THE COMMUNAL ORGANIZATION OF SOLITARY MAMMALS

Paul Leyhausen

Max-Planck-Institute Fur Verhaltenphysiologie, Arbeitsgruppe Wuppertal

(Printed by permission of the Zoological Society of London)

Introduction

Normally we do not think of solitary animals as forming a community of any kind except for the very limited purposes and periods of propagation. Perhaps this is true of a great number of species, even some mammals as, for example, the hamster, the red squirrel, the badger (Eibl-Eibesfeldt, 1950, 1953, 1958) and the wolverine (Krott, 1959). However, if we want to examine more closely what relationships might possibly exist between individuals of an allegedly solitary mammalian species, we are in a very bad position indeed. For the main reason why so many mammals are said to be solitary seem to be that they can only be shot one at a time. Very little field work has been done on such species; field workers — for reasons not to be discussed here — have concentrated on mammals living in social groups or herds. Hence some of my arguments will be of a highly speculative nature. The only justification is my hope that they may help to arouse more interest in the life of solitary mammals and that more field observations will be made over long periods of time and in sufficient detail.

MAMMALIAN TERRITORIES

As far as I know, the existence of a social pattern into which individual, solitary lives might be woven has never seriously been considered. The basis for any such pattern could be found in territorial behaviour. This was first observed in birds, and bird territories have been studied most fully. When similar behaviour was discovered in other vertebrates as well, the characteristics of bird territories were at first thought to apply universally. They have been thoroughly listed and reviewed by Nice (1941). If we exclude colony breeders from our considerations, it may broadly be stated that the breeding territories of most birds — and for that matter fishes — start from a centre which is occupied by the owner, who afterwards stakes out his claim in serious or ritualized fights with occupants of nearby centres, so that after a while territory boundaries can be mapped out quite precisely, each territory owner as a rule keeping to his own boundaries (Curio, 1959; Greenberg, 1947; Kirchofer, 1953; Kluyver, 1955; Koenig, 1951; Lind, 1961; Timbergen & Kluyver, 1953).

Hediger (1949) pointed out that, to mammals, it is not so much an occupied area which is important as a number of points of interest — first-order homes, second-order homes, places for feeding, rubbing, reting, sunbathing, etc. All these places are connected by an elaborate network of paths along which the territory owner travels according to a more or less strict daily, or seasonal, or otherwise determined routine. The areas enclosed by the pathways, though more or less familiar, are seldom or never used. These concepts have been

corroborated and elaborated in detail by the studies of Dasmann & Taber (1956) and Graf (1956) on territorialism in North American deer.

The distinction made by Burt (1943) between home range as an area and situated within the home range) defended against intruding or trespassing regularly used by the animal and territory as an area (usually smaller than conspecifics is not borne out by free-ranging domestic cats because they behave inconsistently; for a full discussion of these concepts see Kaufmann (1962). The terminology adopted for the purpose of this paper is a synthesis between that of Hediger and of Kaufmann.

One outstanding feature of most mammalian territories—the only exception I know being that of the hamster (Eibl-Eibesfeldt, 1958)—is that mammals are not usually in a position to survey the whole of their territory all the time and to spot intruders or trespassers almost instantaneously, because of the nature of the habitat and of inferior methods of locomotion (as compared with birds). This is usually thought to be sufficient explanation of the often considerable overlap of adjacent territories and the shared use of paths running through border areas (Hediger, 1948, 1949, 1951; Eibl-Eibesfeldt, 1958; Krott, 1959; Krott & Krott, 1963; Hall, 1962a 1962b; Koenig, 1960; Kaufmann, 1962; Wynne-Edwards, 1962).

Gustav Kramer (1950) was the first to point out that, in territorial animals, the fixation of an individual in a definite locality obviously facilitates the recognition of this individual by its neighbors. All territorial animals have a good memory for localities and their spatial relationships. Hence they probably "label" the conspecifics encountered by the locality where the encounter took place. This is perhaps of minor importance in species like most song-birds, where neighbours are in almost continuous vocal/auditory contact, but is likely to play a major role under conditions prevailing for solitary mammals, as described above.

Attention has always been focused on the fact that territories in general owe their existence to repulsive forces with the animals, which tend to space out individuals as far apart as possible, and students of territory and territorial behaviour have been almost completely absorbed by studying hostile or agonistic behaviour. However, it has been known that in cases where there is a small population of territorial birds inhabiting a very wide area that is well suited to all conceivable needs of the species, the individuals or pairs are not spaced out evenly as far from each other as the inhabitable area would allow. Clearly there is, in many species at least, not only a minimum but also a maximum size of territory (Kluyver, 1955; Koenig, 1951; Timbergen & Kluyver 1953; for review see Wynne-Edwards, 1962). Many authors have noted the fact and expressed their belief that there must be some agent which keeps a population from dispersing beyond any possibility of contact, but although, as I have already mentioned, dispersing forces have been studied intensively, there has as yet been no attempt to make a close study of the counteracting forces and modes of behaviour which allow a population of solitary individuals to retain contact with each other. Fights, threat displays and the like are very conspicuous and therefore more easily observed in the field than hypothetical centripetal tendencies which, if they can be affirmed, are certainly of a less theatrical nature. To detect them it would be necessary to make an uninterrupted, continuous day and night record of a selected population of solitary mammals. As far as I know this has so far never been done, and the only people who ever seriously set out to do it were my collabo-

rator R. Wolff and myself—on free-ranging domestic cats! The result of this little survey has been published elsewhere (Leyhausen & Wolff, 1959). As measured against the standards set out above, we failed: it was an impossible job. To follow a single cat around day and night without losing sight of it and keep a complete record of all its movements, encounters, etc., requires at least three well-trained, physically fit and inexhaustible observers, plus a lot more equipment than we could command at the time. We carefully selected an isolated farm-house situated in a clearing in a very hilly region. There were two resident cats, and another one in a farm some 600 yards away. Sufficient data was collected for only one of the residents, to form a picture from which we hope no essential feature is missing: even this data was not complete. However, both of us had previously made extensive observations on cat populations under free-ranging conditions, Wolff in two suburbs of Hamburg, myself in the gardens facing the back of my parents' home in Bonn, of some cats in Wales, of a small population in a garden area in Zurich where I lived for approximately two and a half years, and of some individually known cats which night after night populated a small square on the outskirts of Paris. Combined, this was a sizeable amount of data, and our observations confirmed each other in most details. Part of our data fitted well with traditional theories but some simply did not seem to make sense. When we had completed the study, we did not feel it amounted to much in itself and only reluctantly published it, mainly in order to elicit comment and to interest other field workers with perhaps better resources and more time to spend. But on re-examination of our old records, and in the light of old and recent observations and experiments on caged cats, the once odd and ill-fitting pieces suddenly fell into place, and what had previously seemed contradictory became comprehensible. Hence I am quite confident that the picture I shall outline briefly is correct in its essentials.*

SOCIAL AND TERRITORIAL BEHAVIOUR IN THE DOMESTIC CAT

Individual cats own a territory which tallies roughly with Hediger's description (loc. cit.) of the average mammalian territory: a first order home, usually a room or even a special corner in a room of the house where they live, and a home range which consists of a varying number of more or less regularly visited localities connected by an elaborate network of pathways. To draw a line through the outer points of this network and call this the boundary of the home range would be a purely abstract procedure. The concept of such a boundary cannot be based on the actual behaviour of the animals, as we shall presently see. The immediate surroundings of the first order home, as for example the house and the garden, are entirely familiar to the resident cat it uses practically every part of them and there are usually several places in them for resting, sunbathing, keeping watch, etc. Beyond this limited home area the paths mentioned above lead to places for hunting courting, contests and fighting, and other activities. To each of these places there is usually more than one path. The areas between the paths are rarely used, if at all. The places the paths lead to must not, of course, be thought of as mere points. Hunting grounds,

* I am grateful to Dr. Rosemarie Wolff for generously allowing me to use her invaluable records.

for example, like clearings in a wood or freshly cut wheat fields where mice are abundant, may cover areas bigger than the home area, and in the course of time the cat investigates them thoroughly.

There are two snags, however, in our attempt to use observations on free-ranging domestic cats as a kind of substitute for the observation of true wild solitary mammals: (i) domestic cats are not allowed to choose or control their own density of numbers, and as a rule they are not allowed to select their first-order home freely; (ii) their behaviour has been changed in various respects during the course of domestication. Important with regard to territorial behaviour is the fact that domestic cats are less repulsive to one another than their wild relatives and in most cases can be brought to share a home area and often even the first-order home with one or more other cats (Leyhausen, 1956, 1962). At first this might seem to be a serious disadvantage but probably it is simply that the special circumstances mentioned above have brought out more clearly the cohesive factors within the population which are certainly at work in wild populations as well.

As stated above, it is quite normal for the pathway-network of neighbouring cats to overlap, and overlap in this case means the common use of pathways and also of hunting-grounds and sometimes other commodities such as sites for sunbathing and look-out posts. However, common use normally does not mean simultaneous use. In their daily routine, the animals avoid direct encounters, and even cats sharing a home keep separate in the field. According to Hediger (loc. cit.) many species achieve this by following a rather definite timetable, scheduled like a railway timetable so as to make collisions unlikely. Wolff's and my observations have so far failed to produce any positive evidence that the daily routine of domestic cats is subject to such a definite schedule. Where there is a strong tendency towards being in a certain place at the same time every day, this is usually due to human influence, e.g. feeding time. Thus the cat population (up to a dozen or more) of the Welsh farms I saw, gathered about milking time at the barn door or the cowshed to collect their daily ration of milk. Of course, this does show that cats are quite capable of keeping to a time schedule. Our failure to observe anything of the kind in free-ranging cats which are not influenced by human time-fixing does not mean that it could not occur—and, indeed, it does occur in captive groups (see below).

Cats seem to regulate their traffic mainly by visual contact. It is often possible to observe one cat watching another moving a path some distance away —say anything from thirty to one hundred yards—until it is out of sight. Some time afterwards, the watching cat can usually be seen using the same path. On occasion I have observed two cats approaching a kind of cat crossroads from different directions. If they had gone on they would have met almost precisely at the crossing. Both sat down and stared at each other, looking deliberately away from time to time. The deadlock is eventually broken either by one cat moving on towards the crossing while the other is looking away, hesitantly at first, then speeding up and trotting hastily away as soon as it has passed the point nearest to the other cat; or after a while both move off almost simultaneously in the direction from which they originally came. In all these remote visual-contact (or control) cases, it is very rare indeed for one of the animals to walk right up to the other in order to drive it away, or, if it does not move, to attack it. If, however, the animals suddenly and unexpectedly find themselves face to face, a clash of some sort may result. In this way a ranking order is established between

neighbours. There is rarely more than one serious fight between any two adult animals; usually any subsequent close-range encounter will develop almost at once into a chase, with the animal which had been defeated in the previous fight taking to flight, and the victorious one chasing and slashing out at the other if it gets close enough. Females are, on the whole, less tolerant of each other than males. However, the kind of ranking order thus produced does not develop into a rigid social hierarchy within the population. Although the victorious cat is sometimes permitted to visit and inspect the territory and even the first-order home of the defeated one unchallenged it does not make a habit of this and it does not take over the other's home range. Nor is its superiority valid at any place and at any time. If the inferior cat has already entered a commonly used passage before the superior cat arrives on the scene, the latter will sit down and wait until the road is clear; if it does not, its superiority may be challenged successfully. In one case, for example, two females had established homes in two adjacent rooms of the house. The normally superior one had kittens, which enhanced her superiority still further. She wanted to cross into the adjacent room but her neighbour was sitting in the doorway, and when she tried to pass the other spat at her and blocked her path. So she did not fight, but retreated a little way and waited. After a while her neighbour moved away from the doorway, the mother cat crossed and was afterwards tolerated by the resident and in no way inhibited in her investigation of the room. Likewise a superior cat will not normally drive away an inferior one which is already occupying the superior cat's favourite resting place or look-out post. Sometimes the clashes and chasings involved in establishing a locality-priority-dependent hierarchy produce a lasting and irreconcilable hate between two neighbours, so that the superior one chases and hits the other on sight. But this is by no means the rule. Not only is the superior animal allowed to pay visits to the home area of the inferior one, but the latter may also trespass on the former's ground. They may hunt over the same area at the same time, keeping on an average some fifty yards apart, depending on the ground and the vegetation. They do so deliberately, even when there is no other reason for being so close together. This was particularly obvious in the Welsh farm populations. After collecting their daily milk, the animals walked off one by one to their hunting grounds. Normally they were not fed by the farmers but had to sustain themselves largely by catching and eating rabbits which lived in vast numbers in the hedges bordering the fields. Although rabbits seemed to abound everywhere, it was usual to see two or three cats hunting within thirty to seventy yards of each other, rather than one lone cat.

At nightfall there is often something which I can only describe as a social gathering. Males and females come to a meeting-place adjacent to or situated within the fringe of their territories and just sit around. This has no connection with the mating season, which I am excluding from my description throughout. They sit, not far apart—two to five yards or even less—some individuals even in actual contact, sometimes licking and grooming each other. There is very little sound, the faces are friendly and only occasionally an ear flattens or a small hiss or growl is heard when an animal closes in too much on a shy member of the gathering. Apart from this there is certainly no general hostility, no threat displays can be seen except perhaps for a tom parading a little just for fun. I could observe this particularly well and on many occasions in the Paris population. The gathering would go on for hours, sometimes (probably as a forewarning of the mating season) all night. But usually by about midnight or shortly after the

cats had retired to their respective sleeping quarters. There can be no doubt that these meetings were on a friendly, sociable footing, although members of these same populations could at other times be seen chasing each other wildly or even fighting. Indeed, such an urge for social "togetherness" exists also in those wild species in which, according to all available observations, mutual repulsion is much stronger than it is in domestic cats. They are, therefore better capable of close friendship with humans than with conspecifics. A human with sufficient knowledge and understanding can have all the social attractiveness of a conspecific without necessarily possessing its repulsiveness (Leyhausen, 1956).

So far I have been dealing mainly with the behaviour of the females. Resident males are different in that, normally, they are even more tolerant towards trespassers. Their aggressiveness is of course accentuated during the mating season, but this has no relation to territory or home range in the proper sense. Fierce defence of the home and the home area is usually exhibited only by females rearing a litter. Adult tom-cats meeting for the first time are liable to engage in fierce fighting regardless of the season. But once it has been decided which is the stronger or the more tenacious, courageous fighter of the two, they settle their arguments thereafter by display and avoid serious fighting. It is therefore possible to put several adult tom-cats, so far strangers to one another with a number of females in a comparatively small cage, and after a few days of bitter fights there is peace, even when one or more females come in heat. The males may show their threat display but they will rarely engage in actual fighting. Several times I have seen a shifting of rank between the two top cats of such a caged crowd effected by display alone. In an earlier paper (1956) I interpreted all this as a consequence of the animals being forced to live so close together all day that they expended their aggressiveness in "small change" all the time and therefore had no opportunity to build up an aggressive urge strong enough to lead to and sustain actual fighting. This may still play a part but I am quite certain that a similar process occurs in free-ranging tom-cats and that, after some initial fighting, those who pass the test and are not completely defeated and reduced to pariahs form a kind of order or establishment, ruling a great area in brotherhood. They gather in friendly convention as described above, and even in the mating season seldom fight to the bitter end. Such fights as take place between members of the establishment seem most likely to have a mock or **pro forma** quality. The picture is strikingly different if within the established neighbourhood, there is a young tom just crossing the line from adolescence to maturity. The established tom-cats of the vicinity, singly or in twos and threes, will come to his home and yell their challenge to him to come out and join the brotherhood, but first to go through the initiation rites. The challenge is not the piercing, up-and-down caterwauling of the threat display but rather softer and seems to have a good deal of purr in it, as if it were not merely challenging but also coaxing. In fact, the sound is hardly discernible from the call by which a tom tries to entice a female in heat to meet him. If the youngster lets himself be persuaded, hard and prolonged fighting ensues. This is in fact the situation in which most really bitter fights occur. And since the novice, who feels his strength growing from day to day, will not accept defeat as any sensible adult would, he will at first be beaten up and often more or less badly injured. But the wounds have hardly closed before he hurries to battle again, and after a year or so, if he survives and is not beaten into total submission, he will have won his place within the order and the respect of his brethern.

It must be noted that while the territorial ranking order is relative and does not deprive the weak of all rights, the ranking order of the tom-cat brotherhood is an absolute one and is valid wherever and whenever two members meet. But the strongest male normally does not, as is often assumed, become a tyrant, dominating and excluding all others from courting and mating. I have known female cats, free-ranging and in cage situations, remaining faithful to inferior males from one heat period to the next for years. And at least with caged animals I know for certain that the dominant male never made any serious attempt to interfere. The whole social system as described above seems to me designed to ensure that the greatest possible number of strong and healthy males has an almost equal chance of reproduction, rather than to favour exclusively a single dominating individual. Such a situation arises only if, and when, there is one male so overpoweringly superior, in both physique and energy, that he does not find another tom-cat fit to challenge his dominance. For what I rather poetically described above as the "brotherhood" is in fact nothing mythical, but rests on a very real balance of power, risks and deterrents. It can be formed only if there are several males of almost equal strength, so that victories and defeats are decided by a narrow margin and it might cost a higher ranking male his superiority if he provoked an inferior so far as to make him actually fight.

Before describing the interaction of the hierarchical dichotomy in caged cat societies I must make a few remarks on what is called territory marking. Many authors have described how territorial mammals mark their territories by scent, sound, scratching posts, etc. The usual interpretation attributed to this sort of behaviour is that the animal is setting up a warning signal, with the intention of scaring away trespassers and potential intruders. I do not know whether this scaring-off function of an olfactory mark has been established beyond doubt in a species of solitary mammal. In cats I have certainly never observed anything suggesting such an interpretation. Cats, predominately males but also most females, have a habit of spraying their urine against trees, poles, shrubs, walls, etc., and afterwards they often rub their face in it and then the face against other things. No cat has been observed to go up to the mark made by another, sniff it and then retreat. What they almost invariably do is sniff the mark carefully and at leisure, and then either move on quite unconcernedly or put their own mark over it. There is not the slightest hint that the original marking has had anything like an intimidating effect. Of course, this is no proof that is never the case; but there must be at least one other function if not more. One may be to avoid unexpected encounters and sudden clashes, another to tell who is ahead on the road and how far, and whether he can be met if required. However, this is pure speculation and my data do not so far allow me to single out or reject any of the possibilities. The odds are that all of them play their part depending on the situation. But I should like to stress the point that we must not deny territorial behaviour of cats because their markings do not, or only moderately, function as deterrents.

When I first (1956) described the structure of artificial cat societies in cages, I found that there was usually a dominant male and frequently, though not always, one or two animals, male or female, which were so subdued that they hardly dared breathe, and which I called "pariahs". There was some ranking order among the rest of the population, but it seemed very indefinite and unstable. My explanation then was that cats, as essentially solitary animals, simply lack the capacity to build a stable society. When the existence of two dif-

ferent types of ranking dawned upon me, two facts emerged: (i) it is actually possible to find evidence for such a dualism. At the food bowl for example, an absolute rank order is observed. Narrow passages and preferred resting places may, in a sense, belong to top cats, and inferior cats often leave them when the superior one approaches, but if they do not there is no quarrel; and, in particular, the cat already in a passage has the right of way regardless of its status within the absolute hierarchy. Also, there is sometimes a perrogative related to the time of day. Some cats, for example, make full use of the floor for running and playing in the morning, others in the evening, and it is "their" time, when they are superior to all others which happen to come their way, again regardless of their absolute ranking. (ii) there is a direct relationship between the balance of absolute and relative hierarchy, and population density. The more crowded the cage is the less relative hierarchy there is. Eventually a despot emerges, "pariahs" appear, driven to frenzy and all kinds of neurotic behaviour by continuous and pitiless attack by all the others; the community turns into a spiteful mob. They all seldom relax, they never look at ease, and there is continuous hissing, growling and even fighting. Play stops altogether and locomotion and exercise are reduced to a minimum.

It should be noted that all statements so far are based on plain observation and, although they seem reliable enough qualitatively, there as has yet been no quantitative investigation. In the near future, however, I hope to make a detailed quantitative study by means of a new photography recording device.

DISCUSSION, WITH SPECIAL REFERENCE TO HUMAN SOCIETIES

I believe that this basic dualism of social hierarchy is present in many other mammals, and that the interaction of the two and the possibility of the weight shifting from one to the other lies at the root of the ability of some species either to lead solitary, territorial lives or live in small or even quite large groups. But as individual territories shrink and the group emerges, a group territory is formed. Davis (1942) found that the social behaviour of various species of the family of Crotophaginae represents successive steps in a phylogenetic change from individual to group territory. In a number of mammalian species, however, the change need not be brought about by a slow, phylogenetic process, the faculty for both solitary and group life being inherent to the individual. Ecological and perhaps other circumstances determine what kind of social structure a population will have. The North African lion was, as far as one can make out from the reports of hunters and travellers, a solitary animal, living at the most in pairs. This seems also to be true of the West African lion in many regions. Yet in the East African plains, lions live in groups sometimes numbering more than twenty members (Guggisberg, 1961). The same principle seems also to govern the life—both within the group and among the groups—of species, such as the wolf, which habitually live in small groups (Armitage, 1962). In Murie's description (1944) we find examples of strong leadership at times and of relative tolerance and indulgence at others when the rights of the weak are well and, I might almost say, deliberately respected by the strong. In striking contrast are the observations of Schenkel (1947), who decribes the social behaviour of wolves in an overcrowded captivity situation in exactly the same way as I have for the overcrowded cat community.

I should also like to suggest that the fact that territorial dominance in

mammals depends on locality and time might help to settle controveries between various observers with regard to territoriality in some species. Hediger (1951) reports territorial behavior in bull hippopotami; Grzimek (1956) and Verheyen (1954) deny this. Likewise it has always been assumed, and has also been confirmed by field observations, that black and brown bears are territorial animals (Meechan, 1961; Meyer-Holzapfel, -957). Yet Krott & Krott (1963) frantically deny even the remotest possibility of territoriality in bears and describe the species as being 'socially indifferent' (social neutral). It has, I hope, become sufficiently clear from the above that the only mammal one could conceivably speak of as being socially indifferent is a dead one. Apart from this ill-chosen term, I think once again that the controversy may find its solution in the way I have already explained. Only after studying a population for a long period and following the individuals at all times and through all situations will one be able to make a correct and proportional assessment of their social interaction and relationships.

Just as mammals that normally live solitary lives often seem to have a faculty for changing to some form of group life, so many, if not all, mammals normally living in groups and even large herds seem to me to possess a faculty in the reverse direction. The wapiti for example is territorial in some habitats and non-territorial in others (Altmann, 1952; Graf, 1956). I therefore believe that, even in mammals living in herds and not occupying territories in the strict sense, both forms of social hierarchy could be traced, if only the attention of observers were focused on the point. And in that case I should predict that absolute rank order would predominate over relative rank order, the bigger the herd, and the less there is a tendency to subdivide it into small groups.

Although I have no special knowledge of the social life of monkeys and apes I suggest that here again the hierarchial dichtomy could be found. There would be, perhaps almost exclusive, predominance of absolute hierarchy in monkeys living in large bands, like the rhesus (Chance,1959; Chance & Mead, 1953), and a more proportionate balance between the two in monkeys living in smaller groups like the South Indian macaque (Nolte, 1955) or the langur (Jay, 1962, 1963). Whatever the results of pertinent observation of monkey life may be, I feel sure that the dichotomy exists basically in mammals and can be observed in all kinds of human social organizations; I am also convinced that the well-being and even the survival of our species depends on a proper balance between the two types of hierarchy.

In an earlier paper (1954) I gave numerous examples of the fact that in a sort of human social organization territorial behaviour in various forms, both unadorned and sublimated, plays a role which it would be hard to overestimate (Meyer-Holzapfel, 1952; Nippold, 1954; Schmidt, 1937). I described in some detail that, under the conditions of overcrowding prevailing in prisoner-of-war camps, exactly the same symptoms developed as those described above in overcrowded captive cat and wolf communities. I showed that the same symptoms are becoming increasingly conspicuous in modern mass communities. In that sense, the cynical definition of psycho-analysis, as the main symptom of the illness of which it pretends to be the cure, is one hundred per cent correct. My conclusion was that space in its physical or—if I may say so—biological form, not in a sublimated or figurative sense only, is indispensable for the biological, and particularly for the psychological and mental health of human in a human society. For these reasons overcrowding is a menace to mankind

long before general and insurmountable food shortage sets in. The increase in human numbers is not primarily a food problem, it is a psychological, sociological, mental health problem—in short, a humanist problem. And we have to realise that human nature sets a far narrower limit to human adaptability to overcrowding than is commonly believed today.

This I could see as a fact in 1954, but at that time I had no idea why it should be so. The key was given me by Wynne-Edwards (1962) when he formulated and elaborated the principle that natural selection has produced various kinds of social organization because they replace direct competition for the basic needs of life by competition for other goals (i.e. social goals in the widest sense). This controls numbers before the basic necessities of life become so scarce that they need be competed for, thus guaranteeing that the numbers of a given species are kept at an optimum level. Group selection (Wynne-Edwards, loc. cit.) and the mechanisms which are involved in intraspecific balance of numbers do not operate in a void. Other factors, especially ecological ones, are taken into account and their more or less constant presence is "relied upon". If, for instance, a species is suddenly freed of practically all predators, the balance of numbers may break down completely. To what extent the numerical control mechanisms depend on such partial elimination and other environmental factors and whether these feed-back systems are of a direct or an indirect nature, probably varies greatly from species to species. On the whole one might guess that short-lived animals, with an enormous rate of reproduction and regular elimination, can make do with more direct methods of control, i.e. food supply might directly affect numbers, whereas long-lived species have to keep a balance of numbers over longer periods and cannot readily adapt their density to short-term fluctuations in the food situation. In such cases an indirect influence based on the average situation over many cycles comes into operation, and this is precisely the function of what Wynne-Edwards calls 'conventional competition.' In any case, an all too drastic change in such conditions as have been so far "taken into account" in the process of evolving the "homeostatic machine" that they are practically working parts of it, will result in a breakdown of the machine as a whole. This is what happened to our own species during the last few centuries — a mere nothing of time, phylogenetically speaking. The natural biological instruments for balancing our numbers have been reduced to ineffectiveness by man's rational powers and inventions. But our nature has not basically changed. We do not want to suffer from diseases, we do not want our old people to die sooner or our babies to die before they grow up. We certainly cannot wish to restore the original system for balancing numbers. Yet we cannot bear to become more and more numerous and to be in a crowd wherever we turn. The only human and humane answer is to evolve and make effective use of rational, scientific means to restore the balance.

The other point I did not realise in 1954 was the dichotomy of social hierarchy. * I am fully aware that there may be many cases in which the line between territorial or relative dominance (relative hierarchy) and absolute dominance (absolute hierarchy) cannot be drawn as neatly as I have done for the sake of argument. Yet there can be no doubt that the constructive antagonism between the two forms one of the most effective mechanisms for balancing numbers by means of "conventional competition" (Wynne-Edwards, loc cit.). In human history endless examples can be found; constructive balance between

the two marks the periods of peaceful and prosperous development. Perhaps I may reformulate here what I said when describing the cat community, in order to make plain its potentialities for the interpretation of human organizations. Territorial dominance gives the individual, or individual family, superiority over all or almost all other members of the community in certain places and at certain times; it stands for the rights and liberty of the individual It enables the individual to enter a community and co-operate in it with other individuals, as a separate member in his own right, regardless of his status in the absolute hierarchy of that community. On the other hand, absolute ranking order ultimately makes leadership and law possible, law being originally the will of the leader or overlord.

What it may lead to if territorial behaviour runs free of any control by a superimposed absolute order can be amply illustrated, for instance, from the history of exploration and settlement in North America. At the other extreme, the result of unchecked absolute hierarchy is tyranny, when individuals or organizations have acquired excessive power and succeeded in reducing individual liberty more and more in favour of the "common good". In crowded societies, both have a strong tendency to combine and to squash the individual into an anonymous cipher. Sometimes the problem of crowding has been solved socially by the emergence of an elite of "free citizens" or princes, who established among themselves a community based on proper balance between relative and absolute dominance, reducing the rest of the population to the status of mere domestic animals. Striking examples of this were the city-states of ancient Greece and the medieval princedoms of central Europe. Whenever the absolute hierarchy grew too oppressive, rebellions and revolutions were the inevitable course of events. And the coercion exerted by the underlying mechanism described can hardly be better illustrated than by the fact that the great revolution rising in the name of "liberte, egalite, fraternite" set up its own tyranny as soon as it had won victory. This was not because of the wickedness of some of the revolutionary leaders, but was the inevitable consequence of crowding and crowd management, and it is not by chance that under similar circumstances wicked leaders are almost automatically swept into power.

I do not want to oversimplify matters. There is no question of hierarchial antagonism being the one and only agent of human history. All I wish to stress is that it has been one agent and that the fact that it has a biological foundation and forms an indispensable and indestructible part of human nature

* I owe an apology to Dr. Peter Marler, whose important work (1955a, 1955b, 1956 1957) on fighting in the chaffinch escaped my notice while preparing this paper. Marler found both forms of social rank order in his birds and came very close to realizing the potentialities of their interaction; in the chaffinch however, they seem not to exist simultaneously but to be exchanged for each other according to season, with transitional stages in between. I fully agree with Marler that it is not two different types of aggressiveness underlying the dichotomy, but typically differing factors of the internal and external situation. These, especially the internal ones, undergo seasonal changes in the chaffinch but co-exist, to some extent at least, in some mammals. However, Marler's statement that fighting is not sought after "for fun" and does not lead to appetitive behavior if not properly released for some time, certainly must not be applied generally. I do not know about birds, but many fish and Mammals do seek a releasing situation for fighting when they are "in the mood".

has hitherto been utterly neglected. The shift of balance between the two orders of dominance is only possible within limits. The range of such a shift is species-specific and represents the density tolerance of a species defined by this particular mechanism. It seems, unfortunately, that these limits are not hard and fast, so that it is possible for density unobtrusively to increase too much if it is strongly favoured by other factors. Since the human mind is adapted to life in a small group and to co-operating in a neighbourly manner with a small number of other groups, it is often incapable in a modern mass society of singling out individuals for social partnership. In the midst of an anonymous crowd it is faced with hopeless loneliness.

In modern mass democracy, "mass" and "democracy" are incompatible because crowding favours absolute hierarchy to a degree where it becomes tyranny. Democracy has one of its indispensable biological roots in relative hierarchy. Almost daily we can observe how the liberty and free enterprise of the individual are drastically diminished because of the priority given to the communal good, whatever that may be or may be believed to be. Anyone who owns a piece of land and wants to erect on it a house suiting his own needs and taste will know what I mean. The words "own" and "property" have long lost their original meaning. We accept this, rationally and morally, as inevitable and therefore "good". But our nature will not accept it, and open or latent crisis will ensue. This road leads to either rebellion and violence, or neurosis, or both. There is no other remedy than to re-establish the balance of numbers in human societies and quickly to find effective means of controlling them at the optimum level.

Modern psychology and sociology have for far too long been obsessed by the idea that maladjustment between individual and society is almost exclusively due to a faulty construction of the individual, who must therefore be helped to adjust to the demands of a society which is taken as a more or less unalterable system of conditions. In the present situation this is decidedly the wrong way of looking at the problem; as history clearly teaches, societies and their structure have undergone rapid changes all the time, and there is no reason to assume that adaptive changes could not be effected by conscious human effort. But phylogeny has left us with a set human nature, with a basic construction of the species, which cannot be altered at will and needs enormous periods of time for harmonious evolution. For practical purposes, and in striking contrast to common belief even by scientists, the limits within which the individual can adapt and stay healthy are rather narrow and cannot be changed without interfering with the basic pattern of human nature itself, i.e. without danger of destroying the species. We should therefore stop striving vainly to adapt the individual to the impossible demands of a society which regards itself as an end instead of a means to a better and happier life for the individual. We should conscientiously proceed towards altering societies and their structures in order to adapt them — to re-adapt them — to human nature. One of the most effective means to this end would be to pursue a policy of birth control which would gradually reduce our numbers in some parts of the world and in all others ensure that they do not exceed a certain level.

There can be little doubt that the balance between relative and absolute dominance has been one of the mechanisms which controlled human density under primitive conditions. It is, within limits, capable of responding to ecological feed-back, but can presumably work to some extent, perhaps for only

a limited period of time, without such feed-back; it is probably capable of functioning again if its basic functional requirements are restored. A close study of this and other mechanisms which form part of the "homeostatic machine" will perhaps enable us to define objectively "density tolerance" and "desirable or optimum level of density" in our own species.

REFERENCES

ALTMANN, M. (1952). Social behavior of elk, **Cervus cnandensis** Nelsoni, in the Jackson Hole area of Wyoming. **Behavior** 4:116-143.

ARMITAGE, K. B. (1962). Social behavior of a colony of the yellow-bellied marmot **(Marmota flaviventris). Anim. Behav.** 10:3191331.

BURT, W. H. (1943). Territoriality and home range concepts as applied to mammals. **J. Mammal.** 24:346-352.

CHANCE, M. R. A. (1959). What makes monkeys soicable? **New Scient.** 5:520-523.

CHANCE, M. R. A. & MEAD, A. P. (1953). Social behaviour and primate evolution. **Symp. Soc. Exp. Biol.** no 7 : 395-439.

CURIO, E. (1959). Verhaltensstudien am Trauerschnapper. **Z. Tierpsychol.,** Beiheft 3.

DASMANN, R. F. & TABER, R.D. (1956). Behavior of Columbian black-tailed deer with reference to population ecology. **J. Mammal.** 37 : 143-164.

DAVIS, D. E. (1942). The phylogeny of social nesting habits in the Crotophaginae. **Quart. Rev. Biol.** 17 : 115-134.

EIBL-EIBESFELDT, I. (1950). Nber die Jugendentwicklung des Verhaltens eines mannlichen Daches (**Meles meles** L.)unter besonderer Berucksichtigung des Spieles. **Z. Tierpsychol.** 7 : 327-355.

EIBL-EIBESFELDT, I. (1953). Zur Ethologie des Hamsters **(Cricetus cricetus** L.) **Z. Tierpsychol.** 10 : 204-254.

EIBL-EIBESFELDT I. (1958). Das Vehhalten der Nagetiere. **Handb. Zool. Berl.** 8, Lfg 12, Teil 10 (13) : 1-88.

GRAF, W. (1956). Territorialism in deer. **J. Mammal.** 37 : 165-170.

GREENBERG, B. (1947). Some relations between territory, social hierarchy, and leadership in the green sunfish **(Lepomis cyanellus). Physiol. Zool.** 20 : 267-299.

GRZIMEK, B. (1956). Einige Beobachtungen an Wildtieren in Zentral-Afrika. **Z. Tierpsychol.** 13 : 143- 150.

GUGGISBERG, C. A. W. (1961). **Simba. The life of the lion.** London: Bailey Bros. & Swinfen.

HALL, K. R. L. 1962a). Numerical data, maintenance activities and locomotion of the wild Chacma baboon, **Popio ursinus. Proc. Zool. Soc. Lond.** 139 : 181-220.

HALL, K. R. L. 1962b). The sexual, agonistic and derived social behaviour patterns of the wild Chacma baboon, **Papio ursinus. Proc zool. Soc. Lond.** 139 : 283-327.

HEDIGER H. (1948). Kleine Tropen-Zoologie. **Acta trop., Basel** Suppl. 1 : 1-182.

HEDIGER, H. 1949). Saugetier-Territorien und ihre Markierung. **Bijd Dierk.** 28 · 172-184.

HEDIGER, H. (1951). Observations sur la psychologie animale dans les Pares nationaux du Congo belge. **Explor. Parc. nat. Albert, Miss. Hediger & Verschuren** no. 1 : 1-194.

JAY, P. C. (1962). Aspects of maternal behavior among langurs. **Ann. N. Y. Acad. Sci.** 102 : 468-476.

JAY, P. C. (1963). Ecologie et comportement social langur commun des Indes **Presbytis entellus. Terre et la Vie** 110 : 50165.

KAUFMANN, J. H. (1962). Ecology and social behaviour of the coati, **Nasua narica**, on Barro Colorado Island, Panama. **Univ. Calif. Publ. Zool.** 60 : 95-222.
KIRCHSHOFER, R. (1953). Aktinssystem des Maulbruters, **Haplochromis desfontainesii. Z. Tierpsychol.** 10 : 297-318.
KLUYVER, H. N. (1955). Das Verhalten des Drosselrohrsangers, **Acrocephalus arundinaceus** (L.), am Brutplatz mit besonderer Berucksichtigung der Nestbauteshnig und der Revierbehauptung. **Ardea** 43 : 1-50.
KOENIG, L. (1960). **Das** Aktionssystems des Siebenschlafers **(Glis glis** L.) **Z. Tierpsychol.** 17 : 427-505.
KOENIG, O. (1951). Das Aktionssystem der Bartmeise II. **Ost. zool.Z.** 3 : 247-325.
KRAMER, G. (1950). Uber individuell und anonym gebundene Gemeinschaften der Tiere und Menschen. **Studium gen.** 3: 565-572.
KROTT, P. (1959). **Der VielfraB (Gulo gulo** L. 1758). Jena.
KROTT, P. & KROTT, G. (1963). Zum Verhalten des Braunbaren (**Ursus arctos** L. 1758) in den Alpen. **Z. Tierpsychol.** 20 : 160-206.
LEYHAUSEN, P. (1954). Verglenchendes uber die Territorialitat bei Tieren und Raumanspruch des Menschen. **Homo.** 5 : 116-124.
LEYHAUSEN, P. (1956). Verhaltensstudien an Katzen. **Z. Tierpsychol.** Beiheft 2 : 1-120.
LEYHAUSEN, P. & WOLFF, R. (1959). Das Revier einer Hauskatze. **Z. Tierpsychol.** 16 : 666-670.
LEYHAUSEN, P. (1962). Domestikationsbedingte Verhaltenseigentumlichkeiten der Hauskatze. **Z. Tierz. Zucht. Biol.** 77 : 191-197.
MARLER, P. (1955a). Studies of fighting in chaffinches. (1) Behaviour in relation to the social hierarchy. **Brit. J. anim. Behav.** 3 : 111-117.
MARLER, P. (1955b). Studies of fighting in chaffinches. (2) The effect on dominance relations of disguising females as males. **Brit. J anim. Behav.** 3 : 137-146.
MARLER P. (1956). Studies of fighting in chaffinches. (3) Proximity as a cause of aggression. **Brit. J. anim. Behav.** 4 : 23-30
MARLER P. (1957). Studies of fighting in chaffinches. (4) Appetitive and consummatory behaviour. **Brit. J. anim. Behav.** 5 : 29-37.
MEEHAN, W. R. (1961). Observations on feeding and behavior of grizzly bears. **Amer. Midl. Nat.** 65 : 409-412.
MEYER-HOLZAPFEL, M. (1952) **Die Bedeutung des Besitzes bei Tier und Mensch.** Biel (Switzerland).
MEYER-HOLZAPFEL, M. (1957). Das Verhalten der Baren (Ursidae). **Handb. Zool. Berl.** 8 Lfg 8, Teil 10 (17) : 1-28.
MURIE, A. (1944). **The wolves of Mount McKinley.** Washington : U.S. Department of the Interior.
NICE, M. (1941). The role of territory in bird life. **Amer. Midl. Nat.** 26 : 441-487.
NIPPOLD, W. (1954). **Die Anfange des Eigentums bei den Naturvolgern und die Entsehung des Pricateigentums.** s'Gravenhage.
NOLTE, A. (1955). Field observations on the daily routine and social behaviour of common Indian mnkeys with special reference to the bonnet monkey (**Macaca radiata** Geoff.). **J. Bonbay nat. Hist. Soc.** 53 : 177-184.
SCHENKEL, R. (1947). Ausdrucksstudien an Wolfen. **Behaviour** 1 : 81-130.
SCHMIDT, W. (1937). **Das Eigentum auf den altesten Stufen der Menschheit** I. Munster/Westf.
TINBERGEN, L. & KLUYVER, H. N. (1953) Territory and the regulation of density in titmice. **Arch. neerl. Zool.** 10 : 265-289.
VERHEYEN, R. (1954). Monographie ethologique de l'hippopotame (**Hippopotamus amphibius** Linne). **Inst. Parc. nat. Congo Belge. (Explor. Parc. nat. Albert)** : 1-91.
WYNNE-EDWARDS, V. C. (1962). **Animal dispersion in relation to social behaviour.** Edinburgh, London : Oliver & Boyd.

Dr. Paul Leyhausen was born on November 10, 1916. He holds degrees both in zoology and psychology. He started his scientific career as a research assistant in the Institute of Comparative Psychology in Koenigsberg, then under the directorship of Professor Konrad Lorenz. After the war he did research on cat behavior in the Museum of Natural History in Bonn, and lectured in animal psychology at the University of Bonn. For six years he was Head of the Biology Department of the German Scientific Film Institute at Goettingen, and during that time published over a hundred scientific films, mostly on the subject of vertebrate locomotion. He is now Head of the Wuppertal Study Group of the Max-Planck-Institute fur Verhaltenspysiologie in Wuppertal, does his main research on the comparative ethology of carnivores and human behavior, and teaches ethology and comparative psychology at the Universities of Bonn and Dusseldorf. He is Research Associate of the National Zoological Park, Smithsonian Institution, in Washington.

In appreciation for the help of:

Dr. Rosemarie Wolff, for sending a copy of this article to the Year Book.

Dr. Leyhausen for help and permission to use this paper.

Mrs. B. Tonkin, in furnishing the biographical notes.