between the latter forms and the jungle cat *(chaus)*, which was formerly held to be further away by accentuation of its special adaptive characters (Haltenorth, 1953; Schauenberg, 1974; discussion in Hemmer et al., 1976). Our knowledge on the Chinese desert cat *(bieti)* is limited to some morphological characters (Lonnberg, 1926; Haltenorth, 1953), so that special statements on a possibly closer relationship with one of the other species of this

[1] For these groups, morphologically intermediate or transitional forms were shown by Haltenorth (1953) to exist in the Mediterranean Islands *(silvestris* group - *lybica* group) and in the north of the Arabian Peninsula *(lybica* group - *ornata* group).

group cannot yet be made. The use of the os penis morphology (Kratochvil, 1976) does not seem to be advocable for the systematics in this group, when looking on the high variability of this character in the domestic cat (Kratochvil and Kratochvil, 1976).

Most of the morphological and ethological characters of the black-footed cat *(nigripes)* are in accordance with the interpretation which originates it in the same radiation as the sand cat, wild cat, and jungle cat (Hemmer, 1974a). On the other hand, the relative gestation period is somewhat longer in the black-footed cat than in the other species (Leyhausen and Tonkin, 1966; Hemmer, 1976b; Schuerer, in press), perhaps indicating a somewhat more primitive (if not specifically aberrant) condition. Thus, perhaps the branching off of *nigripes* from the relevant phylogenetic stem may also have taken place at an earlier radiation.

We have to look for the division of the *silvestris, lynx* and *manul* branches in such an early radiation, presumably in the Pliocene. The wild cat group and the lynxes have morphological (Weigel, 1961) as well as ethological (Leyhausen, 1956) characters in common, and the Pallas' cat *(manul)* takes an intermediate position between these two groups (Schwangart, 1936; Weigel, 1961; Heran, 1967; Hemmer, 1974a). Later geographical radiation within the lynxes led to the modern forms *pardinus, lynx, canadensis* and *rufus*, the taxonomic status of which is disputed at least for the first three forms. A decision on their subspecific, semispecific, or specific rank should be possible with breeding experiments. The spreading of primitive lynxes over Eurasia and North America took place at the end of the Pliocene, while "the separation of some speciation centers in the Middle Pleistocene by the glacial ecological events apparently led to the recent species" (Hemmer, 1976a).

For decades the caracal *(caracal)* was classified with the lynxes, then Leyhausen (1973) united it with the golden cats and the puma in one genus, although gave no substantiation for doing so. This placement is surely not tenable, as the banding pattern of the chromosomes show: each of these species belongs to a different chromosomal group (Wurster-Hill, 1973; Wurster-Hill and Gray, 1973). The banding pattern ranks the caracal rather with the hitherto studied species of the wild cat line and, therefore, also with the lynx group as formerly supposed. In the anatomy of its tongue it is also near the wild cat and the domestic cat (Sonntag, 1923). In plesiomorphic cranial characters the caracal approaches the puma and golden cat (Lonnberg, 1926), and resembles the lynxes less. The same is true for the relative length of the gestation period. The caracal tends to have a longer gestation than the true lynxes and the wild cat group, though not reaching the upper level of relative gestation in felids (Hemmer, 1976b; Kawata et al., 1975). In this respect it is comparable to the situation with the black-footed cat discussed above. Therefore, the combination of all available data suggests a branching off from the wild cat-lynx line earlier than the radiation to the wild cat group, the Pallas' cat and the lynxes; thus it is nearer to a common origin with puma and golden cat evolutionary lines.

Weigel (1961) found the skin pattern of the serval *(serval)* comparable to that of the lynxes and the wild cat group. Therefore, she supposed that the serval originated in an early side-branch of this whole species group. Characters of cranial and other external morphology agree with this interpretation (Pocock, 1917c; Lonnberg, 1926), as do ethological characters (Leyhausen, 1956). The length of the gestation period is nearly the same as in the caracal, that is, relatively longer than the lynxes and the wild cat group but shorter than the upper range represented by the pantherines. So the origin of the serval seems to be comparable with that of the caracal and perhaps may be traced back to the same radiation.

An attempt to summarize these considerations on the evolutionary systematics of the recent cat species is presented in a simplified phylogenetic tree based on successive geographical radiations (Figure 1). Some closing remarks on felid taxonomy must follow from these results. We found that several branches leading to modern species have obviously existed since the Miocene. Within these main branches several subdivisions originated at different times with the latest ones in the Pleistocene. If classification into taxonomic categories is in some way supposed to express natural relationships which result from evolution, then it seems quite logical to give all branches coming from the early basic radiations the same rank and could mean calling them genera, tribes, or subfamilies. How many lower categories remain available for all later radiations (in descending succession) depends on this decision. When classifying all products of the first, presumably Miocene radiations as genera, we would have 10 genera. Subdividing them into subgenera where subsequent radiations occurred would require us to arrange the wild cat and its closely related species, the lynxes and the Pallas' cat, not only into one genus, but also into the same subgenus. These forms have hitherto been considered variously as belonging to different genera or even subfamilies.

If the main branches are assigned tribal rank, on the other hand, and the later radiations generic rank, we would have many tribes, some of them monospecific. These would include uncommon ones like the Pumini for the puma, the Profelini for the African golden cat, and the Catopumini for the Asian golden cats. This taxonomic solution does not seem to be the best for practical use and would have no chance of gaining general acceptance. A logical approach to this problem would be to unite all species coming from the last radiation of their group, regardless of the time when this radiation happened, as subgenera, and the groups or species resulting from preceding radiations as genera. In this case monospecific lines originating in the basic radiations would also have generic rank. Then we could have the following classification:

the cheetah as genus *Acinonyx* Brookes, 1828, with the one species *jubatus* (Schreber, 1776),

the puma as genus *Puma* Jardine, 1834, with the one species *concolor* (Linnaeus, 1771),

the jaguarundi as genus *Herpailurus* Severtzov, 1858, with the one species *yagouaroundi* (Geoffroy, 1803),

the leopard cat line as genus *Prionailurus* Severtzov, 1858, with two or three subgenera: *Prionailurus* with the species *bengalensis* (Kerr, 1892), *rubiginosus* (Geoffroy, 1843) and *viverrinus* (Bennett, 1833), perhaps *Mayailurus* with the one species *iriomotensis* (Imaizumi, 1967) and *Ictailurus* with the one species *planiceps* (Vigors and Horsfield, 1827),

the African golden cat as genus *Profelis* Severtzov, 1858, with the one species *aurata* (Temminck, 1827),

the Asian golden cats as genus *Catopuma* Severtzov, 1858, with the species *temmincki* (Vigors and Horsfield, 1827) and *badia* (Gray, 1874),

the ocelot line as genus *Leopardus* Gray, 1842, with the species *pardalis* (Linnaeus, 1758) and *wiedi* (Schniz, 1821),

the little spotted cat line as genus *Oncifelis* Severtzov, 1858, with three subgenera: *Oncifelis* with the species *tigrinus* (Schreber, 1777), *geoffroyi* (D'Orbigny and Gervais, 1843) and *guigna* (Molina, 1810), *Lynchailurus* Severtzov, 1858, with the one species *pajeros* (Desmarest, 1816), and, perhaps as separate genus, *Oreailurus* Cabrera, 1940, with the one species *jacobita* (Cornalia, 1856),

the pantherines as genera *Pardofelis* Severtzov, 1858 for the species *marmorata* (Martin, 1836), *Neofelis* Gray, 1867, for the species *nebulosa* (Griffith, 1821), perhaps *Uncia* Gray, 1854, for the species *uncia* (Schreber, 1775), and *Panthera* Oken, 1816, with three subgenera, if the snow leopard originated in the same radiation as the tiger and the lion-jaguar-leopard line, or two subgenera: *Tigris* for the species *tigris* (Linnaeus, 1758) and *Panthera* for the species *onca* (Linnaeus, 1758), *pardus* (Linnaeus, 1758) and *leo* (Linnaeus, 1758),

the wild cat and lynx line as the genera *Leptailurus* Severtzov, 1858, for the species *serval* (Schreber, 1776), *Caracal* Gray, 1843, for the species *caracal* (Schreber, 1776), and *Felis* for all others, divided into the subgenera *Lynx* Kerr, 1792, for the species or semispecies *rufus* (Schreber, 1777), *canadensis* (Kerr, 1792), *lynx* (Linnaeus, 1758) and *pardinus* (Temminck, 1824), *Otocolobus* Brandt, 1841, for the species *manul* (Pallas, 1776), and *Felis* Linnaeus, 1758, for the species *nigripes* Burchell, 1822, if not coming from a previous radiation, *margarita* Loche, 1858, *chaus* Guldenstadt, 1776, *bieti* Milne-Edwards, 1892, and *silvestris* Schreber, 1777.

This taxonomic arrangement does not claim general acceptance, but it is impossible, in the light of the information given here, to term, for example, the lynxes as genus *Lynx* but the puma as genus *Felis*, as is often found in literature. It will be the task of future research in zoology to gain new information for sharpening the outlines drawn here where they were drawn correctly, to correct them where they may be erroneous, and to fill in the gaps of our present knowledge on the evolutionary systematics of the living felid species. At the same time it will be the task of paleontology to look for the fossil documents for all these phylogenetic branches and to complete the picture with the addition of species already extinct in Tertiary and later Pleistocene times.

SUMMARY

The evolutionary relationships of the living felid species are discussed in the light of the results collected in recent years and decades by morphological research on skull and teeth and on external characters, ethological observations, physiological comparisons, chromosome studies and biogeography and palaeontology. The resulting integrative picture of felid systematics seems to be quite clear in some branches, but still vague and blurred and open to future surprises and changes in others due to a considerable lack of knowledge of several species.

This picture shows conformity with former systems as well as differences. In some of the modern cat species believed to be nearly related, as the golden cats and the puma, common characters seem to be merely symplesiomorphic ones, while in some others believed to belong together, as the South America ocelot group and little spotted cat group, common characters obviously evolved convergently. The living cat species are arranged in 10 major evolutionary lines. Some include one species only, as the cheetah, the puma, the jaguarundi, and the African golden cat line. Others include only a few species, as the Asian golden cat line and the ocelot line, and others comprise a larger group of species obviously arising in two to four radiations, as the wild cat-lynx, the leopard cat, the little spotted cat and the pantherine lines.

Some considerations are given to the problem of arranging the results of the dynamic processes of evolution into the static units of taxonomy. The latter is more a thing of convenience than the clear result of biological research. Nevertheless, a classification is given perhaps expressing best the relationships between the modern cat species as derived here.

ZUSAMMENFASSUNG

Die verwandtschaftlichen Beziehungen der rezenten Felidenarten werden im Licht der Ergebnisse diskutiert, die in den letzten Jahren und Jahrzehnten durch morphologische Untersuchungen am Schadel und GebiB und an auBeren Merkmalen, durch Verhaltensbeobachtungen, durch physiologische Vergleiche, durch Chromosomen-Studien und auf den Gebieten der Biogeographie und der Palaontologie gesammelt wurden. Das hieraus resultierende Gesamtbild der Feliden-Systematik erscheint in einigen Bereichen sehr klar, in anderen aber unscharf und verschwommen und zukunftigen Uberraschungen und Anderungen gegenuber offen, nachdem fur einige Arten nur sparliches Wissen existiert.

Dieses Bild zeigt im Vergleich mit fruheren Systemen sowohl Ubereinstimmungen, als auch Unterschiede. Gemeinsame Merkmale mancher als nahe miteinander verwandt angesehener Arten, wie Goldkatzen and Puma, erscheinen lediglich als symplesiomorph, in anderen Fallen, wie bei der Ozelot-Gruppe und der Oncilla-Gruppe, sind Gemeinsamkeiten offensichtlich in konvergenter Evolution entstanden. Die rezenten Katzenarten werden zu 10 Hauptevolutionslinien gestellt, von denen einige monospezifisch sind, wie die Geparden-, die Puma-, die Jaguarundi- und die Afrikanische Goldkatzen-Linie, andere nur wenige Arten umfassen, wie die Asiatische Goldkatzen- und die Ozelot-Linie, und wieder andere jeweils groBere Artengruppen beinhalten, die sich in 2 bis 4 Radiationen entwickelten, wie die Wildkatzen-Luchs-, die Bengalkatzen-, die Oncilla- und die Pantherkatzen-Linie.

Das Problem, die dynamischen Prozesse der

Evolution in die statischen Einheiten der Taxonomie zu fassen, wird kurz diskutiert. Die taxonomische Bewertung erscheint im Gegensatz zur evolutionaren Systematik mehr als eine Frage der Ubereinkunft, denn als eindeutige SchluBfolgerung rein biologischer Forschung. Trotzdem wird eine Feliden-Klassifikation versucht, mit der die hier abgeleiteten Verwandtschaftsverhaltnisse wohl am besten auszudrucken sind.

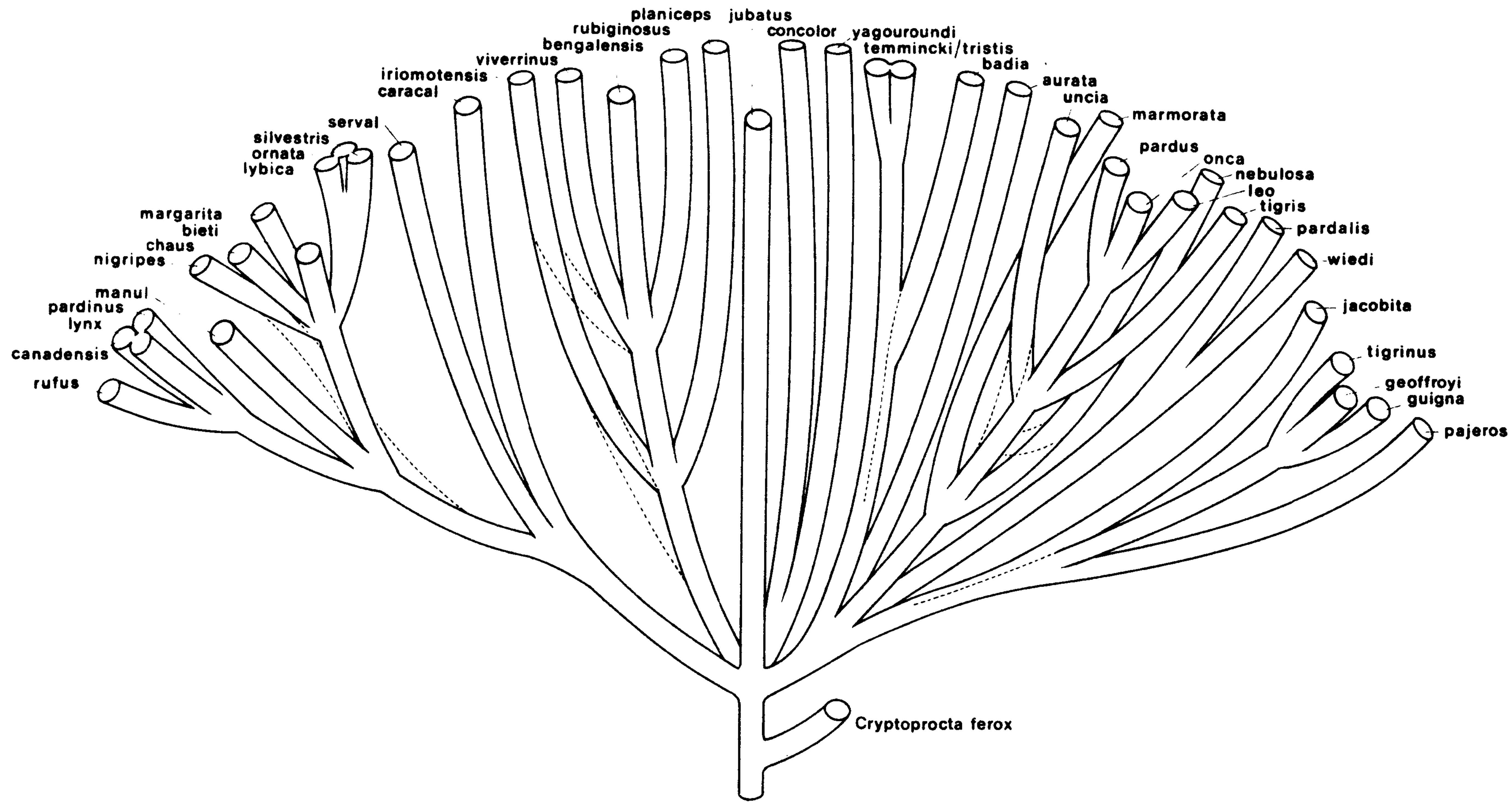

FIGURE 1. Tentative scheme of the evolutionary systematics of the recent cat species, based on the concept of successive geographical radiations.

LITERATURE CITED

Allen, J. 1919. Notes on the synonymy and nomenclature of the smaller spotted cats of tropical America. *Bulletin of the American Museum of Natural History* 41: 341-419.

Beaumont, G. de. 1964. Remarques sur la classification des Felidae. *Eclogae Geologicae Helvetiae* 57: 837-845.

Blonk, H. L. 1963. *Wilde Katten.* Thieme & Cie., Zutphen.

Cabrera, A. 1940. Notas sobre carnivoras sudamericanos. *Notas del Museo de La Plata, Zool.* 5(29): 1-22.

Geisler, M., A. Gropp, P. Leyhausen, and B. A. Tonkin. 1968. Cytogenetische Untersuchungen an Sudamerikanischen Pardelkatzen. *Zeitschrift fur Saugetierkunde* 33: 315-320.

Glass, G. E., and N. B. Todd. 1977. Quasi-continuous variation of the second upper premolar in *Felis bengalensis* KERR 1792 and its significance for some fossil lynxes. *Zeitschrift fur Saugetierkunde* 42: 36-44.

Haltenorth, T. 1936-37. Die verwandtschaftliche Stellung der GroBkatzen zueinander. *Zeitschrift fur Saugetierkunde* 11: 32-105, and 12: 97-240.

____________. 1953. *Die Wildkatzen der Alten Welt.* Geest & Portig, Leipzig.

Hemmer, H. 1966. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). I. *Veroffontlichursen der Zoologische Staatssammlung,* Munchen 11: 1-121.

Hemmer, H. 1968. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). II. Studien zur Ethologie des Nebelparders *Neofelis nebulosa* (Griffith 1821) und des Irbis *Uncia uncia* (Schreber 1775). *Veroffentlichursen der Zoologische Staatssammlung.* Munchen 12: 155-247.

________. 1971. Zur Charakterisierung und Stratigraphischen Bedeutung von *Panthera gombaszoegensis* (Kretzoi, 1938). *N.Jb.Geol. Palaont.* Mh. Jg. 1971: 701-711.

________. 1974a. Studien zur Systematik und Biologie der Sandkatze *(Felis margarita* Loche, 1858). *Zeitschrist der Kolner Zoo* 17: 11-20.

________. 1974b. Untersuchungen zur Stammegeschichte der Pantherkatzen (Pantherinae). III. Zur Artgeschichte des Lowen *Panthera (Panthera) leo* (Linnaeus 1758). *Veroffentlichungen Zoologische der Staatssammlung* Munchen 17: 167-280.

________. 1976a. Fossil history of living Felidae. Pp. 1-14, *In:* R. L. Eaton (Ed.), *The World's Cats*, Vol. 3, No. 2. Carnivore Research Institute, Burke Museum, Seattle.

________. 1976b. Gestation eriod and ostnatal evelopment in Felids. Pp. 143-165, *In:* R. L. Eaton (Ed.), *The World's Cats*, Vol. 3, No. 2. Carnivore Research Institute, Burke Museum, Seattle.

________, P. Grubb, and C. P. Groves. 1976. Notes on the Sand Cat, *Felis margarita* Loche, 1858. *Zeitschrift fur Saugetierkunde* 41: 286-303.

Heran, I. 1967. Beitrag zur Ethologie des Manul, *Otocolobus manul* (Pallas, 1776). (Felidae, Mammalia). *Acta Musel Nationalis Pragae* 23 B: 33-64.

Imaizumi, Y. 1967. A new genus and species of cat from Iriomote, Ryukyu Islands. *Journal of the Mammalogica Society of Japan 3: 73-103.*

Kawata, K., B. Bailey, and D. P. Siminski. 1975. Notes on feline reproduction at the Indianapolis Zoo. *Zoologische Garten* NF 45: 436-440.

Kratochvil, T. 1976. Os penis der Gattung Panthera und das System der Felidae (Mammalia). *Zool. Listy* 25: 289-302.

Kratochvil, T., and Z. Kratochvil. 1976. The origin of the domesticated forms of the genus Felis (Mammalia). *Zool. Listy* 25: 193-208.

Leyhausen, P. 1950. Beobachtungen an Lowen-Tiger-Bastarden mit einigen Bemerkungen zur Systematik der GroBkatzen. *Zeitschrift fur Tierpsychologie* 7: 46-83.

__________. 1956. Uber die unterschiedliche Entwicklung einiger Verhaltensweisen bei den Feliden. *Saugetierkundliche Mitteilungen* 4: 123-125.

__________. 1963. Uber sudamerikanische Pardelkatzen. *Zeitschrift fur Tierpsychologie* 20: 627-640.

__________. 1973. *Verhaltensstudien an Katzen.3.*Aufl. Parey, Berlin/Hamburg.

__________, and B. Tonkin. 1966. Breeding the black-footed cat *Felis nigripes* in captivity. *International Zoo Yearbook* 6: 178-182.

Lonnberg, E. 1926. Notes on some cats from eastern Asia with description of a new subgenus. *Arkiv for Zoologi* 18 A: 1-23.

Mensch, P. J. A. van, and P. J. van Bree. 1969. On the African golden cat, *Profelis aurata* (Temminck, 1827). *Biologia Gabonica* 5(4): 235-369.

Muller, P. 1973. The dispersal centres of terrestrial vertebrates in the neotropical realm. *Biogeographica* 2: 1-244.

Petzsch, H. 1968. *Die Katzen.* Urania, Leipzig/ Jena/Berlin.

__________. 1970. Kritisches uber die Neuentdeckte Iriomote-Wildkatze. *Der Pelzgewerbe* 20: 1-8.

Pocock, R. I. 1907. Notes upon some African species of the genus *Felis,* based upon specimens recently exhibited in the Society's Gardens. *Proceedings of the Zoological Society of London 1907*: 654-677.

__________. 1916a. On the hyoidean apparatus of the lion *(F. leo)* and related species of Felidae. *Annals and Magazine of Natural History,* Series 8, 18: 222-229.

__________. 1916b. On the tooth-change, cranial characters, and classification of the snow leopard or ounce *(Felis uncia). Annals and Magazine of Natural History,* Series 8, 18: 306-316.

__________. 1916c. The structure of the auditory bulla in existing species of Felidae. *Annals and Magazine of Natural History,* Series 8, 18:

__________. 1916d. On some of the cranial and external characters of the hunting leopard or Cheetah. *Annals and Magazine of Natural History,* Series 8, 18:

__________. 1917c. The classification of existing Felidae. *Annals and Magazine of Natural History,* Series 8, 20:

__________. 1917d. The groups of the small and medium-sized South-American Felidae. *Annals and Magazine of Natural History* Series 8, 20:

Pocock, R. I. 19 . On the external characters of the Felidae. *Annals and Magazine of Natural History.*

__________. 1932. The marbled cat *(Pardofelis marmorata)* and some other oriental species, with the definition of a new genus of the Felidae. *Proceedings of the Zoological Society of London 1932:* 741-766.

__________. 1939. *The Fauna of British India. Mammalia,* Vol. I. Taylor and Francis, London.

__________. 1941. The examples of the colocolo and of the pampas cat in the British Museum. *Annals and Magazine of Natural History* 7(11): 257-274.

Robinson, R. 1976. Cytogenetics of the Felidae. Pp. 15-28, *In*: R. L. Eaton (Ed.), *The World's Cats,* Vol. 3, No. 2. Carnivore Research Institute, Burke Museum, Seattle.

Schauenberg, P. 1974. Donnees nouvelles sur le chat des sables "*Felis margarita*" Loche, 1858. *Revue Suisse de Zoologie* 81: 949-969.

Schmid, E. 1940. Variationsstatistische Untersuchungen am GebiB pleistozaner und rezenter Leoparden und anderer Feliden. *Zeitschrif fur Saugetierkunde* 15: 1-179.

Schneider, K. 1932. Das Flehmen (III.). *Der Zoologische Garten* (NF) 5:

Schurer, U. In press. Breeding black-footed cats, *Felis nigripes,* in captivity. *Carnivore.*

Schwangart, F. 1936. Der Manul, *Otocolobus manul* (Pallas), im System der Feliden. *Zentralblattfuer Kleintierkunde und Pelztierkunde,* 12(8)= Carnivoren Studien 2): 19-67.

__________. 1941. Sudamerikanische Busch-, Berg- und Steppenkatzen. *Abh. Bayer.Akad. Wiss., Math.-nat.Abt.,* NF, 49: 1-77.

Sonntag, C. 1923. The comparative anatomy of the tongues of the Mammalia. VIII. Carnivora. *Proceedings of the Zoological Society of London.*

Thenius, E. 1967. Zur Phylogenie der Feliden (Carnivora, Mamm.). *Zeitschrift fur Zoologische Systematic und Evolution forschung* 5: 129-143.

Weigel, I. 1961. Das Fellmuster der Wildlebenden Katzenarten und der Hauskatze in Vergleichender und stammesgeschichtlicher Hinsicht. *Saugetierkundliche Mitteilungen* 9, Sonderheft, 1-120.

Wurster, D. H. 1969. Cytogenetic and phylogenetic studies in carnivora. Pp. 310-329, *In*: K. Benirschke (Ed.), *Comparative Mammalian Cytogenetics.* Springer, Berlin/Heidelberg/New York.

Wurster-Hill, D. H. 1973. Chromosomes of eight species from five families of Carnivora. *Journal of Mammalogy* 54: 753-760.

Wurster-Hill, D. H., and C. W. Gray. 1973. Giemsa banding patterns in the chromosomes of twelve species of cats (Felidae). *Cytogenetics Cell Genetics* 12: 377-397.

Wurster-Hill, D. H., and D. A. Meritt. 1974. The G banded chromosomes of the marbled cat, *Felis marmorata. Mammalian Chromosomes Newsletter* 15: 14.

A MULTIVARIATE COMPARISON OF SOME EXTANT AND FOSSIL FELIDAE

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The reconstruction of phylogenies requires discriminating among contemporary data. Determining whether one is working with a single, variable species or two morphologically similar species influences the development of phylogenetic hypotheses. The conclusion that two separate taxa exist implies that a single taxon could not account for the qualitative or quantitative differences observed between individuals or samples. Within the Felidae such conclusions are often difficult to reach because intraspecific variation is often nearly as great as interspecific variation. This problem is compounded for the fossil Felini since individuals are usually represented by isolated skeletal elements. Portions of the upper and lower tooth rows probably represent the most frequently assigned fossil cat material, but without further cranial or postcranial material it is difficult to assign individuals to a species with much degree of certainty. Unfortunately the cranial characters of recent species most carefully analyzed are those which seldom survive fossilization, while dental morphometry, if considered at all, has been of secondary concern.

Paleontologists reconstructing phylogenetic relationships among taxa usually have at their disposal precisely those data which receive such secondary consideration in neotological studies. The result is that paleontologists and systematists, faced with a group which shows a high degree of interspecific similarity, have no real way to communicate the information they have derived from their respective fields. The present analysis was undertaken to resolve, at least in part, some of these difficulties through a rudimentary and strictly quantitative comparison of dental characteristics in a portion of the Felidae. We are aware that others have utilized dental morphometry studying fossil felids (e.g., Simpson, 1941; Kurten, 1965; Schutt, 1969). However, most of these studies utilize bivariate analyses which have not been (in our opinion) very successful in elucidating the arrangement of North American fossil felids. We have asked if multivariate analysis permits better separation of species based on dental morphology and, if this is so, to what systematic level it is possible to distinguish individuals belonging to different species if only dental characters are analyzed. Assuming that groupings of morphologically similar species can be made, will they agree with taxonomic groupings based on other character suites; and are the presumed ancestors of the modern North American cat species sufficiently distinct from the modern species and each other to be recognized as separate species? Finally, if the hypothesized ancestor-descendant relationships are real, what can be said about the net evolutionary trends in dental morphometry in these lineages?

The usefulness of dental characters in achieving these goals were examined in eight extant species: *Puma concolor*, the mountain lion; *Lynx caracal*, the caracal; *Lynx candensis*, the Canadian lynx; *Lynx rufus*, the bobcat; *Herpailurus yagouaroundi*, the jagouaroundi; *Leopardus wiedi*, the margay; *Leopardus pardalis*, the ocelot; *Leopardus tigrina*, the oncilla; and, six fossil species: *"Felis" trumani*, *"Felis" lacustris*, *"Felis" studeri*, *"Felis" rexroadensis*, *Lynx issiodorensis* and *"Lynx" stouti*.

Although upper and lower dental characters are often highly correlated, analyses were conducted separately on each suite of characters since several of the fossil species are known by only one set or the other.

MATERIALS AND METHODS

Upper and lower tooth rows and mandibles from 130 individuals representing the eight modern species and 15 specimens from six fossil species were used in the present study. Sample sizes for the recent species ranged from five for *L. tigrina* to 36 for *Lynx rufus*. The examined specimens are listed by species in Appendix 1. Only adults were used in the analyses, being defined by the presence of complete permanent dentition which in most cases was fully erupted. Seventeen measurements were taken on each specimen, six from the upper tooth row and eleven from the lower tooth row and mandible. Each measurement is defined in Appendix 2. All measurements of the teeth represent alveolar distances since teeth were occasionally absent from both modern and fossil specimens. Measurements were taken to the nearest 0.1 mm with dial calipers.

The goals of the present study require the solution of three overlapping problems. The first is to determine whether a significant discrimination can be made between species on the basis of available characters. The null hypothesis is that the group mean of each species is equal to all the other group means. The standard methodology for testing this hypothesis is the multivariate analysis of variance (MANOVA). The analysis reduces an array of variables to a single score which is a linear combination of the values for each of the original variables. The goal is to obtain the linear combinations of variables which maximally separate each group from every other group (the discriminant score) by maximizing the between-group mean squares in relation to the within-group mean squares (Harris, 1975). The criteria used for testing the separation of groups is a univariate F-ratio. The second problem is classifying individual specimens into groups which correspond to the *a priori* species groupings which were based on other systematic characters. The analysis compares the discriminant scores of each individual with the group mean for each species and assigns the individual to the most similar group. Clearly, if the group means between species are not significantly different, then classification of individuals is difficult; however, differences between group means does not indicate that assignment of individuals to the proper groups will necessarily occur. Finally, the morphological relationships among the species are compared to determine how different, and in what ways, the groups are distinguished from one another. This analysis is accomplished through a technique termed canonical analysis (Seal, 1964). The analysis transforms the original data variables to discriminant scores and selects an axis which passes through the greatest variation among groups relative to the variation within groups. A second axis is made through the greatest amount of variation not explained by the first axis. Axes can continue to be generated in this manner until all the significant between-groups variation has been explained. This process is usually accomplished with fewer than the original variables which considerably simplifies the description of morphological variation.

RESULTS

The results of the MANOVA test for significant differences between species for the analyzed characters are shown for the upper and lower tooth rows in Tables 1 and 2, respectively. Table 1 shows that the species group means are significantly different from each other except for the pairwise comparisons of *L. tigrina, L. wiedi* and *H. yagouaroundi.* The comparisons of *L. pardalis* with *Lynx caracal* and *L. caracal* with *L. canadensis* are significant, although just barely. Characters of the lower jaw (Table 2) give a better separation of the species. *Leopardus tigrina* is still not distinguished from either *H. yagouaroundi* or *L. wiedi,* but *H. yagouaroundi* and *L. wiedi* are better discriminated and *L. pardalis, Lynx caracal* and *L. canadensis* are easily distinguished from one another.

Puma, 80.0% of all *Herpailurus* and 72.4% of all *Leopardus* were correctly assigned to their respective genera using the upper dentition, and 100%, 100%, 100%, and 93.1% of the same genera using the lower dentition.

The morphological relationships among species are shown in Tables 5 and 6 for the cats' upper and lower jaws. The coefficients for the canonical variable on the first axis of the upper tooth rows (Table 5) show equal weighting on the three original variables, accounting for the most variation contrasting canine length with a combination of canine width and P3 length. Species with positive group means have a relatively round canine in cross section with a relatively longer P3. Thus, for example, *P. concolor* has very round canines and a long P3 while *H. yagouaroundi* has thin, sabrelike canines and a short P3. The second canonical axis contrasts the overall size of the canine with the length of the P3. On this axis all three species of *Lynx* are distinguished from the other three genera by their relatively smaller canines and larger P3's. The three species of *Leopardus,* in contrast, have very large canines in relation to P3 while *Puma* and *Herpailurus* are intermediate. The third axis contrasts the anterior-posterior length of the canine with the anterior-posterior length of P3. *L. canadensis* and *L. rufus* are grouped together on the basis of their short canines and long P3.

Table 6 shows the canonical relationships among species for the lower tooth rows. The first axis shows all the coefficients are approximately equal in weighting and are the same sign, indicating that the first axis corresponds to a

TABLE 1. F-values calculated from MANOVA testing for significant differences between pairs of species using upper tooth row characters. Significant differences for $p<0.05$ occur for values greater than 2.68. Underlined values are for species pairs which cannot be discriminated or are poorly separated. CARAC is *L. caracal,* CANAD is *L. canadensis,* RUFUS is *L. rufus,* CONCL is *P. concolor,* YAGUR is *H. yagouaroundi,* WIEDI is *L. wiedi,* PARDL is *L. pardalis,* TIGRN is *L. tigrina.* F-values greater than 100 are rounded to the nearest unit.

Species	CARAC	CANAD	RUFUS	CONCL	YAGUR	WIEDI	PARDL
CANAD	<u>3.35</u>						
RUFUS	9.26	15.01					
CONCL	260	283	405				
YAGUR	25.74	42.85	35.47	390			
WIEDI	33.09	50.47	38.66	337	<u>1.74</u>		
PARDL	<u>2.74</u>	11.27	14.38	228	33.12	38.18	
TIGRN	21.82	38.48	26.93	252	<u>0.47</u>	<u>0.51</u>	25.79

The classification of individuals into species based on the comparison of the specimen's discriminant score with the species mean scores is shown for the upper dentition in Table 3 and the lower dentition in Table 4. There was a wide range in the correct identification of individuals to the species level, ranging from 35.7% for *L. caracal* to 100% for *P. concolor.* The classification based on the lower jaw (Table 4) provided a much better identification of individuals, with an average correct identification of 95.4%. Classification to the generic level was much better than to the species level. Eighty-seven percent of all *Lynx,* 100% of all

size factor. *P. concolor,* with the longest p3, p4 and m1, has the highest negative score, and *L. wiedi* with the shortest p3, p4 and m1, has the highest positive score. The second axis contrasts p4 length with m1 length, grouping *L. canadensis* and *L. rufus* with a long m1 in relation to p4, while *Leopardus* shows a long p4 in relation to m1. This is especially pronounced in *L. pardalis.* *P. concolor* shows a tendency to have a long m1 while *Lynx caracal* shows a development of the p4 compared to m1 nearly as strong as the species in *Leopardus.* The third axis contrasts p3 length with p4 length and no systematic variation is evident from the results.

TABLE 2. F-values calculated from MANOVA testing for significant differences between pairs of species using lower tooth row characters. Significant differences for p<0.05 occur for values greater than 2.68. Underlined values are for species pairs which cannot be discriminated or are poorly separated. Acronyms for species are as in Table 1. F-values greater than 100 are rounded to the nearest unit.

Species	CARAC	CANAD	RUFUS	CONCL	YAGUR	WIEDI	PARDL
CANAD	19.40						
RUFUS	30.43	28.06					
CONCL	183	213	385				
YAGUR	38.38	63.84	25.44	313			
WIEDI	36.67	71.37	38.44	262	<u>3.71</u>		
PARDL	8.49	53.32	84.57	173	68.41	53.15	
TIGRN	17.62	37.99	18.73	177	<u>2.26</u>	<u>1.40</u>	29.48

TABLE 3. Identification table of individuals analyzed from upper tooth row characters. Reading across the rows shows how the *a priori* classification compared with the generalized (D^2) distance of individuals from the species centroids. Acronmys for species are as in Table 1.

Species	CARAC	CANAD	RUFUS	CONCL	YAGUR	WIEDI	PARDL	TIGRN	% CORRECT
CARAC	5	3	2	0	1	0	3	0	35.7
CANAD	2	17	0	0	0	0	1	0	85.0
RUFUS	5	2	25	0	1	0	3	0	69.4
CONCL	0	0	0	21	0	0	0	0	100.0
YAGUR	0	0	0	0	8	1	0	1	80.0
WIEDI	0	0	0	0	0	5	0	2	71.4
PARDL	1	3	2	0	1	0	10	0	58.8
TIGRN	0	0	0	0	1	0	0	4	80.0

TABLE 4. Identification table of individuals analyzed from lower tooth row characters. Reading across the rows shows how the *a priori* classification compared with the generalized (D^2) distance of individuals from the species centroids. Acronyms for species are as in Table 1.

Species	CARAC	CANAD	RUFUS	CONCL	YAGUR	WIEDI	PARDL	TIGRN	% CORRECT
CARAC	14	0	0	0	0	0	0	0	100.0
CANAD	1	18	2	0	0	0	0	0	90.0
RUFUS	0	1	35	0	0	0	0	0	97.2
CONCL	0	0	0	21	0	0	0	0	100.0
YAGUR	0	0	0	0	10	0	0	0	100.0
WIEDI	0	0	0	0	0	6	0	1	85.7
PARDL	0	0	0	0	1	0	16	0	94.1
TIGRN	0	0	0	0	1	0	0	4	80.0

The relationships between fossil and modern species are shown in Figures 1 and 2 for the upper and lower tooth rows. *"F." studeri* (Figure 1) is distinct from all species considered in this study by its much larger size. In spite of being much larger than *P. concolor* and having a rounder canine, the canine is relatively smaller and the P3 longer than in specimens of *P. concolor*. *"F." trumani* is also separated from *P. concolor* using the upper tooth row (Figure 1) by its smaller canines and longer P3. Similarly, *L. rexroadensis* is distinguished from the lynxes in Figure 1 by its rounder canines and longer P3. *"Lynx" stouti*, however, cannot be separated from the *Leopardus tigrina-L. wiedi* group with the character suite used, and shares the large canines and small P3 which are characteristic of that genus.

TABLE 5. Contribution of original upper tooth row variables to the canonical analysis and the canonical variable evaluated at each species centroid. Acronyms for species are as in Table 1.

	COEFFICIENT OF CANONICAL VARIABLE		
ORIGINAL VARIABLE	AXIS 1	AXIS 2	AXIS 3
CANINE LENGTH	-1.112	0.238	1.115
CANINE WIDTH	1.713	0.325	0.084
P3 LENGTH	1.256	-0.604	-1.356
	CANONICAL VARIABLE AT GROUP MEANS		
CARAC	-1.051	-0.045	0.079
CANAD	-0.433	-0.435	-0.834
RUFUS	-0.997	-0.099	-0.421
CONCL	8.617	0.104	0.208
YAGUR	-4.599	0.095	0.204
WIEDI	-5.362	0.331	0.610
PARDL	-0.726	0.369	1.020
TIGRN	-5.165	0.236	0.541

TABLE 6. Contribution of original lower tooth row variables to the canonical analysis and the canonical variable evaluated at each species centroid. Acronmys for species are as in Table 1.

	COEFFICIENT OF CANONICAL VARIABLE		
ORIGINAL VARIABLE	AXIS 1	AXIS 2	AXIS 3
p3 LENGTH	-0.927	0.173	-2.451
p4 LENGTH	-0.524	-1.748	1.768
ml LENGTH	-0.152	1.641	0.563
	CANONICAL VARIABLE AT GROUP MEANS		
CARAC	0.420	-0.972	0.921
CANAD	-0.003	1.636	1.372
RUFUS	1.816	1.355	-0.436
CONCL	-7.487	-0.016	-0.822
YAGUR	4.376	-0.358	-1.090
WIEDI	4.679	-1.977	-1.275
PARDL	-0.605	-2.494	0.850
TIGRN	3.956	-1.548	-0.404

The analysis of the lower teeth (Figure 2) reveals that "*F.*" *trumani* tends to have a slightly longer tooth row than most *P. concolor* sampled, but is distinguished by the relation between its larger p4 and smaller ml, although the separation is not as distinct compared with the upper jaw (Figure 1). *P. lacustris* is distinguished from *P. concolor* primarily by its smaller overall tooth row size, but the relative proportions of the cheek teeth are the same. *L. issiodorensis* is intermediate in size between *P. lacustris* and extant lynxes; it has a relatively longer p4 and shorter ml than *L. canadensis* or *L. rufus*, but tends to show somewhat more development of ml than *L. caracal*. "*L.*" *stouti* has the smallest cheek teeth of the fossil species analyzed. The relative development of p4 and ml is intermediate to "*F*". *trumani* and *P. lacustris* with p4 relatively longer than ml, but the development is not nearly as pronounced as in the extant *Leopardus* species. Again, it cannot be distinguished from the *H. yagouaroundi*-*L. wiedi*-*L. tigrina* group.

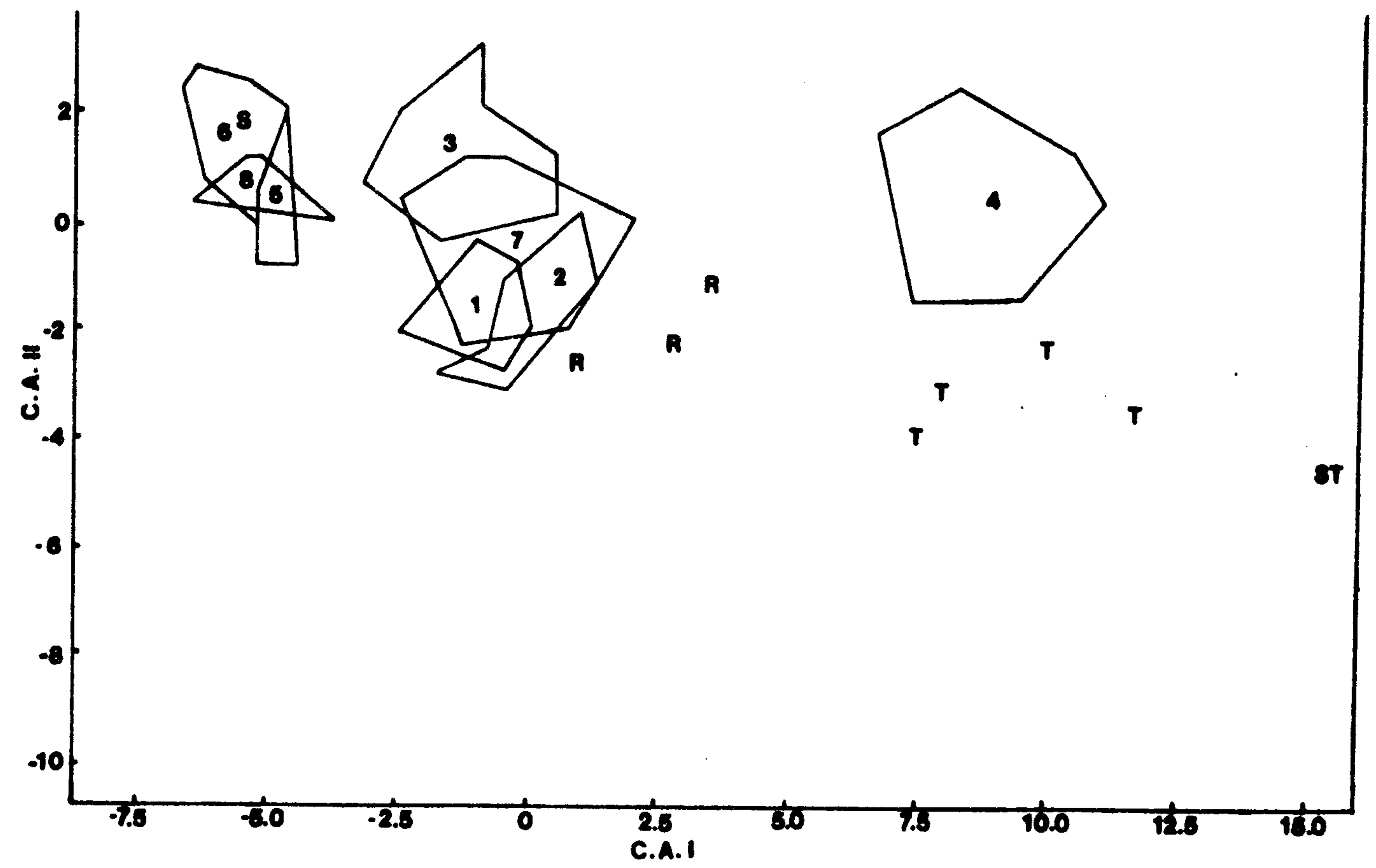

FIGURE 1. Relative positions of modern and fossil cat species on the first two canonical axes for data from upper tooth row measurements. Modern species are numbered 1 to 8. Polygons surrounding each extant species were constructed by connecting outlying points of species. *L. caracal = 1, L. canadensis = 2, L. rufus = 3, P. concolor - 4, H. yagouaroundi = 5, L. wiedi = 6, L. pardalis = 7,* and *L. tigrina = 8. L. rexroadensis = R, "F." studeri = ST* and *"L." stouti = S.*

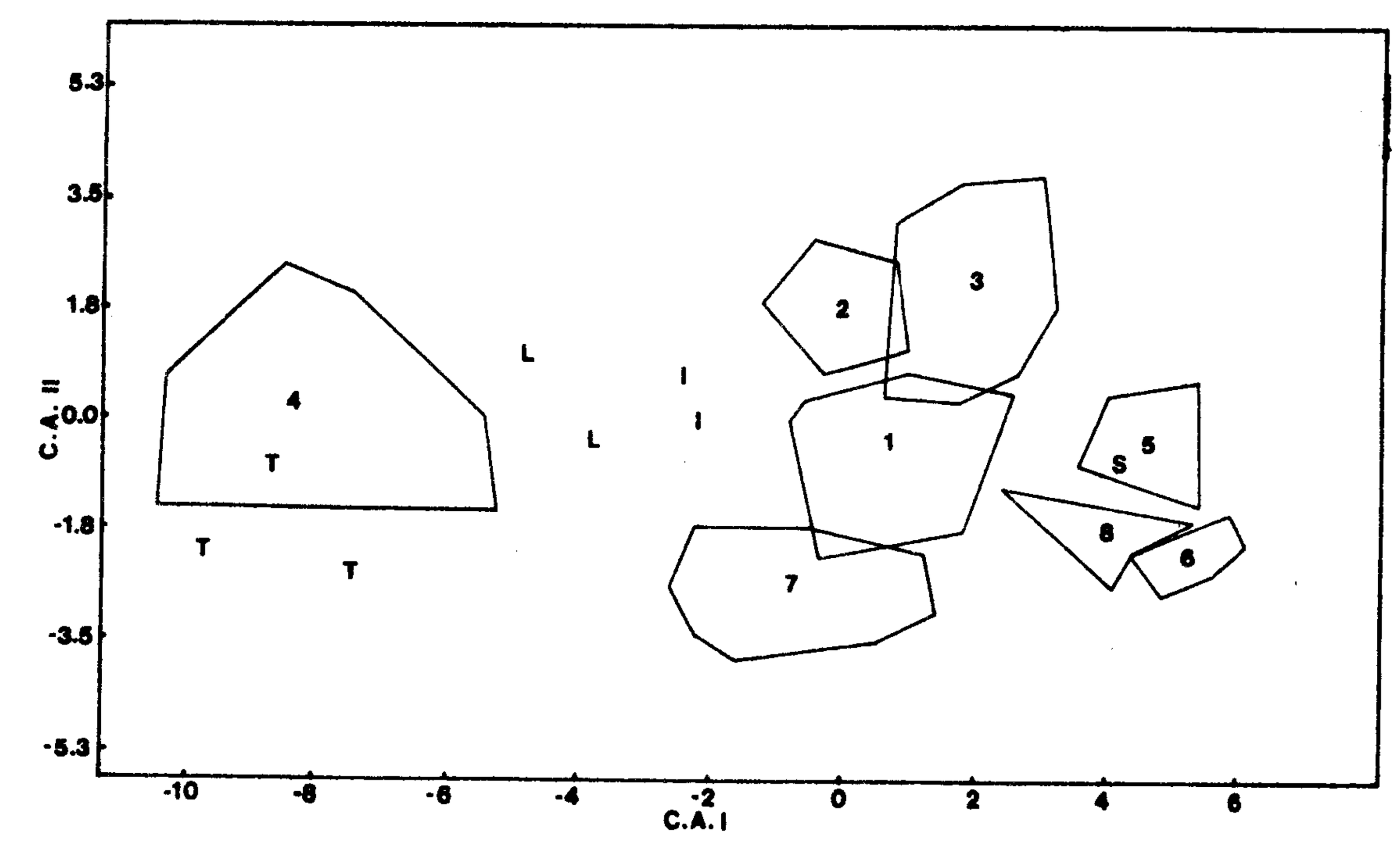

FIGURE 2. Relative positions of modern and fossil cat species on the first two canonical axes for data from lower tooth row measurements. Codes for modern species remain as in Figure 1. *P. lacustris = L* and *L. issiodorensis = I.*

DISCUSSION

The results of our preliminary analysis of dental characters indicate that the answers to our original questions presently depend upon the genera we wish to consider. Perhaps increasing sample sizes for some groups, such as *Leopardus*, or using other character suites may resolve the situation where ambiguity exists. Most of the species are easily separable from one another on the basis of either upper or lower dentition, although lower dentition provides a much better overall discrimination. The inability of the analysis to differentiate the four smallest species may be resolved by including the alveolar widths of cheek teeth in the analysis (Ray, 1964; Gillette, 1976). As with the discrimination of species, identification of individuals to the species level varies and is dependent on whether upper or lower tooth rows are considered. Identification to the generic level is uniformly quite good using either upper or lower tooth rows. Thus identification of isolated tooth rows, using the selected characters, is possible with a high degree of accuracy to the generic level and to a lesser and more variable extent to the species level. The groupings of species shown in Figures 1 and 2 do not reveal clustering of species according to previously accepted taxonomy. Rather, the groupings appear to be accomplished more by the size of each species. Even though the canonical relationships among the species do not strictly accord to systematic relationships, some of the axes suggest affinities. For example, all the extant species of *Lynx* are characterized by small (in cross section) canines and large P3's while all *Leopardus* can be distinguished from the remaining three genera by their relatively large upper canines and small P3's. *Lynx canadensis* and *L. rufus* share the short (in anterior-posterior length) upper canine and long P3, which the remaining species lack (Table 5). This suggests that *L. canadensis* and *L. rufus* share a common ancestor not linked to *L. caracal*, which is in agreement with other studies recognizing *L. caracal* as distinct from other members of the genus (Pocock, 1917; Ewer, 1973). The same relationship is seen in the relative proportions of p4 and ml which show increased development of ml in *L. canadensis* and *L. rufus* compared to *L. caracal*.

Puma, the large, non-roaring cats of the Western Hemisphere, are first found in the Blancan, Hagerman local fauna from Idaho (Gazin, 1933) as *Puma lacustris*, described on the basis of a lower jaw. Since then, Bjork (1970) has added additional material from Hagerman including upper jaws and skeletal elements. Hibbard (1941) referred two rami and skull fragments from the Blancan, Rexroad fauna in Meade County, Kansas to the species. *P. lacustris* was distinguished from modern forms by its smaller size, the shallow, anteriorly rounded margin of the symphysis and the narrow, more slender premolars and molars (Gazin, 1933). While the cheek teeth are smaller, their relative development has remained unchanged and there has been little tendency for reduction of the anteriorly placed cheek teeth seen in *Lynx*. *Felis daggetti* (Merriam, 1918), *Felis hawveri* (Stock, 1918) and *Felis bituminosa* (Merriam and Stock, 1932) are Rancholabrean pumas described from western North America, but the status of Irvingtonian pumas is uncertain because of confusion with a much different cat described by Orr (1969) as *Felis trumani*, a mountain lion from a Rancholabrean cave in Nevada. "*Felis*" *trumani* was originally differentiated by a reduced protocone with a shallow angle in the symphysis and a steeply ascending angle of the ramus when compared to *P. concolor*. Martin et al. (1977) described the recently discovered skeleton of "*F.*" *trumani* from Natural Trap Cave, Wyoming. The new material showed that "*F.*" *trumani* was distinct from *P. concolor* with many cheetah-like adaptations including a reduced protocone, broad forehead, short face, domed skull, enlarged external and internal nares, shallow angle of the ramus, usually a single mental foramen and elongated limbs. The present study supports the distinction of "*F.*" *trumani* from *Puma*, and "*F.*" *trumani* can be characterized by its relatively smaller canines and larger P3. In the lower jaw the relatively larger P4 and smaller ml of "*F.*" *trumani* distinguish it from *P. concolor*. "*Felis*" *studeri* (Savage, 1960) from the late Blancan Cita Canyon, Texas was described as a *Puma*, but was much more massive than *P. lacustris* and larger than nearly any living *Puma*. It resembles "*F.*" *trumani* in that it is distinguished from recent *Puma* by the relatively larger P3, somewhat smaller, rounder canines, the angle of the ramus at the symphysis which is shallow and rounded and a P4 with a reduced protocone. "*F.*" *trumani* and "*F.*" *studeri* share many morphological similarities with *Acinonyx*, suggesting evolutionary affinities between these Old and New World cats. It seems that a common ancestor of the three would have to be at least pre-Blancan.

Several additional extinct species which have been considered pumas might also be related to "*F.*" *trumani*. Cope (1895) referred a P4 from Port Kennedy Cave to *Crocuta inexpectata*. The reference to *Crocuta* (Hyaenidae) was based on the reduction of the protocone on the upper carnassial. In 1899 Cope referred this cat to *Uncia* (= *Panthera)* and added additional specimens to the hypodym. Brown (1908) described *Felis longicrus* from the Conard fissure in Arkansas, noting the strong similarities with *F. inexpectata*. Hay (1920) erected another new species, *Smilodontopsis mooreheadi* from Maryland based on a P4 with a reduced protocone. Simpson (1941) referred *F. longicrus* and *S. mooreheadi* to *F. inexpectata* and stated they were pumas. Since Simpson's paper, large, nonpantherine cat material has usually been placed with *F. inexpectata* (Ray, 1958, 1967; Gut and Ray, 1963) which Kurten (1965) synonymized with *P. concolor*. Since Kurten's study, Martin et al. (1977) and this paper have shown that two large, nonpantherine groups of cats existed in North America and the synonomy of *F. inexpectata* with *P. concolor* deserves reevaluation.

The genus *Lynx* includes from three to five living species. They are medium-sized cats with short faces, usually lacking P2; they have ossified hyoids, "tufts" on their ears, elongated legs, and short bodies. Their fossil record begins with *Lynx rexroadensis* in the Blancan of North America ("*Lynx*" *stouti* will be discussed with the small spotted cats). *L. rexroadensis* was distinguished from *P. lacustris* by the size and shape of its petrosal (Stephens, 1959). Stephens, however, did not compare it closely with lynxes and it was Kurten (1963) who suggested its affinities with *Lynx*. It has not been closely compared with the large Villafranchian

Lynx of Eurasia, *L. issiodorensis* with which it shares its general size. Our analysis supports the assignment of *L. rexroadensis* to *Lynx* based on the small canines and large P3 which are characteristic of extant forms. It is distinguished from living species by its round canines and larger P3. The data support Kurten's (1968) argument that lynxes originated in North America and spread to Eurasia in the Villafranchian. *L. issiodorensis* is widespread in the Villafranchian of Europe (Kurten, 1963, 1968) and China (Teilhard de Chardin and Leroy, 1945), the Blancan of North America (Schultz and Martin, 1972; and possibly Savage, 1960) and the Pliocene of Africa (Hendey, 1974) and is considered the most recent common ancestor of modern lynxes (Kurten, 1963). *L. issiodorensis kurteni* is based primarily on lower jaws from the late Blancan of Cherry County, Nebraska and cannot be directly compared to *L. rexroadensis*. Our analysis shows morphological similarities with other lynxes except that *L. issiodorensis kurteni* has larger cheek teeth. However, this is not unexpected, since later lynxes also tend to be notably smaller than other *L. issiodorensis*. *L. issiodorensis* also has a longer p4 relative to ml compared to *L. canadensis* and *L. rufus*, suggesting a trend to increase the relative size of the carnassial while decreasing tooth row length which results in increased shearing force. The morphological similarities of *L. issiodorensis* and *P. lacustris* (Figure 2) suggest that increased sample sizes could make the distinction between the two difficult. This raises a question which cannot be answered by the present study. Is the morphological similarity of *L. issiodorensis* and *P. lacustris* due to common ancestry of *Lynx* and *Puma* or is it a similarity of independently retained, primitive feline dental characters?

In North America several species and subspecies of Irvingtonian lynxes have been described, including *Lynx calcaratus* (Cope, 1899) from Early Irvingtonian Port Kennedy Cave and *Lynx compressus* (Brown, 1908) from the Early Irvingtonian Conard fissure. Brown also reported *L. rufus* from Conard fissure. Kurten (1965) erected a subspecies, *L. rufus koakudsi*, from Late Irvingtonian localities in Florida. All these Irvingtonian lynxes need review.

L. rufus is not uncommon in Rancholabrean sites, especially in southeastern North America (Kurten, 1965). *L. canadensis* is extremely rare in the North American fauna. Early studies by Matthew (1902) reported it from Whitman County, Washington and Hay (1923) lists it, along with caribou, from Monroe County, Pennsylvania. Guilday and Adam (1967) also tentatively reported it from Jaguar Cave in Idaho. Kurten and Anderson (1972) were able to confirm the presence of this species in Jaguar Cave.

The recent small South American cats do not have a good fossil record in North America and their evolution appears to have been primarily in Central and South America, at least since the Hemphillain. The only records of extant *Leopardus* are *L. pardalis*, represented by a mandibular ramus in the late Irvingtonian, Reddick fauna in Marion County, Florida (Ray et al., 1963), and the proximal end of a femur from Haile IA, Alachua County, Florida (Kurten, 1965). *"Felis" stouti* (Schultz and Martin, 1972) from the Valentinian of Logan County, Colorado, was tentatively assigned to *Lynx*, although the authors suggested that it should be the genotype for a new genus. This cat is one of the earliest felines presently known and could occupy a position ancestral to either the South American small cats or the lynxes. Our analysis affiliates it with the South American small cats on the basis of its large upper canines and small P3. Other qualitative characters, such as the position of the anterior border of the masseteric fossa, the position of the mental foramen and the angle of the anterior border of the coronoid process support this affiliation.

The origins and affinities of *Herpailurus* are presently unknown. There are similarities between *H. yagouaroundi* and *"F." stouti*, but none of the characters appear to be unique to *Herpailurus*. The earliest records of *Herpailurus* are reported from Port Kennedy Cave (Early Irvingtonian), Pennsylvania as *H. yagouaroundi* by Cope (1899). We have not examined the specimen and cannot confirm the identification. All other specimens that have been referred to *H. yagouaroundi* are Rancholabrean. Jagouaroundi are reported from Edwards County, Texas (Dalquest et al., 1969); Ladds, Georgia (Ray, 1967), and several localities in Florida (Gazin, 1950; Ray, 1964; Kurten, 1965). Some of these records were assigned by Gillette (1976) to a new species, *Felis amnicola*. Gillette concluded that this species did not share a close phylogenetic relationship with *H. yagouaroundi* because of several differences in jaw proportions; its status is unclear.

SUMMARY

The present study shows that it is possible to discriminate most cat species using selected characters from either the upper or lower tooth rows. Discrimination of the small South American cats is poor and might be improved with different character suites. Proper species identification of individuals is variable, but identification to the generic level can be done with a high degree of accuracy. At either level, lower tooth rows give a more accurate identification than upper tooth rows.

A comparison of eight recent species with six fossil species shows that five fossil species are distinct from extant species. The analysis suggests that two groups of large, nonpantherine cats existed in North America until the Pleistocene. They are represented by *P. lacustris* and *P. concolor*, as true mountain lions, and *"F." trumani* and *"F." studeri* as a group of cursorial cats with many cheetahlike adaptations.

Evidence is presented that supports assigning *Lynx rexroadensis* to that genus. Comparison of *L. issiodorensis* with modern lynxes suggests a trend of reduced absolute lower tooth row length with an increased relative size of the posterior teeth.

Previously described *"Felis" stouti* is shown to possess characters which are unique to *Leopardus*, suggesting its affiliation with that group and making the origin of the genus one of the earliest for the Felini. The status of *Herpailurus* remains undetermined in this study.

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LITERATURE CITED

Bjork, P. R. 1970. The Carnivora of the Hagerman local fauna (Late Pliocene) of Southwestern Idaho. *American Philosophical Society Transactions* 60: 1-54.

Brown, B. 1908. The Conard fissure, a Pleistocene bone deposit in northern Arkansas: With descriptions of two new genera and twenty new species of mammals. *Memoirs of the American Museum of Natural History* 9: 155-208.

Cope, E. D. 1895. The fossil vertebrata from fissure at Port Kennedy, Pa. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 446-450.

__________. 1899. Vertebrate remains from Port Kennedy bone deposit. *Journal of the Academy of Natural Sciences of Philadelphia,* Ser. 2, 11: 193-267.

Dalquest, W. W., E. Roth, and F. Judd. 1969. The mammal fauna of Schulze Cave, Edwards County, Texas. *Bulletin of the Florida State Museum* 13: 205-276.

Ewer, R. F. 1973. *The Carnivores.* Cornell University Press, Ithaca, New York.

Gazin, C. L. 1933. New felids from the Upper Pliocene of Idaho. *Journal of Mammalogy* 14: 251-256.

__________. 1950. Annotated list of fossil Mammalia associated with human remains at Melbourne, Florida. *Journal of the Washington Academy of Sciences* 40: 397-404.

Gillette, D. D. 1976. A new species of small cat from the Late Quaternary of southeastern United States. *Journal of Mammalogy* 57: 664-676.

Guilday, J. E., and E. K. Adam. 1967. Small mammal remains from Jaguar Cave, Lemhi County, Idaho. *Tebiwa* 10: 26-36.

Gut, H. J., and C. E. Ray. 1963. The Pleistocene vertebrate fauna of Reddick, Florida. *Quarterly Journal of the Florida Academy of Sciences* 26: 315-328.

Harris, R. J. 1975. *A Primer of Multivariate Statistics.* Academic Press, New York, San Francisco, London.

Hay, O. P. 1920. Descriptions of some mammalian and fish remains from Florida of probably Pleistocene age. *Proceedings of the U.S. National Museum* 56: 103-112.

__________. 1923. The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi River and from the Canadian Provinces east of Longitude 95°. *Carnegie Institute* 322: 1-499.

Hendey, Q. B. 1974. The late Cenozoic Carnivora of the southwestern Cape Province. *Annals of the South Africa Museum* 63: 1-369.

Hibbard, C. W. 1941. Mammals of the Rexroad fauna from the Upper Pliocene of southwestern Kansas. *Transactions of the Kansas Academy of Sciences* 44: 265-313.

Kurten, B. 1963. The return of a lost structure in the evolution of felid dentition. *Comment. Biol. Helsigf.* 26: 1-12.

__________. 1965. The Pleistocene Felidae of Florida. *Bulletin of the Florida State Museum* 9: 215-273.

__________. 1968. *Pleistocene Mammals of Europe.* London, Weidenfeld and Nicolson.

__________, and E. Anderson. 1972. The sediments and fauna of Jaguar Cave: II The fauna. *Tebiwa* 15: 21-45.

Martin, L. D., B. M. Gilbert, and D. B. Adams. 1977. A cheetah-like cat in the North American Pleistocene. *Science* 195: 981-982.

Matthew, W. D. 1902. List of the Pleistocene fauna from Hay Springs, Nebraska. *Bulletin of the American Museum of Natural History* 24: 317-322.

Merriam, J. C. 1918. A new puma-like cat from Rancho La Brea. *University of California Publications Bulletin of the Department of Geology* 10: 535-537.

__________, and C. Stock. 1932. The Felidae of Rancho La Brea. *Carnegie Institute* 422: 1-231.

Orr, P. C. 1969. *Felis trumani* a new radiocarbon dated cat skull from Crypt Cave, Nevada. *Santa Barbara Museum of Natural History Bulletin* 2: 1-8.

Pocock, R. I. 1917. The classification of existing Felidae. *Annals and Magazine of Natural History* 20: 329-350.

Ray, C. E. 1958. Additions to the Pleistocene mammalian fauna from Melbourne, Florida. *Bulletin of American Museum Comparative Zoology* (Harvard) 119: 421-449.

__________. 1964. The jaguaroundi in the Quaternary of Florida. *Journal of Mammalogy* 45: 330-332.

__________. 1967. Pleistocene mammals from Ladds, Bartow County, Georgia. *Bulletin of the Georgia Academy of Sciences* 25: 120-150.

__________, S. J. Olson, and H. J. Gut. 1963. Three mammals new to the Pleistocene fauna of Florida, and a reconstruction of five earlier records. *Journal of Mammalogy* 44: 373-395.

Savage, D. E. 1960. A survey of various Late Cenozoic vertebrate faunas of the panhandle of Texas. Part III. Felidae. *University of California Department of Geology Publication* 36: 317-344.

Schultz, C. B., and L. D. Martin. 1972. Two lynx-like cats from the Pliocene and Pleistocene. *Bulletin of the University of Nebraska State Museum* 9: 197-203.

Schutt, G. 1969. Untersuchungemam Gebiss von *Panthera leo fossilis* (V. Peichenau 1906) und *Panthera leo spelea* (Goldfuss 1810). *N. Jb. Geol. Palaont. Abh.* 134: 192-220.

Seal, H. 1964. *Multivariate Statistical Analysis for Biologists.* Methuen and Co., London.

Simpson, G. G. 1941. Large Pleistocene felines of North America. *American Museum of Natural History Novitates* 1136: 1-27.

Stephens, J. J. 1959. A new Pliocene cat from Kansas. *Papers Michigan Academy of Sciences, Arts and Letters* 44: 41-46.

Stock, C. 1918. The Pleistocene fauna of Hawver Cave. *University of California Publications Bulletin Department of Geology* 10: 461-515.

Teilhard de Chardin, P., and P. Leroy. 1945. Les Felides de Chine. *Publication of the Institute Geobiology Peking* 11: 1-58.

APPENDIX 1

Examined Specimens

Measurements for the present study were taken from the following specimens. Museum abbreviations are: FMNH = Field Museum of Natural History, S = Moscow State University Museum, MCZ = Museum of Comparative Zoology (Harvard), KU = University of Kansas Museum of Natural History, UMMP = University of Michigan Museum of Paleontology, USNM = National Museum of Natural History, UNSM = University of Nebraska State Museum, P3a/450 = Western Speleological Institute.

Lynx caracal - FMNH 32945, FMNH 105607, S 69084, S 69082, S 72742, S 69080, S 69109, S 69081, S 69044, MCZ 12611, MCZ 12612, MCZ 20049, MCZ 34634.

Lynx canadensis - KU 89167, KU 28631, KU 28630, KU 2195, KU 2196, KU 39037, KU 21110, KU 28629, KU 4808, KU 38423, MCZ 50520, MCZ 453, MCZ 1955, MCZ B7259, MCZ 34519, MCZ 34161, MCZ 50527, MCZ 50526, MCZ 34520, MCZ 50522.

Lynx rufus - KU 2641, KU 68065, KU 6676, KU 6680, KU 58954, KU 45215, KU 45046, KU 82824, KU 48077, KU 48063, KU 45178, KU 50261, KU 63129, KU 64367, KU 64368, KU 70010, KU 9643, KU 9792, KU 5707, KU 50211, KU 50212, KU 63755, KY 76302, KU 2240, KU 5321, KU 68807, KU 68808, KU 68809, KU 76517, KU 7039, KU 13903, KU 18770, KU 100131, KU 8410, KU 83465, KU 100121.

Puma concolor - KU 73928, KU 73729, KU 73930, KU 73931, KU 84882, KU 54856, KU 54857, KU 2194, KU 6107, KU 2185, KU 48092, KU 48096, KU 48095, KU 48094, KU 2191, KU 35561, KU 35560, KU 35562, KU 35563, KU 89165, KU 14554.

Heipailurus yagouaroundi - KU 93838, KU 886, KU 47305, KU 40179, KU 71942, MCZ B9095, MCZ B5646, MCZ B8428, MCZ 21711, MCZ 21759.

Leopardus wiedi - KU 90988, KU 107872, KU 93836, KU 90532, KU 93837, MCZ 34328, MCZ 51384.

Lepardus pardalis - KU 82202, KU 82203, KU 83582, KU 93835, KU 57005, KU 19281, KU 66228, MCZ 27210, MCZ 17028, MCZ 11066, MCZ B8148, MCZ 27216, MCZ B5647, MCZ 30728, MCZ 28099, MCZ 31822, MCZ 32186.

Leopardus tigrina - MCZ 5358, MCZ 6413, MCZ 24058, MCZ 20979, MCZ 31085.

"Felis" rexroadensis - UMMP 34195, UMMP 34196, UMMP 29644.

"Felis" trumani - P3a/450, KU 26290, KU 26289, KU 26133, unnumbered specimen.

"Felis" studeri - KU 563.

"Felis" lacustris - KU 4665, USNM 12611.

Lynx issiodorensis - UNSM 25504, UNSM 39233.

"Lynx" stouti - UNSM 25490.

APPENDIX 2

Analyzed Dental Variables

Upper tooth row

1. *Length of canine* - greatest anterior-posterior length across the canine's alveolus.
2. *Width of canine* - greatest width of the canine's anveolus measured from some medial point to the point opposite it on the lateral side.
3. *Length of Diastema* - least distance from the posterior of the canine's alveolus to the anterior border of the P3's alveolus.
4. *Length of P3* - greatest anterior-posterior length across the P3's alveolus.
5. *Length of P4* - greatest anterior-posterior length across the P4's alveolus.
6. *Width of P4 at protocone* - greatest width from the medial point of the protocone to the point opposite it on the lateral surface of P4.

Lower tooth row

1. *Length of canine* - Same as 1 above.
2. *Width of canine* - same as 2 above.
3. *Length of Diastema* - same as 3 above.
4. *Length of p3* - same as 4 above.
5. *Length of p4* - same as 5 above.
6. Length of ml - greatest anterior-posterior length across the ml's alveolus.
7. *Length of ramus to condylar process* - distance from the anterior of il to the posterior most point of the angular process.
8. *Length of ramus to angular process* - distance from the anterior of il to the posterior most point of the angular process.
9. *Length of ramus to coronoic process* - distance from the anterior of il to the posterior most point of the coronoid process.
10. *Width of the ramus at the notch in ml* - least distance between the medial and lateral surfaces of the ramus at the carnassial notch.
11. *Thickness of the ramus at the posterior border of ml* - least distance between the dorsal and ventral surface of the ramus at the posterior border of the ml's alveolus.

GROWTH RATES AND OTHER POST-NATAL DEVELOPMENTAL CHANGES IN MARGAYS

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INTRODUCTION

Knowledge of an animal's physiological profile is essential for preservation of a given species, both in wild and in captive environments. Follis and Morse (1974) made a plea for physiologic-normals research, including descriptions of growth parameters. These measurements can provide a barometer of the animals' health and may ultimately be related to their reproduction and conservation. In addition, such data will provide further knowledge about felid life-histories which can be useful for comparative purposes among felid species in particular, and among mammals in general. The information could also be utilized in relation to hypotheses in community and population ecology, and in developmental ethology. Thus, a two-fold purpose can be served by physiologic-normals studies: 1) by contributing toward the conservation of endangered species, and 2) by contributing toward a general knowledge of felid life-histories as it relates to basic science.

To our knowledge, the literature contains no reports of growth rates in margays *(Felis wiedii)*. Indeed, few studies have been conducted on any species of cats with respect to weight gains through adulthood (Crandall, 1964; Cisin, 1967; Veselovsky, 1967; Ulmer, 1968; Volf, 1968; Armstrong, 1975). Three references are made to margay birth weights (Douglas, 1970; Perry, 1973; Treanor, 1974). The latter article also mentions an eye-opening date in this species. Other reports, too numerous to be included in the reference section, give some data on felid growth rates, birth weights, and various developmental parameters. Most of these references are included in the *International Zoo Yearbook* and the *Long Island Ocelot Club Newsletter*.

The objectives of this paper are: 1) to present growth rates (body weight and several body measurements) of captive margays; 2) to describe selected post-natal developmental changes in this species; and 3) to compare these data with those on other felids. It is hoped that the information will be useful as physiologic-normal data for future studies on *F. wiedii* and on other species of cats.

METHODS

Most of the data were acquired on a male (Morgan) and female (Manchita) margay which were subjects of two other studies (Petersen, 1976, 1977). Also included in the current study were two other margays (Ludi, a male, and Emily, a female) which were captive-born to Morgan's sire and dam in 1966 and 1969, respectively.

Morgan was captive-born (January 9, 1970) to a female from western Mexico and a male from Columbia, South America. He was bottle-raised from birth, and was obtained by us at 2.5 months of age. Manchita was wild-caught from near Ayutla, Guerrero in southern Mexico, while still a suckling. We estimate, based on body weight and size, that she was born approximately 1 May, 1969, or 2.75 months before we purchased her from a Mexican trapper. Prior to purchase this cat was kept in a small wire cage. Nevertheless, she seemed to be healthy and quite tame.

During the study, Morgan and Manchita were housed together in a dry basement room. Room dimensions were 35 feet long (10.68 m) by 12 feet wide (3.66 m) by 8 feet high (2.44 m). Numerous furnace ducts (cold and warm), shelves and ledges were available for climbing to various heights. A large window was situated at the south end of the room. Two smaller windows were located on the west wall near the ceiling. Two upright six-foot (2 m) logs were provided as scratching and climbing posts. A 12-foot long (3.66 m) horizontal clothesline rope was available for the cats to jump and swing on. Air temperature ranged from about 66° F (18.9° C) in winter to 77° F (25° C) in summer.

Because of differences in food preferences, Morgan and Manchita each had a separate diet. Morgan was fed two, 4 oz. (114 g) meals per day of a commercially prepared diet, Feline Zu/Preem. Manchita was given two, 3.25 ounce (92 g) meals of Friskies Giblets and Turkey Parts each day. To her food was added 1/2 teaspoon of powdered Squibb's "Vet Nutri" (vitamin supplement) and 12 drops of liquid vitamin ("ABDEC" by Parke-Davis) every day. One 10-grain calcium gluconate tablet was crushed and placed in her food three times weekly. Chicken bones were given once or twice a week for added calcium and to aid in teeth cleaning. Fresh water was available *ad libitum*. Lettuce, celery or carrots were frequently provided to aid the cats in passing hair efficiently through the alimentary canal. Neither cat was declawed, defanged, or neutered. Further details on care of these animals appeared in the two above-mentioned investigations. Emily was bottle-raised on Esbilac and ABDEC vitamin drops, whereas Ludi was raised by his mother.

Weights were taken by placing a cat on a bathroom scale. Pound readings were then converted to the nearest gram. Body measurements were made in millimeters on hand-held, un-anesthetized individuals, so these figures are only approximate. Morgan's weights and measurements were taken on an average of once every 29 days from age 0.23 years to age 6.56 years, while those of Manchita were obtained approximately once every 26 days from age 0.24 years to age 7.25 years.

RESULTS

Weights and Measurements

The growth rates of body weights for Morgan and Manchita are presented in Figure 1. We consider this parameter to be the most accurate growth indicator of all measurements taken. Both cats' curves indicate constant, rapid early growth followed by an abrupt cessation which was more apparent in the female. The female achieved her mature body weight (at 0.67 year) at an earlier age than did the male (1.67 years); however, both had attained about 90% of their adult body weights by ages 0.50 and 0.81 years, respectively. The male's mature body weight was 36.4% heavier than that of the female.

Instantaneous growth rates (IGR) were calculated for the cats' body weights from age 3 months to the ages when their asymptotic body weights were attained. The following equation from Brody (1945) was utilized:

$$\mathrm{IGR} = \frac{\ln m_2 - m_1}{t_2 - t_1}$$

where IGR is the instantaneous growth rate for the period between t_2 and t_1; $l_n m_2$ and $l_n m_1$ are the natural logarithms of the measurements taken at times t_2 and t_1 respectively. For these cats, $t_2 - t_1$ was approximately 27 days. The student's t-test was used to assess statistical differences between mean IGR's. No significant difference in IGR ($P<.05$) was evident between the male (IGR = 1.97) and the female (IGR = 4.65).

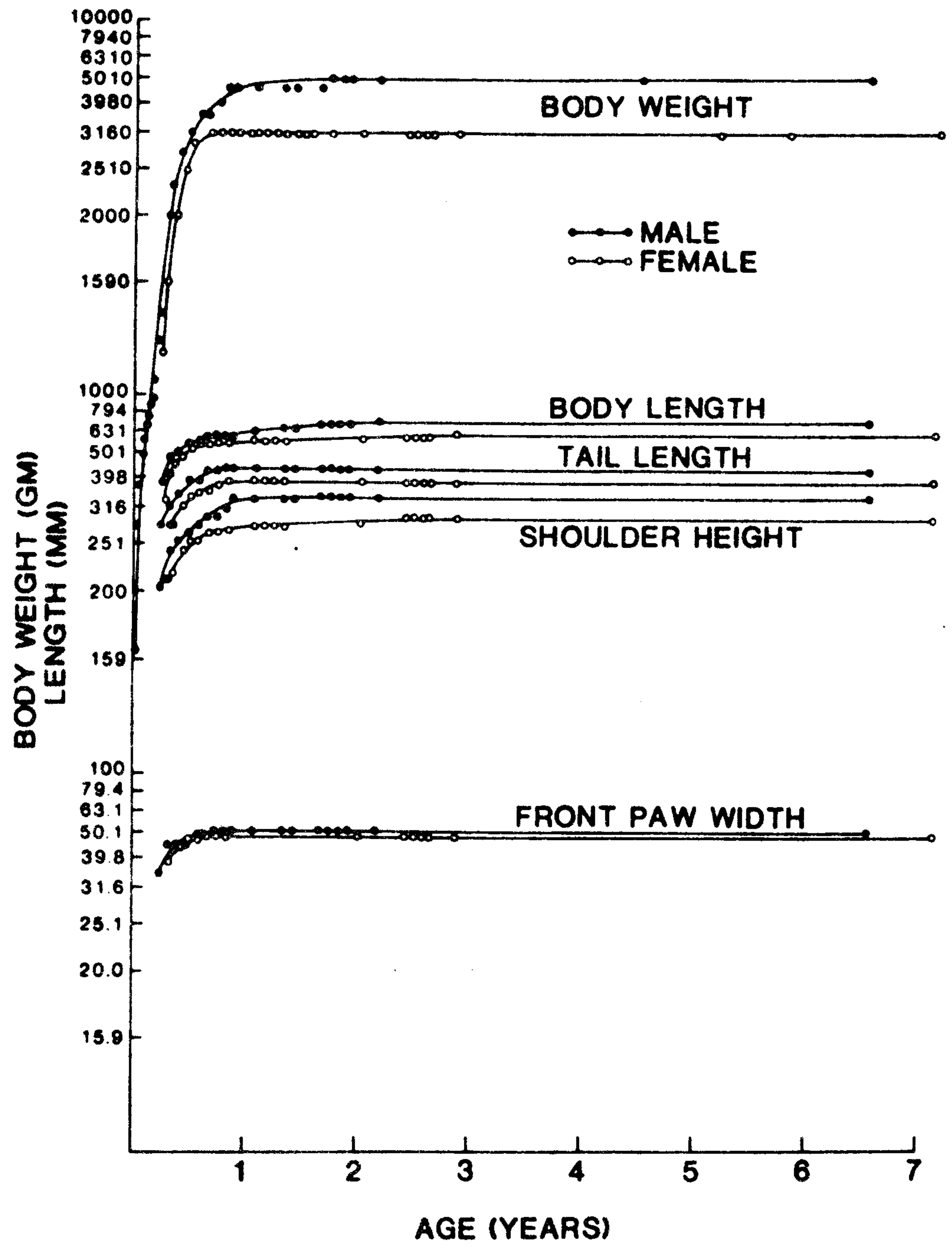

FIGURE 1. Absolute growth curves for body weight and selected body measurements of two captive margays *(F. wiedii)*. Semilogarithmic plots.

IGR's were also calculated for Morgan, Ludi, and Emily from birth to age 3 months. All three were weighed once every 7 to 9 days. No significant differences ($P<.05$) in IGR existed between any of these animals (Morgan's IGR = 12.78; Ludi's IGR = 8.98; Emily's IGR = 10.04). Stated in somewhat different terms, the average daily weight gain for Morgan, Ludi and Emily during their first four weeks of life was 16.20 grams (range = 15.78 - 16.50 gm.). Ludi was weighed at intervals of 2 to 6 days from 16 to 30 days of age; the data indicate that oscillations occurred in his weight gains during this time (see Table 2).

Selected body measurements (body length, tail length, shoulder height and front paw width) for Morgan and Manchita are also given in Figure 1. Growth of body length paralleled body weight gains in both sexes. The male's tail reached its mature length before his mature body weight was achieved, while the female's tail reached full growth somewhat after her mature body weight was attained. Front paw growth for both sexes followed the same pattern as that of the tail. Shoulder height growth also essentially followed the same pattern as body weight growth for both sexes. All body measurements for the male were larger than those of the female at comparable ages.

Post-Natal Developmental Changes

Certain post-natal developmental changes appear in Table 1. Although both eyes were open by the days given in this table, one eye was usually open 2 to 3 days before the other. Manchita began to shed her deciduous canine teeth 10 days before the permanent canines appeared, whereas Morgan did not lose his deciduous canines until about 2 weeks after the permanent canines began to erupt. Even though solid food (Zu/Preem) was first taken by the young cats at 52-57 days of age, all were started on strained chicken (baby food) at about 45 days.

Morgan was able to urinate without external stimulation (tapping) at 52 days of age. Emily groomed her front paws and made gestures toward grooming her face at 8 days of age, and was able to climb from her 30 cm high nest box at 27 days.

Table 3 contains information regarding ontogenetic changes in physical appearance. Adult pelage was acquired at approximately 6 to 7 months of age with respect to texture and at 9 to 10 months with regard to color. The nape hair was reversed at least from the time we acquired both cats (approx. age = 3 months). Changes in the physical appearances of both cats were similar to one another, except that the male seemed to retain his general "kittenish" look somewhat longer than did the female. This was particularly noticeable with respect to the shape of the face. Morgan, Ludi and Emily seemed to have inherited their dam's coat pattern of larger spots and blotches which tended to form a horizontal striping configuration. Their more yellowish background color was similar to that of the sire. The sire's smaller spots and blotches, which formed no definite pattern, were not evident on his three offspring.

DISCUSSION

These margays' birth weights compare favorably with those given by Douglas (1970), Perry (1973), and Treanor (1974). Furthermore, they are in relatively close agreement with respect to birth weights of closely related species: *F. pardalis* - 206 to 340 g (Travers and Travers, 1973; Hauser, 1974; Dunn, 1974; Treanor, 1975), and *Leopardus geoffroyi* - 65 g (Scheffel and Hemmer, 1975). Cisin (1967) lists the adult weight of margays as between 2,724 and 9,080 g. The adult weights of our cats were well within this range, as were their body and tail lengths when compared with those listed by Hall and Kelson (1959).

Few studies have compared male and female growth rates. Veselovsky (1967), Stehlik (1971) and Morse and Follis (1974) found that both sexes of young tigers *(Panthera tigris)*, jaguars *(P. onca)*, and lions *(P. leo)*, respectively, had comparable growth rates, but males' adult weights were generally greater than those of females. Meyer-Holzapfel (1968), however, stated that male *F. silvestris* gained weight faster than did females. Male cats of most species tend to mature at a later age than females. The margays of the current study were no exception. In addition, their average daily weight gains and oscillations in these gains were similar to those reported by Hemmer (1976) for other species of small felids.

Large felids tend to attain their adult body weight at age 3 to 5 years (Veselovsky, 1967), but most of their growth is made in their first 9 months. Small cats, on the other hand, usually mature at 9 months to one year of age (Ulmer, 1968; Volf, 1968; Armstrong, 1975). However, Cisin (1967) indicates that two male ocelots *(F. pardalis)* reached their adult weights at ages 24 and 30 months, respectively. Our margays seemed to follow the pattern of maturation for

TABLE 1. Age (days) when Certain Post-natal Developmental Changes were First Noticed in our Young Margays.

Individual	Birth wt. (g)	Both eyes Open	Deciduous Canines First Noticed	Permanent Canines First Noticed	Solids First Taken
Morgan (male)	163	11	20	165	52
Ludi (male)	---	16	--	---	57
Emily (female)	170	15	--	---	52
Manchita (female)	---	--	--	99	--

TABLE 2. Oscillations in Daily Weight Gains for One Male Margay (Ludi).

Ludi's Age (da.)	Daily Weight Gain (gm.)
16-18	28.50
18-22	7.00
22-24	21.00
24-30	9.50

TABLE 3. Ontogenetic Changes in Physical Appearance of Morgan and Manchita.

Age (months)	Fur Texture	Background Color of Fur	Shape of Face	Eye Color
3	Wool-like	Tan, except yellowish along mid-dorsal area	Round, ears large in proportion to head in male and small relative to head in female	Brown with bluish hue in entire iris
4	Same as above	Same as above except more yellowish on sides of neck and body in female	Same as above	Brown, except bluish around outer rim of iris
5	Beginning to lose wool-like texture	Same as above	Same as above	Same as above
6	Almost entirely smooth and silk-like, but less so in male	Same as above; male beginning to acquire somewhat more yellowish hue	Somewhat more angular, especially in female; male's ears more normal relative to head size	Entire iris brown
10	Smooth as in adults	More yellowish as in adult margays	Angular adult appearance in female; somewhat less so in male	Entire iris brown
17	Adult texture	Adult color	Adult form	Entire iris brown

Although abrupt cessation of growth might be a useful marker in studies of felid development, this phenomenon does not seem to occur, or has not been reported, for other species. In most studies, weights have not been taken past the time that an animal is assumed to have reached adult weight. However, data from Robinette et al. (1961) and Armstrong (1975) do suggest a somewhat abrupt cessation in the growth rates of *F. concolor* and *F. nigripes,* respectively.

It should be noted that growth rates of captive cats are maximized because of supranormal nutrition (Follis and Morse, 1974). Kitchener et al. (1975) demonstrated that hand-raised snow leopard cubs *(P. uncia)* were heavier than those raised by their mothers. This may explain the lower IGR of Ludi compared with those of Morgan and Emily.

According to Table 1, there is some variation in margays' eye opening dates, even among young born to the same parents. The literature also indicates considerable variation among many species of cats, both large and small: *P. leo* - 0 to 6 days (Crandall, 1964); *P. tigris* - 0 to 17 (Ewer, 1973); *F. yagouaroundi* - by day 5 (Herd, 1970); *F. nigripes* - by day 6 (Leyhausen and Tonkin, 1966); *L. tigrinus* - at day 17 (Leyhausen and Falkena, 1966); *L. geoffroyi* - at 12 days (Scheffel and Hemmer, 1975); *F. pardalis* - at 14 to 17 days (Dunn, 1974); *F. wiedii* - at 11 days (Treanor, 1974). Ewer (1973) states that the early eye opening dates in some big cats may be related to the unprotected situations in which many of them are born. Baudy (1971) attributes variation in eye opening dates of tigers to subspecific differences.

Cisin (1967) indicates that some *F. pardalis* are born with their deciduous canines already erupted, and that the permanent canines appear at age 8 months. Armstrong (1975) lists first appearance of canines in *F. nigripes* at day 18, while the permanent canines erupt by day 146. Hatfield (1970) indicated that margays shed their deciduous teeth by age 5 months. Morgan, in the present study, was within this range; but Manchita's permanent canines appeared at an earlier age. Because of this evidence and because this animal was wild-caught, it is possible that she is as much as 2 months older than originally believed.

Most species of small felids are weaned by age 7 to 12 weeks. The large cat species, in contrast, are weaned at a later age (generally at 3-6 months) than are the small felids (Crandall, 1964; Veselovsky, 1967; Sankhala, 1967; Carvalho, 1968). The cheetah *(Acinonyx jubatus)* seems to be an exception. Several reports list an age of about one month when solids are first taken by this cat, or when weaning occurs (Florio and Spinelli, 1967, 1968; Vallat, 1971, Tong, 1974). Perry (1973) indicated that margays began consuming solids at 49 days; Dunn (1974) reported ocelots first eating solid foods at 65 days of age. Leyhausen and Falkena (1966) found that young *L. tigrinus* began eating solid food at a later age (55 days) than did young domestic cats *(F. domestica)*. Our data for margays are consistent with these findings.

Armstrong (1975) reported first voluntary urination at day 15, and patting motions suggestive of grooming with paws at day 4 in *F. nigripes*. Various reports of first leaving the nest box or den include *L. geoffroyi* at 35 days (Scheffel and Hemmer, 1975); *F. nigripes* at 28 days (Leyhausen and Tonkin, 1966); *F. caracal* at 21 days (Kralik, 1967); *F. lynx* at 30 days (Burger, 1966). The larger felids first leave their nest at about the same age as the smaller cats (Sankhala, 1967; Schaller, 1967; Stehlik, 1971), but young *Panthera* spp. generally remain with their mother for a longer period of time than do their small felid counterparts (Ewer, 1973). Information on developmental changes in felid pelage and eye color is sparse. Cisin (1967) mentions that the eye color of *F. pardalis* kittens begins to change from blue to brown at about 3 months of age. She also describes the wool-like texture of ocelot kittens' fur, but the age at when adult pelage is attained is not given.

In conclusion, the margays' growth rates were approximately the same in males and females, although the male's adult weight was greater than that of the female's. Some of the other developmental parameters were roughly comparable to those of certain other small felid species. More data are needed both for margays and other small cats before meaningful comparisons can be made.

ACKNOWLEDGMENTS

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LITERATURE CITED

Armstrong, J. 1975. Hand-rearing black-footed cats *Felis nigripes* at the National Zoological Park, Washington. *International Zoo Yearbook* 15: 245-249.

Baudy, R. E. 1971. Notes on breeding felids at the Rare Feline Breeding Center. *International Zoo Yearbook* 11: 121-123.

Brody, S. 1945. Time relations of growth of individuals and populations. Pp. - , *In: Bioenergetics and Growth*. Reinhold, New York.

Burger, M. 1966. Breeding of the European lynx *Felis lynx* at Magdeburg Zoo. *International Zoo Yearbook* 6: 182-183.

Carvalho, C. T. 1968. Comparative growth rates of hand-reared big cats. *International Zoo Yearbook* 8: 56-59.

Cisin, C. 1967. *Especially Ocelots*. Harry G. Cisin, Publ., Amagansett, New York.

Crandall, L. S. 1964. *The Management of Wild Mammals in Captivity*. The University of Chicago Press, Chicago and London.

Douglas, S. 1970. Another domestic-born margay. *Long Island Ocelot Club Newsletter* 14(6): 7.

Dunn, G. L. 1974. Use of a domestic cat as a foster mother for an ocelot *Felis pardalis*. *International Zoo Yearbook* 14: 218-219.

Ewer, R. F. 1973. *The Carnivores*. Cornell University Press, Ithaca, New York.

Florio, P. L., and L. Spinelli. 1967. Successful breeding of a cheetah *Acinonyx jubatus* in a private zoo. *International Zoo Yearbook* 7: 150-152.

____________________. 1968. Second successful breeding of cheetahs *Acinonyx jubatus* in a private zoo. *International Zoo Yearbook* 8: 76-78.

Follis, T. B., and R. W. Morse. 1974. The need for physiologic-normals research. Pp. 238-242, *In*: R. L. Eaton (Ed.), *The World's Cats - Biology, Behavior and Management of Reproduction*. Vol. 2. Feline Research Group, Woodland Park Zoo, Seattle.
Hall, E. R., and K. R. Kelson. 1959. *The Mammals of North America*. 2 Vols. The Ronald Press Co., New York.
Hatfield, J. 1970. (from) The news. *Long Island Ocelot Club Newsletter* 14(3): 18.
Hauser, E. 1974. (from) Meeting report of Pacific Northwest Branch of *Long Island Ocelot Club Newsletter* 18(3): 10.
Hemmer, H. 1976. Gestation period and postnatal development in felids. Pp. 143-165, *In*: R. L. Eaton (Ed.), *The World's Cats: Contributions to Biology, Ecology, Behavior and Evolution*. Vol. 3, No. 2. Carnivore Research Institute, University of Washington, Seattle.
Herd, Mrs. David. 1970. And then there were seven. *Long Island Ocelot Club Newsletter* 14(1): 8-9.
Kitchener, S. L., D. A. Meritt, Jr., and M. A. Rosenthal. 1975. Observations on the breeding of snow leopards *Panthera uncia* at Lincoln Park Zoo, Chicago. *International Zoo Yearbook* 15: 212-217.
Kralik, S. 1967. Breeding the Caracal lynx *Felis caracal* at Brno Zoo. *International Zoo Yearbook* 7: 132.
Leyhausen, P., and M. Falkena. 1966. Breeding the Brazilian ocelot-cat *Leopardus tigrinus* in captivity. *International Zoo Yearbook* 6: 176-178.
___________, and B. Tonkin. 1966. Breeding the black-footed cat *Felis nigripes* in captivity. *International Zoo Yearbook* 6: 178-182.
Meyer-Holzapfel, M. 1968. Breeding the European wild cat *Felis s. silvestris* at Berne Zoo. *International Zoo Yearbook* 8: 31-38.
Morse, R. W., and T. B. Follis. 1974. Physiologic normals research in lions. Pp. 188-199, *In*: R. L. Eaton (Ed.), *The World's Cats: Biology, Behavior and Management of Reproduction*. Vol. 2. Feline Research Group, Woodland Park Zoo, Seattle.
Perry, P. 1973. Very precious gems. *Long Island Ocelot Club Newsletter* 17(2): 6.
Petersen, M. K. 1976. Behavior of the margay. Pp. 39-59, *In*: R. L. Eaton (Ed.), *The World's Cats: Contributions to Biology, Ecology, Behavior and Evolution*. Vol. 3, No. 2. Carnivore Research Institute, University of Washington, Seattle.
___________. 1977. Courtship and mating patterns of margays. Pp. 22-35, *In*: R. L. Eaton (Ed.), *The World's Cats - Contributions to Breeding Biology, Behavior and Husbandry*. Vol. 3, No. 3. Carnivore Research Institute, Seattle, Washington. 144 pp.
Robinette, W. L., S. Gashwiler, and O. W. Morris. 1961. Notes on cougar productivity and life history. *Journal of Mammalogy* 42: 204-217.
Sankhala, K. S. 1967. Breeding behavior of the tiger *Panthera tigris* in Rajasthan. *International Zoo Yearbook* 7: 133-147.
Schaller, G. B. 1967. *The Deer and the Tiger*. The University of Chicago Press, Chicago.
Scheffel, W., and H. Hemmer. 1975. Breeding Geoffroy's cat *Leopardus geoffroyi salinarum* in captivity. *International Zoo Yearbook* 15: 152-154.

Stehlik, J. 1971. Breeding jaguars *Panthera onca* at Ostrava Zoo. *International Zoo Yearbook* 11: 116-118.
Tong, J. R. 1974. Breeding cheetahs *Acinonyx jubatus* at the Beekse Bergen Safari Park. *International Zoo Yearbook* 14: 129-130.
Travers, T., and J. Travers. 1973. England's first domestic-born ocelot. *Long Island Ocelot Club Newsletter* 17(5): 5.
Treanor, S. 1974. Observation of a margay birth. *Long Island Ocelot Club Newsletter* 18(5): 6.
_________. 1975. The births. *Long Island Ocelot Club Newsletter* 19(6): 16.
Ulmer, F. A. 1968. Breeding fishing cats *Felis viverrina* at Philadelphia. *International Zoo Yearbook* 8: 49-55.
Vallat, C. 1971. Birth of three cheetahs *Acinonyx jubatus* at Montpellier Zoo. *International Zoo Yearbook* 11: 124-125.
Veselovsky, Z. 1967. The Amur tiger *Panthera tigris altaica* in the wild and in captivity. *International Zoo Yearbook* 7: 210-215.
Volf, J. 1968. Breeding the European wild cat *Felis s. silvestris* at Prague Zoo. *International Zoo Yearbook* 8: 38-42.

THE WELFARE OF THE PUMA IN CALIFORNIA, 1976

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California is the only state in which the puma *(Felis concolor)* is protected by a hunting moratorium. This formerly bountied predator was classed as a big game mammal in 1969 but, after 2 years of licensed hunts, public demand brought about protection starting in 1972. During this moratorium the California Department of Fish and Game was to gather data on distribution and numbers and to make plans for puma management. This paper includes some of the results of their studies (1972-1976) and of my independent studies (1973-1976) on the welfare of the puma.

Under legislative mandate the Department of Fish and Game made an interview survey which indicated that the overall distribution of the puma was roughly the same as during the bounty period, 1908-1963, when over 12,000 puma bounties were paid, but that recent occurrence was irregular and spotty. The Department of Fish and Game map of the reported sites of bountied kills showed that some cats were taken dozens of miles from regular puma haunts in the mountains and some taken in every county, save one, San Francisco. To analyze these kill data I classified the kill rates for the 55-year bounty era into three degrees of concentration within overlaid squares of 36 sq mi. These rates were: low, 4 to 15 spots; moderate, 16 to 63 spots; and high, 64 or more spots per square. With student help I outlined the boundaries of each kill rate zone (Figure 1) and measured the square miles in each. For the state, the total area of low kill rate was roughly 5,000 sq mi, moderate rate, 8300 sq mi, and high rate, 600 sq mi totaling in all about 14,000 sq mi.

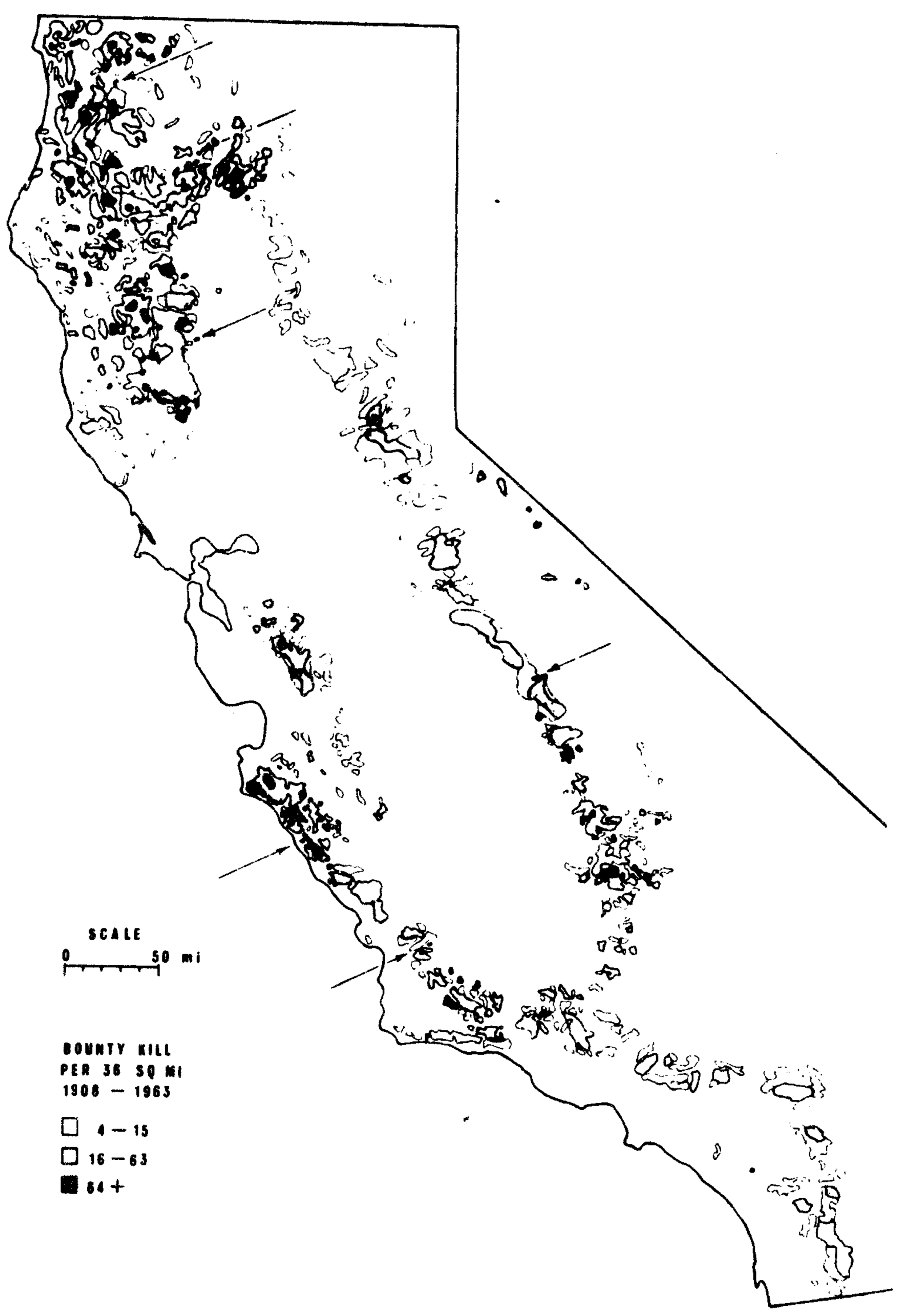

FIGURE 1. Map of bountied kill rate zones, 1908-1963. Arrows indicate centers of six study areas.

To reveal changes in the distribution of kills within counties over the years I compared the mapped zones with the distribution of kill spots during the last quarter of the bounty era, after 1950, allowing for the shorter period. These comparisons showed notable reductions in kill rates after 1950 in large sections of several northwestern counties, including areas with new large reservoirs and intense recreational use (e.g., Shasta Lake, Clair Eagle Lake), as well as in the northern Sierra Nevada and in the mountains just north of Los Angeles. The kill rate was sustained, however, in other sections, especially the southern Coast Range and the central Sierra Nevada. In general, the trend was toward disappearance of puma kills from low kill rate zones and restriction to parts of the earlier moderate-to-high kill rate zones, as one might expect in a decreasing overall population. In addition, the average annual number killed in the state dropped from about 290 during the first 8 bounty years to about 135 during the last 8 years, the major decrease occurring in the early 1940's. The contribution of the original four highest counties to the state kill decreased about two-thirds from the first to the last 8-year period. The rate of kill probably decreased after 1963, when bounty payments ceased, but data are scant. Tag returns for the licensed hunts, 1970-1972, again showed most kills in central counties. Further, 94% of 118 kill sites reported fell within the former bountied kill zones.

In addition to analyzing kill data, from 1973 to 1976 I collected hundreds of puma reports from forest and wildlife men, ranchers, hunters, and other outdoorsmen. Although the validity of these reports is unverified, at least 90% of the sites fell within the former kill rate zones. From these data and my own tracking, it appears that those zones include nearly all of the resident pumas, that is, those present year-around and producing young. Pumas that stay for shorter periods or travel through are termed floaters (= transients of Hornocker, 1970). Some gaps between the mapped patches of range may now include residents, but such additions of area seem to be more than compensated within nearby zones by areas that now lack residents. I conclude, therefore, that the overall range of regular occurrence of the puma in California, or resident range, has been fairly stable for decades and comprises roughly 15,000 sq mi.

Many patches of that range, however, have diminished in size since the bounty era, especially from the southern end of the Sierra Nevada southward through Los Angeles county to the Mexican border. Local decreases have surely occurred in mountains near cities and in heavily used recreational areas. Yet today a locally experienced woodsman can usually find puma tracks within a day or two of search under good conditions, and single pumas are reported at localities where they were thought to be rare a decade ago, such as near Big Sur and Carmel Valley in Monterey County. These current reports might indicate increases in total numbers of pumas under reduced hunting, in boldness under protection, in proportion of far-ranging floaters in the population, in puma travels during a period of deer scarcity, or in public awareness of wildlife.

The ecological range of the puma in California is mostly between 2,000 ft and 6,000 ft elevation among mixed conifers or mixed brush, especially where these types interdigitate. At upper levels pure stands of true firs or lodgepole pine and, at lower levels, pure stands of chamise brush *(Adenostoma)*, rarely include pumas. Several localities where pumas were intensively hunted for bounties have been modified by roads, forest fires, logging, and recreational use, yet they now have pumas. Apparently site attachment and tradition are strong in these cats, as in African lions, elephants, mountain sheep and some other mammals. The most essential area for a mammal is that part of the resident range where the special environmental requirements for the bearing and raising of young are met. This breeding range could be outlined from the locations of birth dens and of mothers with small kittens, but records of these are scant.

The general distribution process in the puma, based on the syntheses of several years of study in Idaho (Hornocker, 1970; Seidensticker et al., 1973) and habits of other mammals, seems to be about as follows. Kittens accompany their mother in her home range, then at about 20 months of age leave her and disperse into a broader range of environments as floaters. During these travels, which may last for months, they sustain high mortality in unfamiliar surroundings. They seek suitable unoccupied home ranges in which to settle but, as the best places are already occupied by residents, in the view of a floater, "good habitat is bad habitat," and the cat may be forced to travel on or to remain in marginal areas. Only a small proportion of the dispersing cats is able to settle down in good home ranges. Although many immatures disperse from their natal range, the fact that distribution occurs in patches of traditional ground supports the idea that pumas rarely colonize a new area in the sense of starting a breeding group in a region where there were no resident pumas. Large areas of the state appear to be suitable for pumas, yet lack them; and there seem to be no clear examples of expansion of resident range in California during this century.

To estimate total numbers in the state one must know both the area of regular occurrence and the average density of pumas. Density means number present per unit area at a particular instant, and comparisons of densities are meaningful only if the measurements are taken at the same season (Dasmann, 1964). I estimated densities from the evidence of distinctive puma footprints found on six study areas in summer. These areas, chosen to represent a variety of puma environments, were located in Fresno, San Luis Obispo, Monterey, Lake, Shasta, and Siskiyou counties and ranged in size from 115 to 280 sq mi (total 1,055 sq mi). Over a period of 3 years I tracked each area 15 to 82 days for total distances of 157 to 495 miles, over 1,600 miles in all. From this tracking I derived a road count index for each study area in terms of the number of different cats detected per 100 miles of road and trail tracking. Then, by comparing these results with the total number of pumas that I was able to detect by intensive search of the study area, I "calibrated" the indices to indicate numbers per 100 sq mi.

Within a study area I think that the footprints of all cats present at about the same time can be distinguished by their size and shape. The most useful single measurement is the width of the hindfoot heelpad, measured as shown in Figure 2. In a quarter inch of dust the hindpad prints of grown pumas (independent of mothers) measured from 42 to 60 mm wide. Those measuring 50 mm or more were judged to be of males. Some other features that aided individual identification were: the shape of heelpad margin, especially the angularity of corners, the depth of heel notches, and the asymmetry of lateral "cheeks"; the pointedness of toes; and the advance of the second toe ahead of the third toe. Sketches of footprints, photographs of prints alongside a millimeter scale, and plaster casts documented characteristics for later comparisons.

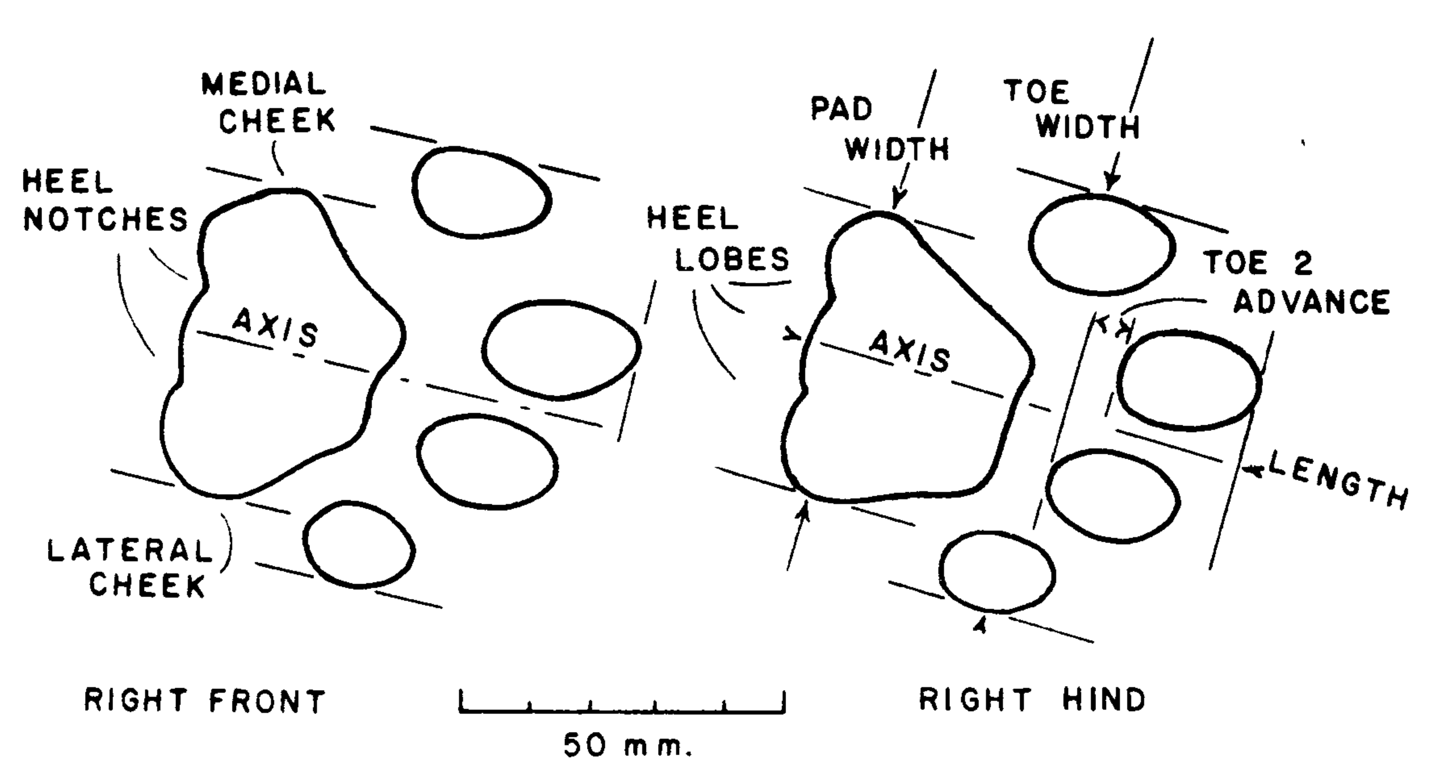

FIGURE 2. Suggested method of measuring puma footprints. Figure based on tracks of a pet yearling male. Width hindpad 44 mm, forepad 50 mm.

The best method of finding tracks on a road was to walk about 2 mph with pauses at curves, passes, turnouts, and other favorable ground. For more rapid travel I drove dirt roads about 7 mph, scanning the ground on one side and, with allowances for spotty coverage, searched the opposite side on the return trip. At the end of each day I summed up the miles tracked and the number of different tracks found. In each study area I made index runs at intervals in order to increase opportunities for detecting all cats present, and I pooled the results of these index runs for each summer to obtain an average track index for each area. These indices ranged from 0.9 to 4.8 cats per 100 miles tracked, excepting one study area where no tracks were found.

To find the number of cats in an area by intensive search for tracks requires several days and the tracks found may be several days old. Hence, a period of ground tracking indicates the number of cats using the area during a period of at least a week, which I call weekly traffic, rather than at one time, or true density. Some cats tracked in a study area also use range outside of it during a tracking period. Hence, in computing the area occupied, I added a strip one mile wide around the peripheral area searched. For any tracking period traffic would equal density only if the number of cats that are detected in the study area, and then depart, is compensated by an equal number that enter and remain undetected. For purposes of comparison, I assumed that the average numbers detected during periods of 2 months (3 to 11 days tracking) was roughly the same as the average one-day density. Average 2-month traffic in the study areas ranged from 0.9 to 3.5 cats per 100 sq mi. To calibrate indices for each study area I divided the traffic by the tracking index to derive a conversion factor. These factors ranged from 0.4 to 0.8, average 0.6. That is, if the index was 3 cats per 100 mi of road tracking, the indicated density was 1.8 (= 3 x .6) cats per 100 sq mi. A 0.5 factor would indicate that, on average, the index revealed the presence of pumas within one mile each side of the road, a 1.0 factor, within a half mile each side of the road. Outside of study areas students and I tracked in 23 counties for a distance of over 1,300 miles. The highest road index was 6.0 cats per 100 miles, which indicated a local density of about 3.6 cats per 100 sq mi in central Santa Barbara County.

Another density estimate was based on a study by the Department of Fish and Game in the Santa Lucia range south of Monterey. Over a period of 3 years they radio-collared 17 pumas and monitored the signals. The average monthly number detected during the highest 3 months of each year was about six grown cats in an area of over 200 sq mi, approximately three per 100 sq mi. Studies in other states have suggested puma traffic of from two to five cats per 100 sq mi, but comparisons with these are difficult because they were based on different seasons, periods of time, categories of animals, and allowances for peripheral movement. Considering all data, including about 3,000 miles of my ground tracking, I conclude that the average summer density in good puma country throughout California is three grown cats per 100 sq mi. This figure is roughly the same as the thumb rule of one per 36 sq mi proposed long ago for the "normal range" of the puma by our first state lion hunter, Jay Bruce (1925).

Assuming an average of three pumas per 100 sq mi in 15,000 sq mi of resident range, the number in that range is 450 grown cats, including floaters.

In addition, there are juveniles with their mothers in the resident range and floaters scattered widely and irregularly outside of it. If we take 1,000 as a working figure for the number of pumas in California, assume that the average proportion of residents, juveniles and floaters derived from the Idaho studies (Seidensticker et al., 1973) applies to pumas in the resident range, and allow an equal number of floaters outside of the resident range, the composition of the California population would be as follows:

		Male	Female
Residents	430	160	270
Juveniles (under 2 years old)	230	110	120
Floaters in resident range	170	110	60
Floaters outside resident range	170	110	60
TOTALS	1000	490	510

This table indicates 600 pumas in the resident range, a third more than my estimate of 450. Further, the sparcity of kitten records suggests that the indicated proportion of juveniles is too high for current conditions. Hence, I think that there are less than 1,000 pumas in California.

For California we have few data on population structure, largely because we have no reliable method for distinguishing age classes. How many females are of breeding age? Bounty records indicated a sex ratio of about 90 males per 100 females, but these included a large proportion of young. The Department of Fish and Game study area captures (17) comprised a ratio of 183 males per 100 females, perhaps because many cats were floaters which are mostly males. The only analysis of birth seasonality showed that births (26) occurred in every month of the year, with most in April (Grinnell et al., 1937). We have little data on rates of birth and survival in California pumas. Idaho studies suggest an average biennial production of two kittens per breeding female, usually at least 3 years old (Hornocker, 1970).

How did pumas survive half a century of bountied hunting? The kill was largely composed of kittens and floaters, I think, rather than of basic breeding stock. And lost residents were probably replaced by floaters from nearby regions, as reported for currently hunted areas in Nevada and Idaho (Fish and Wildlife Service, 1976). It has not been demonstrated that reduction in numbers stimulates reproduction in pumas, as it does in deer.

Deer are the main prey of pumas in this state but large areas of deer range, especially in the Northeast, have few pumas. There is but slight correlation between the deer kill and the puma kill by counties; during the last 8 bounty-years, the average ratio of deer to puma killed ranged from 64 to 1,000 (median 250) in the 15 counties leading in puma kill. Puma kills are hard to find. We have essentially no data for the numbers of deer taken annually by pumas in California, none for the proportion of alternate prey in the diet, and none for scat analysis. Judged by range maps, resident pumas occur in about a third of the winter range of deer, a fifth of summer range, and a tenth of the state area.

The Idaho studies indicated that a grown puma may kill about 30 deer per year. Hence, deer densities as low as four per sq mi, 400 per 100 sq mi, with normal annual mortality (including predation) of 25% to 40%, could continually supply ample prey (100 to 160) for three or four pumas. During the 1950's average densities of deer in the state were over 10 per sq mi, but in the last decade numbers have sharply declined. This diminished supply of prey might be affecting pumas by decreasing the survival of kittens, by making marginal ranges untenable, and by increasing the foraging distance of individual cats.

Some 100,000 cattle and 75,000 sheep graze on National Forests of California; yet apparent losses to pumas occur only about a dozen times a year (Department of Fish and Game, 1976). About half of the incidents involve sheep; but a recent study shows that of all sheep annually lost to predators in California, only about 1.2% are taken by pumas, as compared to over 14% by dogs and more by coyotes (Nesse et al., 1976). Reported kills are investigated by the Department of Fish and Game and, if confirmed, a permit is issued to the landowner to take a puma within 10 miles and 10 days. About half the permits result in the kill of a puma, usually by a federal government hunter. About two-thirds of the stock-killing pumas are males (Department of Fish and Game, 1976), perhaps most of them floaters.

The Idaho studies emphasized the importance of social behavior in pumas, including antagonism between resident males; yet over a period of 8 years there was no apparent evidence of fighting (Seidensticker et al., 1973). In California males may fight. For example, in 1924 hunters found two badly lacerated males, one dead, near a female (Grinnell et al., 1937). More recently the Department of Fish and Game found a dead radio-collared male that was bitten up as by another puma, and at another locality found a collared cat that was cut up at the time of recapture but not located again (Department of Fish and Game, 1976). Infanticide has not been documented in California although other states have reported observations (Hornocker, 1970; Dewar and Dewar, 1975). From what we know about pumas so far, I predict that many features of social behavior described for the African lion (Schaller, 1972; Bertram, 1975), such as kinship groups, synchronous breeding, and effects of male dominance on mating will be found in the puma. For behavior, as for density and population dynamics, we lack sufficient information for proper management of the puma.

Wildlife management is the "process by which closely related needs of wild animals and of people are evaluated, reconciled, and met" (Scheffer, 1974). Sound management, which leaves the wildlife community in good shape and protects esthetic values, must be based on sound biological information. To provide this base, for each major population of pumas we need to gather a wide range of biological data from which to predict the outcome of natural and man-caused influences.

In 1972 California initiated a hunting moratorium which legally protects pumas, except that, under permit, confirmed depredators can be taken and other pumas pursued by unarmed men with dogs. Most Californians seem content with this policy though many object to dog pursuit. It will be years before we have the reliable data needed for a detailed, sound management plan. Hence, the most practical course at present is protection of pumas, ecological education of the public, and careful research. Removal of depredators can be regulated as a form of data collection. Protected, the cats should become increasingly observable for study and enjoyment as California's most spectacular carnivore.

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LITERATURE CITED

Bertram, B. C. R. 1975. The social system of lions. *Scientific American* 232: 54-60, 65.

Bruce, J. 1925. The problem of mountain lion control in California. *California Fish and Game* 11: 1-17.

Dasmann, R. F. 1964. *Wildlife Biology*. J. Wiley and Sons, New York.

Department of Fish and Game. 1976. California Mountain Lion Study. Department of Fish and Game, Sacramento, California. 40 pp. Mimeo.

Dewar, P. E., and P. L. Dewar. 1975. Northwest Bay Cougar Study. Progress report. Nanaimo, B.C. 37 pp. Mimeo.

Fish and Wildlife Service. 1976. *Transactions of the Mountain Lion Workshop*. U.S. Fish and Wildlife Service, Portland, Oregon. 213 pp. Mimeo.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. *Fur-bearing Mammals of California*. Vol. II. University of California Press, Berkeley. Pp. 533-589.

Hornocker, M. G. 1970. An analysis of mountain lion predation under mule deer and elk in the Idaho Primitive Area. *Wildlife Monograph* 21: 39 pp.

Nesse, G. E., W. M. Longhurst, and W. E. Howard. 1976. Predation and the sheep industry in California 1972-1974. *University of California Division of Agricultural Sciences Bulletin* 1878: 63 pp.

Schaller, G. B. 1972. *The Serengeti lion*. University of Chicago Press.

Scheffer, V. B. 1974. *A Voice for Wildlife*. Charles Scribners and Sons, New York.

Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monograph* 35: 60 pp.

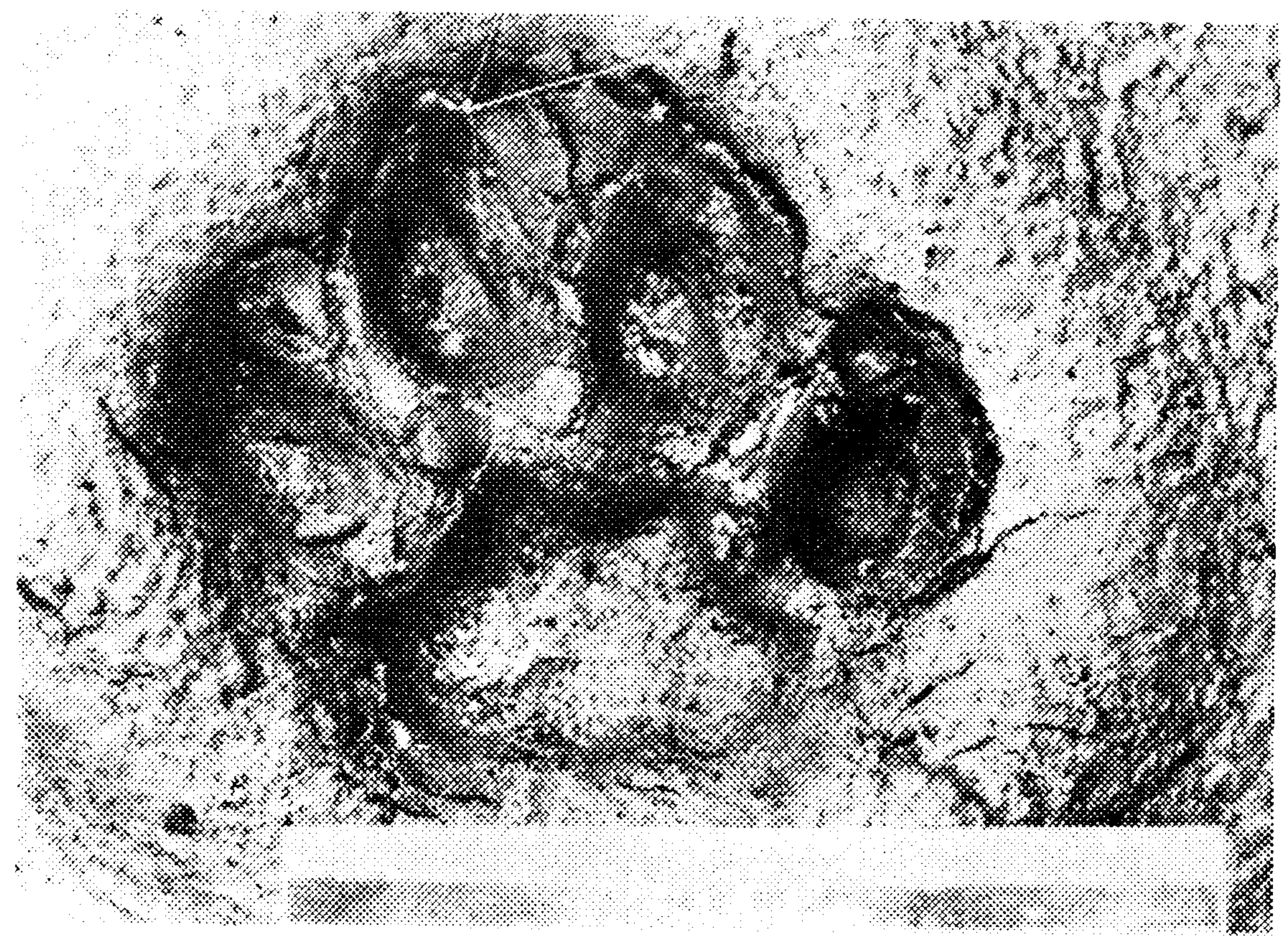

FIGURE 3. Right forefoot of male puma in mud. Scale is 150 mm long.

FIGURE 4. Puma footprints. Across center, tracks of adult male heading to left; above, tracks of adult female or large cub heading to right. At bottom, track of a black bear heading to left.

FIGURE 5. Footprints of male puma and mountain quail in dust.

STATUS AND CONSERVATION OF THE SUMATRAN TIGER

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Of the eight tiger subspecies, one, the Bali tiger *(Panthera tigris balica)* is already extinct and three others, the Javan tiger *(P. t. sondaica)*, the Chinest tiger *(P. t. amoyensis)* and the Kaspian tiger *(P. t. virgata)* are close to extinction with little hope of survival. Poaching and habitat destruction all over the range of the other four subspecies, the Bengal tiger *(P. t. tigris)*, the Siberian tiger *(P. t. altaica)*, the Indochina tiger *(P. t. corbetti)* and the Sumatran tiger *(P. t. sumatrae)* threaten their survival.

On behalf of World Wildlife Fund International and the Dinas-Perlindungan dan Pengawetan Alam (Indonesian Nature Conservation Department), I carried out a study on the status and conservation of the Sumatran tiger. This survey was done in connection with World Wildlife Fund's "Operation Tiger" and Project 884, "Sumatran Rhinoceros."

METHODS

From December 1972 to August 1975 I travelled throughout the Island of Sumatra, spending one to two months in each province and working the rest of the time in Aceh and North Sumatra.

Countless interviews were carried out with officers from the Nature Conservation Department, the local Forestry Department, Army, Police, village-heads, hunters, taxidermists, villagers, and many others. Based on these data, survey areas were selected in every province. I searched for evidence of the tiger on expeditions into these survey areas; for instance, scratching and pug marks, feces, remains of kills, and so on. Based on such evidence, an estimation of the number of tigers in Sumatra was worked out.

DISTRIBUTION AND STATUS OF THE TIGER IN SUMATRA

I have found evidence of the tiger in all of the eight Provinces of Sumatra. The tiger is rare in most of these areas and has found its last stronghold in the lowland forests of Central Sumatra and in the heavily forested areas of the Province of Aceh.

Large parts of the Province of Aceh in the north of Sumatra are still covered with primary forests. I have found evidence of tigers in 12 different locations. The tiger population in the large Gunung Leuser Reserve (4,365 km) is relatively low, as the Reserve consists mainly of mountainous areas. In the east and west coast lowlands, the forest is more favorable to the tiger. But it is also in these areas that timber, farming and plantation activities are progressing rapidly. The tiger is bound to conflict with the human population and is hunted frequently. In 1975 I could confirm that at least 10 tigers were killed in the Province of Aceh.

The Province of North Sumatra (Sumatera Utara) is densely populated. Tigers still occur in the northern part of the province, in the Langkat Reserve (2,100 km^2), and at the southern boundary in the lowlands of Torgamba near the Barumun River. Poaching in the Langkat Reserve seems to be rare. No tiger hunting could be confirmed in the last few years.

In the Province of West Sumatra (Sumatera Barat) tigers still occur in the northwestern and southwestern parts which have a low human population density. Poaching is frequent--a taxidermist at Padang-Panjang claims that he receives about two tiger skins a month (1974).

The largest number of tigers is living in the Province of Riau. Most of the still existing lowland forest of this province is under timber exploitation. Due to the abundance of secondary growth in these areas, the tiger's favorite prey species, pigs and deer, are abundant. In these areas the tiger has its optimal habitat. Poaching is frequent. Six tigers were killed in the surroundings of Duri during my 6-week survey in the area in March-April 1974.

A large part of the Province of Jambi is still covered with forests. Most lowland forests are under timber exploitation, and in the mountainous areas of Kerinci shifting cultivation is very active. Evidence of the tiger can still be found in all parts of the province. Two areas will be important for the conservation of the tiger, namely the lowland reserve of Berbak (1,900 km^2) and the mountain area south of Sungei Penuh in the Kerinci-District. Poaching occurs but is difficult to confirm.

The Province of South Sumatra (Sumatera Selatan) has a rather dense human population, and large forest areas can only be found in the northern part of the province. Tigers still occur in several areas; I found evidence around Pendopo. Here the tigers manage to survive in an area that is covered with Alang-Alang grass and only a few patches of forest. The tigers frequently attack domestic cattle and are hunted ruthlessly. Palembang, the main town of the province, is the center for illegal trading and smuggling of tiger skins. At least six taxidermists are working in this city.

Little is known about the status of the tiger in the Province of Bengkulu, although poaching is frequent. I have found evidence of the tiger in the Sungei Seblat area, and it also seems to occur in the northern and southern part of the province.

In the Lampung Province in the south of Sumatra I have found evidence of tigers in the Wai Kambas area in the east and in the Sumetera Selatan I Reserve in the west. The forest cover in this province is shrinking rapidly and poaching is frequent.

Evidence of breeding was found in several places. In Singkil I could observe a tigress with two cubs.

Pug marks of a tigress with a cub were found in the Mamas and Pinus river area of the Gunung Leuser Reserve and in the Utung river area (Aceh), Torgamba (North Sumatra), Sungei Buluhala and Sungei Kubu (Riau). Tiger cubs were offered for sale in Singkil (1 cub), Tapaktuan (2 cubs), Duri (2 cubs) and Bukittinggi (1 cub). Only in Tapaktuan could the origin of these animals be traced--the mother was shot by a plantation manager near Tapaktuan.

ESTIMATION OF NUMBERS

Due to the difficulties of the habitat, the large area surveyed, and the limited time I could spend on the survey, it is very difficult to make an accurate estimation of the numbers of tigers still surviving in Sumatra.

I have found the tracks of at least 39 different tigers. (The average "largest width" of the forefoot was 14.7 cm. and that of the hindfoot was 12.4 cm.) In addition I had direct observation of three more animals. Taking into account the evidence of tigers which I found, the dimension of the area in which tigers still occur, the different density of tiger population in primary/secondary and lowland/mountain forests, local information and information on tiger hunting, I can make the following approximate estimation:

Province	Approximate Number of Tigers
Aceh	100
North Sumatra	50
Riau	300
West Sumatra	50
Jambi	200
South Sumatra	100
Bengkulu	100
Lampung	50
Total	1,000

The total number of tigers still surviving in Sumatra would therefore be around 1,000 animals.

THREATS TO THE TIGER POPULATION

Habitat Destruction

The main prey species of the tiger, pigs and deer are animals mainly of the forest fringe and not of the large primary forests. The densest tiger populations can be found where the living conditions for its prey species are optimal.

Selective timber cutting is therefore not destroying the tiger's habitat. Selective cutting is, on the contrary, inducing the growth of secondary vegetation, which allows a dense population of pigs and deer. The abundance of prey species is a precondition for the occurrence of a good tiger population. It must be stressed, though, that selective timber cutting is disasterous for some species like the orang utan or the Sumatran rhinocerus.

The opening of the remote wilderness areas by timber and oil companies, however, has facilitated the approach to these areas and, consequently therefore, to local hunting. In opening the hitherto unaccessible areas to local farmers the forest is burnt down and the habitat of the tiger completely destroyed. Due to the loss of its habitat and natural prey species, the remaining tigers are forced to feed on the domestic stock of the farmers and are consequently killed.

Hunting

Sport hunting of tigers was introduced by expatriates and was very popular a few years ago. Sport hunting was done quite openly and is therefore relatively easy to control. Under the Directorship of Ir Priyono Harjosentono, the Indonesian Department for Nature Conservation (Dinas PPA) is doing its best to stop this kind of hunting.

In spite of the fact that the tiger has been protected by law since 1972, it was still common in 1973 for tigers to be killed by sport hunters; and the event was often published in local newspapers. The following example may show how things have changed today.

"Siliwangi" is an army unit stationed in Java which has the tiger as its symbol. The commander of this unit, Colonel Sulaya Sutikna, wanted tiger skins for the hats of the unit's drummers. Two tigers were shot on his order in Aceh and the skins were sent to Java. PPA officials reported the tiger killings and consequently the commander was indicted. The case is still in court at the moment. Of the 10 confirmed tiger killings in the Province of Aceh in 1975, only two were carried out by sport hunters.

Foreign tourists, employees of foreign companies, and rich Indonesians pay over $1,000 U.S. currency for an undamaged tiger skin. As a local villager has an income of less than $50 (U.S.) a month, the incentive for poaching is very high.

Groups of three to four local hunters secretly build traps in the forest. Once a tiger is caught in a sling- or box-trap, the animal is strangled or drowned to prevent damage to the skin through shot wounds. Some of these poachers are operating on their own risk, but many receive a regular salary from taxidermists who prepare and sell the skins or smuggle them out of the country.

As this kind of hunting is done very secretly it is extremely difficult to control, especially outside a reserve. At least 70% of all tigers killed today are hunted by such local poachers. I found no evidence that poisoned meat is used to kill tigers.

CONSERVATION OF THE SUMATRAN TIGER

By a decree of the Minister of Agriculture the Sumatran Tiger is strictly protected since 1972.

Valuable tiger populations are existing in two established reserves, namely the Gunung Leuser/Langkat Reserve and the Berbak Reserve. The Gunung Leuser/Langkat Reserve consists mostly of high, mountainous areas. A large part of the Berbak Reserve is swamp forest which is not optimal for the tiger. Consequently, the tiger populations in these reserves are relatively low.

As a consequence of WWF's Tiger Survey, the Indonesian authorities are now establishing a large reserve especially for the protection of the tiger. The reserve will be situated in the Riau Province between Baramun and Rokan Rivers. Selective timber cutting will be allowed in this reserve, but all human settlements and farming activities will be banned. With this concept, the optimal tiger habitat of lowland forests with an abundance of secondary growth can be protected. The reserve will have an area of approximately 5,000 km^2 and harbor a population of about 100 tigers. This great effort of the Indonesian authorities to save the Sumatran tiger from extinction is supported by the World Wildlife Fund. The tiger reserve is situated in the concession area of the Caltex Oil Company which was asked to contribute funds and equipment to this project.

The Indonesian government is facing many problems in enforcing the protection of the tiger. Due to lack of staff, equipment and funds, the protection of the tiger outside of the reserves is extremely difficult.

The WWF Tiger Survey in Sumatra has, together with concerned Indonesian authorities, worked out several proposals to restrict illegal tiger hunting:

All tiger skins already in private possession should be inventoried; newly purchased skins should be confiscated.

All taxidermists should be strictly controlled. Officials, disguised as tourists, should try to locate tiger skins held illegally.

Most tiger skins are smuggled in small boats from Medan, Pekanbaru and Palembang to Singapore. Army and customs officers should be trained especially to control the illegal traffic of protected animals and products of such animals.

In Singapore and Penang tiger skins are still openly sold in curio and leather shops. The Governments of Singapore and West Malaysia should be asked to prohibit the trading of tiger skins.

If it can be proved that a tiger is killing men, it should be shot by trained PPA personnel. As long as there is a demand from zoos with good reputations, such animals could be captured alive.

The hides, teeth and claws of all shot tigers should be destroyed or should belong to the government that could not sell them.

A small sum of money should be paid to local people when they can prove that they have lost a buffalo or goat by an attack of a tiger.

Nature Conservation Education is a precondition for the long-term survival of the Sumatran Tiger. Special campaigns for the tiger should be launched.

THE TIGER AND MEN

People Killed by Tigers

Many horror stories circulate among the people of Sumatra describing tigers who have killed dozens of people. Villagers claim that in 1972 a tiger killed 30 people in a rubber plantation near Batu Radja (South Sumatra). In most cases such stories are only used as an excuse to kill a tiger. I, myself, could confirm only three cases of human beings killed by tigers. During a geological survey of Riotinto Bethlehem in 1972 in the mountains of the Kerinci area, a tiger entered the field camp at Sungei Seblat in the night and killed one local employee. In 1973 a man who was working in his ladang (farmer's field near the forest) was killed by a tiger near Muara Tembesi (Province of Jambi). In 1974, during my survey in Lampung Province, a man was killed by a tiger in Wai Tebu. Other reports about people killed by tigers in Aceh and South Sumatra could not be confirmed.

Remarkably, the three confirmed killings have one thing in common: none of the victims was in upright position when attacked by the tiger. The man from Kerinci was sleeping, the man from Muara Tembesi was working in a squatting position, and the man from Wai Tebu was urinating, also in a squatting position.

Information and my own observations on encounters with tigers seem to confirm that a tiger gives way to a human being approaching upright. A tigress with two nearly full-grown cubs on a timber road in the Singkil Area (Aceh) watched my approach until about 50 meters before walking off into the forest.

It is obvious that tigers sometimes attack men, but such accidents seem to be very rare.

Raiding of Domestic Stock

In areas where the habitat of the tiger is gradually being destroyed reports of tigers killing domestic stock are frequent.

Such reports could be confirmed from all provinces where the tiger still occurs. I have inspected two such kills, one near the Langkat Reserve (North Sumatra) and one near Pendopo (South Sumatra). The tiger kills cows, waterbuffalos, dogs and sometimes goats.

In most cases the tiger is driven away from the kill, just to return for another kill. Several domestic animals killed in the same area mean a considerable economic loss to the native people and the regional Nature Conservation Department (PPA) is pressed hard for a permit to kill the tiger. PPA is looking for alternatives. In December 1975 the Nature Conservation Department of Aceh caught two such notorious cattle raiders and sent them to the Surabaya Zoo.

The Tiger in the Belief of Sumatra's Local Population

The tiger plays an important role in the mythology of the people of Sumatra. It is regarded with great respect and believed to have strong magical powers. It is believed, for instance, to bring bad luck to pronounce his name (Harimau) in the forest. He is therefore respectfully called

"Radja" (King) or his name is expressed with a gesture of the fingers, forming the claws of a tiger.

He is regarded as a messenger of God and the mighty spirits of the forest. He is said to kill only people who have done bad things. When somebody in a village gets killed by a tiger, it is regarded as a punishment of God and the forest spirits and offerings are made to calm the rage of the spirits.

In some areas people believe that the souls of their ancestors are living in tigers. Thus the killing of a tiger can mean the killing of the body of one's own ancestor. That such an act means bad luck for the whole area is evident.

People still believing in the old traditions are therefore not willing to hunt a tiger. If a tiger is harrassing a village, a "Pawang Harimau" or Tiger Magician is called. The Pawang speaks with the tiger, explaining to the tiger how difficult life is becoming for the villagers when all their cattle are killed. He asks the tiger to go back to the forest. If everything fails, the Pawang can give the permission to kill the tiger, but only after he himself receives permission from the forest's spirits to do so. Various ceremonies to calm the forest spirits have to be carried out before a tiger trap can be built. If a tiger is killed accidently in a trap meant for other animals, the enraged spirits of the forest have to be appeased by the Pawang to protect the hunter and the village from the revenge of these spirits.

People born with a harelip are said to be "tiger men." The inhabitants of certain areas of Sumatra believe that these people can be completely normal during day, but that they can change into a tiger in the night. The "tiger people" are much feared for what terrible things that they are able to do in the night.

A strange animal is the "Cegau." It is believed to live in remote mountain areas of the Seblat region in Bengkuli Province. The front half of the "Cegau" is a lion or a tiger, the back half a horse. The animal is said to be extremely ferocious and very fond of human flesh. Today it is still nearly impossible to convince the local villagers to take part in an expedition to these mountains.

The local beliefs about the tiger have proved to be very valuable for the conservation of this species in Sumatra up until now. Unfortunately these beliefs are vanishing rapidly today.

SUMMARY

World Wildlife Fund International has carried out a 2-year survey on the Sumatran Tiger. About 1,000 animals of this endangered subspecies may still survive, scattered over all the Island of Sumatra. The tiger has found its last stronghold in the lowland forests of Central Sumatra, where selective timber cutting is creating an optimal habitat.

Poaching is still frequent, but the Indonesian Nature Conservation Department is making great efforts to save the tiger from extinction. A 5,000 km^2 large reserve was created in the Riau Province to assure the survival of the Sumatran Tiger.

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I would like to express my thanks to the Nature Conservation Department and its Director, Ir Priyono, for all the help I received during my stay in Sumatra. I am grateful to L.I.P.I. for arranging my visa. I am most grateful to Mr. Poniran, Mr. Bangun, and all the numerous people who helped me on my survey throughout Sumatra.

APPENDIX:

SHORT NOTES ON THE ECOLOGY AND BEHAVIOR OF THE SUMATRAN TIGER

The World Wildlife Fund Sumatran Tiger Survey was aimed at the collection of data concerning distribution and status of the tiger. Only few data could be collected on the ecology of these animals.

The Sumatran Subspecies of the Tiger

Panthera tigris sumatrae (Pocock, 1929) is smaller than the Indian tiger. Sody (1949) reports the length of the animal, including tail, to be around 250 cm. Two animals shot in Duri during my survey in March 1974 were both males and had a length of 236 cm and 252 cm. Another male tiger, shot just one week earlier, was said to be 3 meters. I could not check this information. Similar to the two other Indonesian subspecies, the Sumatran tiger has a darker coloration than the mainland subspecies (Trap, 1973). This dark color was not very evident in the skins I was able to inspect. The three tigers I could observe myself in the Singkil area, however, were extremely dark colored. The ground color between the black stripes was not yellow or ochre, but dark brown. In diffuse light the stripes were hardly visible.

Of all tracks that were found, the largest width of the pug mark was measured. The average "largest width" of the pug mark of the forefoot was 14.7 cm, of the hindfoot 12.4 cm. The largest prints were found in the Kerinci area (Jambi) where a tiger had forefoot measurements of 16 cm and hindfoot measurements of 13.5-14 cm.

Habitat

Like other tiger subspecies, the Sumatran tiger is adaptable to all kinds of environment. I found evidence of the tiger from sea level up to the mountainridges of the Bukit Barisan at altitudes of over 2000 meters.

The tiger seldom ventures into the mangrove forests of Sumatra's East Coast. It is, however, one of the very few large ground-living animals that use the freshwater swampforest. In the large swamp areas of Riau and Jambi, the tiger prefers regions which are not always flooded and have large patches of dry ground.

Evidence of the tiger was found in the primary lowland, hill, submontane and damp-moss forest. It is able to survive in abandoned and overgrown rubber plantations (Jambi, Riau, Sumatra Utara) and even in Alang-Alang grass areas with only a few patches of forest (Pendopo).

The habitat requirements of the tiger are a good water supply, enough cover, and plenty of prey species. In Sumatra water and cover are plentiful in all tiger areas. Food supply seems to be the restricting factor for a tiger population.

Due to the scarcity of undergrowth in the undisturbed primary forests and therefore of food plants for ground-living herbivores, the population density of the tiger's main prey species, pig and deer, is very low. Secondary forest, created by selective timber cutting, is the optimal habitat for the tiger's main prey species. Wild boar, deer and other ground living herbivores find plenty of food in the soft secondary vegetation. These animals are more abundant here than in undisturbed primary forests where food is sparse.

In these selective timber cutting areas the undergrowth is dense and provides an ideal cover for the tiger. Water is plentiful.

Due to abundance of prey species and dense cover, lowland forest under selective timber cutting is the optimal habitat of the Sumatran tiger. About 70% of the tigers still surviving live today in such lowland forests.

Density of Population

Unlike in India, forest area, water and cover are abundant in Sumatra. The limiting factor to the growth of a tiger population appears to be the availability of prey.

Prey species are more numerous in primary lowland forest than in primary submontane or damp-moss forests. In lowland forests that have an abundance of secondary growth due to selective timber cutting, the density of prey species is higher than in undisturbed primary lowland forest. The density of the tiger population is in direct relation to the density of its prey species.

In the mountainous primary forests of the Gunung Leuser Reserve, the tiger's prey species are rare and, consequently, the density of the tiger population is very low. I have only few data about the size of the tiger's home range in these mountains. Relative identification of tigers based on their footprints and tracking of individual animals suggest that they have a home range well over 100 km^2. I guess that about 50 tigers are living in the 4,400 km^2 of the Gunung Leuser Reserve. That would mean a density of about one tiger/90 km^2.

In the lowlands of Central Sumatra, especially in forests with secondary growth, the tiger's prey species are abundant. The density of the tiger population is higher than in the Gunung Leuser mountains. Tracks of different individuals can often be found close together. The home range is probably smaller than in the mountains. Due to the short time I spent in a single area, I could collect only very few data and can therefore not estimate the area of the home range. I guess that about 100 to 150 tigers are living in the 5,000 km^2 of the newly established Tiger Reserve in the lowlands of Riau. That would mean a density of about one tiger/50 km^2. This population density would still be lower than in the Kanha National Park in India, where Schaller (1967) estimated one tiger/30 km^2 and Sankhala (1974) one tiger/12.5 km^2.

Prey Animals

According to the analysis of feces and kills found, the main prey species of the Sumatran tiger is the wild boar (eaten also by the Javan tiger [Hoogerwerf, 1970]) *(Sus scrofa)*. I found the remains of a wild boar killed by a tiger in the Gunung Leuser Reserve. Wild boar hairs were found frequently in tiger feces. Several times the hair of the sambar *(Cervus unicolor)* was found in feces. A tiger kill in Besitang (Langkat Reserve) was a barking deer *(Muntiacus muntjak)*. Twice the remains of a mouse deer *(Tragulus javanicus* or *napu)* were found in tiger feces. The most remarkable kill I found was in Liwa (Lampung). A Malayan bear *(Helarctos malayanus)* had obviously been killed and partly eaten by a tiger.

Occasionally the tiger catches a monkey. Feces analysis showed that the pig-tailed macaque *(Macaca nemestrina)*, the longtailed macaque *(Macaca irus)* and the leaf monkey *(Presbytis)* (one feces sample each) are prey species. N. van Strien (personal communication) found in the Mamas area of the Gunung Leuser Reserve that even an adult orang utan male *(Pongo pygmaeus)* was killed and half eaten by a tiger.

In addition, nails of birds and hair of unidentified small mammals were found in tiger feces.

In newly populated areas where the tiger's habitat is being destroyed rapidly, the tigers also feed on domestic stock. I have seen two such kills--one was a cow, the other a dog. According to local information, water buffalos and goats are also killed by the tiger.

Schaller (1967) found that in India more than half of the tiger feces contained leaves or earth. Nothing similar could be observed in Sumatra.

After the tiger has killed its prey, it eats the prey in a safe, densely covered place. Parts of the barking deer killed in the Besitang area were eaten in different places. All of these places were in an area of about 200 meters in dense secondary growth near a river. The cow killed in Pendopo was dragged over 100 meters from the Alang-Alang grassland to a small area covered with dense shrub before the tiger started to feed.

Scratching Marks

Probably with its forefeet the tiger makes scratching marks on the ground. Such scratching marks are about 20 to 30 cm wide and 40 to 60 cm long. They can be found along animal trails, near kills and saltlicks. Often they are repeated every few hundred meters.

Scratching with the hindfeet was observed in connection with defecation. The droppings however, are not buried. The tiger scratches with both hindfeet before defecation. After placing the droppings in or near the scratching mark, the tiger sometimes scratches again, but not burying the feces. Scratching marks on the soil could be part of the tiger's communication system (Trap, 1973).

Scratching marks on trees are much less frequent. Claw marks on trees were found near a kill, near a saltlick, and along a main trail.

LITERATURE CITED

Hoogerwerf, A. 1970. *Udjung Kulon, The Land of the Last Javan Rhinoceros.* Brill, Leiden.

Pocock, R. I. 1929. Tigers. *Journal of the Bombay Natural History Society* 33(3): 504-541.

Sankhala, K. 1974. *Tiger.* World Wildlife Fund, Zurich.

Schaller, G. B. 1967. *The Deer and the Tiger.* University of Chicago Press, Chicago.

Sody, H. J. V. 1949. Notes on some primates, carnivora and the babirusa from the Indo-Malayan and Indo-Australian regions. *Treubia, Buitenzorg* 20: 121-190.

Trap, L. 1973. On the tiger in Indonesia. *A.L.H. 73-03,* Report No. 164. Agricultural University, Wageningen.

SOCIALIZATION BY INTELLIGENCE:

SOCIAL BEHAVIOR IN CARNIVORES AS A FUNCTION OF RELATIVE BRAIN SIZE AND ENVIRONMENT

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A review of the evolution of sociality in carnivores was given by Eaton (1976), mainly with reference to felids. It seems wise to proceed from that discussion in this paper to avoid needless repetitions. Eaton discussed the evolution of social behavior mainly in terms of natural selection; i.e., social behavior is probably under direct genetical control. Some serious doubts on this assumption arise when social behavior is studied not only in the wild, but in captivity, too. Many species show a broad plasticity of social behavior. There is strong pair bonding in species in which this type of sociality is uncommon in nature; there is help of the male for the female in the care of young, even in the first days after birth, not only in conspecifical pairs, but in heterospecifical ones, too; there is a great variability of social relationships towards man, and so on. Comparative investigations of carnivores in their natural habitat as well as in zoos add to the evidence that many species are capable of a much greater plasticity in social behavior than they usually show in nature. This means that different types of sociality found in different populations of the same species, as is true of the lion and the cheetah (Eaton, 1976), may merely suggest the realization of different behavioral possibilities without specific genetical background but based on a general social plasticity.

The idea that brain size is related to plasticity of social behavior was independently put forward at the same time by Krushinsky (1974) and myself (Hemmer, 1974). Krushinsky found a correlation between the rate of cephalization and the ability for elementary intellectual activity. He concluded on the basis of ethological facts accumulated up to this time that there is a specific relation between the development of animal intellectual activity and the level of complexity in intragroup social relations. He pointed out that mutual help and cooperation are characteristic of the animals with highly developed intellectual activity.

The main problem hindering a much earlier success in the approach to behavioral-brain correlations was how to measure the relative brain size in a truly comparative manner. It was explained in several publications by the author (Hemmer, 1971a, 1971b, 1974a, 1974b) why a reliable calculation of relative brain size has to be based on the intraspecific or intrapopulation allometric relationship between a parameter of the body size, e.g., the body weight, and the brain weight or volume, but cannot result from interspecific relations as it was done by most workers on the evolution of brain and intelligence (e.g., Jerison, 1973). I calculated cephalization constants in form of the value of the allometric equation's integration constant, with the mean mammalian allometric exponent 0.23 for the brain-body relationship.

The only correlations hitherto found with behavioral or other biological parameters are those described by Hemmer (1971a, 1974a) for primates with this cephalization constant. The only other cephalization parameter meaningful in a biological sense is the number of extra neurons as calculated by Jerison (e.g., 1973). As the values of the correlation coefficients for different cephalization parameters show (Table 1), there is a highly significant correlation between the cephalization constant as given by Hemmer and the extra neurons as given by Jerison in Old World monkeys and in apes. The cephalization index as given by Bauchot and Stephan and the cephalization quotient as given by Jerison are also significantly correlated in the monkeys with each other both basing on allometric exponents between 0.6 and 0.7 (0.63 in Bauchot and Stephan; 0.67 in Jerison), but show no correlations at all with the biologically meaningful parameters (Table 2). Although calculating cephalization levels with the interspecific or intergeneric brain-body-allometry with slopes about 0.6 - 0.7 may indeed have some long tradition, it produces less than useful results as shown; for example, in primates by the gorilla ranging below all cercopithecine monkeys and by the chimpanzee, related in all ways to the gorilla, but ranging above the cephalization level of nearly all cercopithecine species except the small *Cercopithecus (Miopithecus)* talapoin.

TABLE 1. Correlation Coefficients for Different Cephalization Parameters in Seven Ape Species, for Which Data Were Given by Bauchot and Stephan (1969), Hemmer (1971a) and Jerison (1973); Means of the Male and Female Values Were Taken in the Three Great Ape Species. All significant correlation coefficients are underlined in both tables.

	Cephalization Index - Bauchot and Stephan	Cephalization/ Quotient - Jerison	Extra Neurons Jerison
Cephalization Constant - Hemmer	0.03	- 0.40	<u>0.97</u>
Cephalization Index - Bauchot and Stephan	-	0.71	- 0.17
Cephalization Quotient - Jerison		-	0.48

TABLE 2. Correlation Coefficients for Different Cephalization Parameters in 20 Old World Monkey Species, for Which Data Were Given by Bauchot and Stephan (1969), Hemmer (1971a) and Jerison (1973).

	Cephalization Index - Bauchot and Stephan	Cephalization/ Quotient - Jerison	Extra Neurons - Jerison
Cephalization Constant - Hemmer	0.28	0.13	<u>0.99</u>
Cephalization Index - Bauchot and Stephan	-	<u>0.88</u>	0.24
Cephalization Quotient - Jerison		-	0.14

It was shown that curiosity as a measure of some part of intellectual activity significantly correlates in primates with the value of the cephalization constant. This indicates that there is an increasing role of individual experience gained by increasing exploratory activity with progressive cephalization. From the prosimians up to man the values of this constant very closely correlate with the duration of youth. Therefore, the whole time a primate can use for learning before reaching maturity is a function of its brain size as a measure of the morphological substratum of learning ability (Hemmer, 1971a, 1974a).

As for sociality in carnivores, we find several informative points which fit well the theory that social plasticity is based on learning ability as correlated with relative brain size. The three levels of socialization in canids described by Fox (1972) coincide well with the cephalization levels in the respective species. The type I "solitary" species with a very limited or more or less absent capacity for the formation of secondary social relationships have relatively low cephalization values (calculated for the different species mentioned here by use of brain and body weights given by Warncke [1908], Crile and Quiring [1940], Count [1947]): arctic fox--7, red fox--7.5. The type II canids with limited socialization capacity comprise somewhat higher cephalization values: from 7.5 in the black-backed jackal to 10.5 in the coyote. Values around 13 are typical for the more sociable type III species as the wolf (13.5) and the Cape hunting dog (13). Calculation of the correlation coefficient for these cephalization data and the levels of socialization of the respective species is significant (r = 0.92).

In the hyenids we found the same pattern. The highly social spotted hyena has a cephalization value about 14.5, while the solitary striped hyena's value is not higher than 8.5. In the felids the lion with its high socialization capacity stands high with a cephalization value of 16. Solitary species living in the same regions, the serval and the caracal, share in contrast mean values between 6.5 and 7. Unfortunately we have not yet a comparable value for the cheetah, which ranges between the lion and the latter-mentioned species in its social behavior (Eaton, 1976) but, according to braincase volume and skull size (Schauenberg, 1971), it seems to range near the puma, which has a mean cephalization value of 12. Thus these results obtained for the three carnivore families Canidae, Hyaenidae and Felidae support the theory that relative brain size level, and thus learning capacity, is correlated with social capacity and plasticity.

The differences in social behavior between carnivore species in zoos and in nature indicate what extremes of environmental condition can do in modifying sociality. The environmental-correlated sociality differences in lions or cheetahs, as discussed by Eaton (1976), obviously show the same. Group size and composition in lions was found tending to vary partly as a function of herbivore productivity and carrying capacity of different habitats (Eaton, 1976). The four hypotheses for socialization in carnivores formulated by Eaton (1976--the first three hypotheses are from Alexander, 1974) can all be effective on the basic assumption of a dependence of social plasticity on the learning capacity and its modification by habitat factors. These hypotheses are: 1) defense against predation, 2) nature of food resources favoring grouping, 3) intraspecific competition for critically limiting resources, and 4) interspecific competition for critically limiting resources.

If the high plasticity of social behavior in the African lion is understood as the result of a relatively high learning capacity based on its relatively high cephalization level, then a problem is why the tiger is not usually a group living species, too. The tiger stands together with the African lion at the top of the felid cephalization, having a mean brain size value of 17. Therefore, this species should also be a highly sociable one. It is to be assumed that the tiger's different habitat compared with the lion's is partly responsible for the tiger's more solitary mode of life. Some observations made in nature (e.g., Schaller, 1967) as well as in captivity suggest that the tiger is basically capable of group living, but may usually be forced by habitat condition not to use this social capacity. At a lesser grade of sociability the same may be true for the leopard and the jaguar which have cephalization values about 13.5 (see Hemmer, 1966, for a compilation of data on group formation and mutual help in these species).

Discussing the social situation of tigers, leopards and jaguars versus lions, a third factor besides brain size and habitat not yet well studied in the pantherines and other cat species seems worth mentioning. This is a factor of general behavior comprising motility, aggressiveness, and what is popularly called temperament. Psychopharmacological research in rodents has shown that manipulation in the neurotransmitter level of the brain can result in drastic changes in social behavior, lowering the aggressiveness and the spontaneous social activity, but raising the sociability (Ernst, in Hemmer, 1976). Examples of this kind occurring naturally include the differences between wild and domestic animals of the same species (see Hemmer, 1976).

In the pantherines such differences seem to exist between the lion and the tiger, the leopard and the jaguar being more on the side of the latter species. The motility of the lion seems to be somewhat lower than that of the other species but, unfortunately, we have not yet exact motility scores (Hemmer, 1966). An experienced circus lion and tiger trainer adjudged the tiger to have a much higher temperament than the lion (Togare, 1940). Objective studies on this character are lacking. In any case, the lion seems to be nearer the basic behavioral traits of domestic animals than the tiger, so that it is not surprising that the lion was tamed in ancient times for different purposes more often than the tiger.

The species of bears reach higher cephalization levels than found in felids, hyenids and canids. Here also we need much more knowledge on the behavioral plasticity given by the presumably high intelligence of bears before we will be able to understand the situation in this family.

Basic studies on relative brain size and related plasticity and complexity of social behavior may be possible by comparative field work and zoo research on African versus Indian lions. The latter are somewhat less cephalized than the African subspecies living south of the Sahara (Hemmer, 1971b; 1974c). Here is an opportunity to check experimentally what such differences in a large carnivore species mean on the whole for their behavior. The same thing should also be possible with wolves. In this species the northern Eurasian and American races have higher relative brain size than the southwestern, southern and central Asian ones (Hemmer, 1975, in preparation). The theory of socialization by intelligence gives rise to a myriad of problems, but here we see the same ways possible to clarify them. We could begin new research programs to throw light on socialization in carnivores and perhaps, at the same time, on basic problems of social life in primates, including man.

LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Systematics and Ecology* 5: 326-383.

Bauchot, R., and H. Stephan. 1969. Encephalization et niveau evolutif chez les simiens. *Mammalia* 33(2): 225-275.

Count, E. W. 1947. Brain and body weight in man: Their antecedents in growth and evolution. *Annals of the New York Academy of Sciences* 46: 993-1122.

Crile, G., and D. Quiring. 1940. A record of the body weight and certain organ and gland weights of 3,690 animals. *Ohio Journal of Science* 40: 219-259.

Eaton, R. L. 1976. The evolution of sociality in the Felidae. Pp. 95-142, *In*: R. L. Eaton (Ed.), *The World's Cats* 3(2). Carnivore Research Institute, Burke Museum, University of Washington, Seattle.

Fox, M. W. 1972. Patterns and problems of socialization in hand-reared wild canids: An evolutionary and ecological perspective. *Zeitschrift fur Tierpsychologie* 31: 281-288.

Hemmer, H. 1966. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Teil I. *Veroffentlichungen der Zoologischen Staatssammlung*. Munchen 11: 1-121.

_________. 1971a. Beitrag zur Erfassung der progressiven Cephalisation bei Primaten. *Proceedings of the 3rd International Congress on Primates*. Zurich, 1970, Vol. 1: 99-107.

_________. 1971b. Intraspezifische Unterschiede der relativen HirngroBe beim Lowen (*Panthera leo* L.). *Experientia* 27: 1500-1501.

_________. 1974a. Progressive Cephalisation und Dauer der Jugendentwicklung bei Primaten, nebst Bemerkungen zur Situation bei Vor- und Fruhmenschen. Pp. 527-533, *In*: W. Bernhard, and A. Kandler (Eds.), *Bevolkerungsbiologie*, Fischer, Stuttgart.

_________. 1974b. Brain size changes in mammalian evolution and domestication. *First International Theriological Congress Transactions* Vol. 1: 217-218 (Moscow).

_________. 1974c. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). III. Zur Artgeschichte des Lowen *Panthera*

(Panthera) leo (Linnaeus 1758). *Veroffentlichungen der Zoologischen Staatssammlung*, Munchen 17: 167-280.

__________. 1975. Zur Abstammung des Haushundes und zur Veranderung der relativen HirngroBe bei der Domestikation. *Zoologische Beitrage* NF 21: 97-104.

__________. 1976. Man's strategy in domestication - a synthesis of new research trends. *Experientia* 32: 663-666.

Jerison, H. J. 1973. *Evolution of the Brain and Intelligence*. Academic Press, New York and London.

Krushinsky, L. V. 1974. Comparative ethological study of elementary intellectual activity. *First International Theriological Congress Transactions* Vol. 1: 309 (Moscow).

Schaller, G. B. 1967. *The Deer and the Tiger*. University of Chicago Press, Chicago and London.

Schauenberg, P. 1971. L'indice cranien des Felides. *Revue suisse de Zoologie* 78: 317-320.

Togare, . 1940. Erfahrungen mit wilden Tieren. *Berliner und Munchener Tierarztliche Wochenschrift Jahrgang*.

Warncke, P. 1908. Mitteilung neuer Gehirn- und Korpergewichtsbestimmungen bei Saugern, nebst Zusammenstellung der gesamten bisher beobachteten absoluten und relativen Gehirngewichte bei den verschiedenen Spezies. *Journal of Psychology and Neurology* 13: 455-503.

CONSIDERATIONS ON SOCIALITY IN FOSSIL CARNIVORES

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Attempts to reconstruct behavioral traits of extinct animals are always puzzling projects, for behavior leaves direct remains in a fossil state only in some cases. Otherwise, we have to look for indirect evidence based on research with living forms. Such behavioral reconstructions depend on the level of correlation of morphology and behavior in modern relatives. Therefore, it is necessary to know correlations of this type in recent carnivores when considering sociality in fossil members of this order.

Such a correlation was shown to exist for the basic behavioral plasticity, the capacity of socialization, and the relative brain size in the preceding paper. The high correlation coefficient of 0.92 for canid cephalization and the pattern of socialization makes it reasonable to begin with this family. Cephalization constants were calculated for fossil species with cranial capacities and body weight estimates given by Jerison (1973). For the oldest real canid genus *Hesperocyon*, living from Eocene to Miocene (Thenius, 1969), a cephalization value of about 2.5 was found, which is lower than all known values of living canids. Therefore, it seems that these early canids belonged to the solitary social type I as defined by Fox (1972). We find the same for the next stage in canid evolution, the Miocene genera *Cynodesmus* and *Tomarctus* with cephalization values between 4 and 6.5 corresponding to the lowest values of recent canids. These predecessors of the extant genera and species (Thenius, 1969) have to be considered as solitary-living, too, because of their relatively low brain size. Members of the upper Tertiary North American genus *Mesocyon* scatter in the same cephalization range (4.5-6.5) and therefore may also have been solitary living forms with a very limited capacity for secondary socialization.

At the other end of the cephalization scale range was the big dire wolf, *Canis dirus*, of the American late Pleistocene. This species, with its brain size value of about 15.5, surpassed the wolf and the Cape hunting dog and therefore has to be considered at least as highly sociable as these and as having a very high capacity to form secondary social relationships. Another carnivore species of the Rancho La Brea fauna was supercephalized when compared with modern relatives. This was the giant American lion, *Panthera leo atrox*, which was as large or even larger than today's Siberian tigers (Hemmer, 1974a). Its brain size value amounts to about 18-19 (calculated from endocast volume and skull size given by Merriam and Stock, 1932, with the formulae published by Hemmer, 1974b for body length and weight). The environment of the region about the tar traps of the type locality Rancho La Brea, in which grass-covered surfaces were interspersed with copses of trees and brush, appears to have been favorable for the development of a diverse population of hoofed animals (Stock, 1930). A rich herbivore production surely allowed the lions to use their wide socialization capacity to form large prides and an even greater range of types of grouping than is to be found in the modern African lions.

There are more problems concerning social life in the large Rancho La Brea dirk-tooth cat, *Smilodon californicus*. According to the discussion by Radinsky (1975) on the brain and body size of this lion-sized species, we can calculate a cephalization value of about 13 with his data. This is in the brain size range of the non-social recent species puma, leopard and jaguar (12 - 13.5). A particularly high frequency of lesions in skeleton elements, mostly to be attributed to injury with subsequent infection (Stock, 1930), seems to reveal a highly aggressive animal not especially stuited to complex sociality. The remarkable representation of dire wolves and dirk-tooth cats in the tar traps of Rancho La Brea reflects in large measure the conditions prevailing in the immediate vicinity of the asphalt accumulations and the availability of a food supply especially for these species, as Stock (1930) pointed out. This suggests scavenging and carrion-feeding habits for these carnivores.

Looking at the sabre-tooth morphology from a functional viewpoint, it seems obvious that the extremely long dirk tooth is useful for stabbing, but is not the right instrument to kill only large pachyderms, as is often believed to have been the usual method of getting food in these cats. The risk of such a canine being broken in violent struggles with such huge victims is surely greater than for a shorter, more compact canine as is typical for the pantherines. On the other hand, the sabre tooth may have been more useful for opening pachyderm carcasses, while the pantherine canine is not specially suitable for this work. The dirk tooth was also certainly a formidable weapon against other competitive carnivores. Together with the powerful front limbs and a high aggressiveness, as indicated by the frequency of injuries, this unique armament must have been very efficient in interspecific competition, without forcing the dirk-tooth cats to socialize for undisturbed feeding or defense against predation. The occurrence of short-legged specimens (Merriam and Stock, 1932) suggests that this species had not much selective pressure to avoid competitors. The chance of such short-leg mutations, which are usually found in domestic animals, surviving in *Smilodon* populations makes the existence of flop-ears and piebald coat suggestive, too. Therefore, taking into account the known factors--brain size and environment--and the presumable aggressiveness which determine socialization, we should not expect a more complex grouping in *Smilodon californicus* than at most that found in the cheetah.

So the Rancho La Brean carnivore scene, on the whole, may be considered as a competition between super-carnivores in terms of their superior relative brain size, intelligence, and thus complex sociality, on the one hand, and a super-carnivore in terms of its mighty physical power and weapons, but less intelligence and hence less socialization capacity on the other.

The situation in the Pleistocene large dirk-tooth cat is not comparable with the biology of early Tertiary cats with the same sabre-tooth specialization. For the hoplophoneine genera *Hoplophoneus* with little, and *Eusmilus* with high, sabre-tooth specialization, cephalization values can be calculated in the range of 4 - 5 using brain volumes and body weights as given by Jerison (1973) and in the range of 5 - 7.5 using the body weight estimate of Radinsky (1975). In any case, the relative brain size of these lynx-sized species was not greater than the range given by the modern species domestic cat (4.5), European wild cat (6), caracal (6.5), and serval (7), and hardly reached the lynxes (7.5 - 8.5), all of which are essentially solitary living forms.

For a large species of the genus *Pseudailurus*, the basic group in the evolution of modern cats, Jerison's (1973) estimates for brain and body size give a cephalization value of 7.5, which is also by no means the value of a social living cat species. Therefore, the beginning of sociality in the cat family has to be considered as occurring not before the Lower Pleistocene about 2 million years ago when the first lions appeared on the scene, or perhaps in the late Pliocene with the evolution of the giant cheetah, *Acinonyx pardinensis*. Unfortunately, we have not yet weight estimates allowing a calculation of cephalization values in the latter species.

The large-brained modern hyenid and canid species with high socialization capacity originated also in the Pleistocene (e.g., Schutt, 1971, 1974). Therefore, we have to assume that the evolution of complex socialization patterns in carnivores occurred chiefly in this time. In the lower Tertiary only the amphicyonide genus *Cynelos*, among all forms for which Jerison (1973) gave some brain and body size estimates, reached a cephalization level perhaps allowing some limited capacity to form social groups (cephalization value 9). At the end of the Tertiary the genus *Plesiogulu* forerunning the recent glutton had a brain giving a cephalization value about 12.5. In the modern glutton the high intelligence is not used in socialization, perhaps because of its high aggressiveness. Therefore, we have also no sure indication of any form of social grouping in this Pliocene glutton stock. The same is true for the Pliocene and Pleistocene evolutionary basis of the recent bears.

We should always keep in mind this obviously relatively late development of sociality in carnivores when looking for any impact of social carnivores in the evolution of hominids (e.g., Eaton, 1976). When the early *Ramapithecus* hominids roamed in Europe, Africa and South Asia, the lion, spotted hyena, wolf, Cape hunting dog and so on were not yet in sight. More advanced hominids were already present in the lower Villafranchian (e.g., Howells, 1973; Groves and Mazak, 1975) when the first members of the genera *Crocuta* and *Canis* appeared at about 3 million years ago in Africa (Howell and Petter, 1976). At the time when the first lions emerged at about 2 million years ago, two or three different hominid lines, i.e., species, lived together and at least one of them was a highly cephalized tool-maker (e.g., Howells, 1973; Groves and Mazak, 1975). Therefore, the high capacity of some modern carnivore species for socialization evolved chiefly after the emergence of man in Africa and Asia.

Otherwise the highest brain size--and thus socialization capacity--levels in felids and canids occurred in the Rancho La Brea fauna's super carnivores before man entered the North American scene in the last glaciation. Thus the existence of man seems to have just as little basic importance for the socialization in carnivores as carnivore sociality obviously had for man's social behavior.

LITERATURE CITED

Eaton, R. L. 1976. The evolution of sociality in the Felidae. Pp. 95-142, *In*: R. L. Eaton (Ed.), *The World's Cats* 3(2). Carnivore Research Institute, Burke Museum, University of Washington, Seattle.

Fox, M. W. 1972. Patterns and problems of socialization in hand-reared wild canids: An evolutionary and ecological perspective. *Zeitschrift fur Tierpsychologie* 31: 281-288.

Groves, C. P., and V. Mazak. 1975. An approach to the taxonomy of the Hominidae: Gracile Villafranchian hominids of Africa. *Casopispro Mineralogica Geologie* 20: 225-247.

Hemmer, H. 1974a. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). III. Zur Artgeschichte des Lowen Panthera *(Panthera) leo* (Linnaeus 1758). *Veroffentlichunsender Zoologischen Staatssammlung*, Munchen 17: 167-280.

_________. 1974b. Korperproportionsunterschiede bei Pantherkatzen (Pantherinae). *Saugetierkundliche Mitteilungen* 22: 233-236.

________. 1978. Socialization by intelligence: Social behavior in carnivores as a function of relative brain size and environment. *Carnivore* 1(1):
Howell, F. C., and G. Petter. 1976. Indications d'age donnees par les carnivores de la formation d'Hadar (Ethiopie orientale). *Comptes Rendus del Academiede Science de Paris* 282 Series D: 2063-2066.
Howells, W. 1973. *Evolution of the Genus Homo*. Addison-Wesley Publ., Reading, Mass.
Jerison, H. J. 1973. *Evolution of the Brain and Intelligence*. Academic Press, New York and London.
Merriam, I. C., and C. Stock. 1932. *The Felidae of Rancho La Brea*. Publications of the Carnegie Institute, Washington, D.C. No. 422.
Radinsky, L. 1975. Evolution of the felid brain. *Brain Behavior and Evolution* 11: 214-254.
Schutt, G. 1971. Die Hyanen der Mosbacher Sande (Altpleistozan, Wiesbaden/Hessen) mit einem Beitrag zur Stammesgeschichte der Gattung Crocuta. *Mz.Naturw.Arch.* 10: 29-76.
________. 1974. Die Carnivoren von Wurzburg-Schalksberg. Mit einem Beitrag zur biostratigraphischen und zoogeographischen Stellung der altpleistozanen Wirbeltierfaunen vom Mittelmain (Unterfranken). *N.Jb.Geol. Palaont.Abh.* 147: 61-90.
Stock, C. 1930. Rancho La Brea. A record of Pleistocene life in California. *Los Angeles Museum Publication* 1: 1-84.
Thenius, E. 1969. Stammesgeschichte der Saugetiere (einschlieBlich der Hominiden). *Handbuch der Zoologie* 8,Bd. 2. T.W. de Gruyter, Berlin.

AN ENCOUNTER BETWEEN CHIMPANZEES AND A LEOPARD IN SENEGAL

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This paper reports an encounter between chimpanzees *(Pan troglodytes)* undergoing rehabilitation into a natural habitat and a wild leopard *(Panthera pardus)* at Mont Assirik in the Parc National de Niokolo-Koba, Senegal. This is the first recorded meeting of the two species in the park. Only a few observations of encounters between wild chimpanzees and leopards or lions have been reported before (Izawa and Itani, 1966; Kano, 1972; Nishida, 1968; Pierce, unpublished; van Lawick-Goodall, 1968).

No conclusive evidence exists for leopard predation upon wild chimpanzees, although Rahm (1967) gave an account of game scouts having surprised a leopard which was attacking an adult female chimpanzee and had fatally injured her infant. Of the potential predators at Mont Assirik, leopards would appear to be the most likely candidates since they are agile when climbing trees, the usual refuge of chimpanzees when threatened and at night. Of the other large carnivores in the park, hyenas *(Crocuta crocuta)*, wild dogs *(Lycaon pictus)*, and jackals *(Canis adustus)* cannot climb trees, and lions *(Panthera leo)* are not skilled in doing so (Schaller, 1972: 129). There is some evidence that leopards prey on the other two pongid species. Schaller (1963: 302-304) listed a number of second-hand reports of mountain gorillas *(Gorilla gorilla berengei)* having been killed, apparently by leopards, as well as observations of leopards eating gorilla flesh, and stalking a gorilla group. Rijksen and Rijksen-Graatsma (1975) reported that a clouded leopard *(Neofelis nebulosa)* which was subsequently captured, caused the deaths of seven orangutans *(Pongo pygmaeus)* undergoing rehabilitation in North Sumatra.

The rehabilitation camp for chimpanzees lies at the eastern base of Mt. Assirik. The climate of the area is characterized by a dry season (November to May) in which daily maximum temperatures are about 40°C and minima about 25°C, and a wet season (June to October) in which maxima are around 32°C and minima about 22°C. Annual rainfall averages less than 1,000 mm. The Guinea-Sudan vegetation includes open areas of short grass, tall, monospecific grassland, open deciduous woodland, bamboo thicket, and strips of gallery forest usually along seasonal water courses. Dupuy and Verschuren (1977) described other environmental aspects of the park.

Brewer established the rehabilitation camp in 1974, and was later joined by Savinelli (Brewer, 1977; Brewer and Savinelli, unpublished). The project aims to introduce or reintroduce sub-adult chimpanzees which have been in captivity to a natural habitat containing wild chimpanzees. Guided by human caretakers and by other partially rehabilitated chimpanzees, the newly arrived animals learn how to survive in the unfamiliar habitat: where and what to eat, how to build a nest, how to recognize predators, and how to interact with other chimpanzees.

At the time of the event reported here, Gandini had been working at the rehabilitation camp for 4 months and Baldwin had been studying wild chimpanzees in a nearby area for 12 months.

DESCRIPTION OF THE ENCOUNTER

Specific behavioral terms used in the description follow van Lawick-Goodall (1968). At 1000 hours on February 19, 1977, we departed from camp accompanied by the six chimpanzees described in Table 1. It was a typical dry season day, hot and sunny. We walked to a place where there were suitable wild fruits for them to eat, and they fed and rested intermittently for several hours. At 1430 we began the return journey to camp, following a valley by walking along the edge of its rim.

At about 1 km from camp, Tina began to approach Gandini repeatedly, pant-grunting, extending her hand towards his and looking alternately towards him and the valley below. This was typical of her behavior when wishing to be accompanied to a specific food item. She took lead of the group, and we followed her down into the valley, a distance of about 200 meters. The other chimpanzees showed mild excitement with slight hair erection and general alertness. Nini seemed fearful and climbed onto Baldwin's back, whimpering. Tina led us to the stream bed, by which time Bobo was lagging behind by about 20 meters.

had climbed to the upper branches of the same tree and was feeding. Tilly remained in the ventral position. Papoose began to food-grunt and climbed into the same tree. Nini climbed down from Baldwin's back. Yula, still with hair

TABLE 1. Chimpanzees Undergoing Rehabilitation at the Time of the Leopard Encounter: Individual Histories.

Name	Age	Sex	Place of birth	Experience in Captivity	Arrival in park
Tina	14 years	Female	Wild-born in Guinea-Bissau	Captured at the age of 6, confiscated soon after, and kept in a large enclosure in the Gambia.	1972
Tilly	1 year, 3 months	Male	Wild-born at Mont Assirik	None	1975
Papoose	8 years	Male	Wild-born, location not known	Captured as an infant and kept as a pet in the Gambia.	1974
Bobo	6 years	Male	?	Bought and kept as a pet in Italy.	1974
Nini	7 years	Female	?	Bought and kept as a pet in Italy.	1975
Yula	8 years	Female	London Zoo	Raised in captivity with other chimpanzees at London Zoo.	1975

When we were about 60 meters from a large tree *(Treculia africana)* covered with leaves and fruit, a group of baboons *(Papio papio)* descended from it and other nearby trees and retreated from us. We approached the tree, following Tina; the other chimpanzees showed little interest in the baboons. Tina, with Tilly ventral, walked quadrupedally to the tree and climbed up a thick liana toward the fruit.

Within 30 seconds, she was on a branch 8 meters above the ground. Baldwin, with Nina still clinging to her back, and Gandini were under the tree; Yula and Papoose were behind us, and Bobo was approaching us from about 20 meters behind. Suddenly Tina, with her hair erect, gave a series of loud waa-barks, raising her arm in an arm threat, and rushed towards something only she could see in the foliage of the tree. A young adult leopard rapidly descended from a branch at the same height as Tina, and less than 5 meters from her. It avoided her and jumped to the ground from a height of 3 meters, landing 3 meters from us. It then fled, in a direction opposite to that of our approach. The chimpanzees reacted in the following ways: Nini clung onto Baldwin's back with hair erect throughout the incident; Papoose stood bipedally with hair erect and an arm raised in an arm-threat, and gave a waa-bark; Yula stood bipedally with hair erect; Bobo was too far behind for us to see his reaction. He ran toward us, quadrupedally, with hair erect after the leopard descended. Following its departure, we each gave a waa-bark, and Gandini shot the rocket flare gun towards the fleeing leopard. Our behavior was intended to demonstrate an appropriate chimpanzee response and to indicate that leopards are dangerous. Within a minute, Tina erect, climbed a small sapling and gazed in the direction of the leopard's disappearance. Bobo sat down on the ground beside us.

DISCUSSION

In order to consider whether or not this is a typical reaction, similar to those of truly wild chimpanzees, we must examine the other observed encounters with leopards or lions, all recorded in Tanzania. Van Lawick-Goodall (1968: 173) reported two chimpanzee-leopard interactions in the Gombe National Park. In the first case, a juvenile, seeing a leopard in the ravine below, gave loud screams for 5 minutes. Its mother, who had a small infant, looked down into the ravine, but continued to feed. In the second case, chimpanzees paid no attention to a leopard which "coughed" 50 meters away.

Pierce (unpublished) gave a detailed account of a meeting at Gombe between a group of six chimpanzees and a leopard, which was partly concealed in a thicket on the ground, 10-15 meters from them. They showed signs of general excitement, e.g., hair erection and curiosity, peering towards the leopard. They also gave alarm and threat calls. Some climbed trees, and an adult male displayed by shaking vegetation and charging away from the leopard. The leopard eventually departed but was followed a short way by several chimpanzees.

During a study in the Kasakati Basin, Izawa and Itani (1966: 140) heard a young adult male chimpanzee scream for an hour before they saw it in a tree. It continued to scream and shake the vegetation, but when it saw the observers it descended and disappeared. The observers then noticed an adult male leopard resting in a tree 25 meters from where the chimpanzee had been.

In the Mahali Mountains, Nishida (1968: 175) was observing an adult male chimpanzee as it fed, when it suddenly stopped and began to throw down pieces of vegetation. Although other chimpanzees were nearby, it did not vocalize. After it had descended, Nishida saw a leopard rush into the undergrowth 40 meters away.

Finally, Kano and Itani (Kano, 1972: 67; Itani, in press), while in the Ugalla region, saw a young male lion which had apparently driven a group of 15 chimpanzees up into trees. They were screaming as they moved through the trees. The lion fled when it saw Itani.

Added to these episodes, our observation indicates that the behavior of wild chimpanzees toward large carnivores varies. This is also the case with small carnivores (Teleki, 1973) and when wild chimpanzees are exposed to a mechanized stuffed leopard (Kortlandt and Kooij, 1963). The latter experiment revealed a wide range of responses, including the use of sticks as weapons to throw and strike at the mechanical leopard. Thus, there seems to be no "typical" reaction of wild chimpanzees toward large carnivores. They may respond with fear, curiosity, or even threatening behavior.

These reactions may depend on the age and sex of the individual, and the size of the group involved. The relative positions of the chimpanzee and the carnivore may also be important. In all cases previously reported, the carnivore was at least 10-15 meters away from the chimpanzees, which were either in trees or had access to trees, while the carnivore was either on the ground or in a different tree: the chimpanzees could remain and watch in safety. In the episode we record here, Tina was confronted with a leopard in the same tree, and less than 5 meters away. Probably the best tactic available was to take the initiative and direct an intimidating display towards the leopard.

We cannot say, however, to what extent Tina's behavior was influenced by our presence. The direct charge toward the leopard with hair erection, loud vocalization and arm-threat, apparently before the leopard had moved at all, indicates that she took the initiative in the interaction. It was a bold and, to us, very impressive display. Her apparent calmness immediately after the encounter, as indicated by the lack of hair erection and any reassurance-seeking behavior directed toward us or the other chimpanzees (which she *has* shown in other fearful situations when human beings were present) suggests that she was confident, and not intimidated by the leopard, and that her response would probably be the same were she alone.

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LITERATURE CITED

Brewer, S. 1977. Chimpanzee rehabilitation. *International Primate Protection League Special Report*: 10 pp.

__________, and R. Savinelli. Project report: Chimpanzee rehabilitation. Paper submitted to *Journal of Human Evolution*.

Dupuy, A. R., and J. Verschuren. 1977. Wildlife and parks in Senegal. *Oryx* 14(1): 36-46.

Itani, J. In Press. Distribution and adaption of chimpanzees in an arid area (Ugalla Area, Western Tanzania). *In*: D. A. Hamburg and J. Goodall (Eds.), *Behavior of Great Apes*. W. A. Benjamin and Co., Menlo Park, California.

Izawa, K., and J. Itani. 1966. Chimpanzees in Kasakati Basin, Tanganyika. *Kyoto University African Studies* 1: 73-156.

Kano, T. 1972. Distribution and adaption of chimpanzees on the eastern shore of Lake Tanganyika. *Kyoto University African Studies* 7: 37-129.

Kortlandt, A., and M. Kooij. 1963. Protohominid behavior in primates. *Symposia Zoological Society of London* 10: 61-88.

Nishida, T. 1968. The social group of wild chimpanzees in the Mahali Mountains. *Primates* 9(3): 167-224.

Pierce, A. H. An encounter between a leopard and a group of chimpanzees at Gombe National Park. Unpublished manuscript.

Rahm, Y. 1967. Observations during chimpanzee captures in the Congo. Pp. 195-207, *In*: D. Starck, R. Schneider, and H. J. Kuhn (Eds.), *Neue Ergebnisse der Primatologie*. Gustav Fischer Verlag, Stuttgart.

Rijksen, H. D., and A. G. Rijksen-Graatsma. 1975. Orang-Utan rescue work in north Sumatra. *Oryx* 13(1): 63-73.

Schaller, G. B. 1963. *The Mountain Gorilla: Ecology and Behavior*. University of Chicago Press, Chicago.

______________. 1972. *The Serengeti Lion*. University of Chicago Press, Chicago.

Teleki, G. 1973. Notes on chimpanzee interactions with small carnivores in Gombe National Park, Tanzania. *Primates* 14: 407-411.

Van Lawick-Goodall, J. 1968. The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monograph* 1(3): 161-311.

THE EVOLUTION OF TROPHY HUNTING

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"From the day I was born I was born for meat."

Toma of the !Kung Bushman

" . . . not only was hunting a privilege respected by all, but those on the bottom demanded it of those on top, because they saw in hunting, especially in its superior form . . . a vigorous discipline and an opportunity to show courage, endurance, and skill, which are the attributes of the genuinely powerful person."

Jose Ortega y Gasset

Whether of modern or so-called primitive societies, hunters everywhere tend to collect preferentially and to display trophies. A trophy documents a hunter's performance at killing an exceptionally large individual of a typical game species such as a large herbivore, or a species which is extremely difficult to encounter, either because it is rare or secretive and difficult to locate, or a dangerous species such as large carnivores or other formidable humans. Although trophy hunting and display--termed trophyism--has come under attack recently (e.g., Amory, 1974), no adequate explanation has been given for this widespread human behavior. Leopold (1949) said that the trophy hunter is the caveman reborn, but he carried this provocative metaphor no further.

My hypothesis is that trophyism has for thousands of years affected the reproductive success of males, and thus has been strongly influenced by natural selection. Males would benefit in competition for females if they could demonstrate and advertize their hunting prowess. Display of hunting prowess to other males could also affect the probability of a male being accepted as a hunting partner, thus increasing his fitness. A trophy usually communicates bravery or skill, both desirable traits for a hunting or warring associate.

The social status of males and their corresponding fitnesses should tend to correlate with their hunting capability. Size or formidability of prey taken by a male should be a measure of his suitability as a mate, including when mate selection is governed by older, higher-ranking males. Individuals of hunting societies (hunting is probably the critical niche dimension for all societies categorized by anthropology as hunter-gatherers so I simply use "hunting societies") should discriminate the status of males according to their trophies. The effect of such a system would be hunting of certain animals; for example, a relatively small but dangerous species, so as to display them regardless of any immediate value of the prey itself.

As the ability of males to kill larger herbivores would be favored by selection because of reproductive benefits, selection would also favor the demonstration of minimal hunting ability for admission into adult male groups and candidacy for marriage. Competition among males of groups should favor those males who kill the largest, most elusive or most dangerous prey, and this would accelerate trophyism.

Selection would favor the tendency of males to advertize their hunting skills. Any male who has killed a trophy-class animal stands to gain, especially if his hunting prowess relative to other males is verifiable, which would favor possession of part of the prey which either verifies its kind or correlates with its exceptional size.

Trophyism would appear in the early stages of hunting societies. But selection also would favor it in more advanced hunting societies and both pastoral and agricultural societies; ability to kill competing or dangerous species such as large carnivores or humans of competing groups could be as important as killing large herbivores among some hunters.

TESTS OF THE HYPOTHESIS

First Prediction: Males Benefit in Competition for Females If They Advertize Hunting Prowess.

The ideal test of the hypothesis would be a correlation of hunting success with fitnesses of individuals. Inadequate ethnographic data do not permit such a precise comparison; however, strong supportive evidence is available.

In a general statement about mate selection among hunting peoples, Coon (1971: 191) says, "Usually the groom will give his proposed in-laws a modest present, including meat that he has secured by his own prowess as a huntsman." Among the !Kung Bushman, a male could not marry until he had killed a "buck," some large herbivore (Marshall, 1957; Thomas, 1958). Only one Bushman studied by the Marshalls had never married (Thomas, 1958); he was an old man who was unmarried because he had never killed an antelope. One male, Toma, who was not a !Kung and therefore unlikely to be accepted as a mate by the !Kung, was allowed to marry the daughter of the clan's headman only because of his exceptional hunting success.

Although nomadic hunters would not be expected to transport larger animal parts with them, any portable item would constitute a trophy as long as it clearly identified the prey or its esteemed class (size, sex). The semi-nomadic Akoa pygmies wear elephant hair bracelets. One !Kung, admired for killing four gnus in one hunt, displayed this feat with their tails (Marshall, 1957). Bushman hunters customarily cut strips of skin from the foreheads of the antelope they kill and make them into bracelets, which their wives wear on their arms (Thomas, 1958). The forehead skin communicates the particular species killed, a significant measure of hunting prowess. The abundance and kind of these trophies correlates with the success of the hunter and his esteem as a hunter.

The elephant-hunting Akoa pygmies traded ivory to Fang Negroes for products used to court females (Trilles, 1932). In an Akoa legend (Coon, 1971: 232), probability of reproductive success is linked to hunting ability and trophyism:

> "His arrows felled all game, and he had already killed two elephants and he wore a necklace of hairs from their tails (trophies). All the women ran after him."

In order for a Mbuti pygmy male to marry he had to ask permission of the female's parents. If they agreed, he had to kill one of the larger species of antelope and give it to them (Turnbull, 1961). Among Alaskan Eskimos the completion of full eligibility for marriage came after a male had killed a succession of animals of increasing size and difficulty, ending with a bearded seal or a polar bear, the former being especially difficult, the latter especially dangerous (Nelson, 1969).

Some Alaskan Eskimos take grizzly bear trophies by killing them with a special spear thrust in the neck. The grizzly bear is not a reliable source of food, but it is very risky, which suggests that bears are killed for trophies. In a population studied by Binford (1972) only three old men had taken such trophies, all while young. Two equally old males had not done so and none of the younger males had either. Of the three collectors of grizzly bear trophies, one did not marry, one had a long marriage to a sterile woman but raised a large family by adoption, and the third had an average-size family. On this basis, J. Spuhler (personal communication) and an anonymous reviewer argued that males with the highest class trophies do not necessarily have higher reproductive success. Not only is this sample quite small, the objection to the hypothesis overlooks inclusive fitness; for example, the adoption of kin, which could be influenced by social status.

In the Sciriono of the southern Amazon Basin, males become chiefs by virtue of their hunting ability (applicable to second prediction) (Meggers, 1971). The principle way for a man to achieve status is by being a good hunter. The chief of a group and one or two other outstanding hunters are the only males in a group who are polygynous. Although no details are available as to trophies, their only dress is necklaces including canine teeth of prey such as the coati and spider monkey, which would appear to constitute trophies.

Among the Kurelu of New Guinea, there can be little doubt that the fitnesses of males correlates with their status as established by their bravery in war. A man who has not killed an enemy is considered cowardly, without valor and worthless. Their position in the tribe is determined by their comportment on the field of battle. Matthiessen (1962: 15) says, "Unless they (a man who has not killed) have strong friends or family, any wives or pigs they may obtain will be taken from them by other men, in the confidence that they will not resist; few 'kepu' men have more than a single wife, and many of them have none." Men who have killed in battle have more wives, more children, and receive more pigs more often. The men who have killed the greatest number of enemies tend to have the most wives and children. Among warriors, the number of kills are well established and are an important measure of status; kills are permanently recorded by tufts of hair taken from victims. Thus, selection must favor males who successfully collect trophies.

Additional examples of males having more wives and resources owing to their trophies are given in the following section.

Second Prediction: Status Among Males Should Correlate with Success in Trophy Hunting.

The selective benefits to a male of trophy hunting extend beyond simply qualifying for marriage to status in male groups, which is related to numerous factors influencing personal and inclusive fitness. Based on his review of hunting peoples, Coon (1971: 110) said, " . . . big game hunting bears some of the dangers [note use of the word "bear" with "hunting" and "danger"] and the rewards in prestige, or fighting . . . those who do [hunt big game] are outstanding individuals, both for the amount of meat they supply to their fellows, and for the respect that they receive, if they survive."

If hunting prowess is important in competition among males for leadership (and its probable advantages in resources, number of mates, control of mate selection of kin and so on), succession to leadership should not be hereditary. In cultures in which subsistence is primarily by hunting, where a headmanship is present, succession is non-hereditary (13 of 18), while among other cultures succession tends to be hereditary (93 of 160) (Textor, 1967) ($\chi^2 = 7.45$, $p = .0064$).

Among the Andamanese Islanders, succession of males to leadership depends on their hunting ability (Coon, 1971). Able hunters became band chiefs and arranged matings which, regardless of effects on personal fitness, could mean considerable inclusive fitness. Hunting prowess correlates with social status in other hunting peoples. In the Nunivak Eskimo, the son of a rich man could not maintain wealth and obtain leadership except by being a good hunter and trader. Highest prestige was associated with killing bearded seals from Kayaks in spring hunts, as bearded seals are large and difficult to capture when struck (Lantis, 1966). Inheritance of wealth is insufficient for a Nunivak hunter to gain high status, but ability to kill certain species under difficult conditions could earn status, and probably enhance reproductive success.

Whaling is dangerous and also highly rewarding in terms of food resources. Among the Tikerarmiut, Eskimos of Tigara, the most prominent males in a "house," holding a number of related families, were usually a boat owner and its captain (Rainey, 1947). While a man could inherit a whaleboat from his father, he could not become a captain unless he commanded the respect of other males. Captains had to have been notably successful in killing whales: they signified their success with bands of white fur trimming their boots. Boat captains received more food resources on the average from a group kill than any other males, and the captain of the boat that first harpooned a whale received by far the greatest share of food. Equally important, Eskimos hunted whales to demonstrate bravery. Selection would favor competition for status measured by hunting success.

Among the Nootka, northwest coastal Indians, whales were hunted and highly valued (Drucker, 1951). Although the boat captains distributed meat according to status of the individuals more than each individual's role in the hunt, whale meat may not have been nearly as important a food source as to the Eskimo. Moreover, the Nootka hunted whales as a test of valor. The dorsal fin of the whale was highly prized as a trophy, being hung in the house of a Nootka who first harpooned it (Drucker, 1951).

The killer whale is the dominant predator of the marine environment. It was normally considered too dangerous to hunt by whaling peoples (Boas, 1895; Slettebak, 1976) and may have deterred other coastal peoples from whaling (e.g., the Haida, Anon., 1952). However, young men of the Nootka attempted killing killer whales (or riding them) as demonstrations of valor to become great whalers (boat captains) (Slettebak, 1976; Boas, 1895), indicating that trophy hunting was a significant factor in achieving highest social status.

In the few hunting societies in which succession to headman is by inheritance, hunting ability of individual males may take precedence over genetic relatedness. A previously low-ranking, unrelated male eventually became headman of a group of !Kung because of his superb hunting success. Toma's hunting skill attracted the attention of the headman, who offered his daughter in marriage; when the headman died, Toma took leadership, and the rightful heirs did not contest (Thomas, 1958). Toma's position as leader was not held by force but "by wisdom and ability, and people prospered under him" (Thomas, 1958: 183). Wisdom, ability and prosperity all refer to his hunting prowess and its benefits for individuals of the group: "it was said of him that he never returned from a hunt without having killed at least a wildebeest, if not something larger. Hence the people connected with him ate a great deal of meat and his popularity grew" (Thomas, 1958: 182). Although Thomas (1958) said that Toma's good fortune as leader was due to his marriage, it was actually his hunting ability that gained the status for the marriage as well as the headmanship.

As Toma was not related to breeding members of his group, the high status he achieved through hunting could not affect his inclusive fitness. He did have a wife fatter than most women, and three of his five offspring born by the end of the study had survived infancy and were apparently healthy (Thomas, 1958), which apparently is better than average survival of infants (Harpending, 1971).

As a general rule, survival of !Kung and other hunting peoples' infants probably depends largely on abundance of animal protein, especially during limiting seasons (a point still not generally appreciated by anthropology [e.g., Yellen and Lee, 1967], which tends to describe many primitive peoples as having an abundance of resources and males as hunting merely for "sport." The reader should see Orians, this issue, for similar criticisms). The common knowledge of the !Kung, for example, should not be taken lightly. Hunters said (Marshall, 1957) that if they did not kill game soon, their wives' breasts would dry up and their babies would die. It seems that the differential reproductive success of males is most influenced by their hunting success, and, secondarily, among some peoples by their leader's hunting ability and knowledge. Regardless of the relative abundance of resources, selection should always favor those individuals who acquire more animal protein or acquire it more efficiently in terms of time, energy and risks.

Although details about trophies per se tend to be lacking, in numerous Indian societies of South America the status of individual males is largely affected by their hunting or warring ability. Status in male groups affects share of resources and number of wives and, consequently (probably), number of offspring. Among the Jivaro of the Upper Amazon Basin (Meggers, 1971), the status of adult males depends on their skill and accomplishment in warfare. The Jivaro collect heads of enemies as trophies; success at head hunting affects the probability of a male being appointed chief of a war party, and acquiring a large number of wives.

Among the Kayapo of the Lower Amazon Basin, large herbivores and the jaguar are hunted as trophies; but an adult male does not achieve full status until he has killed an enemy in warfare (Meggers, 1971). This feat is signified with a tatoo on the chest. The highest ranking males, chiefs, are selected on the basis of their demonstrated success in warfare, which they lead. As chiefs they especially receive a portion of any large game killed by hunters, and they typically have more wives, some of which are stolen in raids, than do other males.

Among the Waiwai of northern Amazonia, "Hunting is the favorite pastime of men . . . Being a good hunter is a way to achieve prestige . . ." (Meggers, 1971: 91).

Trophy hunting should be less prevalent among peoples in which most or all able hunters participate in a hunt, especially when the methods employed make it difficult to determine who played a crucial role. Trophyism might not be favored because it would reduce cooperation or enhance strife, thus reducing the success of foraging and individuals' fitnesses. Examples include some pygmies who hunt in large groups by driving prey into nets. However, even among such extreme "altruists" trophy hunting occurs and apparently benefits individuals. The Mbuti are normally net hunters, but some men kill elephants, the largest and most dangerous prey, to gain prestige (Coon, 1971). The Mbuti are the only pygmies among whom some individuals hunt elephants solitarily, surely the most dangerous strategy. Although the tusks go to the special patron of the elephant hunter, who sells them, the hunter receives a share. Thus, even where there is an active reduction of competition for status within groups, individuals may assume very high risks for benefits such as resources and status among males.

Third Prediction: Trophy Values Should Evolve According to Rank of Hunters Among Predators.

Selection should progressively favor the ability of individuals to acquire more animal protein. Certainly this is the overall theme of human evolution; in other words, exploitation of animal protein has been the critical niche dimension in human evolution. The factor limiting hunting success by man may have been interspecific competition (Eaton, 1976, in press). Thus, trophy values should correlate with the rank of a people, extinct or extant, among competing predators.

The immediate advantages of killing dangerous carnivores include: reduction of the probability of predation; reduction of exploitive competition for prey resources; and reduction of interference competition, as for carcasses or other clumped and limiting resources such as water. As humans become more successful at killing dangerous carnivores, avoidance of man by these species would be favored. The avoidance of hunting males by large carnivores should greatly enhance hunting success; for example, within an area, prey would be less wary and less concentrated. Killing of predators is not only advantageous in reducing predation and competition, it is also very difficult; for both reasons, predator trophies would carry high status and reproductive benefits.

If interspecific competition (which can encompass predation and interspecific aggression: Eaton, 1976, in press) has been a primary influence in the evolution of human social behavior and niches, then the cost-benefit ratio of warfare should be inversely related to the interspecific rank of humans in predator guilds. The relative importance of interspecific versus intraspecific competition would be revealed by the relative importance of carnivore and human trophies.

When humans are subordinate in a guild, warfare should be relatively costly and rare, and thus trophy values would be highest for larger herbivores. When humans are co-dominant in a guild, inter-group competition should tend to be more important and trophy values should be highest for larger carnivores and enemy humans. When humans are dominant in a guild, warfare will be most important and trophy values would be highest for the very dangerous carnivores and enemy warriors. These predictions should vary somewhat according to the relative formidability of sympatric top-ranking predators and the nature of limiting resources; for example, whether they are sparse or clumped or whether or not they are defendable.

Among hunters who are subordinate in predator guilds, large herbivores constitute the highest-ranking trophies. The killing of dangerous carnivores is rare; in most cases groups of hunters are involved and the prey does not constitute a trophy. A good example is the !Kung Bushman who are (or were until the recent intervention of European man and firearms; see Eaton, in press) subordinate to the lion which they fear and normally avoid (Thomas, 1958). The !Kung occasionally kill leopards, which are far less formidable than lions, but normally only when the !Kung are grouped and have dogs. Leopards are killed not because they provide tangible products but, rather, because they pose a threat of predation or have stolen prey wounded by the Bushman. Their elimination can have a longer-term value. There is no evidence that leopards or any other risky carnivores or men constitute trophies for the !Kung. Their trophies are large herbivores.

A similar example is the Tapirape Indians of Brazil, whose highest-ranking trophies appear to be herbivores (Wagley, 1977). Rarely they may kill jaguars close to camp with the aid of dogs, but jaguars are not hunted as trophies. Moreover, their and many other relatively low-ranking peoples' taboos against killing the largest herbivores appear to be adaptations to avoid interference competition with large predators. The Tapirape do not make war.

Among peoples who are co-dominant in predator guilds, the most esteemed trophies are dangerous carnivores or enemy warriors. Examples include some (not all) types of Xingu hunters who hunt and display jaguar trophies. The jaguar is the most dangerous and competitively important sympatric species; it is considered a chief, comparable in status to a headman of a male group, by the tribesmen (Boas and Boas, 1970). Among some warring societies of South America, only the jaguar rates as high in trophy value as an enemy human.

Among the Plains Indians of North America, after the horse the primary resources were mobile but also clumped and relatively defendable. Such semi-nomadic societies warred among themselves and hunted large carnivores as trophies. The grizzly bear was commonly used as a trophy; it is a symbol of power (W. Holm, personal communication). In numerous hunting societies of the Holarctic region, brown bears have ranked as high or higher than a human trophy, such as a scalp taken in war, as evidence of warring ability.

The Eskimos major competitor for seals, their most important prey (Weyer, 1932), is the polar bear. Prior to the advent of firearms, Eskimos were at best co-dominant with the polar bear. If a man killed one, he was held in high esteem (Nelson, 1969). According to Nelson (1969: 202), one Eskimo had killed a polar bear with his knife: "This feat proved him one of the greatest of the old-time hunters."

The most sedentary and warlike of recent hunting peoples include the northwest coastal Indians. Bears, especially the grizzly bear, were important trophies; the claws of grizzly bears make up the vast majority of crowns worn by Shamans (W. Holm, personal communication). These people also collected heads in war (Curtis, 1915).

In pastoral societies protein resources are livestock. Hunting ability would not be important to reproductive success as far as directly provisioning wives and offspring. The reproductive advantages of predator control are obvious, since the major food resource is mobile, clumped and vulnerable to predation. Pastoralism as a niche would be impossible unless males were able to defend livestock against predation; thus pastoralists must be co-dominant or dominant in predator guilds. Males would serve their interests by advertizing their suitability as mates by displaying trophies of predators. Typical examples include the Zulu, Suk, Marakweet and Turkana males who adorn themselves with leopard skins (Adamson, 1967).

Semi-nomadic pastoralists such as the Masai typically warred among themselves and with agricultural societies for grazing lands. Display of a trophy from a dangerous animal should be especially important as a means of selecting warring associates or war leaders. Among pastoral societies, hunting of large carnivores can be ritualistic, done in such a way as to give individuals the opportunity to demonstrate warrior skills. The best known example is the Masai who hunt lions (Roosevelt, 1921).

Generally, as warring becomes more important to the reproductive success of males, emphasis should shift from trophies of game species to those of dangerous animals, including horns, teeth and claws. Males of numerous East African pastoralist societies, known for their recently frequent warring, adorn themselves with skins and teeth and claws of larger felids (Adamson, 1967), as well as with tusks and large teeth worn conspicuously around the head, as in the Luo. The Masai and Njemps warriors wear a headress resembling a lion's mane (Adamson, 1967). Among the Masai, the headress, which is composed of hair from the lion's mane, is worn only by males who were first to grab the wounded lion's tail.

A secondary benefit of dangerous or difficult-to-kill animal trophies could accrue in warfare, as a means of intimidation, reducing risks when enemies submit (flee) rather than fight. Interspecifically high-ranking or dangerous predators (for example, the bear, lion and eagle) are the most common symbols of might and aggression in warring peoples. Warriors not only don the skins and weapons of dangerous predators, they often label their groups with these animals' names--for example, the Leopard Group of the Turkana (Adamson, 1967), and the Lion Hunters of Niger.

Males who are able to demonstrate their warring skills by taking dangerous game should benefit from perfecting skills transferable to warfare, as well as from gaining status in groups. Considering the great number of wars since the advent of agriculture, warrior skills should be valued by agrarian societies. Trophyism is prevalent in agricultural societies. Males hunt dangerous animals for trophies which are kept and displayed as status symbols. With civilization, the opportunity increased for display of otherwise burdensome parts of large animals, such as tusks or whole specimens.

Advances in weapon technology accelerated to the point of sophisticated firearms, the use of which involves lower risks. As a consequence, trophy value should shift from what previously had been dangerous animals, indicative of the hunter's bravery and suitability as a warrior, to extremely rare or difficult-to-kill prey, indicative of leadership qualities. Among males of agricultural-industrial societies, a trophy of an extremely rare species has become as significant as one of a dangerous species. Today, the most valued trophies are the rarest on den walls. The previously esteemed "Big Five" of Africa--elephant, rhinoceros, Cape buffalo, lion and leopard--include species which are either exceptionally large or potentially dangerous, but not especially rare. The "Grand Slam" includes trophies of North America's rugged mountain game, which are valued not for rarity, size or danger, but because the successful hunter has to possess qualities desirable in a warring society. These include self-control, physical conditioning and stamina, patience, tenacity and wealth. It may be no mere coincidence that a disproportionate number of males with high status or great wealth in our society--business tycoons, military leaders and holders of high state office--are trophy hunters; for example, the members of the Safari Club International, Game Conservation International, and Mzuri Safari Foundation (see *Safari, Mzuri Drumbeat* or *Hook 'n Bullet News*).

With such apparently high gains to males from displaying trophies, individuals could benefit by cheating. In primitive settings, this probably could not usually occur, as more than one male would normally be engaged in hunting or processing the prey. Occasionally, an individual on a solo hunting trip, or alone tending livestock, could acquire a trophy from a dead or dying animal, and thereby benefit himself by deceiving females and other males. The response to a cheating male should be considerable, as other males stand to lose if a male is not really worthy as a hunting or warring mate, or if they lose inclusive fitness from permitting a less productive marriage to a kin female.

If selection has so strongly favored trophyism as a social evaluator, cheating and attempts at detection by males are to be expected in any society in which trophies are displayed. Among hunting societies, testimony is insufficient--the prey must be located or presented (e.g., in the !Kung, Thomas, 1958). Among warring societies, claims of kills not observed or substantiated by a trophy, such as a scalp, are not recognized (e.g., in the Kurela, Matthiessen, 1962). Hunter organizations such as the Boone and Crockett Club act as detectors, demanding clear proof of the kill. I have personally observed extreme ostracism extended to hunters who buy their trophies. This has become especially prevalent among recent oil millionaires, some of whom buy their trophies and then move to a new town before tacking them on the wall (R. Taber, personal communication). No form of deceit is more contemptible among modern hunter organizations.

DISCUSSION

Objections to the Hypothesis and Trophyism in Other Species

An earlier but radically similar version of this paper was rejected by *Evolution*. To the four reviewers, some and possibly all of whom were ethnographers or anthropologists, the hypothesis does not account for what they consider to be cultural behavior. Reviewers said that I should demonstrate a genetic basis for the desire to hunt trophy animals. Cultural behavior is not exempt from natural selection so long as there is any correlation between behavior and genetic fitness. Although precise comparisons of the fitnesses and trophies of males in groups is impossible, owing in part to their being ignored by anthropology, the hypothesis need only find support for its predictions, which I believe it has.

Trophy hunting should not be unique to humans. Especially among predators, females would serve their reproductive interests by evaluating potential mates according to their predatory abilities. Thus, selection would favor males which demonstrated hunting ability to females. Among some felids, specialized predators tending to be polygynous, males courting females may make kills--"love gifts" (McCord, 1974) and either give them to or share them with females. Males of some predatory birds demonstrate their flight and predatory capabilities to females they are courting. Since females depend upon assistance from males in raising young, collection and display of trophies by the male should signal his suitability as a mate. In these and probably many other species, the tendency of males to "hunt trophies" would appear to be favored by natural selection.

Group Solidarity and "Group Trophies"

Tiger (1969) suggested that hunting and trophies could increase male group solidarity. Considering that male hominids probably lived in small groups, which may have been kin, selection could favor male group loyalty as well as personal hegemony over the gene pool. Although hunting would surely favor cooperative behavior (group solidarity) among males in groups, competition for rank by trophy hunting is an individualistic matter even when individuals hunt together. If anything, trophy hunting could lead to strife among males contesting credit for a trophy; this is precisely why males of hunting societies take great efforts to individually discriminate their weapons. For example, among the !Kung, each male carefully marks his arrows with his own insignia (Marshall, 1957). This same idea probably explains the oldest known designs, which occur on weapons and utensils of European Paleolithic man (Eaton, in preparation a). On the other hand, trophy hunting tends to establish standards or norms of rank, which result in classes of male status measured by a hierarchy of trophies, as we have seen in several societies.

There is a mutually inclusive hypothesis that would explain trophyism as a function of group solidarity. I refer to "group trophyism" as a spacing mechanism. It would serve the interests of males of groups to advertize their presence in hunting areas and to avoid areas occupied by other hunters for two reasons: reduced wariness of prey is likely to enhance hunting success, and the risk of intergroup aggression would be reduced. Indicators of the proximity of other hunters would include the remains of prey. Conspicuous display of animal remains would enhance communication and reduce probability of congestion or confrontation. Display of very large or dangerous prey would be more effective as these would involve either more skilled hunters, likely to be more skilled warriors, or larger groups of hunters. An animal's head is largely inedible and costly to transport relative to amount of meat; it also signifies species, size, and often sex, critical factors in assessing bravery or skill of hunters. The head of esteemed trophy species displayed conspicuously would constitute maximal deterrent as a territorial marker.

A recent fossil discovery appears to offer a possible example among Paleolithic hunters of North America. Frison (1976) speculated that prehistoric hunters stacked mammoth bones to protect fresh meat from carnivores. If such stacks were above ground, carnivores could climb them and birds of prey would scavenge them as well; if bone stacks were in caches, carnivores could dig the meat out. It is conceivable that piles of bones were visual displays intended to deter competitors. Placement of mammoth skulls on top of the piles suggests that groups may have communicated by display of formidable prey, in this case prey probably requiring a minimal number of cooperative hunters.

Group trophyism would not be expected to evolve until groups of human hunters were competing with one another for territory or temporarily clumped prey resources. I do not believe this would normally occur until human groups were relatively large or sedentary, and hunters were already co-dominant in predator guilds. Trophyism as a form of competition for mates and status among group members would appear much earlier. In any event, among living hunters and primitive warring societies, such as in New Guinea, I found no evidence of trophies being used as territorial markers. But symbols apparently derived from trophyism demarcate territories; such symbolic depictions are not trophies per se, but they may communicate the antagonism of residents to intruders.

Pseudo-Trophyism: Intergroup Mimicry?

There are societies in which males typically adorn themselves with what appear to be trophies, but these are acquired by trade or some other means than hunting. A male's status in a group may be indicated by these "pseudo-trophies" since they correlate with his wealth. The Mehinaku of Brazil rank low among human groups in their area, and they do not hunt jaguars. They are frequently attacked by warring groups, the males of which do collect trophies of jaguars and humans (Gregor, 1977). The wearing of jaguar pseudo-trophies--claw necklaces--by the Mehinaku males could deceive enemies and thereby benefit males who wear them.

I speculate that "pseudo-trophyism" could evolve because it deceives enemies as to the formidability of males, which would be mimicry. Accordingly, males of a society which is inferior to neighboring groups in warfare can be expected to mimic the appearance of enemy warriors, including their highly esteemed trophies.

Trophyism and the Origin of Art

The oldest paintings and sculptings of Paleolithic hunters may have represented trophies. The predominance of large herbivores and dangerous carnivores, the accuracy of depiction as to species, sex and age, and the emphasis on the head region all suggest trophyism (Eaton in preparation a), as do conventions such as the turning of antlers and horns sideways (to dramatize the trophy value of an animal), the clumping together and superimposition of animal paintings (as if representing individual collections), and the association with handprints, which could have been a hunter's means of identifying trophies. Moreover, species painted are organized in cave chambers according to trophy values. There would have been several advantages to hunters of symbolizing rather than storing trophies; for example, reduced loss of trophies to predators and scavengers and other hunters during seasonal vacancy. The fundamental qualities expected of trophyism exist in all the earliest Paleolithic arts, whether of northern and southern Africa, Europe and Eurasia, North America or Australia (Eaton, in preparation a).

Trophy art may even have given rise to written language. Within each of the Paleolithic art traditions presently known, there appears over time a point where big game art ceases to be used only as an intragroup record of individuals' hunting feats and begins to appear in modified form as intergroup communication. In the former case, trophy art is usually well secluded, while in the latter, it is placed conspicuously as if intended to be a visual marker of territory. However, while the older form of art consistently implies recording of actual events (trophy hunting), new, exposed art is for the first time anticipatory or impressionistic. It tends to depict groups of hunters *about* to kill some formidable species. In the trophy art, hunters are relatively insignificant and stylized, with emphasis given to the prey itself. In the exposed art, hunters are embellished, with equivalent or greater emphasis given to them, their weapons and sex organs. The evidence indicates that as foreign groups begin to pose significant threats, the art becomes stylized to the point of graphic abstraction intended to communicate to group members but hide information from competitors. Character displacement by intergroup competition can explain the origin of written language as well as the diversification of verbal language.

Trophyism and Its Possible Relationship to Totems, Cults and Myths

Many spiritual practices and cults of hunting peoples may have originated from trophyism. Choice of predators, with highest status often given to the highest-ranking species, suggests trophy values and an origin from trophy hunting. Among the sedentary Ainu, patrilineages were totemic; each was designated by the name of a predator: bear, wolf, fox, eagle, hawk and eagle-owl. The male lineage of the bear ranked highest and live bears were central to the ceremonial life (Coon, 1971). The highest ranking male cults of the Nootka were the killer whale and wolf; pelts of wolves were worn in rites (Drucker, 1951).

Totems also appear to originate from trophyism. Among the northwest coastal Indians moieties and lineages were depicted with crests--representations of animals or supernatural beings. Coon (1971) points out that these totems originally were more like heraldic devices, indicating status and prestige of individuals. Prior to totem poles (after introduction of metal tools and the appearance of competitive European man), crests were painted on houses and boxes. The species most often depicted were killer whale, wolf, eagle and raven. The species and their use in display of status by individuals suggest an origin from trophy hunting.

Many anticipatory rituals including magic appear to have originated from the prestige and power associated with killing dangerous predators. For example, prior to a raid on other Indians, the Nootkans painted their faces black with charcoal; however, the war chiefs used charred wolf or mountain lion bone instead (Clark, 1953). The bone from such animals was believed to impart greater power; such a belief would derive from the higher status given males who were powerful enough to have killed these species. Such men would be more likely to become war leaders.

A majority of totems, cults and magical rituals tend to emphasize a few species of larger game and carnivores, especially high-ranking predators. Myths purported to explain the origin of totemism almost universally trace it to events involving an encounter between an individual and an animal for which a clan or rite is named (Jensen, 1963). The high esteen originally given to hunters with trophies of certain species may account for the origin of these cultural phenomena.

A possible progression of the cultural extension of trophyism is seen in the uses of the dorsal fin of whales by the Nootka, described by Drucker (1951). It was hung as a trophy in the house of the whaler who harpooned it--probably the original use. It was symbolized in totems, probably originally as an individual trophy, and on a whaler's hat, worn by very few individuals of high status, i.e., men who had killed a whale. The depiction on the hat included the scene of the whale hunt. The hump was also used in anticipatory rituals for hunting which were probably a succedant of trophyism.

Trophyism and Predator Symbols

A basic theme of religion among hunting peoples, and their descendants including European man, is a predominance of predator symbols which represent: a) "good"--qualities or entities strived for by individuals; and b) "evil"--qualities or entities which, if not avoided by individuals, threaten serious, even fatal consequences due to exceptional, often invisible powers. The origin of spiritualism and its widespread association with predator symbols appear to lie in two phenomena: 1) the competition for status among males, i.e., trophyism; and 2) selection favoring an imprinting form of learning which reduces the threat of predation or interference competition from dangerous predators. By mere verbal communication, often enhanced by ceremony, individuals learn *without relevant experience* to conform their behavior in ways that are adaptive for them and their kin. Spiritualism includes fear of behaving in certain ways even though the actual danger is unexperienced and its source is unseen.

In a discussion of Shamanism in northwestern North American Indians, Spencer (1977) says that shamans have fundamental religious preoccupations with the conceptual unity of the spiritual realm of animals. He says (1977: 356), "It is well enough known that the basic premise of the religious world view of the North American hunting peoples involved the concept that animals were morally, intellectually, and spiritually superior to men." He refers to animals that were hunted and adds that inhabitants of the animal world could in themselves become sources of power for the persons morally and perhaps intellectually prepared to receive it. Spencer poses a question (1977: 357): "Why the Eskimo, for example, at least those in the west, should single out land animals, bears, wolves, foxes, etc., as a source of power, while ignoring the spirit power potential of sea animals is an interesting but unanswerable question."

Among hunting societies, males compete for status by trophy hunting. Their status must be earned. By killing such wary and difficult-to-kill animals as bears or wolves or almost any predator, a man must develop himself. By collecting such trophies he demonstrates superior power as a hunter and acquires power (rank and esteem) among his associates--thus the belief that such species can actually impart power to men. As for Eskimos placing greater spiritual power in terrestrial predators than marine mammals, this might be expected considering the more demanding requirements of hunting these predators. Hunting of elusive terrestrial predators would be more difficult in general, as they are better adapted to avoid men than are marine mammals.

Conceptions of power and the supernatural tend to parallel trophy values. For example, among the Tzeltal of Mexico, it is believed that all true humans have individual animal soul companions, whose fortunes coincide with and help determine the fortunes of their human counterparts (Stross, 1977: 280). The most powerful humans have jaguar soul companions; less powerful individuals are associated with lesser soul companions, all of which can be organized in a power hierarchy: individuals of high status are associated with dangerous animals of high status and so on. Comparable examples in the western tradition, including contemporary American society, are endless (see the *Oxford English Dictionary* under "lion."

A belief in powerful, invisible spirits is adaptive since it reduces the threat of predation (or aggression or wife-stealing and so on). A widespread example is instructing children to avoid wandering away from camps or fires at night because invisible spirits, demons or devils will kill them if they do, as in the !Kung (Thomas, 1958). Similarly, among the Waiwai Indians, it is believed that bush spirits will kill people who wander in the forest alone at night (Meggers, 1971). Regardless of the rank of a society among predators, especially children but even adult males are vulnerable to serious attack by predators at night. Herein may be the adaptive significance of fear of graveyards. The !Kung, for example, actively avoid grave sites, the reason given being that evil spirits dwell there. Almost all predators readily scavenge; thus graves, especially of the flimsy type made by the !Kung, should attract predators and be dangerous locations. The belief in the supernatural and the no-trial learning associated with it appear to reduce risks.

In societies that are predator regulated (subordinate), spiritualism conforms behavior adaptively without relevant experience. Like the lion to the Bushman (Thomas, 1958) and the jaguar to some Indians of Brazil (Boas and Boas, 1970), the tiger is regarded by Sumatrans as a messenger of God and the mighty spirit of the forest (Borner, 1978). The tiger is said to kill only people who have done bad things, i.e., committed evil deeds. Being killed by a tiger is considered a punishment by God. It is adaptive to consider a man who is killed by a tiger as having been guilty of bad deeds punished by supernatural, powerful God because individuals will not imitate his behavior. Except by imprinting, learning to avoid tigers would usually involve one trial and one error. Such belief systems are likely to favor individuals.

Man's belief in supernatural being or power--that which is real but cannot be seen or doubted without reprisal--conforms behavior adaptively. Together with trophyism, here is a model for the evolution of spiritualism, which accounts for the symbolic significance of predators to man. This hypothesis would appear to apply to the Judeo-Christian tradition.

The lion is a symbol of magnanimity, representing good or godly qualities, as well as a symbol of evil and ferocity in the Bible. The lion is referred to more than 100 times in the Bible, second among animals only to the sheep (Fisher, 1834). It represents the devil (e.g., Peter 5:8), a formidable obstacle (e.g., Proverbs 22:13), a tyrannical ruler (e.g., Timothy 4:17) and conquest and courage (e.g., Psalm 91:13). The same pattern applies to the ancient books of the East; for example, comparisons of the Buddha to a lion and the ascension of Buddha on six tigers, and to both Mayan and Aztec civilizations regarding the jaguar.

The greatest hero of the Old Testament, David, is also the greatest trophy hunter. He had nearly as many wives as trophies, which included a lion and bear and the penis foreskins of thousands of enemies killed in war. Genesis (49:9) associates the lion with the warring Hebrews: "Judah is as a lion's whelp; from the prey [conquered enemies], my son, thou art gone up." The power of Jesus is likened to a lion in Revelations (5:5), "Behold the lion of the tribe of Judah, the root of David . . ."

Trophyism, Interspecific Rank and Historical Interpretation

Until hominids achieved co-dominant or dominant status in predator guilds, and resources were clumped and defendable, intergroup competition (warfare) would not have become more important than interspecific competition (for reasons discussed above and in Eaton, 1976, in press). Trophy values and related cultural phenomena should indicate the status of a people among predators and the relative importance of interspecific and intergroup competition. I showed that the trophies of several societies indicate interspecific rank, subsistence patterns, and the importance of warfare. Thus, fossil and historical evidence of trophies and their symbols could be used to interpret the ecologies and social behavior of extinct societies, as well as the histories of extant societies.

Viewed as trophyism (Eaton, in preparation a), the upper Paleolithic art of Europe (12-33,000 years old) (Leoroi-Gourhan, 1976) and Rhodesia (2-4,000 years old) (Cooke, 1974), suggests that neither of these hunting peoples had achieved full dominance over large carnivores (Eaton, in preparation a). For example, the rarest and most sequestered depictions in cave art are of the *most dangerous* species, big cats, especially the lion. Apparently intraspecific aggression was rare compared to confrontations with some larger carnivores, such as bears. Hominids are very rare among Ice Age fossils in Europe, but some species of large carnivores (not the lion) are common (Kurten, 1968). It should be recognized that the cave lion was larger than its living descendant and it was probably social. It is reasonable to believe that the lion was dominant to the large bears, which were probably asocial (Herrero, 1978). Trophies buried with Paleolithic hunters of Europe include large herbivores and bears, but not lions, indicating that full dominance had not been achieved (Eaton, in press). As we learn more about the carnivore faunas associated with hominids, and their diets and trophies, a clearer picture should arise about human evolution and the possible importance of domestication of the dog, weaponry, and so on, in man's achievement of dominance. The following section supports a view that dominance occurred very recently in human evolution, and that trophyism may have been involved.

An Overview of Trophyism in Western Civlization

I outlined a few points in support of the hypothesis that art originated as trophyism (Eaton, in preparation a). I also suggested that picture writing could be traced directly to trophy art. Hieroglyphics resemble the pictographs of several extinct and extant hunting peoples, and apparently represent the first fully developed written language. Hieroglyphs are phonograms or sound pictures, which were decoded by relating the symbol of the lion to the letter "L" in Greek (Casson, 1965). In the Indo-European language system, the root form for the word lion has the same sound as the lion's roar (Eaton, in press), which made decoding possible. It is conceivable that hieroglyphs originated from depiction of trophies, which the Egyptians sought.

That the lion was a trophy and probably had been an important competitor of the early Egyptians is indicated by several things. Pharaohs went hunting for lions in the desert to prove their power; such feats were depicted on the walls of royal buildings (Casson, 1965; Guggisberg, 1961). The war goddess, Sekhmet, was part woman, part lioness; Bes, a lion-headed dwarf, scared off evil spirits (Casson, 1965). The chief Egyptian god, Rā, was symbolized as a serpent with a lion's head (Gaskell, 1960: 676).

The most common headress of the Pharaohs and many animal gods was symbolic of the lion's mane, resembling the headress of Masai (above), which may have a neohaemetic origin. The Sphinx is a lion's body and a man's head; this, the oldest huge structure built by man may have communicated the power of its builders to their enemies in Upper Egypt (see Casson, 1965). The Sphinx has a headress of the type representing a lion's mane. Rā assumed the form of the Sphinx when he desired to protect his friends and adherents (Gaskell, 1960: 716).

Priests were exceptionally high in status among Egyptians; they were considered powerful and godly. Priests wore animal skins as their outer garment, especially those of dangerous predators such as the leopard (Casson, 1965).

Both household furniture as well as tomb furnishings often were decorated with animal figures, especially the head, paws and tails of the lion (Casson, 1965). Tutankhamen's throne rests on carved lion's paws and handles of the two arms are the heads of lions, a form of decoration practiced into the 19th Century throughout much of Europe.

Pharaohs were buried with symbols of their might. The most impressive figure in Tutankhamen's tomb, for example, was a six-foot-long wooden lioness situated in the antechamber. It was designed as a bier; the word bier has a common origin with that of bear, and the first objects to be placed in graves were the teeth of bears (Howell, 1965), trophy necklaces worn by Paleolithic hunters in Europe. Some graves of young adult males of European hunters contain a single canine tooth of a deer. To this day in Europe a hunter's first kill of a big game animal, normally a deer, is symbolized by the animal's canine tooth (Guggisberg, 1970).

An unfortunate behavior of conquering warriors is the defacing of art. This practice can be traced back to European caves where trophy art, especially of large carnivores and bears in particular, was demolished, apparently by hunters of foreign groups (Eaton, in preparation a). The art of more recent societies often communicates power and status by depiction of leaders' exploits, as in hunting or war. The Greek mercenaries who served Egypt in Nubia carved a record of their exploits on one of Ramses' colossal statues, "a custom followed by military expeditions since time immemorial" (Casson, 1965: 161).

The culture of the Greeks similarly reflects the importance of trophyism and its possible role in domination of predators in their history. The coins of Greek cities commonly depicted successful hunting scenes which include a hunter, his weapon, the prey and a dog (Bowra, 1965). The coins of Abdera had a griffin, the combination of a lion and a bird of prey; the eagle symbolized Abydos and other cities nearby Troy. In Cyrene, the head of Zeus is shown on a coin with the horns of a ram, which had been a prized trophy species.

In the 5th Century B.C. the Greek highlands, mountainous and covering three-fourths of the country, had been covered with scrub forests, since declining due to overgrazing by goats (Bowra, 1965). Greeks hunted here for hare, lynx, bear, wolves and lions, partly to protect flocks but also to collect trophies and train for war. The warlike Spartans had famous hunting grounds, some of which became the only areas containing formidable predators, where they abandoned children believed to be unfit for military life. In this way they may have fed larger predators while also making them more dangerous adversaries for hunting meant to improve skills and gain status. Even Plato, the father of pious idealism, advocated hunting as desirable in the training of young men; moreover, Plato himself was a hunter (Ortega y Gasset, 1972).

Much of Greek life concerned trophyism and its cultural outgrowths. Here are a few examples: the goddess Athena had a sphinx on her helmet; the shields of Greek warriors often depicted lions and birds of prey; and, Dionysus, youngest of the gods and lord of the good life, wore a panther-skin cloak, symbolizing his power as god of wild things (Bowra, 1965). Incidentally, the Greek historians noted that in the Persian wars, Xerxes troops included eastern Ethiopians who dressed in lion and leopard skins.

It seems probable that dancing, like song and music, evolved from imitation of animals to enhance hunting success (Eaton, in preparation a). Acting stemmed from dancing, and the oldest Greek dances portray human victory over predators (Bowra, 1965). The word tragedy in Greek stems from the word meaning goat song, which probably meant the cry of the lost or dying goat. The goat was the primary source of animal protein for the Greeks; competition with predators was important (above).

Trophyism and Heroism

I have argued that the myths of a people often derive from trophyism, especially involving dangerous predators, and that trophies and associated myths can reveal the history of a people's competitive relationships with predators and human groups. Heroism is intimately connected to trophyism; nowhere is this more obvious than among the Greeks. To this day in the West, the greatest heroic figures are those of Greece. Some of the most famous tales of the Greek heroes reflect what I believe was the culmination of the last major adaptive strategy in human evolution: successful domination of predators.

The greatest hero of the western world is Hercules, whose most famous feat, his first, was killing the "invulnerable lion of Nemea" with his bare hands. Hercules wore the mane of the lion over his head and shoulders. The arche-hero's other feats are also "trophic" (the pun carries weight linguistically): capturing a golden horned ram after chasing it for one year--the valuable horns symbolize the feat of the hunter; running a great boar to death; shooting voracious, livestock-eating birds; and so on.

Other heroic figures include Oedipus, who challenged the sphinx, a humanized lion and monster which ate all passersby, but which could not solve the riddle of human development. Could this mean that men who did not evolve, i.e., achieve dominance, were eaten by the lion, but those who did, the men who gave rise to the Greeks and to us, used their bravery and intelligence to save themselves from the lion?

To build Thebes, Cadmus had to slay a dragon which killed and ate all his companions. This legend could mean that civilization, represented by the ancient city of Thebes, was possible only after man assumed high risks to dominate dangerous predators, i.e., trophyism could explain man's rise to dominance. Cadmus planted the dragon's teeth--trophies?--which gave rise to people from which he populated the city. The legend connects trophyism and procreation.

Theseus was said to have united Attica after he cleared the roads of bandits and killed the half-human, half-bull Minotaur. He also hunted the terrible boar and centaurs, and generally was a great leader because he was a good hunter.

Bellerophon killed the Chimaera, a fire-breathing monster with a lion's head. Using Pegasus, the flying horse, he was able to soar above the Chimaera and wound her with arrows; then he killed her with molten lead poured down her throat. This story suggests that it was the horse, coupled possibly with the use of metal weapons, that gave man indisputable domination over the lion. It is noteworthy that arrows alone were insufficient; the same applies to arrows of primitive hunters living today, such as the !Kung, who say that their wood arrowheads and spears are not powerful enough to be used against lions. Heavy metal weapons, as used by the Masai, are sufficient.

These and similar legends of many peoples need be taken seriously by evolutionary biology. For example, the 12 feats of Hercules could well represent the pattern of evolution from subordinate hunter to co-dominant hunter-warrior to dominant pastoralist-warrior. The theory of natural selection could profitably be joined with the theory of history known as *vital* or *historical* reason advanced by Ortega y Gasset (1941).

The symbol of Rome was the wolf. The pastoralists who gave rise to Rome hunted wolves and demonstrated their feats by wearing wolf skins, which communicated high status (Ortega y Gasset, 1941; Summers, 1946). Interestingly, these men wearing wolf skins gave rise through mistranslation of a Greek observer to the belief in werewolfery (although other factors contributed later, such as men wearing wolf skins to raid livestock; see Eaton, in preparation b). To this day in Italy, it is believed that possession of hair from a wolf will bring the man who killed it many children (Summers, 1946). This belief historically connects interspecific competition to trophyism as a form of reproductive competition.

An overview of trophyism in Egyptian and Greek history suggests that these great civilizations rest upon the domination of dangerous predators. That the same may apply to Rome, the greatest civilization and the one which has most influenced the modern world (Ortega y Gasset, 1973), is suggested by its sumbol being the wolf. Lucretius (Book V, 1st Century B.C., *On the Nature of Things)*, in speaking of the "sweet solaces of existence" which resulted from agriculture, says that these attributes of man and their advantages greatly surpass the "deeds of Hercules." He adds, "For what would yon great gaping maw of Nemean lion now harm us . . .?" Hercules' domination of the lion represents the ultimate pre-Roman achievement by mankind, i.e., the triumph of civilization was made possible by the struggle against predators, not other humans (e.g., as Alexander [1971], with whom I disagree, purports. Moreover, Alexander (personal communication, 1978) has since changed his view: "I think that interspecific competition could well have primed humans for their intraspecific competition, and it could explain about four million years that I have always been very uneasy about."). Lucretius' statements imply that the memory of struggle to dominion over aggressive or powerful animals was still much alive; in fact, they indicate that dominance was recent and still incomplete in outlying areas. He says, "And all other *monsters* [my emphasis] of the kind [lion, bear, poisonous snakes] which have been destroyed, if they had not been vanquished, what harm could they do, I ask, though now alive? None methinks; the earth even now so abounds to repletion in wild beasts and is filled with troublous terror throughout woods and great mountains and deep forests; places which we have it for the most part in our power to shun." However, Roman males did not shun such areas; they went there to collect trophies. It is pertinent to add that the singular event most socially esteemed throughout the Roman Empire was Marcus Antonius' ride through the streets of Rome on a chariot pulled by 20 lions.

What About Us?

I mention just a small number of examples of trophyism in modern Western society. Eight monarchies of Europe are symbolized by the lion (as are seven in Asia by the tiger). In a recent *Newsweek,* President Carter and his cohorts were depicted lionlike in the lion's den. Many beers, some for over 600 years, are symbolized by the lion. The most common name given to taverns for hundreds of years has been "Red Lion." The names of automobiles suggest trophy animals--cougar, bobcat, mustang, jaguar--powered by "putting a tiger in your tank." As one anonymous reviewer said, "Perhaps this is enough to explain the failure of the Edsel. Driving a car with a name like that is not going to affect the reproductive success of an American male." Along the lines of mate selection, the most esteemed fur coats have been those of the big cats; imitation fur coats have the same appearance (pseudo-trophyism?). In both classical and popular music, novels, poems, paintings and so on, the European peoples have emphasized animals of high trophy class. A large proportion of movies and television programming features trophyism threat of predators and, among animal films, there is a great concentration on predators and especially big cats. Within a few weeks during 1977, I saw advertisements for "Jaws," "Grizzly," and "Orca," all of which pitted man against extremely formidable predators. There was even a film, entitled "Day of the Animals," about predators overthrowing man. From May 20-21, 1977, the following programs appeared on national television in the U.S.: "Wolf Man," which was about a great trophy hunter who turned to hunting men. The culprit was described as "the real tiger of the house." "Spectre" was about sorcery and the occult; one line was, "legend has it that he [the devil] takes the form of a great cat." Our hero killed the devil.

Today we are most familiar with the awarding of trophy cups. This particular form of trophy appears to have originated in the late upper Paleolithic hunters of Europe, who may have used trophy skulls as drinking cups, a practice continued in Europe until a few hundred years ago (Howell, 1965).

In a more serious and perilous vein, I submit that since science became a profession the behavior of scientists tends to conform with that of trophy hunters. Each science--each cult--has its esteemed leaders, males who have the highest ranking trophy, e.g., the Nobel Prize. Lesser trophies include publications in *Science* or *Nature,* especially full-length articles; lesser still are doctoral diplomas, which *are* hung on walls, and so on. Intragroup competition for paper trophies is intense, but intergroup competition verges on combat, with each refusing to give status to the trophy standards of other cults. Hunters of ideas strive so much for trophies acceptable to members of their cults that their perception becomes highly conformed, the effect of which is diminishing creativity, and a scarcity of new ideas. In this sense it could be that trophyism threatens the future of science, and thus the possibility for a better human life.

Trophyism and Conservation

Recent cultural values in the West associate sport hunting with destruction of nature and "ecotrauma" generally. However, pious (see Ortega y Gasset, 1972) or misinformed advocates especially attack trophy hunting as an expression of male ego (Amory, 1974). The criticism appears to be biologically correct: I have tried to show that trophyism is a matter of competition among males for status. However, the moral judgment against trophyism is not necessarily valid. For the past several thousand years, trophyism has been the primary motivation for conservation of wildlife (see Guggisberg, 1970). Throughout the history of Western civilization, powerful men have set aside preserves for the purpose of trophy hunting. In American history, the greatest conservationist of wilderness was this country's best-known trophy hunter, Theodore Roosevelt.

CONCLUSION

The hypothesis appears to explain the origin and function of trophy hunting and its persistence in contemporary society. It may well apply to a wide range of problems of interest to several disciplines including paleobiology, sociobiology, history of art, anthropology and philosophy.

ACKNOWLEDGMENTS

I especially thank Sievert Rohwer, who, on a hunting trip, played ear to the question giving rise to the hypothesis: that question was "Why do you suppose so many duck hunters put the tail feathers of mallard drakes in their hats?" I have since become convinced of two things, possibly important to science: the need for taking mental play seriously and the need for recreating our evolutionary heritage to better see ourselves.

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LITERATURE CITED

Adamson, J. 1967. *The Peoples of Kenya.* Harcourt, Brace and World, New York.

Alexander, R. D. 1971. The search for an evolutionary philosophy of man. *Proceedings of the Royal Society of Victoria* (Australia) 84 (1): 99-120.

Allen, D. L. 1962. *Our Wildlife Legacy.* Funk and Wagnalls, Philadelphia.

Amory, C. 1974. *Man Kind?* Harper and Row, New York.

Anon. 1952. *Haida.* Provincial Museum. Victoria, British Columbia.

Binford, L. 1972. *An Archaeological Perspective.* Seminar Press.

Boas, F. 1895. *The Social Organization and the Secret Societies of the Kwakiutl Indians.*

Reports of the U.S. National Museum, Washington, D.C.
Boas, O. V., and C. V. Boas. 1970. *Xingu: The Indians, Their Myths.* Farrar, Straus and Giroux, New York.
Borner, M. 1978. The status and conservation of the Sumatran tiger. *Carnivore* 1 (1): 98-103.
Bowra, C. M. 1965. *Classical Greece.* Time, Inc., New York.
Casson, L. 1965. *Ancient Egypt.* Time, Inc., New York.
Clarke, E. E. 1953. *Indian Legends of the Pacific Northwest.* University of California Press, Berkeley.
Cooke, C. K. 1974. *A Guide to the Rock Art of Rhodesia.* Trustees of the National Museum and Monuments of Rhodesia, Salisbury.
Coon, C. S. 1971. *The Hunting Peoples.* Atlantic, Little Brown, Boston.
Curtis, E. S. 1915. *In the Land of the Head Hunters.* Yonkers, New York.
Drucker, P. 1951. *The Northern and Central Nootkan Tribes.* Bull. 144, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
Drucker, P. 1963. *Indians of the Northwest Coast.* Natural History Press, Gordon City, New York.
Eaton, R. L. In preparation a. *The Origin of Art.*
Eaton, R. L. In preparation b. Review of *Werewolfery,* by M. Summers. To appear in *Carnivore.*
Eaton, R. L. In press. Interspecific competition between carnivores and hominids and its implications for human evolution. *Carnivore.*
Eaton, R. L. 1976. The evolution of sociality in the Felidae. Pp. 95-142, *In:* R. Eaton (Ed.), *The World's Cats III* (2). Carnivore Research Institute, Burke Museum, University of Washington, Seattle.
Fisher, J. 1834 (1972). *Scripture Animals.* Weathervane Books, New York.
Frison, G. C. 1976. Cultural activity associated with prehistoric mammoth butchering and processing. *Science* 194: 728-730.
Forde, C. D. 1956. *Habitat Economy and Society: A Geographical Introduction to Ethnology.* Dutton, New York.
Gregor, T. 1977. *Mehinaku: The Drama of Daily Life in a Brazilian Indian Village.* University of Chicago Press, Chicago.
Guggisberg, C. A. W. 1970. *Man and Wildlife.* Arco, New York.
Guggisberg, C. A. W. 1962. *Simba.* Chilton Books, Philadelphia.
Harpending, H. C. 1971. !Kung hunter-gatherer population structure. Ph.D. Dissertation, Harvard University, Cambridge, Mass.
Herrero, S. 1978. A comparison of some features of the evolution, ecology and behavior of black and grizzly brown bears. *Carnivore* 1(1): 7-17.
Howell, F. C. 1965. *Man.* Time-Life, New York.
Jensen, A. E. 1963. *Myth and Cult Among Primitive Peoples.* University of Chicago Press, Chicago.
Kurten, B. 1968. *Pleistocene Mammals of Europe.* Aldine, New York.
Lantis, M. 1966. *Alaskan Eskimo Ceremonialism.* University of Washington Press, Seattle.
Leopold, A. 1949. *A Sand County Almanac.* Oxford University Press, Oxford.
Leroi - Gourhan, A. 1968. The evolution of Paleolithic art. Pp. 55-65, *In: Avenues to Antiquity: Readings from Scientific American.* W. H. Freeman, San Francisco.
Marshall, J. 1957. "The Hunters." McGraw-Hill, New York.
Matthiessen, P. 1962. *Under the Mountain Wall.* Ballantine Books, New York.
McCord, C. M. 1974. Courtship behavior in free-ranging bobcats. Pp. 76-87, *In:* R. L. Eaton (Ed.), *The World's Cats II.* Feline Research Group, Woodland Park Zoo, Seattle.
Meggers, B. J. 1971. *Amazonia: Man and Culture in a Counterfeit Paradise.* Aldine, Chicago.
Nelson, R. K. 1969. *Hunters of the Northern Ice.* University of Chicago Press, Chicago.
Ortega y Gasset, J. 1973. *An Interpretation of Universal History.* W. W. Norton, New York.
Ortega, y Gasset, J. 1972. *Meditations on Hunting.* Charles Scribner's Sons, New York.
Ortega, y Gasset, J. 1941. *History as a System.* W. W. Norton and Co., New York.
Rainey, F. G. 1947. The whale hunters of Tigara. *Anthropological Papers of American Museum of Natural History* 41(2):
Roosevelt, K. 1921. *The Long Trail.* Scribners, New York.
Slettebak, A. 1976. Indian whalers of the northwest coast. *Sea Pen* 5(2): 4-7.
Speck, F. G. 1940. *Penobscot Man.* University of Pennsylvania Press, Philadelphia.
Spencer, R. F. 1977. Shamanism in northwestern North America. Pp. 351-363, *In:* R. F. Fogelson and R. N. Adams (Eds.), *The Anthropology of Power.* Academic Press, New York.
Stross, B. 1977. Tzeltal conceptions of power. Pp. 271-285, *In:* R. F. Fogelson and R. N. Adams (Eds.), *The Anthropology of Power.* Academic Press, New York.
Summers, M. 1946. *The Werewolf.* Bell Publishing Co., New York.
Taber, R. D. Unpublished manuscript. Man as a hunter: Origins and cultures. College of Forest Resources. University of Washington, Seattle.
Textor, R. B. 1967. *A Cross Cultural Summary.* Human Relations Area File, New Haven, Connecticut.
Thomas, E. M. 1958. *The Harmless People.* Vintage, New York.
Tiger, L. 1969. *Men in Groups.* Random House, New York.
Trilles, R. P. 1932. *Les Pygmies de la Foret Equitoriale.* Bloud and Gay, Paris.
Turnbull, C. 1961. *The Forest People.* Simon and Shuster, New York.
Wagley, C. 1977. *Welcome of Tears: The Tapirape Indians of Central Brazil.* Oxford University Press, New York.
Weyer, E. M. 1932. *The Eskimos: Their Environment and Folkways.* Yale University Press, New Haven, Connecticut.
Yellen, J. E., and R. B. Lee. 1976. The Dobe-/Du/da environment. Pp. 27-46, *In:* R. B. Lee and I. DeVore (Eds.), *Kalahari Hunter-Gatherers.* Harvard University Press, Cambridge, Mass.

BOAT TOWING BY A BOTTLENOSE DOLPHIN

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For the three months June through August 1977 I followed a wild adult male bottlenose dolphin *(Tursiops truncatus)* around the coast of Cornwall, England, swimming with it frequently in order to study its behavior. This report is concerned mainly with the dolphin's unusual behavior: towing large boats, small boats and swimmers. It is preceded by a brief summary of the dolphin's history.

A description of the appearance, history, behavior and movements of this dolphin has been given by Lockyer (in press) and an anthropomorphic book about the dolphin has been written by Dobbs (1977). Lockyer measured the dolphin to be about 360 cm long in May 1976 and estimated him to weigh 400 Kg. This is large, but his teeth are not worn down yet, so he is probably a young adult, perhaps 10 to 15 years old. Certain permanent body scars on the head (visible in Figure 1) and dorsal fin area, and a chipped tooth have provided a convenient means of identification. Lockyer and Dobbs have both traced the movements of the dolphin back to March 1972. Between then and March 1975 he was resident in harbors around the southern end of the Isle of Man in the Irish Sea. Between April 1975 and January 1976 he remained in the region.

Milford Haven lies at the southwest extremity of Wales, about 150 miles to the south of the Isle of Man. In January, 1976 he moved south again, arriving off the coast of Cornwall, at the southwest extremity of England--a distance of about 100 miles, which he covered within a few days of leaving Wales. Until the present (December 1977) he has frequented an area stretching from St. Ives on the north coast of Cornwall to Mevagissey on the south coast of Cornwall (see Figure 2). During this time he has favored certain localities, such as St. Ives, Mousehole, Penzance, Newlyn, St. Michael's Mount, Falmouth, the Helford River and Coverack (and other smaller harbors), where he has remained for periods varying from days to months with short daily excursions. These preferred areas show similarities in that boating, fishing, mooring and human diving and swimming activities were present. More details of the dolphin's range of travel and behavior during the summer of 1977 will be described elsewhere (Webb, in preparation).

Lockyer (in press) reports behavior including: playing with, chasing and maneuvering boats; playing with divers, swimmers and floating objects; interfering with boat propellers and outboard engines; indiscriminate sexual activity with boats; and a generally sociable disposition towards people. I have observed similar behaviors. The dolphin is a solitary animal and, apart from one brief incident in the Isle of Man, and a possible incident in Cornwall, has not been reported to have been seen with other dolphins.

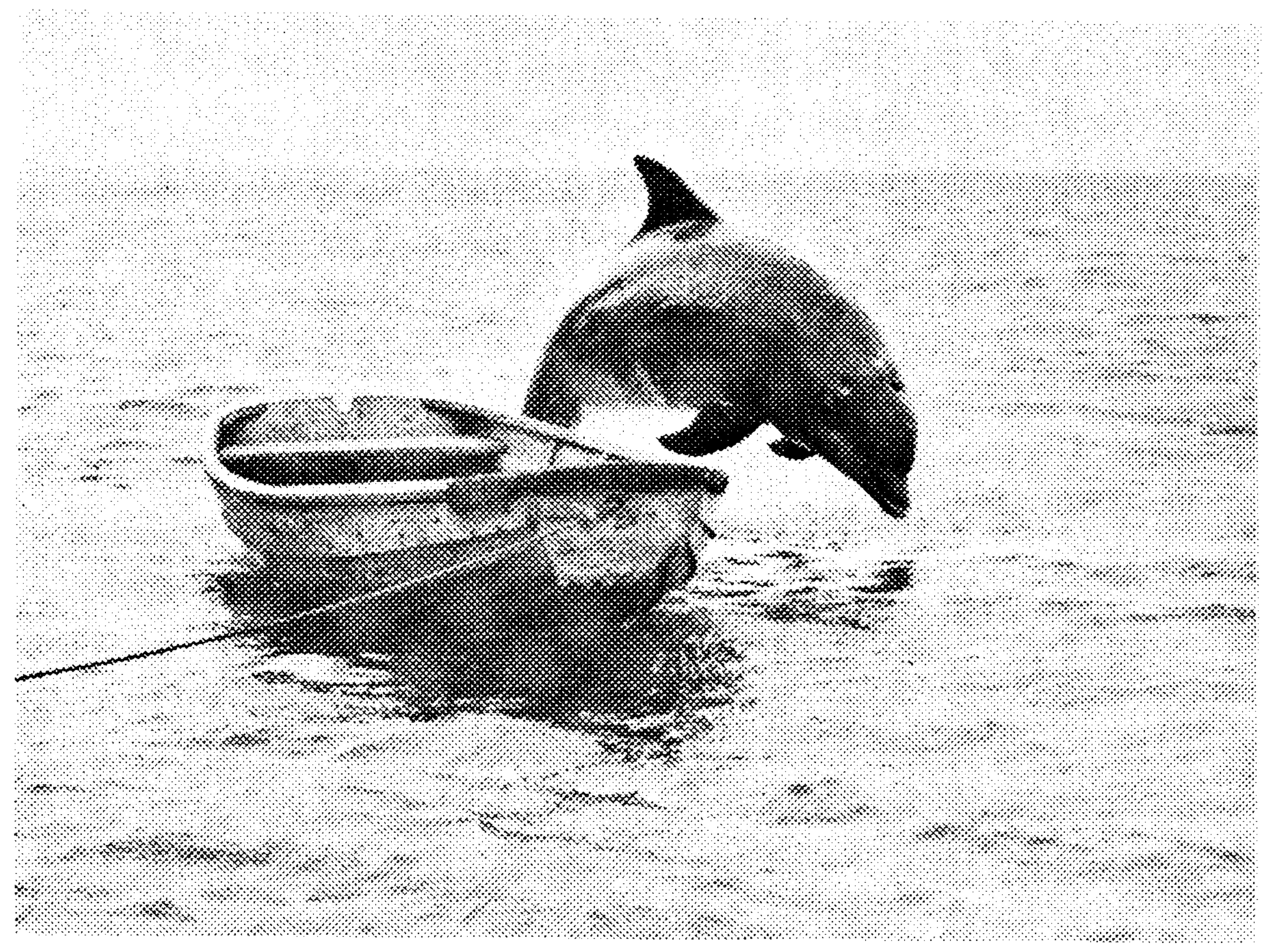

FIGURE 1. The dolphin playing around the tender to the "Sharen" made fast to its usual mooring in Martins Haven, Wales, in 1975. The pit above the right eye and the light scar behind the blowhole are two of the distinctive scars that help identify the dolphin, and are visible in photos taken two years later in Cornwall. Photo by The Institute of Oceanographic Sciences.

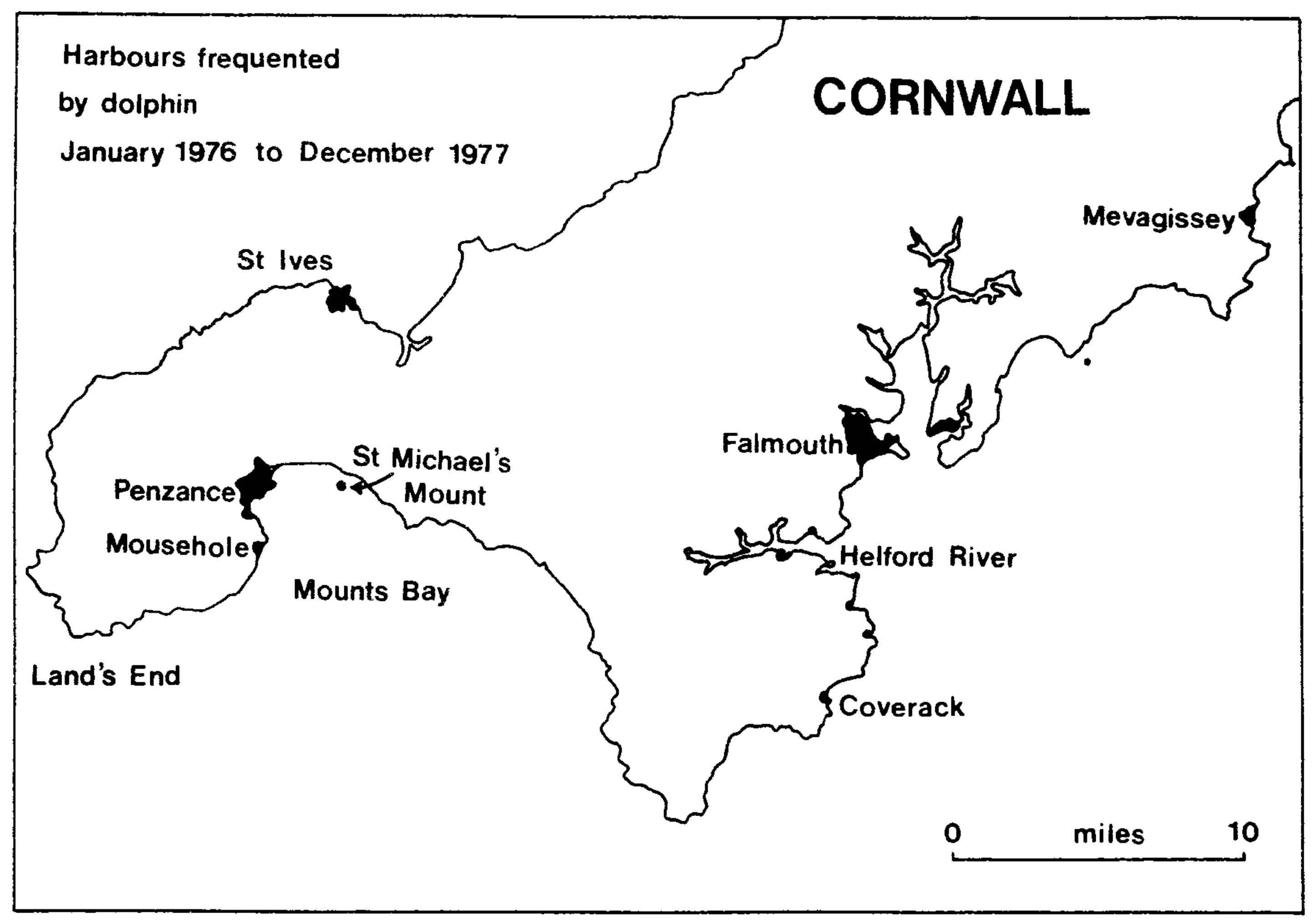

FIGURE 2. Harbors frequented by the dolphin from January 1976 to December 1977. Assembled from sighting reports compiled by C. Lockyer of The Whale Research Unit, by H. Dobbs, by G. Bold, and from my own fieldwork following the dolphin during the summer of 1977, and from interviews with fishermen and other residents in each of the areas depicted.

TOWING LARGE BOATS

While numerous large boats have been towed, this section deals only with a 2-week period of intensive towing activity in August 1977 when the dolphin resided almost continuously in Coverack Cove, except for brief excursions of a few hours each day. The half-mile diameter bay has a shelving sandy bottom, 30 to 40 feet deep. It contains seven permanent mooring buoys outside a small stone harbor which dries twice daily, at low tides.

From August 4 to August 12 the dolphin towed every boat that dropped anchor outside the harbor (i.e., visiting boats that did not enter harbor to moor, or moor at the permanent mooring buoys outside the harbor). Two larger vessels that dropped anchor further out in the bay, an ore carrier and a dive boat, the "Harry Slater" of Falmouth, were visited by the dolphin but did not appear to be towed, possibly because they were too large. At 1800 hours on 4 August two bermuda rig sailing schooners dropped anchor - the 6-ton "Pennylass," a 26-ft. Snapdragon class boat which released 45 feet of anchor chain, as did the "Woodpecker," a 5-ton bilge keel sloop. Both boats were towed a few yards almost immediately, but the crew, below decks, did not know this. The skippers were warned by a local fisherman, but they remained at anchor until each received a short second tow, as shown in Figure 3. They then moored in the harbor. The dolphin floated alongside in the crowded harbor for most of the night and the next morning until they left. On hearing of my interest in the dolphin, the skipper of the Woodpecker obligingly agreed to re-anchor outside the harbor for short periods on the evening of 12 August and the morning of the 13th. Although the dolphin accompanied us out of harbor, and watched the anchor drop, it did not tow the Woodpecker, but returned to the harbor until we restarted our engines. It immediately reappeared and accompanied us back to harbor.

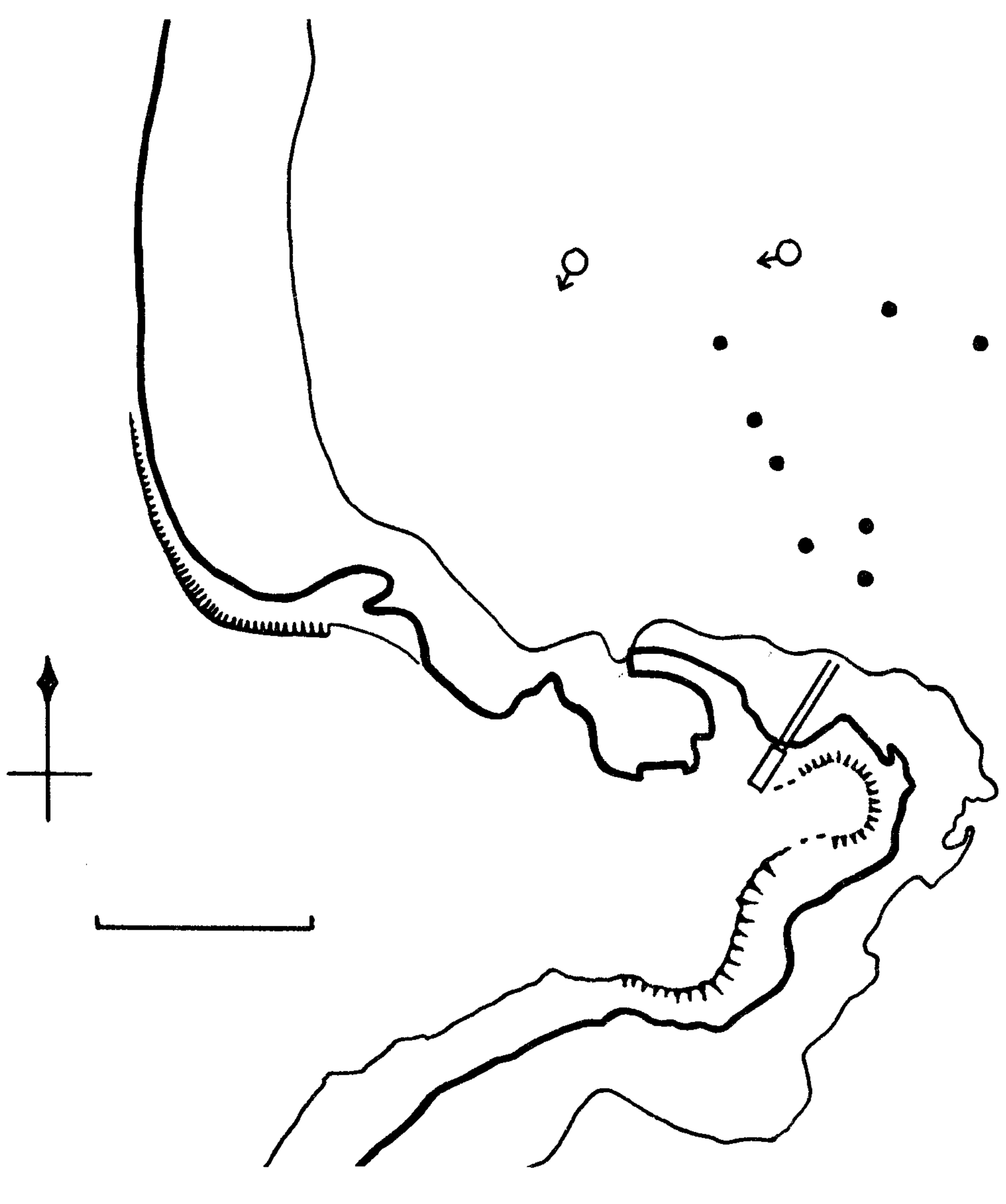

FIGURE 3. Arrows represent the paths of the "Woodpecker" (5 tons) and the "Pennylass" (6 tons) during their tow by the dolphin at Coverack on 4 August 1977. Thick line means high water mark. Thin line means low water mark. Black dots represent mooring buoys, and open circles represent the position of ships on dropping anchor. Horizontal scale mark represents 100 yards.

At 2000 hours on 5 August the 7-ton masthead schooner "Aquarius of Arne" anchored with 8 fathoms of 5/16th inch-thick chain and a 35-lb. anchor. It was towed 100 yards in a semicircle through the permanent mooring buoys, as shown in Figure 4. The crew speedily returned from shore and took the ship into harbor.

Previously, on 3 August, the dolphin had tangled the anchor of the small cabin cruiser "Phoenix" in some mooring chain on the sea bed. On 4 August the dolphin watched closely while I untangled it (Figure 5). The Phoenix was again towed by the dolphin on 9 August after dark. The 1600 lb. fiberglass boat with a 45 horse power outboard motor, was towed 500 yards into the center of Coverack Cove and brought back to rest close to the harbor wall. The dolphin then towed it out 10 yards to its initial position (Figure 6). The cruiser was unattended, but an assistant observer, Colin Swaler, was snorkelling with the dolphin when the tow started. At 0700 the next morning the Phoenix was found 500 yards away around a headland and close to rocks (see dotted line in Figure 6). While it may have drifted during the night, local fishermen thought this improbable.

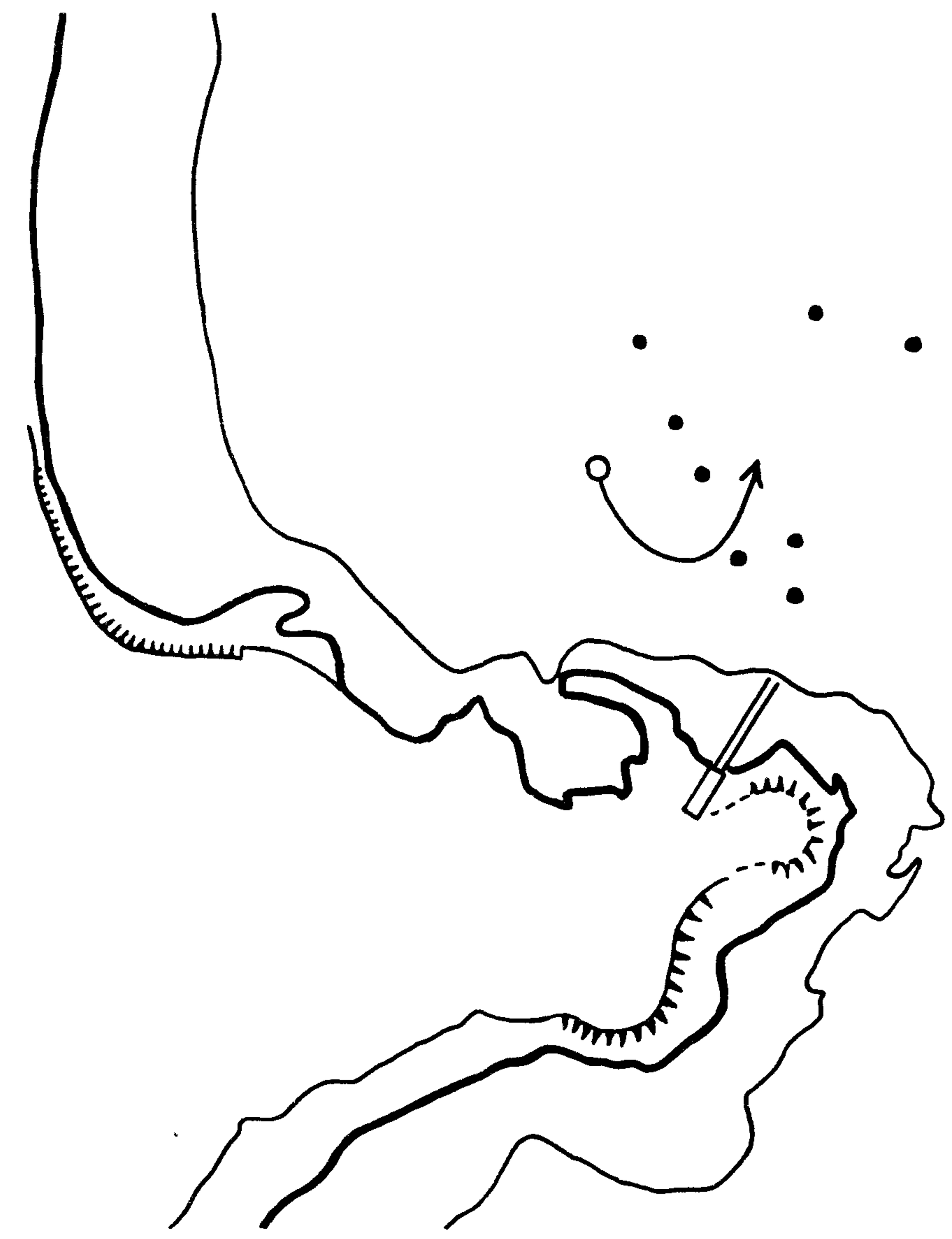

FIGURE 4. Arrow represents the path of the "Aquarius of Arne" (7 tons) during its tow by the dolphin at Coverack on 5 August 1977.

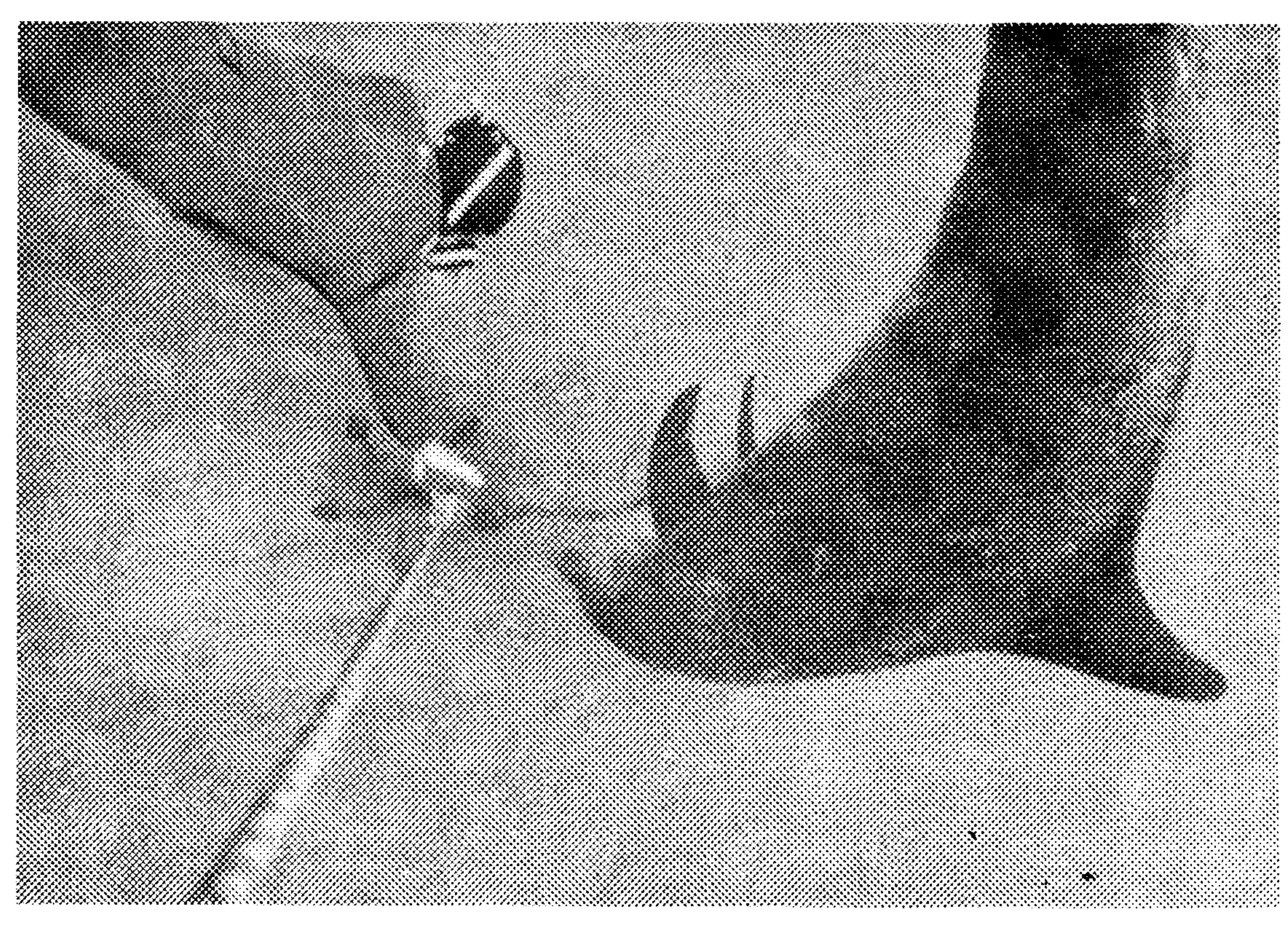

FIGURE 5. Dolphin watches without interfering as I untangle the anchor of the "Phoenix" at Coverack of 4 August 1977.

On 11 August from 1630 to 1800 hours three medium-size family sailing cruisers dropped anchor. The first, on being towed, tried to re-anchor, then left the bay. The second, on being towed a few yards, moored with difficulty to a permanent mooring buoy. The dolphin was observed repeatedly pushing the mooring buoy just out of reach of the crew, behavior which has frequently been observed in Falmouth Harbor and the Helford River. (Falmouth Harbor police reported one skipper who spent over an hour trying to pick up his mooring buoy before giving up and mooring somewhere else.) At 1800 the third sailing cruiser dropped anchor and the crew went ashore. The dolphins apparently left the boat alone (i.e., the boat did not move) until 1945 when Colin Swaler entered the water. They swam together for 5 minutes, then the dolphin picked up the anchor and towed the boat 20 yards until it was almost on top of Swaler, and stopped close to a permanent mooring (Figure 7). A brief "tug-of-war" ensued between Swaler and the dolphin, who were both pulling on the anchor chain. Swaler observed the dolphin's jaws slip up the anchor chain, away from the anchor, so he dived and wrapped the anchor around the mooring buoy rope. He observed that the dolphin was watching. The dolphin then found that it could not move the boat. It swam back and forth repeatedly between the tangled anchor and Swaler, nodding its head at him. (Variations on this gesture are frequently seen, but the meaning is not clear. I do not think it is a threat gesture.) As this was happening the skipper rapidly returned to his boat and winched up the anchor and mooring against the dolphin's counterpull, the dolphin held on to the tangle until it was well clear of the water. Then it swam towards Swaler with its mouth open and gave him two sideways swipes of the tail (a definite threat gesture, discussed below), making firm contact with Swaler, who rapidly swam away. The sequence of events on the surface was independently confirmed by observation from the shore.

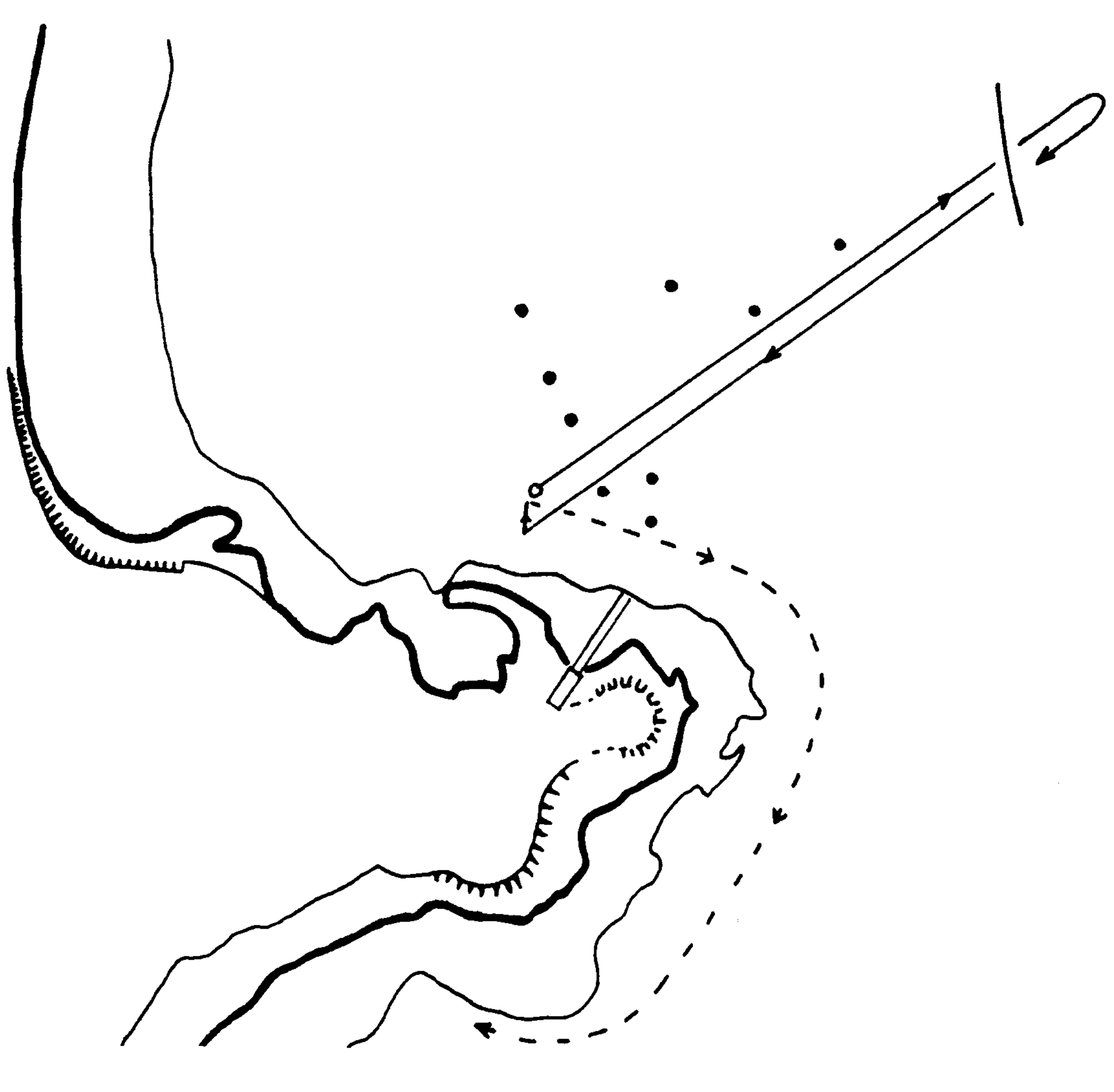

FIGURE 6. Path of "Phoenix" (1600 lb. plus 45 h.p. outboard motor) during tow by dolphin on 9 August 1977. Dotted line represents presumed path during the night, when the boat could have been towed, or may have drifted.

At 1900 on 12 August a 21-foot Bermuda-rig yawl "Slim 3) dropped anchor. It was towed immediately and continuously until 1940 and intermittently until 2100. The skipper, A. van Duin of Rotterdam, stood on deck taking photos of the dolphin as it rose to breathe (Figures 8 and 9 clarify the dolphin's position in the water). He reported that, throughout the towing period, whenever the dolphin surfaced the chain was held in its jaws and wrapped over its head, as if to cushion the strain on its teeth. Figure 8 shows the dolphin actually exhaling through the links of the chain, which rest across the blowhole. This tow was unusual in that the skipper did not try to stop it. The route traced out by "Slim 3" is shown in Figure 10, which was reconstructed from 26 photos such as that in Figure 11, which I took of the towing between 1900 and 1940. As can be seen, the sea was calm and there is absolutely no possibility that the boat was simply drifting. The dolphin expended a great deal of effort during the towing. His general level of arousal could be judged from his frequent breaths and occasional jumps, such as that in Figure 12, which shows the dolphin jumping over two children who attempted to swim nearby while Slim 3 was being towed. Usually the dolphin is very passive around young children; but on this occasion it jumped over them several times, showing that the towing had made him quite excited. (The children were unharmed but badly frightened.) During the tow three mooring buoys were wrapped together. Next morning I inspected and photographed the tangle on the sea bed as the dolphin looked on (Figure 13). From the boat the anchor chain dropped 20 feet almost vertically to an 18 x 12 x 12-inch concrete mooring block. Here the anchor chain was wrapped around a mooring chain attached to the block. The two chains were tangled together in loops and figures of eight. The anchor chain then extended in a straight line for 70 feet to a 30-lb. plough-type anchor. Scars in the sand showed that both the 70 feet of anchor chain and the heavy "thrasher" chain attached to the concrete block had been dragged. The yacht was immobile for 2 days, until the concrete block was winched to the surface and the anchor chain was unshackled from the yacht and untangled. The dolphin watched the whole process, inches away from the concrete block as it hung at the surface. On 13 August there was a regatta in Coverack Cove. A score of boats were anchored, but none was towed, although the dolphin was present. On 16 August the dolphin left during a storm, turning up in Mounts Bay, 20 miles to the west, where it has largely remained until the present (December 1977).

FIGURE 7. Paths taken by three unknown sailing cruisers (estimated weight 4 to 6 tons) during tow by dolphin at Coverack on 11 August 1977.

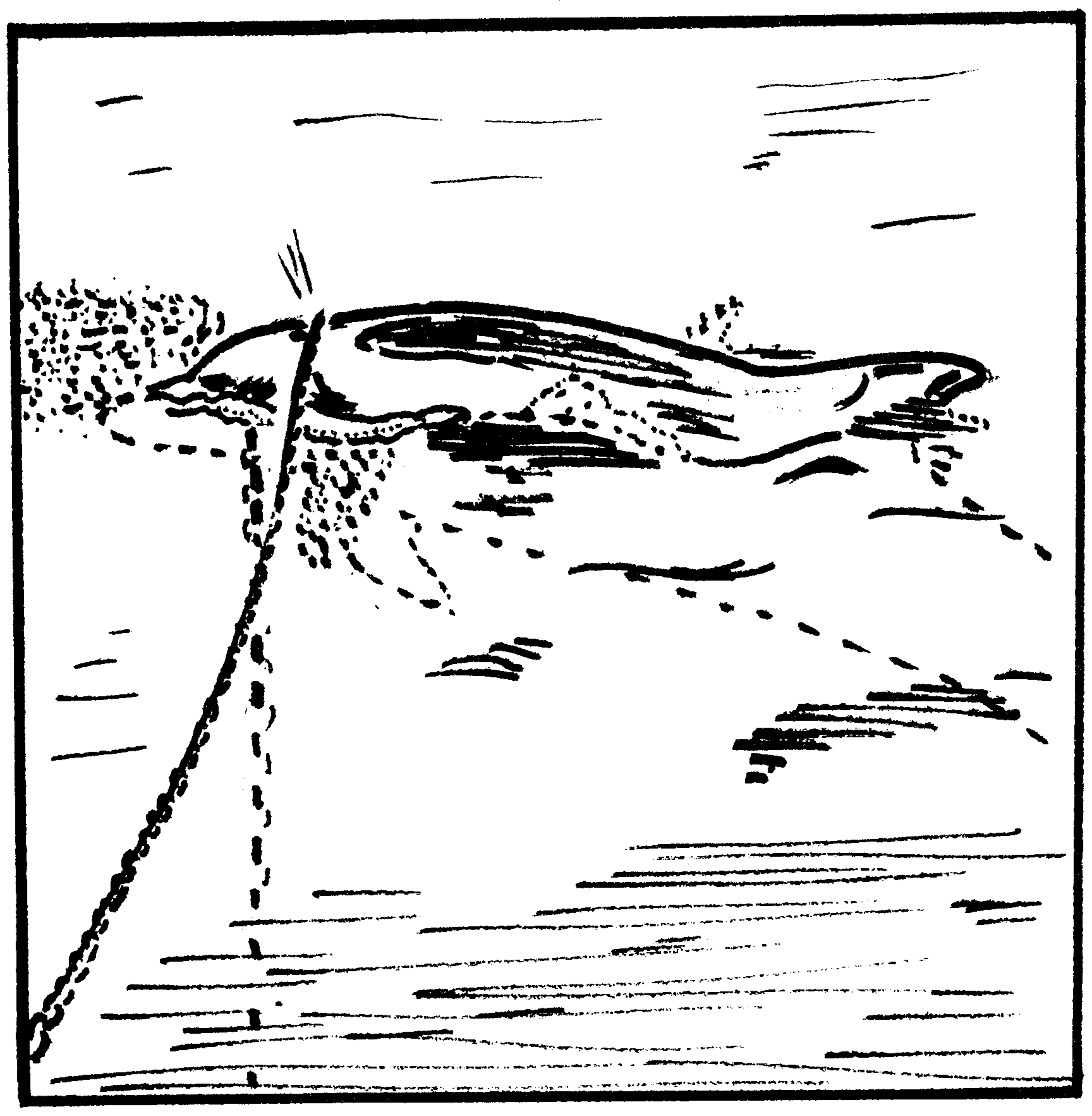

FIGURE 8. Sketch from photo showing position of dolphin and anchor chain. The dolphin rises to blow while towing "Slim 3" at Coverack on 12 August 1977. Notice dolphin exhaling through the links of the anchor chain which are almost occluding its blowhole. The chain is held in the dolphin's jaws. From photo by A. van Duin, skipper of "Slim 3."

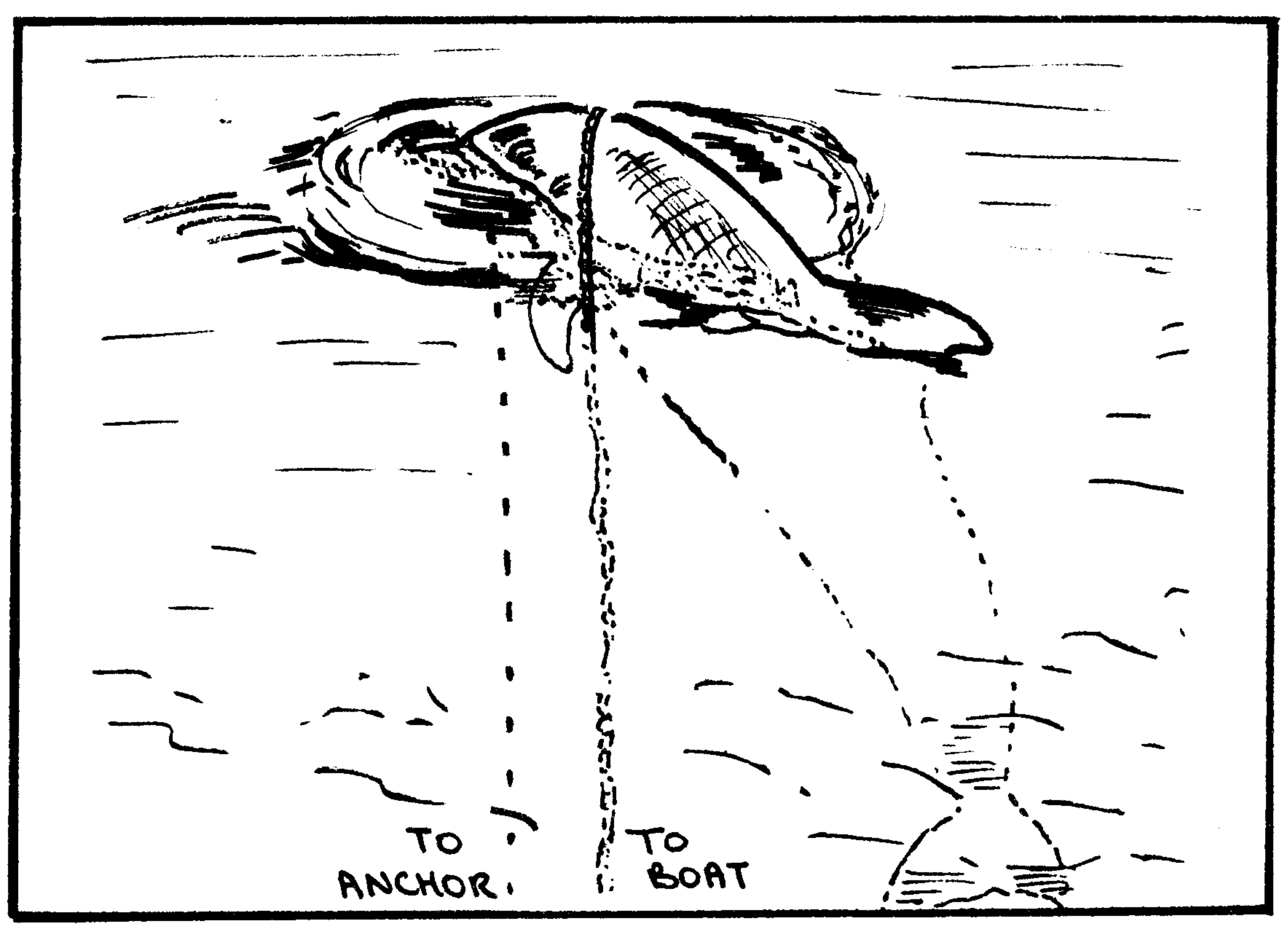

FIGURE 9. Sketch interpreting position of dolphin and anchor chain. From a second photo taken from "Slim 3" as the dolphin surfaces to blow during towing on 12 August 1977. Again, the chain is held in the dolphin's mouth and across his head. Photo by A. van Duin.

OTHER REPORTS OF BOAT TOWING

During the summer of 1977, while following the dolphin, I received several reports from local boat owners of instances of towing large and small boats. The largest boat towed was a 31-foot, 10-ton catamaran owned by D. Eastburn of Truro, who was anchored overnight at Durgan, near the mouth of the Helford River. He alleges that at dawn on 26th June 1977 he and three crew members awoke to find themselves being towed nearly half a mile out toward the mouth of the Helford at speeds of up to two knots. This incident was reported in the *West Briton* on 30 June 1977 and in the *Sunday Express* on July 3 1977.

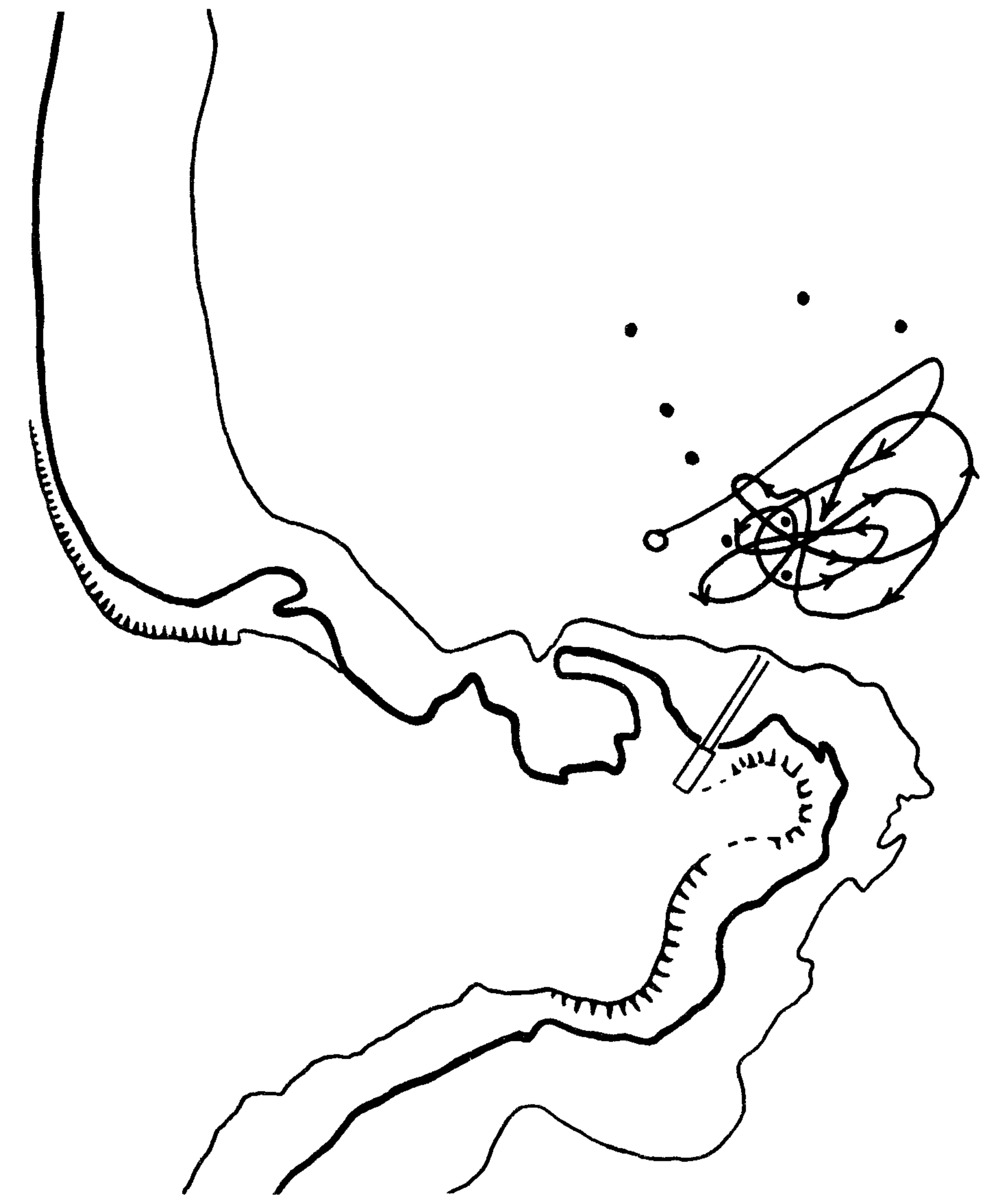

FIGURE 10. Path taken by "Slim 3" (estimated weight 3 tons) during tow by dolphin at Coverack on 12 August 1977 between 1900 and 1940. Reconstructed from 26 photos (such as Figure 11).

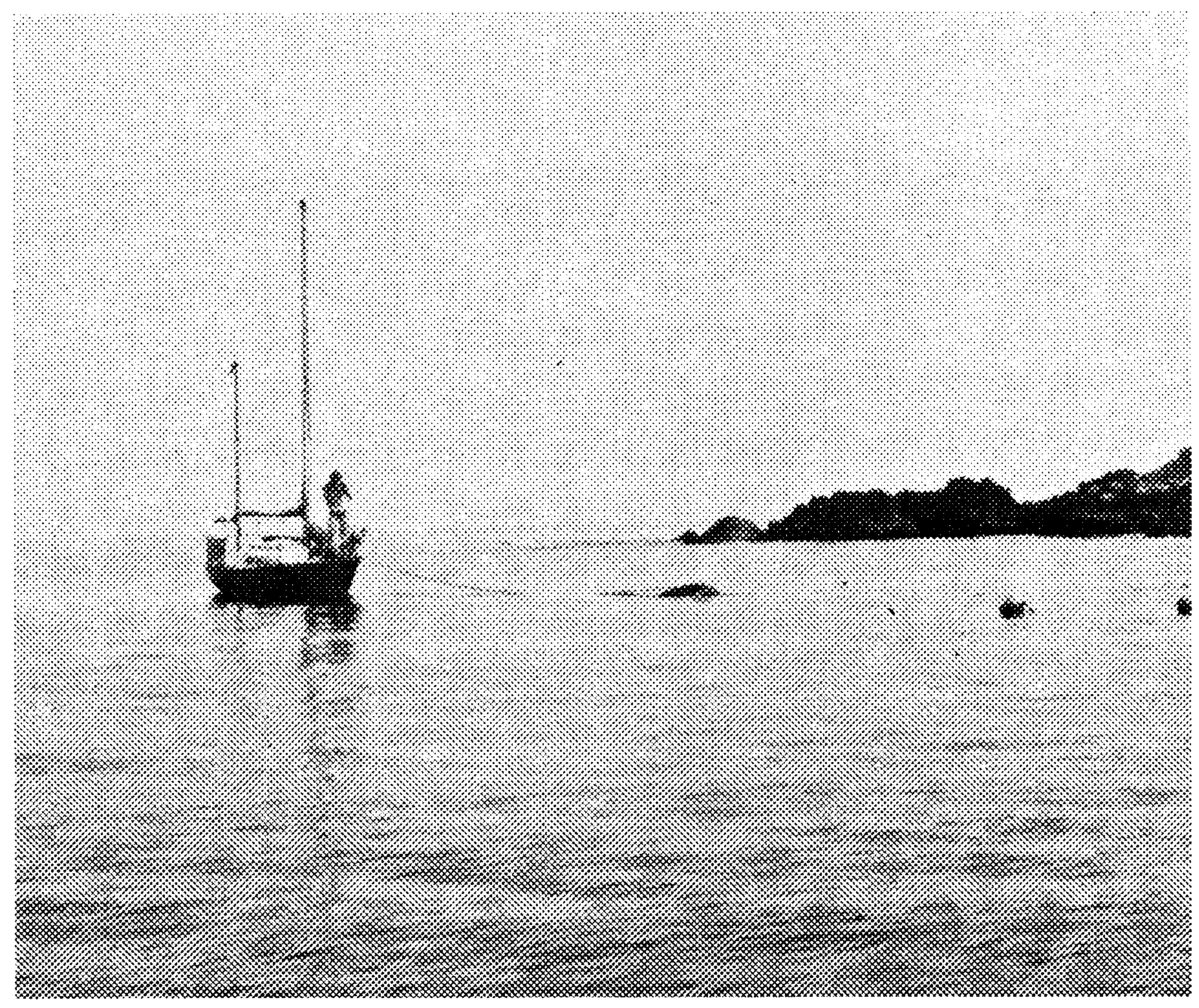

FIGURE 11. The dolphin tows "Slim 3". The skipper can be seen photographing the dolphin (Figures 8 and 9).

On 29 May 1977, R. Brandon, owner of a Nicholson 36, was lying at anchor in the Helford opposite the village of Helford during a flood tide. This was one of the dolphin's preferred locations during the spring and early summer of 1977. Brandon reported that the yacht suddenly "started to charge about as though it was a child's toy being pulled by a string." "A few moments later, a large dolphin, believed to be of the bottlenose type, surfaced alongside with a huge splash and blast of breath. The whole crew was now on deck with torches and saw this animal repeating this maneuver with a smaller unoccupied boat before returning to 'play' with our anchor." The behavior lasted an hour. During a strong N.E. wind that night, the yacht dragged anchor, narrowly missing some moored craft. The next day, on winching up the anchor, the trip line was found to be wound many times around the anchor--this was the reason the yacht dragged. The owner was sufficiently worried about the possible danger to yachting to report the incident to *Yachting Monthly* (August 1977). While the dolphin was not positively identified by the skipper, the location and the incident itself almost certainly identify the dolphin as the same one.

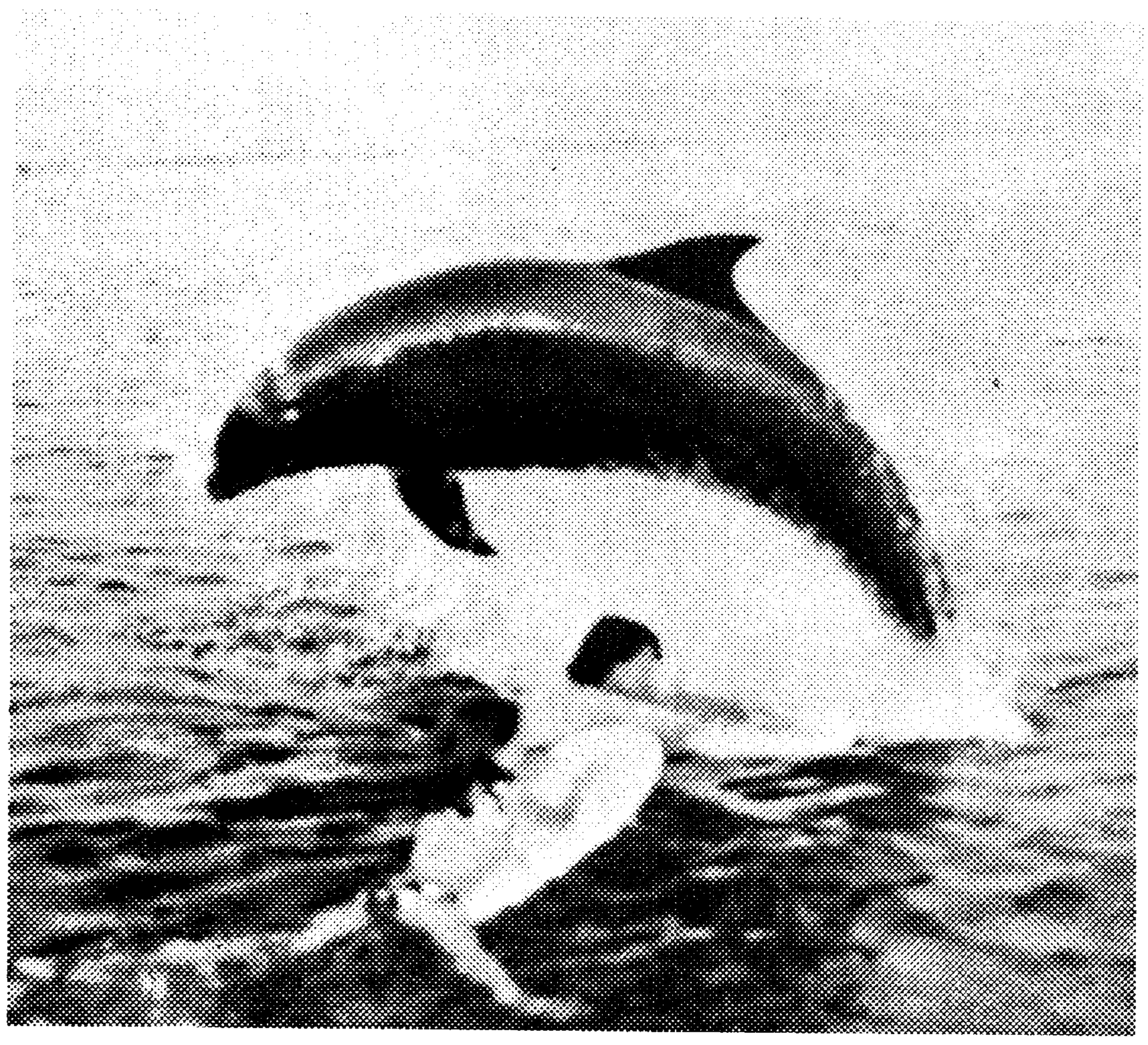

FIGURE 12. The dolphin jumps repeatedly over two children during a pause in the towing of "Slim 3" at 2000 on 12 August 1977.

FIGURE 13. The author inspects the anchor chain of "Slim 3" on the morning of 13 August 1977. The dolphin looks on but does not interfere. Self-portrait, taken one-handed with a Nikinos II camera and Vizmaster wide-angle lens.

Inshore oyster fishermen in the Helford River and Falmouth Harbour, unknown to each other, have each had their work disrupted as a result of the dolphin moving the anchor, either repeatedly returning it to the boat, or towing the boat along. Bert West, ex-coxswain of the Falmouth lifeboat, claims that he was towed across an oyster bed while his oyster dredge was down and caught 16 oysters, but that the next time he got nothing, because he had been towed right off the oyster bed.

TOWING SMALL BOATS AND MOORINGS

During the late afternoon and evening the dolphin is usually found next to one of its preferred mooring buoys, which may or may not be occupied by a boat or pram dinghy. The dolphin sometimes splashes vigorously and jumps against the bows of boats encroaching within a few yards of a preferred mooring, in a manner which appears to be aggressive and which suggests a territorial defense. Much of the dolphin's activities when alone and next to a mooring appears to be masturbatory: towing mooring rope with his penis, and rubbing his ventral surface and genital regions against moorings and the bottoms of small boats. He sometimes lifts the boat and occupants a few inches, and sometimes swims vigorously and jumps close by, as in Figure 1. Behavior such as this has been reported by observers since his earliest appearance in 1972 at the Isle of Man. Interposed between such periods of activity are periods of quiet, during which the dolphin lounges or rests next to the mooring. Further details of the dolphin's preferred rest and play areas, and his behavior in their vicinity, and of our interactions while swimming together, will be given elsewhere (Webb, in preparation).

A consequence of the dolphin rubbing its ventral surface against boats or moorings is that the boats will move, so a reliable way of spotting the dolphin in a large harbor is to see if any moored boat is moving in an unusual manner. I have observed the dolphin moving moored craft on numerous evenings in Falmouth Harbour, during daylight and after dark until about 0200 when observations were terminated. Observations were possible at night because the dolphin's preferred rest and play area was within a few yards of shore; the harbor lights illuminated the water surface, and it was generally calm and quiet at night, so the dolphin's explosive exhalation and inhalation of breath could be heard even when the dolphin was on the far side of a boat.

Occasionally it appeared that the dolphin deliberately tried to entangle small moored boats or make them collide. On several evenings in Falmouth Harbour I saw a 12-foot clinker-built sailing dinghy travel rapidly and directly toward a neighboring dinghy and collide vigorously with it. The sailing dinghy was then pushed or towed in the opposite direction more slowly, turned round, and brought back with a rush. The alternating pace between the rush before collision and the slow return, and the straight line path the dinghy followed, always directed at the second boat, suggests that the dolphin was deliberately making the boats collide. The dolphin has severely entangled the moorings of boats on numerous occasions, and has thus made considerable extra work for the Falmouth Harbour Commission and private individuals, who have often required a scuba diver to untangle the mooring chains.

TOWING SWIMMERS

Swimmers frequently solicit a tow by gripping the dolphin's dorsal fin as he floats alongside. The dolphin responds either by pulling the swimmer along (Figure 14), by sinking out of reach, or by rolling over to present its ventral surface and genital region for rubbing (Figure 15). Very rarely the dolphin will do nothing. Occasionally the dolphin has carried a swimmer on its forehead, or has pulled a swimmer by grasping an arm in its jaws, causing minor scratches.

Figure 14 shows a 16-year-old boy, Robert Sutton of Truro, Cornwall, being towed outside

Falmouth Harbour during July 1977. He was given about fifteen tows, hanging on to the dorsal fin as shown. After each tow the dolphin returned to the boy and floated quietly alongside until its dorsal fin had been grasped once more. In all these and other tows I have witnessed or participated in, the dolphin starts the tow gently. Tows accelerate for 10 to 15 seconds until the participant lets go, or else they level off at a few knots. A tow ends when the participant loses his grip or when the dolphin "barrel-rolls" and dives. On this occasion the dolphin towed the boy repeatedly for about half an hour until the boy became tired and cold and began to swim back to his father's yacht which had been following. I was observing from an inflatable rubber sportsboat, a few yards away. While the boy swam towards the yacht, his progress was impeded by the dolphin, who gently obstructed and pushed the boy away from the yacht for about one minute before letting him leave the water. On another occasion, after swimming alone with the dolphin in the Helford River, I experienced a similar deliberate attempt by the dolphin to hinder me from reaching my inflatable boat. The dolphin floated passively in the water across my path as I swam the last 10 feet to the boat. I pulled myself over and past his dorsal fin. As I did so the dolphin repositioned itself very rapidly between me and the boat, then floated there quietly in a deceptively passive manner. I had to repeat the maneuver three times to cover the 10 feet to the boat. When I reached and held onto the underwater rope ladder the dolphin made a brief open mouth gesture toward my arms, then swam off.

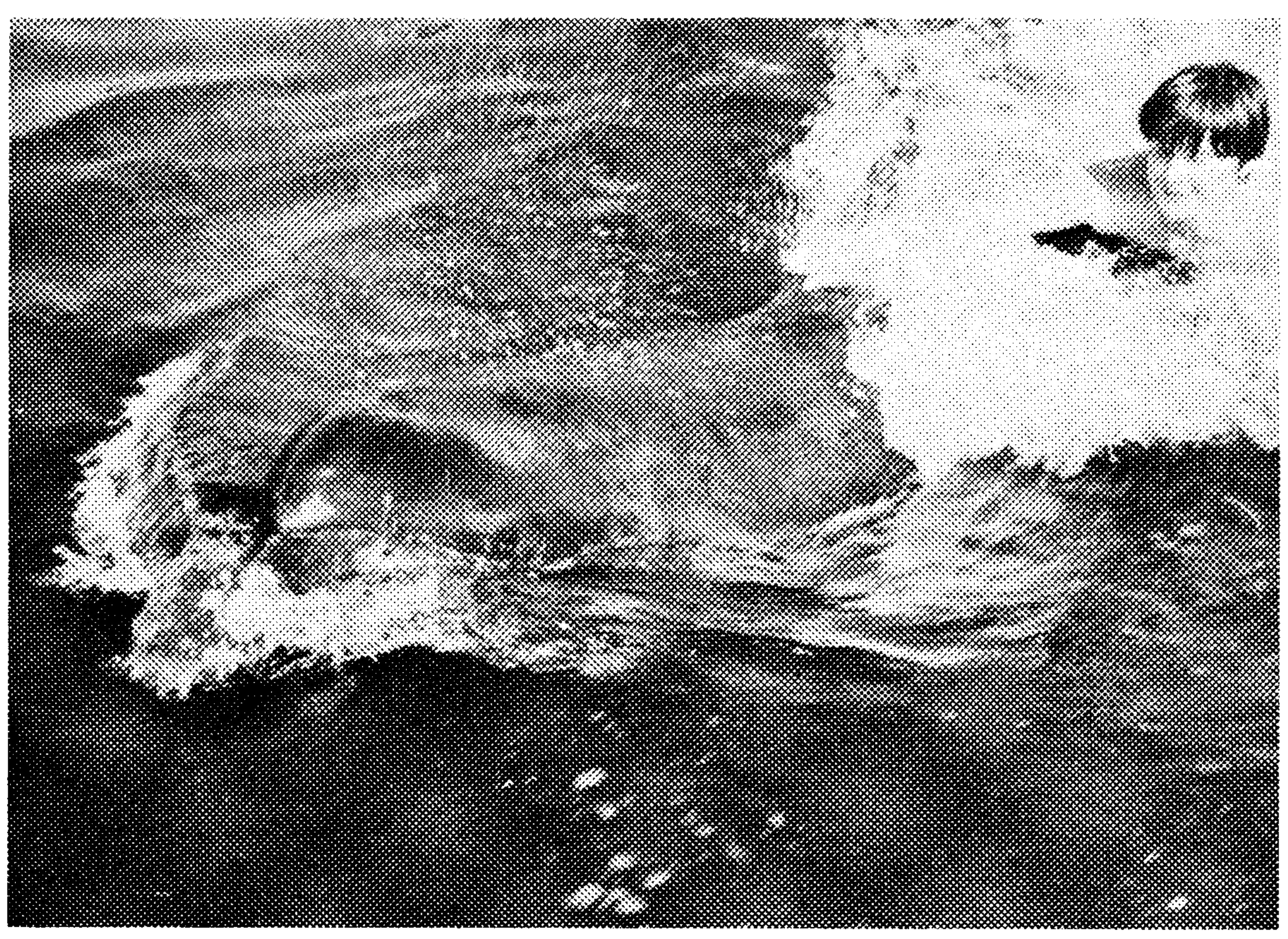

FIGURE 14. Photo showing Robert Sutton (16 years) being towed by the dolphin outside Falmouth Harbour, July 1977. Photo by W. Sutton, Truro, Cornwall.

One way of gaining the dolphin's attention, and of exciting him into giving tows, is to tow a swimmer through the water with a rope attached to a boat. This was used in the towing incident with the boy described above. Another instance occurred in Coverack in August 1977. In Figure 16 the swimmer is soliciting a tow from the dolphin by holding on to the dorsal fin with one hand and to an aquaplane with the other. (An aquaplane is a board with a handle, rigged to allow a diver to steer as he is towed through the water.) On this occasion three swimmers, including myself, took turns at being towed behind my inflatable rubber boat. Each swimmer found, within a few minutes of commencing a tow on the aquaplane, that the dolphin would grip the forearm or elbow of the arm holding onto the aquaplane in a series of gentle bites of increasing pressure. Between each bite the dolphin would let go and continue swimming alongside for a few seconds; then it would return with a slightly firmer bite. Each swimmer held on until about the third or fourth bite, when the dolphin's teeth, which are conical and sharp, began to pierce the neoprene wetsuit and become painful. (Eventually I found that if I pushed the dolphin away with my free hand, it would not bite it - only the hand holding on to the tow. Thus it was possible to rapidly change hands in order to interpose my free arm between my towing arm and the dolphin. However, the animal's strength enabled it to reach across and bite my towing arm anyway. Finally, a few days later, I struck upon the notion of pushing him in the eye with the palm of my hand. This worked; he veered off immediately and did not attempt to bite after that.)

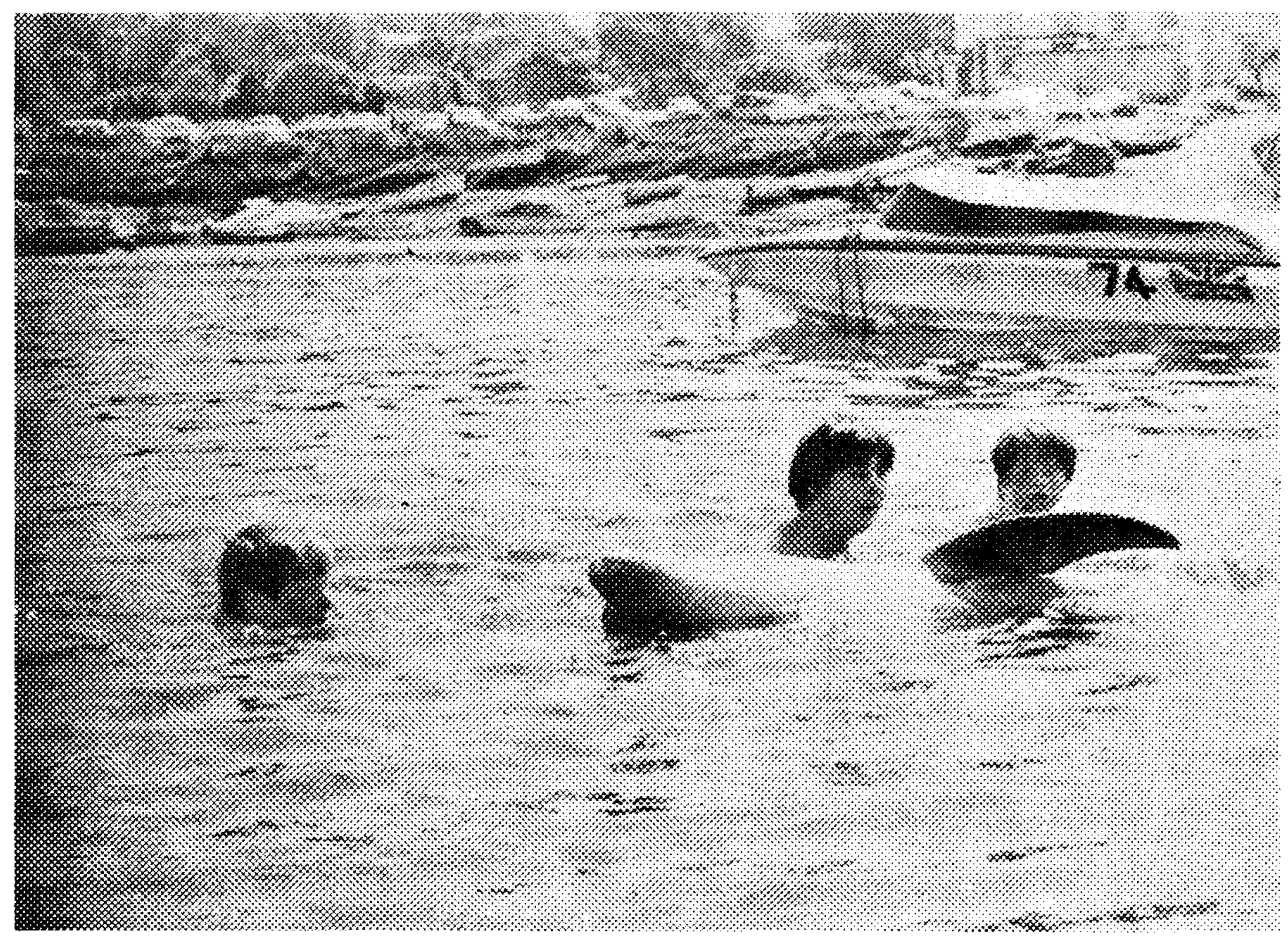

FIGURE 15. The dolphin rolls over for rubs in Falmouth Harbour, in one of its preferred rest and play areas. The swimmers, from left to right, are Kevin Stanton (13 years), Robert Sutton (16 years), and Adrian Sutton (13 years). Photo by W. Sutton, Truro, Cornwall.

When the swimmer was forced to let go, the dolphin either stayed with the now-stationary swimmer, and would usually give him a tow, or it would follow the aquaplane, occasionally contacting it. Several times the dolphin towed the swimmer after the boat, catching up and remaining level with the aquaplane, even when the boat was given a zig-zag course. Sometimes when the boat circled back to enable the stationary swimmer to recatch the aquaplane, the dolphin made one or more "abbreviated tail-swipe" (keep away) gestures. The swimmer's head is characteristically under the tail flukes, which are being lifted rapidly over the diver's head and into the water on the other side, causing the diver to rock in the turmoil. If the leading edge of the tail flukes makes contact it can cause a nasty jolt; but on average the tail either misses, or the contact is firm but not sharp. The term "abbreviated tail-swipe" is used because I have once witnessed a full tail-swipe against the rubber inflatable boat in which I was sitting, and which swamped it. Nothing remotely resembling such a violent impact has been directed against swimmers. While swimming I have frequently received abbreviated tail-swipe gestures in situations where the dolphin has clearly taken possession of inflatable toys, string, and even women and children. It appears to be a threat gesture against a potential or perceived competitor for the possession of someone or something, and was also observed during boat towing (described above).

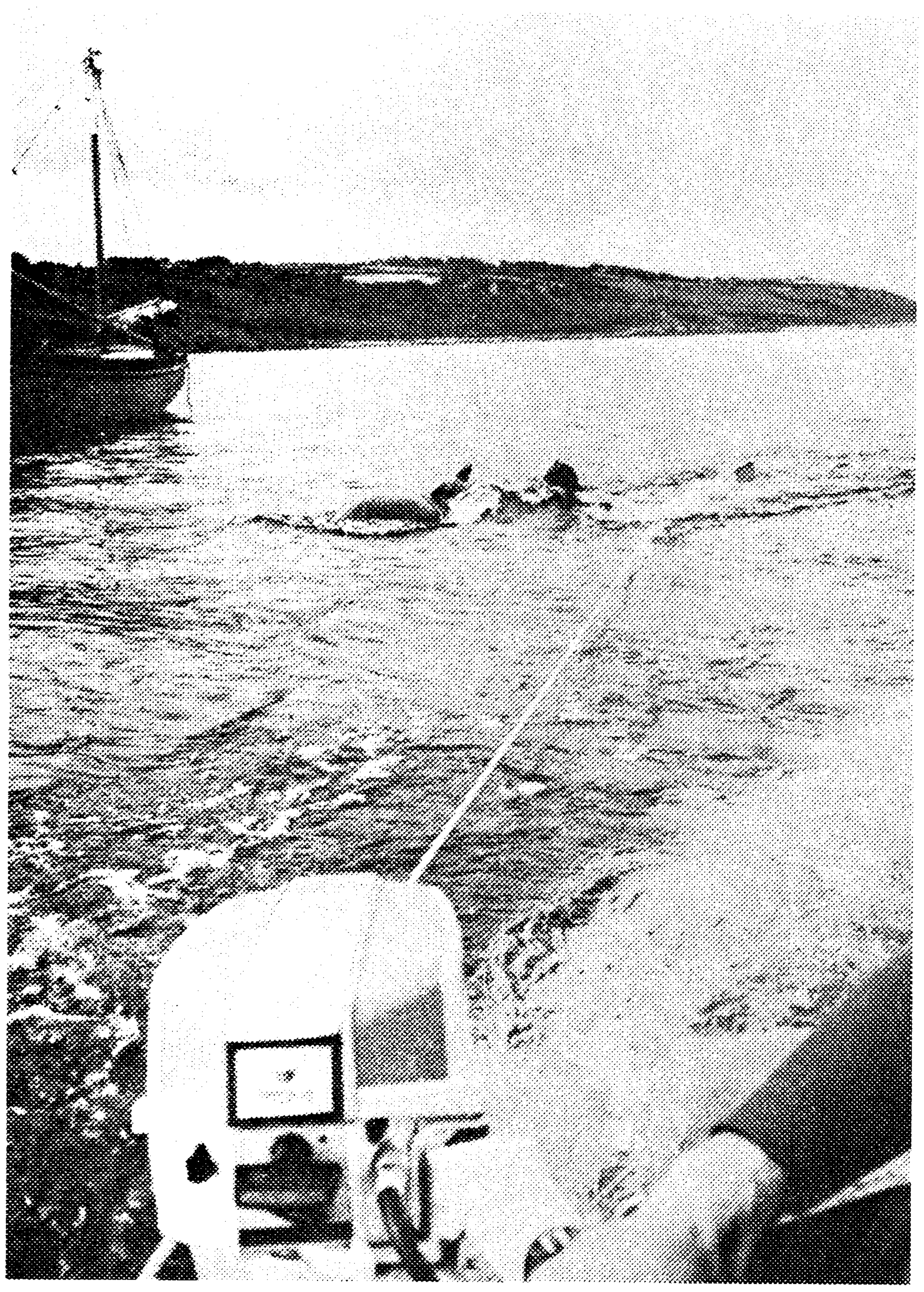

FIGURE 16. Ashley Dobbs solicits a tow from the dolphin by holding onto his dorsal fin with the right hand, while being towed along by an aquaplane, held in the left hand. Coverack, August 1977.

Having delivered the abbreviated tail swipe to the swimmer waiting for the approaching aquaplane, the dolphin followed the aquaplane and contacted a piece of string attached to it with his jaws and rostrum (Figure 17). Subsequently the dolphin dived and tension could be felt in the tow rope.

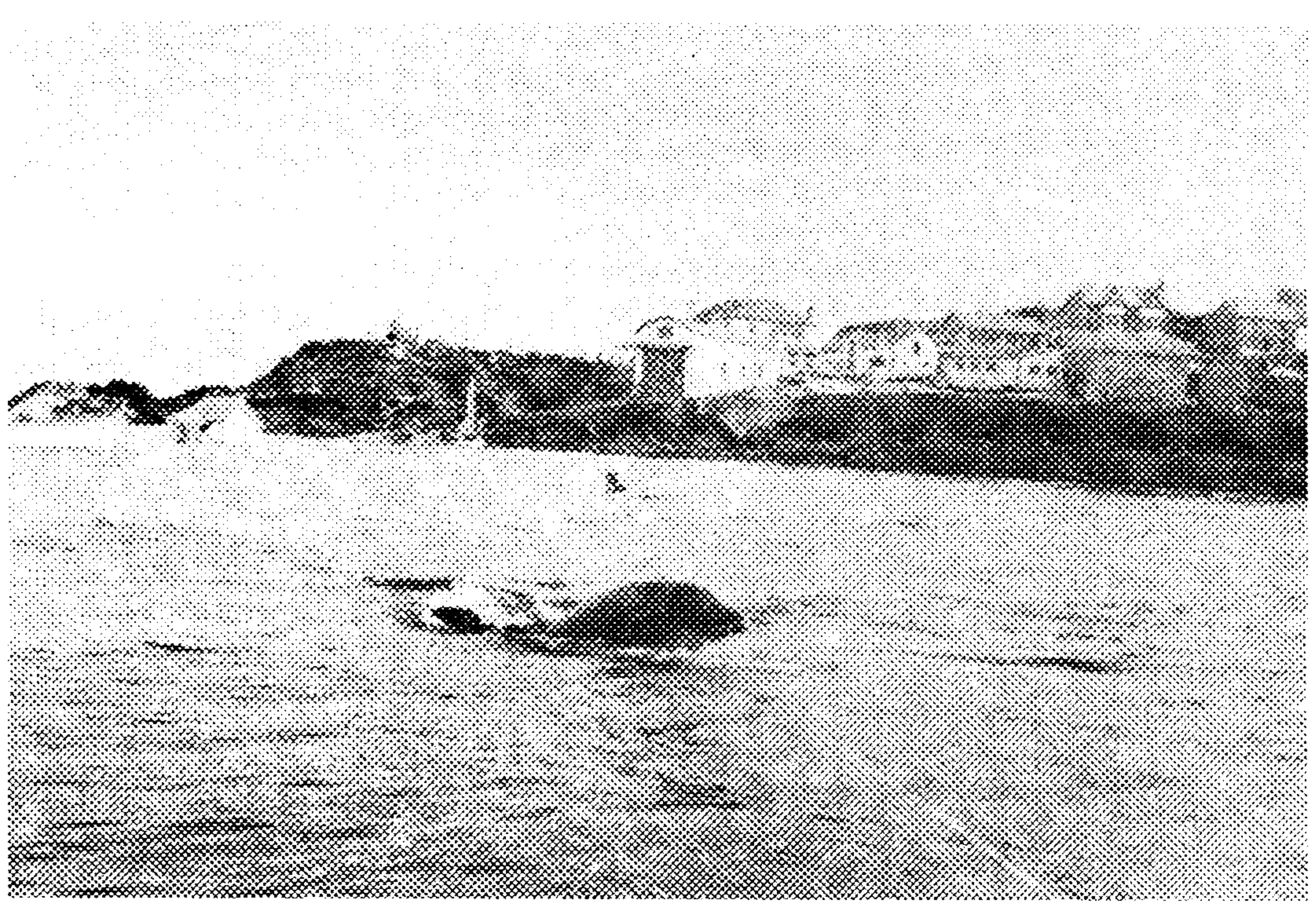

FIGURE 17. Having successfully prevented the swimmer from grasping the aquaplane by using the "abbreviated tail swipe" gesture, the dolphin swims after the aquaplane and contacts it. He is holding a piece of string in his mouth, which is attached to the aquaplane.

One of the swimmers, H. Dobbs, reported experiencing a similar sequence of events a year earlier, the dolphin forcing him to let go with a graded series of bites to the forearm, and then following on and contacting the aquaplane.

I have also received an unsolicited report from a fisherman who claimed that this dolphin had brought one of his otter boards to the surface during trawling. Otter boards are used to keep the mouth of a trawl open. It seems unlikely that the dolphin could lift the combined weight of the otterboards and trawl net, made heavier by the drag of the water. However, this dolphin, with its characteristic scarring and unusual behavior, frequently accompanies fishing boats, especially in the winter months when there is little activity in harbors. Quite possibly it could have played with otter boards and learned to use one like an aquaplane, using the force of the water to lift it to the surface.

I experienced another type of towing in September 1977. I looped a rubber deck quoit, attached to a rope, over the dolphin's rostrum, and swam to the tail, pulling the string taut in order to measure the dolphin's length. On feeling the tension the dolphin started to move, towing me about 100 yards. B. and H. Carswell, dive-boat operators at Mousehole, have reported observing scuba divers towed along underwater in a similar fashion, using a rubber ring and a rope. The dolphin is reported to have returned to the diver if he let go, allowing him to regrasp the rope for a further tow.

DISCUSSION

What possible sequence of events could have influenced the dolphin to tow large boats? Much of the behavior described above has not been seen before among wild or captive dolphins. One explanation is that the dolphin is not wild but has been trained in captivity. While this possibility cannot be disproved, it is unlikely for the following reasons. The dolphin has consistently refused to eat dead fish despite numerous attempts over the years by fishermen, tourist boat operators, and others who have tried to feed him. It is not normal or safe for a wild dolphin to accept dead fish, whereas acceptance of dead fish as food and as a reward is a primary feature of dolphinarium training. As the total record grows of this dolphin's unusual behavior, the possibility that he has been deliberately trained, or conditioned by the fortuitous juxtaposition of events becomes increasingly more remote.

It has also been said that the dolphin's obvious masturbatory behavior around small boats and moorings is a sexual aberration, and that therefore there must be something wrong with the dolphin, which explains why it is solitary, and so no useful purpose is served by studying it (J. Miller, personal communication). There are good grounds for rejecting these hypotheses. Firstly, a high level of sexual activity, including masturbation and homosexual behavior, is considered normal for dolphins (Caldwell and Caldwell, 1972). Secondly, having swum with the dolphin frequently during the 3-month period of observation, I can find no defect in its behavior. Thirdly, the dolphin's solitary status is not adequate grounds for supposing that something is wrong with it. Observations of captive dolphins suggest that the dominant bull of a school, while tolerant of sexual play between a young male and the females in the harem, becomes less tolerant as the youngster matures and becomes a potential competitor (Caldwell and Caldwell, 1972). Thus it may be normal for a young adult male to be expelled from his school and be forced either to join other young males or to remain solitary for a period.

The dolphin's frequent towing, rubbing and pushing behavior toward small boats, moorings and swimmers, although unusual, can be interpreted as having its origin in the social and sexual rubbing and pushing behavior which is common among dolphins (Caldwell and Caldwell, 1972; Norris, 1974; Bateson, 1974). The dolphin's initial encounters with small boats and moorings may have been a chance event which aroused his curiosity and provided an outlet for his needs for social and sexual rubbing. Rubbing may also help keep the skin streamlined by sloughing off dead skin and marine organisms. The initial movements of small boats could have been a secondary product of his rubbing. However, since towing and pushing is an integral part of this dolphin's social and sexual behavior (Caldwell and Caldwell, 1972; Bateson, 1974) and, since dolphins are known to be adept at devising new games (Caldwell and Caldwell, 1972), it is possible that the towing and moving of small boats could have gradually developed from a secondary effect into a play behavior. Repeatedly biting the arm of the swimmer towed by the aquaplane and subsequently towing the swimmer level with the aquaplane certainly appears to be complex play behavior.

The dolphin's towing of larger sailing and cabin cruisers showed no sexual connotations, and also appears to be a form of play. However, the dolphin often showed a great deal of effort and single-mindedness. In trying to move a boat securely moored to a concrete block at Coverack, the dolphin was observed from underwater to be pushing the chain with its back, beating its tail forcefully, and rising frequently for air. Because of such efforts the dolphin's back always had fresh wounds, some deep enough to bleed. The dolphin's lower jaw was also observed to be bleeding one morning when one of the heavy concrete mooring blocks was found upside down, even though the sea had been calm all night. On the occasion, described above, when the diver, C. Swaler, prevented the boat-towing from continuing, the dolphin's disciplinary abbreviated tail-swipes were unmistakable gestures indicating that the diver should keep away, and these gestures suggested that the activity of towing or possessing the boat was preferred to the diver's company. However, I think that a simple sensory-motor game of possessing and towing boats adequately explains neither the dolphin's apparent effort and single-mindedness nor the rich complexity of his behavior.

If Groos' notion of play as a sort of exercise for later life is to be applicable to human infants and the more intelligent mammals, such as the chimpanzee, then one has to allow not only for the exercise of sensory-motor skills during play, but also for the exercise of developmentally more advanced levels of brain function. Thus a 2- to 3-year old human infant may play games, such as imitating the action and sound of a church bell (Piaget, 1962), which appears to exercise the infant's developing ability to think in terms of symbols and images. Examples of symbolic play of this type have been reported for chimpanzees - such as Koehler's chimpanzee, which cradled and rocked its hind leg like a doll or baby (Piaget, 1962).

Saayman has carefully observed and reported unusual and complex imitative behaviors by captive bottlenose dolphins at Port Elizabeth, South Africa, which show a determination and single-mindedness comparable to that of the boat-towing dolphin discussed here, and which show a level of cognitive development in imitation comparable to that of the chimpanzee described above. For instance, a dolphin, Daan, on repeatedly observing a diver clean an observation window, was seen to clean it himself, using a seagull feather. Daan made a sound almost identical to that of the diver's air demand valve and released a stream of bubbles in a manner similar to that of exhaust air escaping from the diving apparatus. This was tape-recorded and filmed. Daan subsequently used food fish, sea-slugs, stones and paper to perform similar cleaning movements, orienting his pectoral flipper toward the metal frame of the window in imitation of the diver, who held the frame with his free arm while cleaning. The dolphin commandeered the vicinity of the window *for 54 days*, during which time he kept it meticulously clean and prevented other dolphins and divers from approaching the window by using open mouth threats and jaw clapping, or forcibly pushing them away. The dolphin also changed its resting pattern so as to remain next to the window (Taylor and Saayman, 1973).

Another example reported by Saayman was of a dolphin, Haig, that imitated in fine detail the swimming, resting and comfort movements of a Cape fur seal, both when the seal was absent, and when it was present but engaged in other behavior. The imitative behavior, though anatomically very difficult for the dolphin, was kept up for several months, culminating in abortive attempts at copulation between the two (Taylor and Saayman, 1973).

These examples of imitation are remarkable not only because of their attention to detail, but also because they were kept up for so long, and because they were made in the face of conflicting behavior from the model. It would appear that the dolphins have the ability to internally represent the sounds and action of a model and to imitate the internally represented model. If this is so, one might expect that dolphins are capable of "deferred imitation," that is, the correct first-time imitation of a new model after a delay. As far as I know, reports of dolphin imitation have not been detailed enough to decide this, although apparent examples of immediate imitation of complex new models, and the imitation of a possibly long-observed model (a diver and a seal) have been seen. The bottlenose dolphin is quite capable of imitating the way boatmen possess, move and moor boats, and the complexity of such behavior suggests its interpretation in terms of cognitive development (Webb, 1976, 1977).

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LITERATURE CITED

Bateson, G. 1974. Observations on a cetacean community. *In:* J. McIntyre (Ed.), *Mind in the Waters.* Scribners and Sierra Club, San Francisco.
Caldwell, D. K., and M. C. Caldwell. 1972. *World of the Bottlenose Dolphin.* Lippincott, Philadelphia.
Dobbs, H. E. 1977. *Follow a Wild Dolphin.* Souvenir Press, London.
Lockyer, C. In press. The history and behavior of a solitary wild, but sociable, bottlenose dolphin *(Tursiops truncatus)* on the West Coast of England and Wales. *Journal of Natural HIstory.*
Norris, K. S. 1974. *The Porpoise Watcher.* Norton, New York.
Piaget, J. 1962. *Play, Dreams and Imitation in Childhood.* Norton, New York.
Tayler, C. K., and G. S. Saayman. 1973. Imitative behaviour by Indian Ocean bottlenose dolphins *(Tursiops aduncus)* in captivity. *Behaviour* XLIV(3-4): 286-298.
Webb, N. G. In preparation. The behavior and intelligence of a friendly wild bottleneck dolphin.
Webb, N. G. 1977. Symbolic thinking in dolphins. *Search* 1(1): 38-44.
Webb, N. G. 1976. Dolphin imitation interpreted in terms of Piaget's stages of cognitive development. Unpublished manuscript.

NOTES

OBSERVATIONS ON THE AQUATIC GENET IN ZAIRE

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The aquatic genet, *Osbornictis piscivora,* recently has been termed "by far the rarest African carnivore" (Coetzee, 1977). Most of the few museum specimens in existence were purchased from local hunters. The reports of aquatic genets in the literature provide little information concerning natural history. In this paper, we review what is known of the distribution for *Osbornictis piscivora,* report new records of occurrence, and present information on habits based upon field observations made by Hart and the Bambuti Pygmies. The nomadic Bambuti with whom Hart lived from July 1973 through February 1975 reside in villages and hunting camps in the Ituri Forest, 60 to 100 kilometers west and northwest of Beni, Republic of Zaire.

We have information on three new specimens of *Osbornictis piscivora,* as follows: 1) adult female (weight 1,500 g) captured on 31 December 1973 at Masange, 60 km west of Beni; 2) adult male (total length 785 mm, tail length 340 mm, length of hind foot 83 mm, length of ear 41 mm, weight 1,430 g) captured at the same location on 16 January 1974; 3) adult of unknown sex (no measurements available) captured on 10 March 1974 at Masenze, 70 km west of Beni. Both locations have coordinates of 00° 30' N, 28° 45' E. The female from Masange contained a single embryo about 15 mm in length. The skull of the specimen from Masenze has been deposited in the James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis, Minnesota, USA (catalog number 13071).

FIGURE 1. A Mbuti hunter holding an adult male aquatic genet (right) and an adult female black-legged mongoose (left) captured at Masange, Republic of Zaire, 16 January 1974.

The Masange specimens, captured by hunters, were flushed by dogs near a small stream. The Masenze animal was snared in a hidden noose attached to a springy sapling and set on a small game trail on the forest floor.

Only 13 specimens of aquatic genets have been reported previously; all were captured in the Republic of Zaire, east or north of the Zaire River (see Rahm, 1965, 1966; Verheyen, 1962). All specimens, with one exception, were reported from heavily forested districts between 500 and 1,500 meters in elevation. The single exception is a locally tanned skin purchased near Butembo (see Schouteden, 1948). Quite probably this animal was actually captured in the lowland forest region to the west where people from Butembo have trade contacts. Butembo, at about 1,700 meters elevation, was originally covered by montane forest. The character of this original cover and ensuing second growth, quite unlike the lowland forest where all other aquatic genets have been captured, coupled with heavy human settlement, makes it unlikely that *Osbornictis piscivora* occurs in the area.

Our three aquatic genets were captured in a hilly district, between 700 and 1,000 meters in elevation, covered by extensive stands of virgin timber intermixed with second growth vegetation of varying age. The area is well drained and there are many streams and small rivers.

Osbornictis piscivora appears to be generally solitary in its habits, as hunters usually encountered this genet alone. Nevertheless, the two individuals taken at Masange, a pregnant female and an adult male, were captured only two-and-a-half weeks apart from the same local area of forest.

The two specimens from Masange were captured by Bambuti with the use of basenji, a small breed of dog. Hunters release one or more dogs, each wearing a wooden clapper, in a suitable area of forest. The dogs move ahead, crisscrossing back and forth until one encounters a fresh animal scent. A change in the sound of the wooden clapper informs hunters when a dog is on a trail. The hunters cannot know what game is being tracked so they follow the dogs until the game is flushed, put to bay or lost. This opportunistic method means hunters capture a wide variety of small game. In addition, hunters cover many microhabitats in their area, including rocky hill sides, bottom lands, virgin forest, and second growth.

The results of such hunts yield a sample of the diurnal mammalian fauna of the area. The proportion of the different species captured over a number of hunts may indicate their relative abundance. The following small carnivores (followed by number of captures and percentage of total) were taken with the use of dogs by Bambuti in the Masange-Masenze area in 53 hunts that resulted in 113 captures: Alexander's mongoose, *Crossarchus alexandri*, (76 - 67.3%); black-legged mongoose, *Bdeogale nigripes*, (28 - 24.8%); marsh mongoose, *Atilax paludinosus*, (5 - 4.4%); aquatic genet, (2 - 1.8%); spotted-necked otter, *Lutra maculicollis* (1 - .9%); and unidentified mongoose, (1 - .9%).

It seems unlikely that the habits of aquatic genets could account for their infrequent capture. Even if aquatic genets were nocturnal or crepuscular, thus rarely encountered by hunters, one would still expect them to be captured in snares. Hart, however, learned of only one *Osbornictis piscivora* snared in the Masange-Masenze area between 1973 and 1975, despite active inquiry among local trappers. This contrasts with several of the nocturnal genets which are regularly captured, judging from reports of trappers, and the numbers of skins preserved in the villages and offered for sale along the roadsides.

Both the Bambuti and neighboring Bantu agriculturalists consider aquatic genets to be rare. Most hunters and trappers have rarely if ever encountered it, and many local people are not even familiar with its name. Furthermore, the meat of the *Esele*, as the aquatic genet is known in the local languages Kibila and Kipakombe, is taboo and cannot be eaten, except by male elders.

The food and foraging habits of aquatic genets are an unknown but contested issue. The choice by Allen (1919) of the specific name "*piscivora*" implies that aquatic genets eat fish. Prigogine (cited by Schouteden, 1948 and Verheyen, 1962), on the other hand, reported learning from local people near Butembo and Katshungu, from whom he purchased skins, that the aquatic genet "feeds exclusively on Crustacea."

The Bambuti told Hart that aquatic genets primarily eat small fish, but on occasion will eat cultivated cassava tubercules (*Manihot* sp.), which have been left to soak in small streams as part of the preparation of flour. The stomach of the adult aquatic genet snared on 10 March 1974 contained numerous bones of small fish and one entire spineless catfish (family Clariidae), about 10 cm in length. At the time, the Bambuti suggested this fish was the favored prey of aquatic genets.

Additionally, dental morphology supports our observations that aquatic genets are piscivorous. According to Ewer (1973), the dentition of *Osbornictis* is adapted to deal with slippery vertebrate prey such as fish and frogs. She found it surprising that Verheyen (1962) reported that aquatic genets eat only crustaceans.

We also suggest that the distinctive bare palms of *Osbornictis* may be associated with specialized foraging habits and diet. The clariid catfish, which may represent a major element of the diet of aquatic genets, are nocturnal and live in small muddy holes in undercut stream banks. Bambuti often fish for these catfish by stirring up mud in likely holes, and then either feeling for and grabbing the fish with their hands or catching them with hooks baited with worms. Aquatic genets also may catch clariid catfish from muddy holes, bare palms being an adaptation which allows them to feel and handle these slippery prey.

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LITERATURE CITED

Allen, J. A. 1919. Preliminary notes on African Carnivora. *Journal of Mammalogy* 1: 23-31.
Coetzee, C. G. 1977. Order Carnivora. *In*: J. Meester and H. W. Setzer (Eds.), *The Mammals*

of Africa: An Identification Manual. Smithsonian Institution Press, Washington, D.C.
Ewer, R. F. 1973. *The Carnivores.* Cornell University Press, Ithaca, New York.
Rahm, U. 1965. Distribution et ecologie de quelques mammiferes de l'est du Congo. *Zoologica Africana* 1(1): 149-166.
_______. 1966. Les mammiferes de la foret equatoriale de l'est du Congo. Ann. Musee Royal de L'Afrique Centrale (Tervuren, Belgique), serie in-8°, *Sciences Zoologiques* 149: 37-121.
Schouteden, H. 1948 (1950). L'Osbornictis piscivora. *Bulletin du Cercle Zoologique Congolais* 20(1): 10-11.
Verheyen, W. 1962. Quelques notes sur la zoogeographie et la craniologie d'Osbornictis piscivora Allen 1919. *Revue Zoologie Botanique Africaines* 65(1-2): 121-128.

HOME RANGE OF A YOUNG FEMALE GEOFFROY'S CAT IN PARAGUAY

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INTRODUCTION

During the period from late August through early November, 1972, an ecological survey was made in the Gran Chaco region of the Republic of Paraguay. The survey was designed to determine the feasibility of a long-term study of the spotted cats, and other field species of concern to man.

The felid fauna of this region of South America is unique, as eight of the ten Neotropical species occur sympatrically (Cabrera, 1961). Spotted cat species in the Chaco include Geoffroy's cat *(Felis geoffroyi)*, little spotted cat *(Felis tigrina)*, margay *(Felis wiedii)*, ocelot *(Felis pardalis)*, and jaguar *(Panthera onca)*. The "non-spotted" species include jaguarundi *(Felis yagouarundi)*, pampas cat *(Felis colocolo)*, and puma *(Felis concolor)*.

The vegetation is predominantly mesquite of the genus *Prosopis*, with vinal *(P. ruscifolia)* the most obvious. This is an invader species that has come into the Chaco region of Northern Argentina and Paraguay since the drought years of 1936-37, when occasional fires no longer kept the subclimax grass stages in prominence (Morello, 1970).

MATERIALS AND METHODS

Two areas were sampled for botanical and faunal material during the survey, which included a limited live-trapping program for the smaller cats. The first area, at estancia Juan de Zalazar (21°45"S, 59°50"), produced a young female Geoffroy's cat after 120 trap-nights using tomahawk live-traps set at game trail intersections. No cats were captured in a second area approximately 150 km northwest along the Trans-Chaco Highway, near the military garrison of Teniente Ochoa. Jaguar and puma "sign" was observed in both areas.

The Geoffroy's cat was immobilized using phencyclidine hydrochloride, and a pulse-type, collar-mounted transmitter in the 150 Megahertz range was attached 16 September. The cat was captured 18 hours earlier, but had been held until the temperature had dropped below 32°C (90°F), when it was safe to administer the drug. Standard body measurements were made and the cat was released at the capture site.

RESULTS

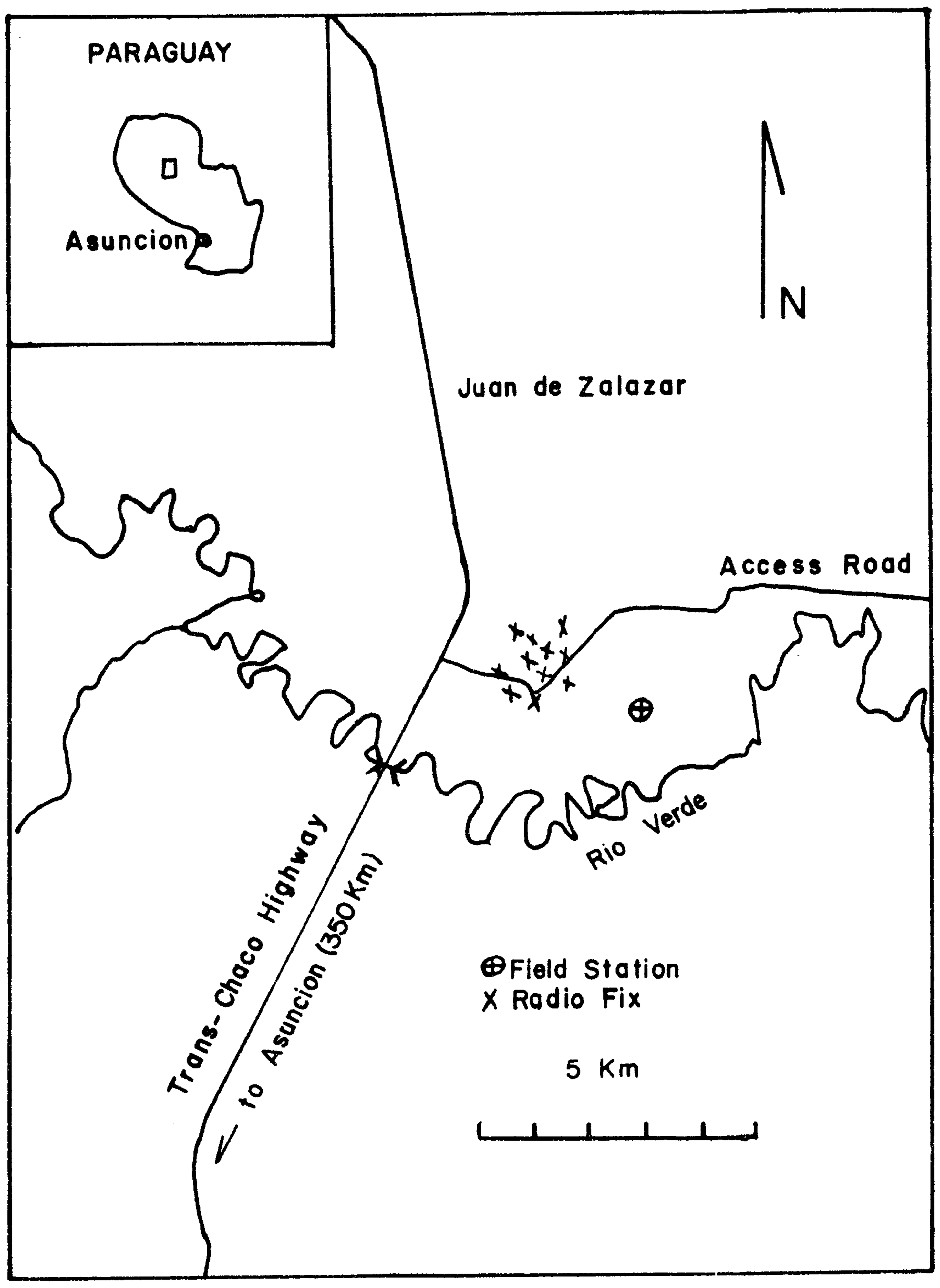
The standard mammal measurements were: total length 54.3 cm, tail length 25.4 cm, ear length 9.5 cm, weight 2.0 kilograms (4.4 pounds).

A marked change from expected behavior in response to phencyclidine hydrochloride was observed. A full milligram of drug per kilogram of live body weight was administered on three separate occasions. The first immobilization period lasted 20 minutes, and a second dose of two milligrams was given before recovery from the first dose was complete, as the cat was rapidly becoming unmanageable. This second dose lasted approximately 19 minutes, when a third dose had to be administered, again before complete recovery. The last dose was effective for 18 minutes, but was adequate to finish collar adjustments and body measurements. A similar dose would have immobilized an adult male mynx of 20 kilograms for a 4-hour period (Berrie, 1973).

A total of 12 radio locations was made during a 24-day period following release of the cat. An initial series of five fixes was made during the firest 3 days following release, and a second series of seven fixes was determined during the last 7 days of the study. Most radio locations were made at night in order to avoid the adverse effects of heat and wind on signal reception during the daylight hours. The cat's home range was estimated to be less than 1.8 km^2 based on the capture location and 12 radio fixes. The cat did not appear to leave a fairly restricted area during the 24-day monitoring period (Figure 1). This is the first home range and movement information available on this species.

CONCLUSIONS

Subadult felids generally have a slightly larger home range area than adults (Berrie, 1973) since the more favorable areas are occupied and defended by adults. If this generalization is true for Geoffroy's cat, the home range for adults may be less than 1.8 km^2. The population of Geoffroy's cat may be quite high in the Gran Chaco region of South America, since home ranges of these cats appear to be small, and felids have a tendency to overlap their individual home ranges (Leyhausen, 1965; Berrie, 1973). The dense mesquite cover of the Chaco and the nocturnal secretive habits of Geoffroy's cat may explain why they have not previously been considered abundant. This concept would also apply to the other small spotted cats in the Chaco, and perhaps other areas of the world as well. Clearly, more research is needed to confirm home range sizes and population densities.



Population estimates for the smaller spotted cats based on trapping rates probably should be viewed more conservatively than has been the case in the past (e.g., Grimwood, 1968). Population estimates based on home range sizes and range sharing are probably more accurate than estimates based on perceived harvests by trappers. Before an investigator or wildlife manager may declare a species threatened or endangered, population estimates must first be determined. Population estimates and range requirements for the smaller spotted cats have not been made for South America, other than the rather limited home range data presented in this paper. More home range and population information is needed before any meaningful management programs can be implemented, and before meaningful harvest estimates can be obtained.

SUMMARY

A subadult female Geoffroy's cat was equipped with a radio transmitter in September, 1972. The home range based on 12 radio fixes and the capture location was estimated to be slightly less than 1.8 km^2.

Resistance to the immobilization agent phencyclidine hydrochloride proved to be greater than expected based on data from other felids. This was the first known use of this drug with Geoffroy's cat in the wild.

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LITERATURE CITED

Berrie, P. M. 1973. Ecology and status of the Canada lynx *(Lynx canadensis)* in Interior Alaska. Pp. 1-44, *In*: R. L. Eaton (Ed.), *The World's Cats I*. World Wildlife Safari, Winston, Oregon.

Cabrera, A. 1961. Los felidos vivientes de la Republica Argentina. Tomo IV, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires.

Grimwood, I. R. 1968. Notes on the distribution and status of some Peruvian mammals. American Committee for International Wildlife Protection and the New York Zoological Society, Special Publication No. 21: 86 pp.

Leyhausen, P. 1965. The communal organization of solitary mammals. *Symposium of the Zoological Society of London* 14: 249-263.

Morello, J. 1970. Modelo de relaciones entre pastizales y lenosas colonizadoras en el Chaco Argentino. *IDIA* 276: 31-51.

REVIEWS

Marks, Stuart A. 1976. *Large Mammals and a Brave People: Subsistence Hunters in Zambia*. University of Washington Press, Seattle. 254 pp. $15.00

To his study of the hunting culture of the Valley Bisa of Zambia, Stuart Marks brings backgrounds in both ecology and anthropology; and his book has an orientation different than expected from a specialist in either of these disciplines. In the first part of the book, Marks explores the culture and society of the Valley Bisa, a cultural group which, though modified by contacts with Europeans, nonetheless maintains many of its traditional patterns of social organization and resource harvesting. The second part explores the cultural dimensions of the hunting process in greater detail, examining the many guilds associated with hunting and the elaborate system of ritual and beliefs that surround initiation into and the practice of hunting. The third part deals with the configurations of the hunting system, including the effects of the Valley Bisa on vegetation and through it, game; data on the ecology of the larger game animals of the region; and details of the hunting activities of individual men and the postulated effects of this activity on prey numbers. Marks utilizes insights gained from a childhood in the Congo, a Bachelor's degree in Animal Ecology from Michigan State University, and a graduate program involving an advisory committee drawn from the departments of Fisheries and Wildlife, Zoology, Botany, Plant Pathology and Anthropology.

Field work for the project was carried out in 1966-67 and many details of the findings were checked with valley residents in 1973.

The most useful parts of the book are its excellent and detailed descriptions of the hunting system in its broader cultural context, its better-than-average treatment of local vegetation types, vegetation successsion, population structure and habitat preferences of the major game species and how these are influenced by the activities, primarily agricultural, of the Valley Bisa. The population ecological data are not sufficiently detailed to form the basis for management decisions but, given the limitations under which Marks and his wife worked, the data provide a valuable context into which hunting activities can be placed. There are also interesting and stimulating bits of interpretation of patterns scattered through the book that give the reader food for thought. For example, the possible role of omens in randomizing the hunting routes of an individual, the best strategy for avoiding previously hunted areas, and the influence of ritual, particularly that associated with the killing of a large animal, in crystalizing the norms and social values of the group, are sensitively treated. These are not new ideas, but they achieve deeper meaning in the context of the wealth of detail about the hunting process of the Valley Bisa.

A very significant fact highlighted by this study is that the importance of protein from wild game is far out of proportion to the amount of time members of the tribe actually spend hunting. It is now fashionable in some circles to argue, pointing to the fact that there is a low input of time and energy into hunting compared to farming, that the role of hunting in human history has been greatly exaggerated. However, in most tropical cultures carbohydrates are readily obtained, but proteins are usually in short supply. Therefore, the value of hunting may be much greater than a time and energy study would suggest. Added to this is the fact that hunting is a risky business, and individuals may be killed or wounded by encounters with large prey or with other predators. The Valley Bisa are clearly much afraid of large and dangerous prey and large mammalian carnivores. Lions are regarded as chiefs of the bush, and killing a lion is comparable to killing another person in terms of associated prestige and prohibitions. Hunters avoid spending the night in the bush, and fears obviously play an important role in the extent to which certain habitat types are exploited.

In other respects, however, the book falls far short of its potential. The study was not designed to test any hypotheses about the role of hunting in the social organization of technologically simple societies or the effects of such societies on the population dynamics and distribution of their major prey. This means that those interpretations offered cannot be tested by the data gathered during the study. This would not be serious were the ideas and concepts utilized in discussions and interpretations not so strongly out of date. Only two of the 115 references cited are more recent than 1970, one for 1971 and one for 1972. Neither of these are anthropological and Marks' thinking reflects anthropological thought of the mid-sixties. Turning to biology, one looks in vain for any recognition of recent advances in the theory of predator-prey interactions, optimal foraging, habitat selection, kin selection, reciprocal altruism (reciprocity), or mate selection, despite the fact that many of the observations are highly pertinent to current ideas in these important areas. For example, the strongly matrilineal organization of the Valley Bisa suggests that certainty of relationships has exerted a strong influence on the evolution of beliefs and norms. The most important ancestral spirits are associated with one's senior collateral kin such as one's mother's brother or one's mother's mother's brother. Victims of sorcerers are also thought to be mostly matrilinearly related. Most hunters are taught their skills by their mother's brother or their maternal grandfather. The elaborate rules by which meat from large game animals is distributed to other individuals reflect matrilinearly dominated kinship. A major cause of social unrest among the Valley Bisa stems from perceptions of neglect by one's relatives. These and other related patterns do not prove a causative role for uncertainty of paternity, but the value of the study is weakened by the lack of any serious attempt to synthesize and interpret any of the results in the light of current ideas. Similar arguments could be advanced for other patterns uncovered by Marks during his field work.

Determining the evolutionary roots of human behavior is an important but extremely difficult task. Studies such as this one can contribute valuable information that may be consistent with one or another interpretation of the long-term course of events, but observational data from within a single tribe can at best provide weak evidence for or against any particular hypotheses. Therefore, it is a pity that no comparisons are made with other hunting groups about any of the traits that characterize the Valley Bisa. The extent to which these traits are or are not shared by other groups can add an important dimension to our understanding of the molding of social systems by environments and of the influence of our evolutionary past on our current behavior. Unfortunately, this book, despite its recent publication date, is a product of an earlier period in scientific thought and does not exploit the opportunities many would perceive today. It provides tantalizing signs and signals, but each reader will have to provide whatever trail or map seems most appropriate.

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Baer, A. S. 1977. *The Genetic Perspective.* W.B. Saunders Co., Philadelphia, London and Toronto. 279 pp. $12.95.

This book is basically elementary: that is, it assumes no previous knowledge of genetics and leads the reader steadily into the basics of the subject. This is accomplished by a very readable style (one hopes an easily assimilable style), ample diagrams and photographs (not all of these are directly relevant to the text but all are illustrative). The device of boxes is freely used to focus on biographies (e.g., Mendel), genetic diseases (phenylketonuvia), and ideas (population genetics), to bolster the main stream of text. For instance, the illustration of genetic drift due to small population size by this procedure as a "party game" is particularly worthy of mention. There is a glossary of terms which is not up to the standard of the text, but this is offset by an adequate index.

The elegance of the book should not obscure the fact that genetics is a serious discipline and considerable ground has to be covered. The writing is fluid but concise and soon one is grappling with genetics at the undergraduate, if not graduate, level in many chapters. Some idea of this is revealed by treatment of such topics as DNA replication, operos, biochemical pathways, immunogenetics, mutation processes, group behavior and genetic counselling. The book is to be recommended to anyone with some biological knowledge who wishes for a rapid overview of genetics. The intelligent layman (to whom the book is presumably aimed) will find it heavy reading unless he or she is exceptionally perseverant or gifted. There is a fair amount on plant genetics but little on mammals. The predilection of the book is towards human genetics, particularly as these are impinged on society. The effects of medical progress, the "green revolution" and the "population bomb" are all discussed. Only one of these topics is directly genetic, but they all have profound effects upon human evolution. The implications for society and for the environment are not shirked. Baer admits that the outlook is gloomy.

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Wright, S. 1977. *Evolution and the Genetics of Populations. Volume 3. Experimental Results and Evolutionary Deductions.* University of Chicago Press, Chicago and London. $35.00.

After the highly mathematical theory of the previous two volumes of Professor Wright's magnum opus, we now have a volume which interprets experimental results in terms of the theory. The present volume discusses laboratory and field experiments of unidirectional and bidirectional selection and of inbreeding. A later volume 4 will discuss observations on natural populations.

The non-mathematical biologist will doubtless find the present volume of considerable interest. Wright is no narrow theorist, but a mathematical biologist (not the reverse) who has worked intimately with laboratory animals (the guinea pig) and has involved himself in practical livestock genetics (selection and inbreeding in cattle). There is evidence that Wright has indulged himself in these volumes. The coverage is comprehensive and detailed. The outcome is that the volume has a somewhat old-fashioned look. Only occasionally is an experiment of note dismissed in a short paragraph. This is not to say that there are not many passing references to work only indirectly related to the immediate discussion but which the reader should be aware of and may follow up as he or she thinks fit.

This detailed treatment of importantly regarded experiments can be a revelation. Wright has a singularly penetrating and finely grinding mind. When an experiment is explained and dissected, one gains an insight into how a geneticist's analytical mind is operating. The volume may be viewed as something more than a theoretical treatise, as an exposition of methodology. The reasoning is so high a level that a non-geneticist will probably find much of it incomprehensible. This cannot be avoided; there are many biological topics which can baffle a geneticist at first meeting. However, there is sufficient in this volume to stimulate a non-geneticist to equip himself with the knowledge to tackle the text in a knowledgable manner.

The volume is to be recommended to all students of evolution and analytical genetics. It is not self-contained. There are frequent references to ideas and formulae of previous volumes. This is not to be unexpected since these give the basis for the ideas and indicate how the formulae are derived. One may criticize the delay in publishing the volume. Volume 1 and 2 were published in 1968 and 1969, respectively. Despite the lapse of some 7 years, few references in volume 3 are dated later than 1969. This dates the contents of the books a little but does not distract from its importance. Many of the fundamantal experiments on selection and inbreeding were completed decades ago. Modern methods may be more refined and may be applied with more confidence of success. The reason: because they are based upon the earlier results. There is a list of corrections to errors in volumes 1 and 2.

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Coppens, Yves, F. Clark Howell, Glynn Ll. Isaac and Richard E. F. Leakey (Editors). 1976. *Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleoecology, and Evolution.* The University of Chicago Press, Chicago. 615 pp. paper $8.50, cloth $17.50.

The fascinating excavations in the Lake Turkana (formerly Lake Rudolf) area, which consists of the Omo Valley in the north, the Turkana region in the west and the "East Rudolf" area in the east, have yielded in the last two decades an enormous bulk of information on the evolution of Plio/Pleistocene East African faunas in general, and especially on human evolution during this period. The result of a workshop-symposium held in September 1973, this extensive volume deals with information available at that time. In three sections and 50 papers the participants in this symposium give the results and current problems in the fields of geology and geochronology, of paleontology and paleoecology, and of paleoanthropology. A rich bibliography terminates the volume, which stands among the foremost modern cooperative monographic studies on important fossil vertebrate localities and locality groups. It reveals a step of mammalian and hominid (including cultural) evolution set within a clear lithological framework and uniquely calibrated by a combination of isotopic and paleomagnetic methods.

One main problem with undertaking comprehensive publication on a series of fossil localities is to limit the size of the volume on the one hand and to give, nevertheless, as much information as possible on the other. This resulted here in a limitation of material descriptions, which are given without photos or drawings and frequently even without measurements in the papers dealing with the mammalian remains. Although there is indeed an excellent overview on the fossil assemblages of basic importance for all paleoecological considerations, there is some lack of comparative data for other specialists working with the respective animal groups, and also a lack of information about where particular fossils are preserved. It remains the task of special publications to provide this enlarged information.

This volume certainly has a particularly high importance for anthropologists, providing them with much information and discussion on the hominid remains and their cultural context, and on all the background for the hominid position in the changing ecosystems of the time span in question. Concerning the hominids themselves, F. C. Howell and Y. Coppens summarize the following provocative implications for their early diversification and evolution: *Australopithecus africanus*, or an allied, diminutive species is characteristic of the 3 to 2.3 million years ago range. This, or a larger descendent species, persists until 1.9 million years ago. A related though morphologically quite distinctive species, *Australopithecus aff. boisei*, of unknown origin, appears 2.1 million years ago and persists for more than a million years. By 1.85 million years ago another hominid taxon, *Homo habilis*, may be present, and by 1.1 million years ago, at least, typical *Homo erectus* has appeared.

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Richard Dawkins. 1976. *The Selfish Gene.* Oxford University Press, New York. 224 pp. $8.95

"Life is a veil of tears"

Dawkins' book is highly readable, provocative and entertaining. It is accessible to nonprofessional biologists, which is a great credit at a time when sociobiology is so controversial and important to human perception. Several reviews cover the primary scientific concepts in this book (e.g. see W. D. Hamilton, *Science* 13 May 1977: 757-759, and E. L. Charnov, *Quarterly Review of Biology* September 1977: 295). I prefer instead to reflect on the philosophical problems it raises.

The preface is written by R. L. Trivers, a significant thinker in sociobiology. The most potent idea in the book could well be this: natural selection should favor the evolution of self-deception in communication, "rendering some facts and motives unconscious so as not to betray--by the subtle signs of self-knowledge--the deception being practiced. Thus, the conventional view that natural selection favors nervous systems which produce ever more accurate images of the world must be a very naive view of mental evolution" (p. vi). On the one hand, sociobiology penetrates human nature more successfully than any scientific theory to date by providing a coherent explanation for social behavior as selfishness. On the other hand, it is Trivers' nervous system that questions our images of the world, leaving us in a vacuum about the possibility of sociobiology as a theory capable of giving us "a deeper understanding of the many roots of our suffering" (p. vii).

"Our suffering" can be translated into "our problems in urgent need of solution" (Ortega y Gasset, 1969). The philosophy of Ortega y Gasset (1946), ratio-vitalism, precedes and surpasses sociobiology in its even more radical idea that the nature of living is problematical, that is struggle, which implies selfishness. The most difficult thing for us to see is in fact what is most operative: that life is struggle, that life is problematical at the core. (Here we must credit Dawkins for having the courage to defend natural selection as "nature red in tooth and claw" or as struggle for survival.) Every moment I am concerned with the next. My compulsion is to live *better* if at all possible, which to sociobiology would mean to invest constantly at enhancing my inclusive fitness even if this involved suicide.

Introspection, originally set out by Dilthey and developed by Ortega y Gasset (1946) as the ultimate methodology for a true psychology reveals to each one of us that all of our mental life, including ideas, hopes, fears and so on, originates from our will, our selfishness. The breadth of our self-interest may be immense, but no less selfish. That living is problematical--selfish--is the most radical datum of the universe, i.e. the first principle and thus the foundation of all life and thought. Sociobiology predicts this radical reality.

Science is the construction of theory to solve problems (Ortega y Gasset, 1960) (theory is constructed solely by deduction; there is no such thing as inductively derived theory [Ortega y Gasset, 1960, 1971]). The present human crisis is the problem of human social behavior, but science has failed to understand man. Science has become a matter of half-problems (Ortega y Gasset, 1960) because of its idealistic-positivistic-mechanistic tradition. Science cannot afford to avoid the grave problems of human life. There is a loss of belief in science by society precisely because the earlier promise of physics has not been realized in terms of theory that encompasses human life. A scientific theory of human social behavior, such as sociobiology, must do what physics and idealism have not done and cannot do, which is to contain itself. Such a theory, in other words, must contain the scientist, in which case we would have a superior form of knowledge.

Science is ignorant of its origin in either a philosophical sense *(historical reason,* Ortega y Gasset, 1946) or an evolutionary (scientific) sense. It is a vital and adaptive--selfish--phenomenon; neither science nor any form of problem solving is intellectually "pure". Such a notion is the very sin of idealism. Science functions consciously or not to serve the vital interests of society and the scientists themselves. "Pure" science in its superlative form is mental play, an evolved form of self-deception (investing in no immediate reward) which is not pure at all but vitalistic or selfish.

Dawkins and other sociobiologists (and biology generally) have grossly confused their theory by emulation of idealistic physics (a vitally important but inferior form of knowledge, see Ortega y Gasset, 1960). For example, Dawkins refers to "survival machines" serving the interests of their genes, which are selfish. Machines that function to survive or perpetuate their genes are not machines at all but vital entities. Selfishness is precisely not mechanistic but vitalistic. Sociobiology hypothesizes that our selfishness is in our genes; the philosopher would say "*I* am selfish" because he seeks the undeniable reality. On the philosophical plane sociobiology shows us that self itself is broader than the individual. Whatever the level or agent identified, sociobiology contributes to human life the awareness that selfishness is the essence of living.

Dawkins develops the theory of sociobiology and then steps outside it with pious idealism about memes (the cultural equivalent of gene), such as ideas, supposed by him to have their own evolutionary course separate from those of our selfish genes. Dawkins says that genes lack foresight or conscious foresight. With the aid of memes, Dawkins proposes, we can override genes to solve man's problems in living. But natural selection accounts for foresight and consciousness; in fact, life is entirely futuristic. Dawkins provides no adequate reason why culture and memes do not fall within sociobiology. So long as there are genetic correlates, culture and memes, which are products of evolution, will feedback upon genes via natural selection. Ideas and all things meme have vital origins and functions; indeed, we would not give thought to the possibility of control of genes to solve problems unless we were selfish in the first place!

This is an appropriate place to hint at how natural selection encompasses physics, and how biology could become, if it dares to turn its theory in on itself, the cardinal science since its theory contains the scientist as well. All so-called *a priori* principles of knowledge, such as 1=1, have their origin in evolution, their explanation in natural selection. 1=1 is undeniably true, I propose, because I am I, not you. At a time when a scientific theory promises to unite all science and human life under one true philosophy--philosophy is the adaptive response to problem--namely natural selection, it seems a pity that so few scientific thinkers grasp the meaning--*for life*--of their discovery but instead retreat to idealism.

According to sociobiology and the philosophy of *ratio-vitalism,* our problems exist only because we are selfish by nature. If theories will sufficiently change our view of life, which is philosophy, they will do so only because they are adaptive, which is to say they serve our selfish interests. Since the solution to human problems depends on accurate perception of our selfishness in such matters as competition for resources and war, we can hardly afford to imagine with Dawkins and other "culturalists" that something independent of selfishness is the solution. The very promise of sociobiology, which is awareness of the reality of living, is undermined by Dawkins' idealistic recourse to memes as a solution to fundamentally vitalistic problems. I dare say that he fails to see that *all* human behavior including the construction of theory has its origin and function in selfishness, nothing else. That we are suddenly aware of our fundamental reality at a time when only such awareness can possibly solve our problems is demonstration that we are not "robot vehicles blindly programmed to preserve the selfish molecules known as genes" (p. 4), but rather that we go about with foresight because it has been and is so adaptive. Whether we do so for our genes is, and will remain for science, strictly hypothetical. No matter, whatever value memes have can be measured only by vital or selfish interest.

Dawkins perpetuates one of the greatest misunderstandings of Western thinkers over the past two centuries when he ridicules Leibnitz's statement, "this is the best of all possible worlds." Actually this is the perfect formulation of the principle of natural selection on its grandest scale. The phrase bothers us because we are "geared" by natural selection to make the world better--we are selfish. This is *here and now* the best of all possible worlds precisely because we have--and have had--no choice but to always strive to make it a better one for ourselves. So potent is this concept, and so much in agreement with sociobiology, that Dawkins contradicts himself in the way he uses it (a consequence of evolved self-deception?).

I believe that for the first time in human history we recognize that we are united by a common destiny. We have not changed except by awareness of the cost/benefit situation which exists globally for each one of us. It is the awareness of the threat of our behavior to our success that extends self-interest and makes possible the salvation of man and his world. If we are saved, it will be our selfishness which saves us. Memes do serve selfishness and probably genes, and have no other significance.

Ortega y Gasset, J. 1946. *Concord and Liberty.* W. W. Norton Co., New York.

________________. 1960. *What Is Philosophy?* W. W. Norton Co., New York.

________________. 1969. *Some Lessons in Metaphysics.* W. W. Norton Co., New York.

________________. 1971. *The Idea of Principle in Leibnitz and the Evolution of Deductive Theory.* W. W. Norton Co., New York.

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BOOKS RECEIVED FOR REVIEW

Argyle, M. 1975. *Bodily Communication.* International Universities Press, New York. 403 pp. $20.00

Beach, F. A. (Editor). 1976, 1977. *Human Sexuality in Four Perspectives.* John Hopkins University Press, Baltimore, Maryland. 330 pp. $15.00

Chauvin, R. 1975. *Ethology.* International Universities Press, New York. 245 pp.

Cody, M. L., and J. M. Diamond (Editors). 1975. *Ecology and Evolution of Communities.* Belknap Press of Harvard University Press, Cambridge, Mass. 543 pp. $29.50

Cohen, M. N. 1977. *The Food Crisis in Prehistory: Overpopulation and the Origins of Agriculture.* Yale University Press, New Haven, Connecticut. 341 pp. $15.00

Cole, H. H., and P. T. Cupps (Editors). 1977. *Reproduction in Domestic Animals.* 3rd Edition. International Universities Press, New York. 414 pp. $39.50

Coleman, W., and C. Limoges (Editors). 1977. *Studies in History of Biology.* John Hopkins University Press, Baltimore. 218 pp. $14.00

Devereaux, G. 1976. *A Study of Abortion in Primitive Societies.* 2nd Edition. International Universities Press, New York. 414 pp. $4.95

Flader, S. L. 1974. *Thinking Like a Mountain: Aldo Leopold and the Evolution of an Ecological Attitude Toward Deer, Wolves, and Forests.* University of Missouri Press, Columbia. 284 pp. $12.50

Fletcher, R. 1968. *Instinct in Man.* 2nd Edition. Unwin University Books, London. 348 pp. $3.45

Fogelson, R. D., and R. N. Adams (Editors). 1977. *The Anthropology of Power: Ethnographic Studies From Asia, Oceania, and the New World.* Academic Press, New York. 429 pp. $19.50

Frankfort, H., H. A. Frankfort, J. A. Wilson, T. Jacobsen, and W. A. Irwin. 1946, 1977. *The Intellectual Adventure of Ancient Man.* University of Chicago Press, Chicago. 401 pp. $4.95

Hausfater, G. 1975. *Dominance and Reproduction in Baboons: A Quantitative Analysis.* Contributions to Primatology No. 7, S. Karger, New York. 150 pp. $29.95

Hooks, S., P. Kurtz, and M. Todorovich (Editors). 1977. *The Ethics of Teaching and Scientific Research.* Prometheus Books, Buffalo, New York. 212 pp. $11.95

Hunsacker, II, Don (Editor). 1977. *The Biology of Marsupials.* Academic Press, 111 Fifth Ave., New York, N.Y. 10003. 560 pp. $36.00

Isaac, G. Ll. 1977. *Olorgesaille: Archeological Studies of a Middle Pleistocene Lake Basin in Kenya.* University of Chicago Press, Chicago. 272 pp. $7.00

Lewis, I. (Editor). 1977. *Symbols and Sentiments: Cross-cultural Studies in Symbolism.* Academic Press, New York. 300 pp. $16.95

Liederman, N. J. 1977. *Playfulness.* Academic Press, New York. $12.00

Luckett, W. P., and F. S. Szalay (Editors). 1975. *Phylogeny of the Primates: A Multidisciplinary Approach.* Plenum Press, New York. 483 pp.

Malins, D. C., and J. R. Sargent (Editors). 1975. *Biochemical and Biophysical Perspectives in Marine Biolgoy.* Academic Press, New York. 359 pp. $30.00

Masterton, R. B., N. Hodos, and H. Jerison (Editors). 1976. *Evolution, Brain, and Behavior: Persistent Problems.* Lawrence Erlbaum Associates, Hillsdale, New Jersey, distributed by Halsted Press Division of John Wiley and Sons, New York. 276 pp.

Mayr, E. 1976. *Evolution and the Diversity of Life: Selected Essays.* Belknap Press of Harvard University Press, Cambridge, Mass. 721 pp. $20.00

Money-Kyrle, R. E. 1961. *Man's Picture of His World.* International Universities Press, New York. 190 pp. $10.00

Robinson, R. 1977. *Genetics for Cat Breeders.* Pergamon Press, Fairview Park, Elmsford, N.Y. 10523. 200 pp. $12.00

Romer, A. S., and T. S. Parsons. 1977. *The Vertebrate Body.* 5th Edition. W. B. Saunders Co., W. Washington Square, Philadelphia, Pa. 19105. 624 pp. $14.95

Schaller, G. B. 1977. *Mountain Monarchs: Wild Sheep and Goats of the Himalaya.* University of Chicago Press, Chicago. 425 pp. $25.00

Sheldon, W. G. 1975. *The Wilderness Home of the Giant Panda.* University of Massachusetts Press, Amherst. 196 pp. $12.50

Stoddart, D. M. 1976. *Mammalian Odours and Pheromones.* Institute of Biology's Studies in Biology No. 73. Crane, Russak and Co., New York. 60 pp. $3.50

Tuttle, R. H. (Editor). 1975. *Socioecology and Psychology of Primates.* Aldine Publishing Co., Chicago. 474 pp.

Wagley, C. 1977. *Welcome of Tears: The Tipirape Indians of Central Brazil.* Oxford University Press, New York. 328 pp. $12.95

Winn, H. E., and B. L. Olla. 1972. *Behavior of Marine Animals: Current Perspectives in Research.* Plenum Press, New York. 503 pp.

Witherspoon, G. 1977. *Navajo Kinship and Marriage.* University of Chicago Press, Chicago. 137 pp. $3.95

FIRST INTERNATIONAL CONFERENCE ON DOMESTIC CAT POPULATION GENETICS AND ECOLOGY 27 June--1 July 1978, Syracuse, Italy

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