UNIVERSITY OF SOUTHAMPTON

VISUAL AND TACTILE COMMUNICATION IN THE DOMESTIC CAT (*Felis silvestris catus*) AND UNDOMESTICATED SMALL FELIDS

by

Charlotte L. Cameron-Beaumont

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ABSTRACT
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VISUAL AND TACTILE COMMUNICATION IN THE DOMESTIC CAT *(Felis silvestris catus)* AND UNDOMESTICATED SMALL FELIDS.

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The domestication of the cat is thought to have resulted in two important changes to its behaviour; firstly the presence of a high density of food around human settlements caused an increase in its intraspecific sociality, and secondly, the cat developed an increasing tolerance for humans. In this thesis the effects of domestication on the signalling methods of the domestic cat are investigated and compared with those of undomesticated species from the family Felidae.

Captive groups of undomesticated felids were selected for observation with the intention that different degrees of relatedness to the domestic cat were represented in the sample. These were *Felis silvestris ornata* (Indian desert cat: domestic cat lineage), *Felis chaus* (jungle cat: domestic cat lineage), *Caracal caracal* (caracal: pantherine lineage) and *Oncifelis geoffroyi* (Geoffroy's cat: ocelot lineage). All were found to exhibit the majority of social behaviours and signals that are known to be part of the domestic cat ethogram, with the exception of the Tail Up signal, which was not performed in the affiliative context in which it is used in domestic cat colonies. It was therefore concluded that Tail Up evolved to function as a signal in the domestic cat, possibly during domestication. All four species were found to have adapted well to an enforced social life in captivity, and to show much social behaviour, despite being solitary in the wild. This suggests that social plasticity, a trait which may have been the basis for domestication, is widespread among the felids.

The Tail Up signal in the domestic cat was subsequently investigated in more detail, by analysis of field observations of interactions in which it occurred, and via a manipulation experiment (using cat silhouettes as stimuli). Tail Up was found to occur in affiliative situations, and to be particularly temporally connected with social rubbing. Social Rub (affiliative) interactions were most likely to occur if preceded by an initiator Tail Up Approach which had been reciprocated by a Tail Up by the recipient. Cats approached Tail Up silhouettes faster, and with less hesitation or fearfulness, than they did Tail Down silhouettes. It was concluded that in the domestic cat, Tail Up acts as a signal of intention to be affiliative (*i.e.* an intention indicator). This signal is likely to have evolved as a mechanism for reducing aggression caused by unwanted advances in the high density colonies which are thought to have formed around human settlements during domestication.

Human-directed signals in the domestic cat were investigated by (a) comparing domestic cat human-directed and cat-directed behaviour, and by (b) comparing human-directed behaviour in domestic and undomesticated captive felids. The latter was carried out by means of a questionnaire to zoo cat keepers. Contrary to expectation, the highest proportion of human-friendly cats was found in the ocelot lineage (*Oncifelis geoffroyi*, *Leopardus pardalis* and *Leopardus wiedii*), and not the domestic cat lineage (five *Felis* spp.). The pantherine lineage (*Prionailurus* spp., *Caracal caracal*, *Leptailurus serval*, and three *Lynx* spp.) had the highest proportion of human-unfriendly individuals. In the domestic cat, intraspecific signals were found to be the basis for all interspecific (*i.e.* human-directed) signals, although the signals were both physically and contextually different in the two situations, such that human-directed signals have developed to be distinct from cat-directed signals. Meiowing and kneading with the front paws, both commonly performed by domestic cats towards people, were virtually absent from the human-directed repertoire of the undomesticated felids, and are therefore likely to be a product of domestication.

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Glossary:

DEFINITION OF COMMON TERMS AS USED IN THIS REPORT

Throughout this thesis I have used captial initial letters to symbolize an ethogram component (e.g. Social Rub, Allogroom, Cuff). I have also used the term 'behaviour' to mean single behavioural acts (i.e. single ethogram components, such as Cuff) as well as entire patterns of behaviour (e.g. sexual behaviour).

Behavioural element: Any behaviour carried out by a cat . This could be a behavioural event (calculated in frequencies) or a tail position or stance of a cat calculated in duration (length of time).

Behavioural event: A single action of behaviour carried out by a cat. This refers only to behaviours that can be recorded as frequencies. (*i.e.* They occur once and cannot be recorded as a duration of time); for example, Cuff, Run Away. Tail positions are therefore not considered to be behavioural events. All behavioural events used in this report are defined in the ethogram in *Appendix I.*

Behavioural sequence: A sequence of behavioural elements that are performed one after the other by one cat in one interaction.

Bout: a series of repeated behaviours of the same type, not interrupted by another behaviour, nor by a short pause.

Human-directed behaviour: Any behaviour which constitutes part of a social interaction with a human, and which is exhibited by a cat towards a human.

Cat-directed behaviour: Any behaviour which constitutes part of a social interaction with a cat, and which is exhibited by a cat towards another cat.

Cat-cat interaction: A social interaction between two cats.

Cat-human interaction: A social interaction between a cat and a human.

Cat-cat signal/behaviour: A signal/behaviour exhibited by a cat towards another cat.

Cat-human signal/behaviour: A signal/behaviour exhibited by a cat towards a human.

Dyad: a pair of cats

Social Interaction: A sequence of behavioural elements occurring between 2 cats until one of them moves over a metre away or until no behavioural events have occurred for 5 minutes.

Social structure: the structure which social rank and dominance takes in a colony, caused by the presence of a **social system** (see below)

Social system: This term is almost synonymous with social structure. It implies the ranking and dominance system within a group of individuals, as described by Alexander (1974). This is often maintained by signalling methods.

Tail posture/position: The position of a cat's tail. Tail positions are mutually exclusive from one another and can be recorded as durations of time rather than frequencies.

COMMON NAMES FOR FELID SPECIES

(Only felids mentioned in the text are included.)

The domestic cat lineage

Felis bieti	Chinese desert cat
Felis chaus	jungle cat
Felis margarita	sand cat
Felis nigripes	black-footed cat
Felis silvestris catus	domestic cat
Felis silvestris ornata	Indian desert cat
Felis silvestris silvestris	European wildcat
Felis silvestris lybica	African wildcat
Otocolobus manul	Pallas' cat

The Panthera lineage

Acinonyx jubatus	cheetah
Caracal caracal	caracal
Catopuma temmincki	Asian golden cat
Herpailurus yaguarondi	jaguarundi
Leptailurus serval	serval
Lynx canadensis	Canadian lynx
Lynx lynx	European lynx
Lynx rufus	bobcat
Neofelis nebulosa	*clouded leopard*
Panthera pardus	leopard
Panthera leo	lion
Panthera tigris	tiger
Prionailurus bengalensis	leopard cat
Prionailurus iriomotensis	Iriomote cat
Prionailurus rubiginosa	rusty-spotted cat
Prionailurus viverrinus	fishing cat
Profelis aurata	African golden cat
Puma concolor	puma
Uncia uncia	snow leopard

The ocelot lineage

Leopardus pardalis	ocelot
Leopardus wiedii	margay
Oncifelis colocolo	pampas cat
Oncifelis geoffroyi	Geoffroy's cat
Oncifelis guigna	kodkod

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Chapter 1: INTRODUCTION

The domestic cat (*Felis silvestris catus*) is generally considered to have "domesticated itself" via natural selection (Serpell, 1988), along with the ferret and the mongoose (Zeuner, 1963, Pg. 385). This is contrast to many other domesticated animals which were domesticated via artificial selection, which is driven by human intervention. In the domestic cat, however, evolution favoured the cat's increasing tolerance of man as a result of the increased amount of food and shelter available around human settlements, although subsequent human interference may have contributed to the process (Serpell, 1988).

It has been suggested that the innate behavioural (particularly social) flexibility of the Felidae (Macdonald, 1983, Macdonald *et al*,1987, Kruuk, 1975, Leyhausen, 1988) enabled the domestic cat to adapt naturally to the human-orientated niche. It is perhaps as a result of this behavioural flexibility, coupled with the novel method of domestication, that the cat stands out from other domesticated species in its degree of independence from man. The cat lives in close proximity to humans, eats their food, uses their shelter, and yet is still able to maintain the degree of independence which is so characteristic of this species. An indication of this is the ease with which it may return to ferality (Bradshaw & Horfield, in press). This species is thus positioned somewhere on the line between wildness and domestication.

Despite this, there is no doubt that the domestic cat now primarily occupies a human-orientated niche, in contrast to its wild ancestor whose environment was not occupied by man. This change in niche has caused a change in the selection pressures acting on the species, resulting in two important changes in its behaviour. Firstly, the cat has become tolerant of and sociable towards humans; secondly, the cat has become tolerant of and sociable towards members of its own species, in contrast to the ancestral species which was solitary and territorial. This latter change was probably driven by the high density of food which exists around human settlements (*e.g.* rodents on rubbish tips and direct hand-outs from humans); this led to a corresponding high density of cats in the same area. Signalling systems are then likely to have evolved as a mechanism to reduce aggression, causing the formation of close-knit colonies, rather than mere aggregations. This combination of human presence and a high density of food has therefore led to an increased social interaction in the domestic cat towards both its own and other species.

This chapter will outline the evolution of the Felidae (in particular the domestic cat), followed by a literature review of the behaviour of both the domestic cat, and of the undomesticated felids. This will particularly emphasize felid communication. Finally I will outline current thinking on signalling theory.

1.1 EVOLUTIONARY ORIGINS OF THE DOMESTIC CAT

1.1.1 Direct Ancestors

The domestic cat is thought to have descended mainly from the African Wildcat (*Felis silvestris lybica*). In the past, however, other species have been suggested as possible sources of gene input, in particular *Felis chaus* and *Felis silvestris silvestris* (for review see Kratochvil & Kratochvil, 1976, Robinson, 1980). The oriental breeds (*e.g.* Siamese and Persian cats) have been suggested to have descended from *Felis margarita, Felis bengalensis*, *Otocolobus manul*, *Felis silvestris ornata*, and even *Catopuma temmincki* (for review see Kratochvil & Kratochvil, 1976, Hemmer, 1978, Zeuner, 1963, Pg. 399). These suggestions were mostly based on the species' position in records of Egyptian life (paintings, mummies, *etc.*), or on an external appearance of similarity to the domestic cat.

Recent studies have provided firmer evidence for the genetic links between the domestic cat and the aforementioned undomesticated species. A morphological study by Kratochvil

& Kratochvil (1976) demonstrated that all types of domestic cats (Siamese, Persian and the tabby) had a common ancestor in *F. lybica*[1], but that they evolved from different subspecies; the Siamese cat from *F. lybica ornata* (now known as *F. silvestris ornata*), the basic tabby domestic cat from *F. lybica lybica* (now known as *F.s.lybica*), and the Persian cat from another subspecies which they call *F. lybica nestorovi.*

Ragni & Randi (1986) similarly concluded from morphological evidence that the domestic cat should be included in the same species as *F.s.silvestris and F.s.lybica.* Randi & Ragni (1991) subsequently confirmed using biochemical genetics that the domestic cat was more closely related to *F.s.lybica* than it was to *F.s.silvestris.* This agrees with Kratochvil & Kratochvil's (1976) findings that the domestic cat was strongly related to *F.lybica*[1]. The inclusion of the other suggested species (*P.bengalensis, F.margarita, C.temmincki*) in the line of the domestic cat have been ruled out (Hemmer, 1978, Zeuner, 1967, cited in Hemmer, 1978).

Behavioural studies support the theory that the domestic cat is more related to *F.s.lybica* than it is to *F.s.silvestris.* The ease of taming the African Wildcat (*F.s.lybica*) has frequently been cited (Guggisberg, 1975, Smithers, 1968, Hillaby, 1968), along with sightings of this species in and around villages, in close proximity to man, feeding on rubbish and rodents (Smithers 1968, Robinson, 1984). In contrast, the European Wildcat (*F.s.silvestris*) has proved much more intractable (Tomkies, 1977, Pitt, cited in Guggisberg, 1975).

1.1.2 Domestication

Cats are thought to have lived commensally near and with humans since at least 2000BC (Serpell, 1988), and possibly longer (Robinson, 1980). The initial attraction of wildcats to human settlements was probably the high density of rodent pests living around the stored grain and rubbish dumps of Egyptian villages. Pest-management was a problem for the

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[1] The species *Felis lybica* is no longer accepted as a taxonomic group (for new subspecific classification of *Felis silvestris*, see Kitchener, 1991). However, by *F.lybica*, Kratochvil & Kratochvil (1976) were implying the Asian and African forms of *F.silvestris, i.e. F.s lybica & F.s.ornata.*

Egyptians, and so the cats are likely to have been encouraged, possibly by direct handouts, and probably tamed, given the Egyptians' propensity for pet-keeping (Serpell, 1988). The niche occupied by the domestic cat therefore became human-orientated, causing the selection pressures to alter accordingly. As a result, natural selection must take a different path to that which it would follow under fully wild conditions (Todd, 1977, Price and King, 1968), and the sequence of domestication is set in motion. Species thus become adapted to their domesticated niche (Hafez, 1968, Kretchmer and Fox, 1975, Ratner and Boice, 1975, Price and King, 1968).

Domestication is a constantly evolving process and not a static state (Ratner and Boice, 1975). Kretchmer and Fox, (1975), describe domestication as "an evolutionary process resulting from the changes in the selection pressures on a species or population created by an altered or artificial environment". This definition encompasses the entire spectrum of domestic animals, from those that have been strongly artificially selected for in captivity, to those, like the cat, which have naturally evolved to life in an altered man-made niche. Interestingly, some definitions of domestication restrict it to having occurred in *captivity* (Zeuner, 1963, Pg. 63, Ratner & Boice, 1975), which questions whether the domestic cat has been truly domesticated. Indeed, Zeuner (1963, Pg. 399) states that it is a species only in the first stages of domestication. This is likely to be true at least, for mongrel cats. Pure bred cats, however, are more tightly controlled by humans, and are frequently kept indoors, with their breeding more closely monitored.

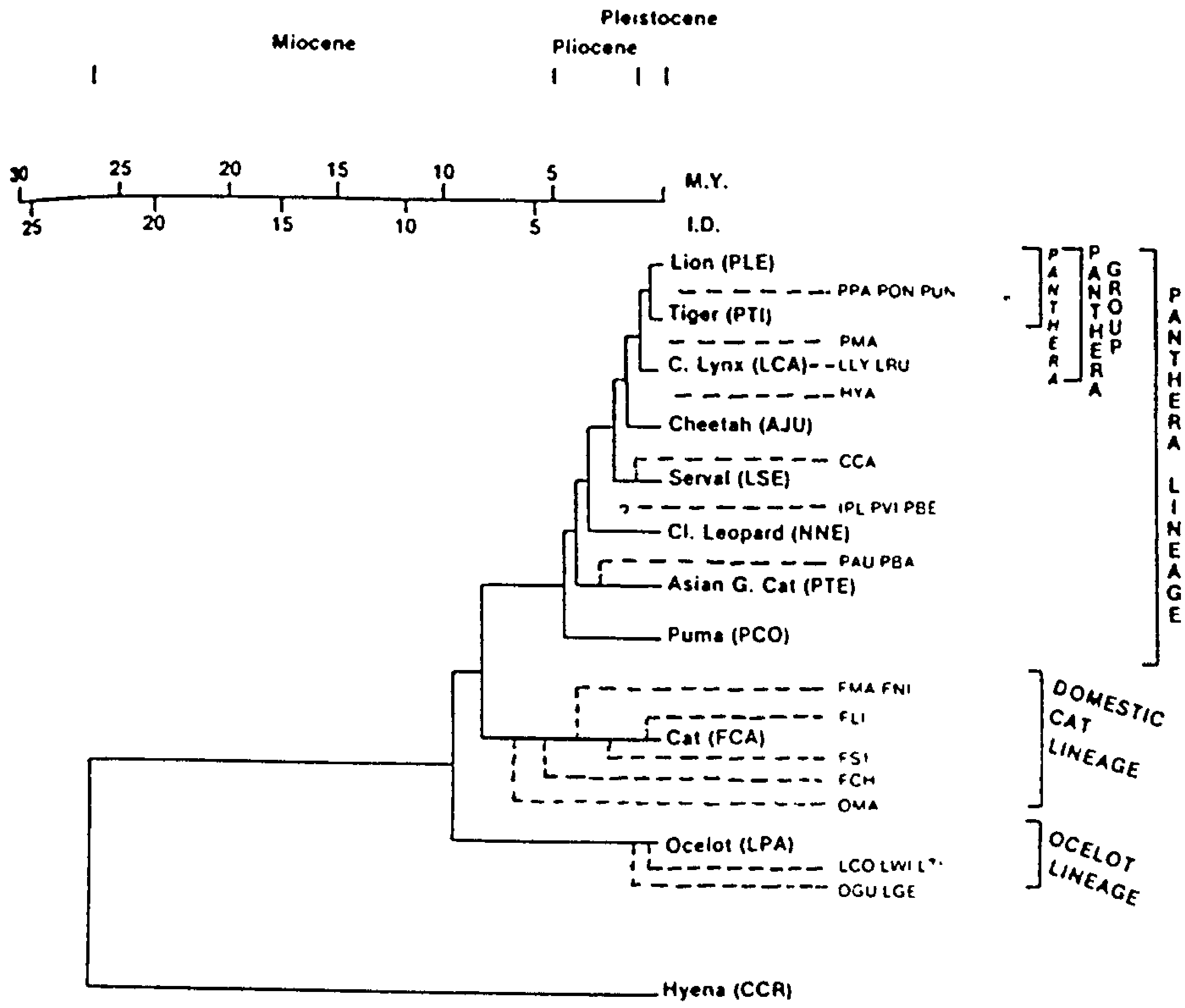
The traditional view of domestication assumes domestication to be a form of degeneracy (Smellie, 1938, cited in Ratner and Boice, 1975), bringing with it a smaller brain and an intellectual decline. Boice (1973) points out that domestic animals are not inferior to wild animals, but instead, merely adapted to a different, artificial environment. The activities of man have been to the detriment of a vast range of species; the domestic cat, however, is widespread and successful, having expanded into new, albeit artificial niches which would otherwise have been unavailable (Todd, 1977).

1.2 EVOLUTION OF THE FELIDAE

Past studies of Felidae taxonomy and evolution have been ambiguous, with a variety of different classification systems having been used (*e.g.* Ewer, 1973, Wilson & Reeder, 1993, Kitchener, 1991) However, recent molecular work has defined the evolutionary links between species more satisfactorily, using albumin immunological distance (Collier & O'Brien, 1985) and isozyme genetic distance (O'Brien *et al*, 1987)(for review see Wayne *et al*, 1989). These studies demonstrated that three lineages exist; the *ocelot* lineage which includes the small South American cats, the *domestic cat* lineage which includes the small Mediterranean cats, and the *Panthera* lineage, made up of large and small cats from many continents (See *Fig.1.1* for evolutionary tree). This broad picture of three felid lineages is supported by studies using mitochondrial gene sequence analysis (Masuda *et al*, 1996), and by past work on the morphological patterns in skulls (Werdelin, 1983). *Table 1.0* gives a summary of the species examined in the various studies.

Studies of specific lineages or genera provide more detailed support to this overall picture: the *ocelot* lineage was studied by Slattery *et al* (1994), and found to contain the species predicted by the above studies (See *Fig 1.1*), as was the *Panthera* lineage (Janczewski *et al*, 1995). Studies of particular species have also confirmed their attachment to the *Panthera* lineage (*P. bengalensis* & *P. iriomotensis* (Masuda & Yoshida, 1995, Susuki *et al*, 1994), *Lynx* species. (Werdelin, 1981)).

Fig.1.1 Evolutionary tree of the Felidae, from Wayne *et al*, 1989. The positions of species in **bold** are based on average reciprocal microcomplement fixation measurements (Sneath & Sokal, 1973, Collier & O'Brien, 1985). The positions of species attached by dotted line are based on albumin immunological distance (Collier & O'Brien, 1985). I have quoted the Latin names exactly as quoted in the original text (Wayne *et al*, 1989); as a result some names do not match exactly to the Latin names that I have used in this thesis. In this case, the name that I have used for the equivalent species is given in parentheses (see *Chapter 2, Section 2.1*, for explanation of felid classification used in this thesis).



AJU *Acinonyx jubatus*
FCA *Felis catus (Felis silvestris catus)*
LPA *Leopardus pardalis*
LSE *Leptailurus serval*
LCA *Lynx canadensis*
NNE *Neofelis nebulosa*
PLE *Panthera leo*
PTI *Panthera tigris*
PTE *Profelis temmincki (Catopuma temmincki)*
PCO *Puma concolor*
CCA *Caracal caracal*
FCH *Felis chaus*
FLI *Felis lybica (Felis silvestris lybica)*
FMA *Felis margarita*
FNI *Felis nigripes*
FSI *Felis silvestris (Felis silvestris silvestris)*
HYA *Herpailurus yagouaroundi*
IPL *Ictailurus planiceps*
LWE *Leopardus wiedii*
LTI *Leopardus tigrina*
LGE *Leopardus geoffroyi (Oncifelis geoffroyi)*
LCO *Lynchailurus colocolo (Oncifelis colocolo)*
LLY *Lynx lynx*
LRU *Lynx rufus*
OGU *Oncifelis guigna*
OMA *Otocolobus manul*
PON *Panthema onca*
PPA *Panthera pardus*
PUN *Panthera uncia (Uncia uncia)*
PMA *Pardofelis marmorata*
PAU *Profelis aurata*
FBI *Felis bieti*
LPA *Lynx pardina*
MIR *Mayailurus iriomotensis (Prionailurus iriomotensis)*
OJA *Oreailurus jacobita*
PRU *Prionailurus rubiginosa*
CCR *Crocuta crocuta*

Table 1.0 Phylogeny studies of the Felidae; species studied. Different authors use different genus names; I have therefore only listed the species names, as these never change. Species studied in this thesis are shown in bold.

Reference	**Methodology**		**Species studied**
Collier & O'Brien, 1985	Albumin Immunological Distance	(average reciprocal measure)	jubatus, **catus, pardalis, canadensis,** nebulosa, leo, tigris, temmincki, concolor
		(one way immunological distance)	**caracal, chaus**, lybica, **margarita, nigripes, silvestris, yagouarundi**, planiceps, **wiedii**, tigrina, **geoffroyi,** colocolo, **lynx, rufus**, guigna, manul, onca, pardus, uncia, marmorata, badia, **bengalensis, viverrinus.**
Janczewski *et al*, 1995	Mitochondrial cytochrome b & 125 RNA sequences.		leo, pardus, onca, uncia, tigris, nebulosa, jubatus, concolor, aurata, temmincki
Masuda *et al*, 1996	Mitochondrial cytochrome b & 125 RNA sequences		manul, **pardalis, wiedii, geoffroyi**, guigna, colocolo, tigrina, **catus, silvestris, chaus, margarita**, bieti, **nigripes.**
Masuda & Yoshida, 1995	Mitochondrial DNA		**bengalensis**, iriomotensis.
O'Brien *et al*, 1987	Isozyme genetic distance.		**catus, silvestris, margarita, chaus**, lybica, **nigripes, caracal, bengalensis, wiedii,** leo, tigris, pardus, uncia.
Slattery *et al*, 1994	Protein electrophoresis		**pardalis**, tigrina, **wiedii**, colocolo, **geoffroyi,** guigna, onca
Suzuki *et al*, 1994	Ribosomal DNA		**bengalensis**, iriomotensis, **catus, pardalis.**
Werdelin,1981	Morphology		**lynx, canadensis**, pardina, **rufus, caracal.**
Werdelin,1983	Skull morphology		**silvestris**, temmincki, nebulosa, **chaus, serval, rubiginosa, viverrinus**, manul, marmorata, planiceps, badia, **bengalensis**, onca, leo, pardus, tigris, concolor, **rufus, lynx**, pardina, **canadensis, caracal.**

1.3 BEHAVIOUR OF THE DOMESTIC CAT

1.3.1 Spatial and Social Organisation

The domestic cat is one of the three species of Felidae which show a high degree of gregariousness, along with the lion (Schaller, 1972) and the cheetah (Caro, 1989, Caro & Collins, 1987, Eaton, 1970). However, it is by no means an entirely group-living species, and has been frequently documented to lead a solitary life (*e.g.* Corbett, 1979, Apps, 1986, Jones & Coman, 1982, Fitzgerald & Karl, 1986, Leyhausen, 1965b). The determining factor is thought to be the distribution of resources; of food in the female, and of females in the male (Liberg & Sandell, 1988). The effect of resource distribution on carnivore and other societies is documented both in theory (Resource Dispersion Hypothesis, Macdonald, 1983; Ideal Free Distribution, Milinski & Parker, 1991), and empirically (*e.g.* hyenas (Kruuk, 1972); badgers (Kruuk & Parish, 1982)). Liberg & Sandell (1988) found that a clumped distribution of high density food gave rise to a high density of resident cats, and a group organisation, while a low density of sparsely distributed food was characterized by a low density of cats, and solitary organisation.

High density resources may cause high cat density, but not gregariousness as such. However, a high cat density will increase the likelihood of the occurrence of aggressive encounters, as a result of resource competition. This factor may increase the adaptive value of living a group life, due to the fact that groups have mechanisms for reducing aggression (Alexander, 1974). These mechanisms act through the formation of known relationships between individuals, which are maintained by signalling systems. This is termed a social system (Alexander, 1974) and frequently takes the form of a dominance hierachy.

The domestic cat species may therefore exhibit either solitary or social behaviour, depending on the available distribution of resources. For cats (or, indeed, any predator) living far from human settlement, feeding on sparsely distributed small prey, non-overlapping hunting areas are predicted (Kleiman and Eisenberg, 1973, Ewer, 1973), because a solitary lifestyle is the optimum strategy. This is the case for the majority of wild undomesticated cats, which also feed on sparse small prey. However, when food is clumped, it is more advantageous for the cat to live in groups. The presence of human settlements frequently causes an artificial clumping of food and therefore for many domestic cats living nearby it is advantageous to live in a group. Thus the change in niche caused by domestication causes a decrease in the adaptive value of a solitary life (Liberg, 1980) (see also Liberg and Sandell, 1988).

Some authors have even found that cats will change their social arrangement with time, both between seasons (Corbett, 1979), and during the course of a day (Laundre, 1977), according to the food distribution at the time. It is likely that the cat is particularly well-equipped to do this as a result of its flexible behavioural repertoire (Leyhausen, 1988, Macdonald *et al*, 1987, Laundre, 1977). However, Caro, (1989) suggests that felids would be more likely to live socially if they caught larger prey, which would make it advantageous to hunt in a group.

So far, I have concentrated on the explanation of resource distribution as a factor causing sociality in the domestic cat, because in this species it is thought to be the primary factor involved. However, in the Felidae as a whole, there are various other factors which may affect the social organisation of a population. These have been reviewed by Eaton (1979) (see also Eaton, 1976). These factors are the extent of predation (in particular of young offspring), and extent of inter- and intraspecific competition for critical resources. Members of a group can jointly defend both young offspring and resources from inter- and intraspecific outsiders. There is evidence for this amongst the domestic cat, where cat colonies have been found to jointly maintain exclusive territories from other colonies (for review see Liberg & Sandell, 1988). Female domestic cats have also been observed jointly defending their young from visiting males (Macdonald & Apps, 1978). It has been suggested that these behaviours arose in the domestic cat as secondary benefits once the colonies had already formed as a product of the resource dispersion (Macdonald, 1983). Communal nursing, which is known to occur amongst domestic cat colonies (Macdonald & Apps, 1978), has also been suggested as a secondary benefit (Macdonald, 1983).

Despite these advantages, there are many costs to group-living, which are outlined by

Caro (1989). He argues that the absence of group-living in the majority of felids is as a result of the *costs* of group-living, rather than a result of the *absence of conditions which would allow the benefits* to be reaped. One factor which could reduce these costs is the maintainance of kin-based groups. Domestic cat groups have been found to be largely matriarchal based; this factor may help to decrease the costs (*e.g.* share food & shelter with kin, rather than non-kin) and increase the benefits (*e.g.* through communal nursing, joint defence of young).

1.3.1.1 Spatial Organisation

Group-living domestic cats tend to have largely overlapping territories, particularly over the core area of food source (*e.g.* Laundre, 1977, Liberg, 1980, Dards, 1978, Panaman, 1981, Turner & Mertens, 1985). However, very little overlap has been documented *between* groups (*e.g.* Turner & Mertens, 1985, Liberg, 1980, Dards, 1978; see Liberg & Sandell, 1988, for review), suggesting that colonies may jointly defend a group territory (Liberg & Sandell, 1988).

Solitary individuals maintain more exclusive territories (*e.g.* Langeveld & Niewold, 1985), though overlap still occurs (*e.g.* Apps, 1986, Jones, 1977, Corbett, 1979). Leyhausen (1965b) observed that paths through territories tend to be utilised by several cats, with spacing maintained by the constant scent marking of paths by users.

In both cases male territories are bigger than females, though to a variable extent (Liberg, 1980, Corbett, 1979), and tend to overlap more than one female's territory (in the case of solitary cats), and more than one group's territory (in the case of group-living cats) (Liberg, 1980).

1.3.1.2 Social Organisation of Cat Colonies

Cat colonies are usually matrilineal; males are less tightly associated and may encompass the territories of more than one group (for review see Kerby & Macdonald, 1988). Females exhibit communal nursing of kittens and joint defence of young (Macdonald &

Apps, 1978). As mentioned earlier, signalling systems help to reduce aggression and maintain non-agonistic relationships between individuals.

Many colonies of mammals are documented as having rigid social systems in order to reduce aggression. This frequently takes the form of a dominance hierarchy (*e.g.* in wolves and primates), with each individual having a specific ranked position within the group. Studies of domestic cat colonies have also provided evidence for a hierarchical system; however, the extent of its linearity appears to depend on the conditions.

Initial studies of hierarchies in cats took place under laboratory conditions. Several of these studies found linear hierarchies, defining dominance as food-getting success (Masserman and Siever, 1944, Baron *et al*, 1957, Cole and Shafer, 1966). De Boer (1977) took a behavioural approach to dominance and found that no hierachy existed below that of the alpha and beta individuals. However, these studies may not be applicable to free-ranging domestic cats, as laboratory conditions may have caused unnatural effects, due to the unnaturally high density of cats.

More recently, studies of free-living groups have been concentrated upon. These have tended to look, not so much for evidence of linear hiearchies, but instead for sub-groups of cats, in which members are of similar rank. Liberg (1983) classified the males living in an area habited by farm cats into four hierarchical groups; breeders, challengers (frequently involved in aggressive encounters with breeders), outcasts (young males avoiding the more dominant males), and novices (yearling males). Kerby and Macdonald (1988) preferred to talk of simply breeders and non-breeder males in their colony of feral cats. Additionally, they divided the females into peripheral and central females; central females on average had higher reproductive success and were more interactive and aggressive with other members of the group. Natoli and de Vito, (1991) also classed their males into two groups, but classed them as regular males (who spent a long time courting the females), and occasional males (who relied on chance encounters). These two categories may be parallel to the breeders and non-breeders mentioned by Kerby & Macdonald (1988). However, Natoli & de Vito found no sign of the existence of central and peripheral females mentioned by Kerby and Macdonald.

These studies suggest that rigid linear hierachies do not exist in free-living groups of cats, or at least that they are difficult to detect if they do. Social systems in laboratories may be more strict and linear due to the very high density of cats, but free-ranging cats appear to have looser ranking systems.

How is dominance maintained in a colony? Various laboratory studies have looked at the relationship between aggression and dominance. Baron *et al* (1957) looked at aggression between pairs in competition for food and found no relationship between aggression and dominance as defined by food-getting success. Fonberg *et al* (1985) similarly concludes that aggressive behaviour and competitive dominance are not always related. Cole and Shafer (1966) found that threat behaviour appeared to be more instrumental in maintaining high dominance status rather than full aggressive behaviour. They suggest therefore, that distant stimuli (*i.e.* threatening behaviour) provide more cues for the subordinate-dominant relationship than do contact stimuli (*i.e.* a physical attack). Podberscek *et al* (1991) similarly found that threat behaviour is more indicative of dominance than contact aggression, while Leyhausen (1965b) noticed that a shifting of rank between caged cats could occur by display alone.

Aggression is therefore not always the key to dominance. The studies above suggest that cat social systems are likely to be maintained, not by overt attacks and aggression, but by more subtle defensive displays, and possibly other types of communication and signalling. This is perhaps not unexpected, as direct fighting in a well-armoured species is detrimental to at least one, and sometimes both, participants. Kerby and Macdonald, (1988), agree that subtle behavioural signals may be more important in maintaining the social ranking system than overt signals of aggression. Signalling in the domestic cat group and its effect on maintaining social structure within the group will be discussed in more detail in the next section.

1.3.2 Cat-Cat Communication

Otte, (1974) defines a signal to be "a characteristic fashioned or maintained by natural selection because it conveys information to other organisms". He stresses that characteristics that can be perceived, but which have not been selected for as an information conveyor, are not signals, but can be referred to with such expressions as cues, or signs.

Signals of any sort, whether conspecific or interspecific, must, in order to be selected for as signals, be distinguishable from the usual pattern of life in that species. This applies to all types of signals, including both affiliative and aggressive, and to signals conveyed in all sense modes. In addition, they must be discriminable from other signals with different meanings, and memorable enough to be learnt by the receiver (Guilford and Dawkins, 1991). These three features of the receiver's 'psychological landscape' contribute to the design of all animal signals and explain why there is such a variation in signals across species.

Most species use several senses to communicate but often specialise in one or two. As signals must ultimately be detectable, and discriminable from other signals, it is clearly advantageous to convey the message using the mode of sense most highly developed in the receiver. The design of conspecific communication signals is therefore governed by the strengths and weaknesses of the different senses in that species.

Cat social communication appears to be largely sight orientated, with the senses of touch and sound following in a close joint second (Wemmer and Scow, 1977, based on Eisenberg's (1973) tabulations of numbers of signal patterns involving each sense). Numbers of signal patterns involving the olfactory sense therefore appear to be fewer, although they may have been underestimated, since cats are known to be macrosmatic (Bradshaw, 1992, Pg. 39).

1.3.2.1 Olfactory signalling

Olfactory signalling is likely to be of more importance to solitary individuals than group members, due to its long-lasting nature, and its specificity to certain individuals (Bradshaw 1992). In addition, the message involved can be transferred from emitter to receiver without any form of social contact between the two. This form of signalling is therefore of advantage to solitary animals because the information can be transmitted without a face to face confrontation, thus excluding the possibility of aggression. In these cases, olfactory communication is most commonly used as a marker of territorial boundaries, indicating presence of an individual, or the length of time since an individual had been there (Leyhausen, 1965b), and in the attraction of a mate.

Sources of odour include urine, which is presented via spraying (Natoli, 1985a, Feldman, 1994a, Verberne & de Boer, 1976, Leyhausen, 1965b), and faeces, which are sometimes left in prominent dung-heaps (Feldman, 1994a). Felids also have the following odour-secreting skin glands, (Prescott, 1974, cited in Fox, 1975), many of which appear to have a communicatory function:

- Submandibular gland beneath the chin.
- Perioral glands at the corners of the mouth.
- Temporal glands on each side of the forehead.
- Caudal glands (diffuse clumps of sebaceous glands along the tail).
- Anal glands (the secretions of which collect in the anal sacs).
- Glands at the base of the tail (Schaffer, 1940, cited in Ewer, 1973)
- Glands in the feet (Fox, 1975, Ewer, 1973), which secrete scent during scratching.

Odour from scent glands can be presented asocially by rubbing and scratching (possibly also kneading) on prominent items and thus leaving the scent there (Feldman, 1994a), - whilst at the same time picking up scents already deposited (Rieger, 1979) - or via a more sociable method through tactile communication with other individuals (Wemmer and Scow, 1977). This is brought about by the rubbing of one cat on another, most frequently by the head, but additionally by the flank, tail and neck. In this way the scent glands of the initiator are rubbed on the recieving individual, leaving an olfactory mark (Wolski,1982). It has been suggested that scent gland secretions (from either the anal or caudal gland) may also be contributing to the liquid which is sprayed (Wolski, 1982, Schaller, 1967, Bradshaw, 1992). Wolski (1982) found that sprayed urine was different in content to that produced in squat urinations, which are thought to be mainly eliminatory in function. Passanisi & Macdonald (1990) showed that domestic cats can discriminate between sprayed and squat urine, indicating that there must be some difference between the two.

Scent gland secretions may also be contributing to the scent of dumped faeces, as is the case in other carnivores (Bradshaw, 1992).

1.3.2.2 Visual and tactile communication

Visual and tactile communication is particularly important in close interactions between individuals, because it is necessary to be relatively nearby to receive the signal. This is in contrast to acoustic and olfactory signals which can be recieved from a long way off. As a result, visual and tactile signals are particularly important amongst social colonies.

Leyhausen (1979) was the first to describe the tactile and visual communicatory sequence of aggressive and defensive patterns within the domestic cat's behavioural repertoire, through both facial expressions and entire body signals. Various other studies have attempted to categorize behaviours in a manner that would throw light on the causation and/or functional associations between behavioural elements. Dards (1979) recorded a list of the behavioural elements exhibited by her dockyard colony. Kerby (1987) attempted to categorize behavioural elements in an objective fashion, but was unsuccessful and resorted to a subjective method. Brown, (1993; see also Bradshaw and Brown, 1992), studied three neutered feral colonies and used the temporal positioning of behavioural elements in order to classify them objectively. A dendrogram was produced from a cluster analysis, with each cluster of behaviours assuming a different function. Van den Bos & de Vries (1996) carried out a similar analysis on three entire laboratory colonies, using a factor analysis of dyadic relationships to develop an idea of the functional associations between behaviours.

Within social groups of cats, the most obvious signals are those involving either rubbing or allogrooming. Macdonald *et al* (1987) found distinct asymmetries in the direction of rubbing within a dyad, finding that rubbing was skewed (a) from adult females to an adult male (b) within adult females, (c) from adult daughters to mothers, (d) from kittens to adult females, and (e) from previously dominated cats to previously aggressive ones. He therefore suggests that rubbing tends to flow from the less dominant individuals to the more dominant individuals. He thus hypothesizes that rubbing behaviour may act to maintain the ranking system within the colony, by acting as a subtle indicator of social rank, and thus acting to cement the social structure (see *Glossary*) within a group. However, his data do not conclusively support this hypothesis, and no other data has been published on this subject. Furthermore, we would perhaps expect rubbing to occur at a higher levels in females than males because object rubbing (and possibly also social rubbing) is characteristic of a female in oestrous (see *Section 1.4.3*). Macdonald also finds assymmetries in the direction of total interaction initiation within a dyad, and suggests that this may also act as an indicator of social rank. However, I am sceptical of this as he does not take into account the type of interaction (*i.e.* affiliative/aggressive). Allogrooming behaviour was not significantly asymmetrical.

Brown, (1993; see also Brown & Bradshaw, 1996), looked at flows of rubbing in a colony of five neutered feral cats, and found some significant assymmetries to occur. However, the results cannot be used to either accept or reject the hypothesis of Macdonald *et al* (1987) above, because the dominance status of each cat was not known, and because differences between males and females may not be so clear in neutered cats.

It is possible, therefore, that rubbing may act to maintain the social ranking system in cat colonies. If this is so, then this behaviour may be an example of the 'subtle behavioural cue' suggested by Kerby and Macdonald (1988; see *Section 1.3.1.2*). However, more evidence for this is needed before any certain conclusions can be made.

1.3.2.3 Acoustic communication

The domestic cat's documented acoustic repertoire varies anywhere between 11 (Bradshaw, 1992), and 16 (Moelk, 1944). Acoustic signals are difficult to characterize because call types often exist on a continuum, such that it is difficult to define where one call ends and another begins (Brown *et al*, 1978). On a broad scale, the domestic cat has three distinct types of call, the sound being produced differently in each type. Within these three types, there are a variety of different calls on a continuum; these are more difficult to tell apart, although some authors have attempted this.

The three basic types of call are as follows (Bradshaw, 1992):

(1) Calls produced with the mouth shut (termed 'murmur calls' by Moelk, 1944). These include purrs, and the greeting trill/chirrup. Generally they are of an affiliative nature.

(2) Calls produced with the mouth open and then gradually shut during the call (Moelk, 1944, terms these 'vowel patterns'). This include the whole variety of meiows, from short intense kitten calls to the longer more drawn meiow often exhibited by a cat towards a human. It also includes the Mowl (male call), and the female call. All these calls are generally attention-seeking in one way or another.

(3) Calls produced with the mouth held open in one position (Moelk, 1944, calls these 'strained intensity patterns'). These include growls and yowls, hisses, spits, and snarls. These occur in an agonistic context.

Call types 1 and 2 contain calls that may be on a continuum within type. Amongst Type 3 calls, the growl and yowl may also be on a continuum as cats frequently move from one into the other without a break in sound.

In the kitten, Moelk (1944) categorized only 9 acoustic behavioural elements, as against 16 in the mature cat. Representatives from all three types of call were present, but there were less distinctions within these.

The domestic cat is unusual in that it purrs and meiows whilst an adult, in a wide range of circumstances (Kiley-Worthington, 1984). In the majority of felids these two calls are exhibited only in juveniles. It may be that humans have selected for an acoustic characteristic in some way (Kiley-Worthington, 1984). Or it may be that cats have learnt to utilise kitten behaviours in a human-orientated manner. This may be the case for meiowing, which is an attention-eliciting behaviour and therefore very useful in cat-human interactions.

1.3.3 Sexual behaviour

The highly stereotyped sexual behaviour of the cat will be summarized in this section. It is important to know which behavioural elements are associated with sexual behaviour in order to distinguish between behavioural elements that are associated with an everyday social context and those that occur in the sexual context. Michael (1961) characterises 4 periods of the female's hormone cycle (anoestrous, pro-oestrous, oestrous and metoestrous). Anoestrus is the usual hormonal state for the majority of the year, with peaks of oestrus occuring in mid-January to March, and May to June in northern latitudes (Fox, 1975).

Pro-oestrus is the hormonal state of the female just before oestrus. It is behaviourally characterized (in the female) by crouching, constant object rubbing and rolling, kneading, and by a soft short vocalisation (Michael, 1961, Rosenblatt & Aronson, 1958). This behaviour may stimulate the male to approach and begin courtship, during which the male's behaviour consists of sniffing the female's genitalia, circling around the female and by a mating call. However, if the male attempts to mount at this stage the female will become aggressive and will not be receptive. This period may last from 10 seconds to 5 minutes (Rosenblatt & Aronson, 1958).

The onset of true oestrus is characterized by the female's receptivity to the male. Behaviours may continue as above, but the female allows the male to grip her neck and mount. Eventually the female assumes lordosis (crouching, with rear end lifted, and tail held to the side), and intromission occurs, which is characterized by a copulatory cry by the female, who is immediately aggressive towards the male. The post-copulatory period is characterised by both cats licking their genitals, the male sitting near the female, and the female rolling and rubbing as before, sometimes also pawing and watching the male. Copulation may take place up to ten times in an hour (Rosenblatt & Aronson, 1958, Michael, 1961, Fox, 1975).

The hormonal state after oestrus is termed metoestrus by Michael (1961), and is characterized by the behaviours described above, and by the female allowing the male to mount, but not to acheive intromission. This lasts at the most about 24 hours (Michael, 1961).

1.4 BEHAVIOUR OF SMALL WILD FELIDS

Small wild felids are found living in numerous habitat types, from dense tropical forest (*e.g.* Geoffroy's cat), to temperate forest (*e.g.* Geoffroy's cat, kodkod), scrub (*e.g.* pampas cat), and grassland (*e.g.* caracal, serval), and the same species is often able to inhabit a variety of different habitats in different areas. They are found living in four continents; America, Europe, Asia, and Africa, though are generally more common in the tropical regions. However, cats of all species are becoming increasingly endangered with the exception of perhaps the bobcat and the caracal, which are sometimes viewed as pests.

1.4.1 Spatial and Social Organisation

There is a wealth of information available on the spatial and social organisation of the large species of cats, in particular the lion, tiger and cheetah, (*e.g.* Caro & Collins, 1987, Hornocker, 1969, Seidensticker *et al*, 1973, Sunquist, 1981, Schaller, 1972, Smith *et al*, 1989). However, the information available on the behaviour of the smaller species of cats, is more limited, partly due to their solitary and often nocturnal behaviour. Here I will discuss only the *smaller* species of felid[2] because these are the most comparable to the domestic cat, and because I only studied small species in this thesis.

Small species of felid (*i.e.* of a *Lynx* size and smaller)[2] tend to feed on sparsely distributed small prey. On the basis of the theories for the evolution of sociality (discussed in *Section 1.3.1*), we would therefore predict that these felids would be solitary with exclusive territories. This prediction is born out by the field studies of the ranges of small felids (*F.s.silvestris*, European wildcat (Corbett, 1979, Stahl *et al*, 1988); *F.s.lybica*, African wildcat, (Fuller *et al*, 1988); *O.geoffroyi*, Geoffroy's cat, (Johnson & Franklin, 1991); *P.iriomotensis*, Iriomote cat (Izawa *et al*, 1989); *L.pardalis*, ocelot, (Emmons, 1987, 1988); *Lynx rufus*, bobcat (Bailey, 1974, Fendley & Buie, 1986), and of some slightly larger species which are difficult to categorize as large or small; *Puma concolor*, puma

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[2] I have arbitrarily categorized these as cats of a Lynx size and smaller, as there is no objective grouping available. This includes cats of the following genera: *Prionailurus, Lynx, Oncifelis, Caracal, Felis, Catopuma, Herpailurus, Leopardus, Leptailurus, Oreailurus, Otocolobus, Profelis, Neofelis.*

(Seidensticker *et al*, 1973, Hornocker, 1969); *Panthera pardus*, leopard (Ilany, 1986).

Though the exact details vary from study to study, the broad picture of spatial organisation of small felids is as follows (compiled from references mentioned in the above paragraph): Individuals live a solitary life, and maintain a territory. Female territories are generally contiguous and do not overlap greatly. Male territories tend to be at least twice as big, and overlap those of several females. They are generally contiguous with the territories of other males, although there are some instances of male-male range overlap. Juveniles separate from the mother at a variable age depending on the species, and become transient until they settle into a territory, either by ousting another cat, or by moving in when a cat dies. Females settle into territories quicker than males, due to the small size of the territory; this can sometimes gives the impression that the males are non-territorial (Fendley & Buie, 1986). This spatial behaviour is parallel to that observed in solitary domestic cats.

Despite the fact that all scientific studies to date have found small felids to live a solitary life, there are many anecdotal accounts which report citings of, for example, long-term social groupings, pairings out of the mating season, co-operative hunting, and of males helping to rear cubs. Information on the domestic cat demonstrates its ability to adapt its social behaviour according to the conditions prevalent at the time. It is therefore not out of the question to suggest that wild felids may be able to do the same. I have therefore listed these anecdotal accounts of social living in *Table 1.1*, for reference.

1.4.2 Cat-Cat Communication

There are no published studies on small felid communication in the wild, due to the difficulty of studying a solitary, small, and often nocturnal animal. Even acoustic and olfactory behaviour is unreferenced from free-ranging cats. All of the information on felid communication is therefore taken from captive studies.

Table 1.1 References which report felid social organisation. This includes both anecdotal and scientific reports. When I have written 'solitary', I mean that the species was reported to hunt and live generally by themselves, with exclusive territories, meeting up with members of their own species only for mating and during mother-young care.

SPECIES	DETAILS GIVEN	CITATION
Domestic cat lineage		
Felis silvestris silvestris, European wildcat	Usually solitary, but has been sometimes seen in pairs out of the mating season, and even occasionally in groups	Ragni, 1978
	solitary	Stahl *et al*, 1988
Felis silvestris lybica, African wildcat	Usually solitary but does sometimes hunt in pairs or as a family group	Kingdon, 1977
	solitary	Smithers, 1983, Fuller *et al*, 1988
Felis silvestris ornata, Indian desert cat	implies that they are solitary by no mention of any social behaviour	Sharma, 1979
Felis chaus, jungle cat	seen in communal groups	Schaller, reported in Guggisberg, 1975
Felis nigripes, black-spotted cat	solitary	Smithers, 1983
***Panthera* lineage**		
Caracal caracal	solitary	Smithers, 1983, Kingdon, 1977, Guggisberg, 1975, Grobler, 1981, Pringle & Pringle, 1979
Leptailurus serval, serval	normally solitary , but pairs sometimes move and hunt together. Females have been reported with quite old juveniles.	Smithers, 1983
Herpailurus yaguarondi, jaguarundi	solitary in Mexico	Guggisberg, 1975
	reports that they live in couples, and that they are often in close contact with other members of their species	Rengger, cited in Guggisberg, 1975
Prionailurus bengalensis, leopard cat	solitary	Guggisberg, 1975
Prionailurus iriomotensis, Iriomote cat	solitary	Yasuma, 1981, Izawa *et al*, 1989
Prionailurus viverrinus, fishing cat	seen fishing in a pair	BBC video footage
	Captive males reported helping take care of the young (several separate observations).	Guggisberg, 1975, Eaton, 1977.

Uncia uncia, snow leopard	talks about 'resident pairs', though gives no other details about their social behaviour	Sitwell, 1972
Lynx canadensis	generally solitary but gives 2 anecdotal reports of them being seen hunting in pairs co-operatively	Guggisberg, 1975
	anecdotal account of 3 cats seen hunting co-operatively	Barash, 1971
Lynx rufus, bobcat	solitary	Guggisberg, 1975, Fendley & Buie, 1986.
	generally solitary, but he reports an anecdotal account of seeing 2 males & 2 females together when food & shelter was scarce.	Bailey, 1974
Puma concolor, puma	solitary	Hornocker, 1969, Seidensticker et al, 1973, Emmons, 1987, Guggisberg, 1975
Panthera pardus, leopard	male stays with during birth and upbringing of cubs	Ilany, 1986
	Writes about a 'pair' of leopards, but does not make it clear whether they merely have overlapping territories or whether they lived most of their life together.	Wilson, 1977
Acinonyx jubatus, cheetah	live both in groups and solitarily, depending on conditions	Eaton, 1968, Caro, 1989, Schaller, 1970
ocelot lineage		
Leopardus pardalis, ocelot	solitary	Emmons, 1987, 1988
	lives in couples with exclusive territories	Rengger, in Guggisberg, 1975
Oncifelis guigna, kodkod	reported to live in groups	Blonk, cited in Guggisberg, 1975
Oncifelis geoffroyi, Geoffroy's cat	solitary	Berrie, 1978, Johnson & Franklin, 1991, Yanosky & Mercolli, 1994.

1.4.2.1 Visual and tactile communication

Mellen (1993) observed 20 species of captive cats of the *Felis* genus and recorded the behavioural components that each species was capable of. The results were restricted to presence/absence data for each behaviour in each species, as the evaluation of visual modes of communication was not the primary aim of the study. She found that most species possessed a rich repertoire of signals despite their naturally solitary existence. However, the rates of social behaviour were low, representing only 1-2% of the total time budgets of each cat, although a similar measurement for the domestic cat has never been made. She found that small felids exhibited remarkable uniformity in their social behavioural repertoire. Social affiliative behaviours observed included Social Rubs, Allogrooming, Sniffing and Sniff Rear. Agonistic behaviours observed included Chase, Bite, Cuff (and acoustically, Hiss, Spit and Growl). The contexts that these behaviours were exhibited in were not mentioned; it therefore cannot be deduced whether these behaviours were occurring in an everyday social situation or whether they were restricted to sexual or mother/young interactions, or to territorial disputes, as one would expect in the wild.

Petersen (1979) observed a pair of captive margays (*Leopardus wiedii)* and found that although close social contact (including Social rubbing, Allogrooming, and social play) did occur, it was only ever very brief. Agonistic threat behaviours included Crouch and Ears Flat (and acoustically, Hiss and Growl). Social interactions in a pair of captive sand cats (*Felis margarita*) were observed by Bennett and Mellen (1983). They found this species to be unsociable, time sharing their cage so that when one was active, the other was asleep. Social rubbing was not included in the ethogram (and so was presumably absent), and social grooming was only observed on 2 occasions. Tonkin & Kohler (1981) do not mention any visual or tactile social behaviours in their observation on the Indian desert cat (*F.s.ornata*); Mellen (1993) similarly found no evidence of any social behaviour exhibited by this species. Ragni & Possenti (1990) looked at the reproductive behavioural repertoire of the African wildcat (*F.s.lybica*), in comparison to the domestic cat, and found that, "No observations were made of any components (either added or alternative) that differentiate from those already observed for the domestic cat." However, they did not include any nonsexual behaviours in this ethogram.

1.4.2.2 Acoustic communciation

The description of sounds can be expressed using the 3 types of call described for domestic cats in *Section 1.3.2.3* (Bradshaw, 1992). Petersen (1979) lists the sounds heard in his two captive margays (*L.wiedii*): Purr (type 1), 3 types of meiow (type 2), and Hiss, Spit, Growl and Snarl (type 3). Tonkin & Kohler (1981) report the sounds heard in several captive Indian desert cats (*F.s.ornata*): Purr (type 1); 3 types of meiow (type 2); Growling, Hissing, Spitting, and Caterwauling (type 3), and also the gurgle. Decriptions of a gurgle range between it being similar to a purr, and being similar to a meiow, so I am unsure which type it may belong to, if any. Peters (1984) describes close range vocalisations in the Felidae, of which there are three types (Gurgle, Prusten, and Puffing), each species having only one type . He suggests that all three have the same function in the different species; that of a friendly signal of appeasement. Most small felids exhibit the gurgle, including *Lynx* species (Peters, 1987).

There has not been a great deal of research into acoustic communication in felids, but the little there is suggests that these sounds may be fitted into the 3 categories already described for the domestic cat by Bradshaw (1992). However, the individual behavioural components within each type differ from species to species.

1.4.2.3 Olfactory communication

Avenues of olfactory communication described for undomesticated felids are similar to those already described for the domestic cat; urine spraying, faeces depositing, and the rubbing and scratching of scent glands against objects (Smith *et al*, 1989, Hornocker, 1969, Schaller, 1972, Wemmer & Scow, 1977, Solokov, 1995, Bothma & Leriche, 1995). (See *Section 1.3.2.1* for more details). Urine spraying occurs more frequently in the male than in the female (Wemmer & Scow, 1977)

1.4.3 Sexual behaviour

Even solitary living cats need to socialise during mating. All the reports of wild felid mating behaviour are from captive cats, but as the sequence of behaviours is very stereotyped we can presume that the behaviour would not differ greatly in the wild.

The mating behaviour of undomesticated cats is very similar to that of domestic cats. The female's oestrous period is characterized by her behaviours of rolling, object rubbing, and presenting her anogenital area to the male (Petersen, 1977, Freeman, 1983, Foster, 1977). However, various authors report that these overt signs of oestrus are less obvious in small species of felids than in the larger felids or in the domestic cat (Petersen, 1977, Bennett & Mellen, 1983). These behaviours attract the male to begin courtship, during which he follows the female around, sniffing her anogenital area.

During copulation the male grips the neck of the female, having given a few light nips at first, and then mounts, and holds her sides with his two front paws (Ewer, 1974, Petersen, 1977). Copulation may then occur when the female assumes lordosis (crouching, rear end lifted, tail to the side, as in domestic cats). Vocalisations occur in both the male and the female at some point but accounts of this vary, as do the names given to the vocalisation so it is difficult to combine reports. The male treads his feet on the ground (Ewer, 1974, Petersen, 1977), and the female has also been reported to 'skate' with her feet (Petersen, 1977). Post-copulatory allogrooming is sometimes observed (Petersen, 1977, Freeman, 1977, Foster, 1977, *pers. obs.*). There are no published mentions of *social* rubbing being involved with courtship (as against *object* rubbing); however, I observed social rubs in as part of courtship in casual observations of one group of *O.geoffroyi*.

Table 1.2 Non-aggressive behaviours that are observed as part of courtship are tabulated below: (Vocalisations have not been included for the reasons described above)

Species	**Citation**	***Female***	***Male***
Snow leopard *(P. uncia).*	Freeman, 1983	Rolling, 'social affiliative behaviours'	'Social affiliative behaviours', Sniff Rear
Snow leopard *(P. uncia).*	Freeman, 1977	Not mentioned.	Allogroom
Cheetah *(Acinonyx jubatus)*	Foster, 1977	Rolling, Allogroom, 'Flop response', Object Rub, pawing	Follow, Tread, Investigative behaviour, Nip neck of female.
Margay (*L.wiedii*)	Petersen, 1977	'Skates' hind feet during copulation, Rolling, Object Rub, Allogroom.	Sniff Rear, Head shake, Growl, Treads, Allogroom.
Puma *(Puma concolor)*	Eaton & Velander, 1977	Object Rub,	Sniff Rear, Follow, Flehmen
Sandcat *(F.margarita)*	Bennett & Mellen	No overt signs of oestrous observed.	Not mentioned.
Geoffroy's cat *(O.geoffroyi)*	*pers.obs.* (casual observations)	Social Rub, Object Rub, Roll, Allogroom.	Sniff Rear, Follow, Chase.
Indian desert cat *(F.s.ornata)*	Tonkin & Kohler, 1981	Restless wandering, frequent licking of genitals. No mention of any other behaviours.	Not mentioned.

1.5 THE FELID-HUMAN RELATIONSHIP

1.5.1 Domestic cats and man

Human-animal relationships have the potential to be mutualistic, commensal, competitive, parasitic, or even very occasionally, ammensal (Bradshaw, 1995). The relationship between the domestic cat and man has swung through the whole range of possibilities: Prior to 7000BC it is likely that cats and human hunter-gatherers were competing for similar foods such as birds and small mammals (Robinson, 1980). With the appearance of early villages in Egypt, cats would have acted as pest controllers, when the relationship became mutualistic, with cats gaining easy access to food, and the Egyptians enjoying the benefits of pest management. There is evidence of human attachment to cats at that time through paintings and sculptures (Serpell, 1988). Cats then became a worshipped animal, with humans going into mourning when their cat died, and dead cats being mummified and buried in consecrated places (Zeuner, 1963, Pg. 391).

However, through the Middle Ages, and up to the 18th century, the attitude of Western Europeans towards the cat swung dramatically in the opposite direction; cats were suspected of being witches' counterparts, and were accordingly burned and boiled alive in rituals (Serpell, 1988). This relationship can be described as ammensal. The popularity of the cat is now once again high, with the numbers of households owning pet cats in the USA increasing constantly (Karsh and Turner, 1988); among the Western world it is now the most popular pet (Turner and Bateson, 1988). Whether this present relationship is mutualistic, commensal, or even possibly parasitic in some cases, could be disputed; the health benefits of cat-keeping on humans has been documented (Anderson *et al*, 1992), but these are unlikely to affect the long-term fitness of a human. It is therefore difficult to generalise this present relationship as the situation is likely to be different in every case.

Any animal-human relationship relies upon two-way communication. Interspecific communication differs from intraspecific communication in that the two individuals involved have different senses. Guildford & Dawkins, (1991) state that the design of signals is affected by the psychology (and physiology) of the receiver. As cats and humans are different animals in both physiology and psychology, we would expect the signals produced by a cat towards these two types of receivers to be slightly different in some way. This is discussed in more detail in *Chapter 6.*

Despite this, many cat-human signals are also used conspecifically. It is clear, even without experimental evidence, that many parallels can be drawn between inter- and intraspecific communication in the domestic cat. For example, interactions involving rubbing and grooming appear to act as affiliative or 'friendly' behaviours whether directed towards another cat, or towards a human. Aggressive behaviour is similarly connected; cats will cuff and hiss at a human as they would a cat (Bradshaw,1992).

Leyhausen (1979) theorises that an adult cat's communication with humans is based on juvenile behaviour which is stifled when with other cats due to the necessary barriers put up through defence and fighting. However, the fact that not all cat-human signals stem from juvenile behaviour indicates that this may be only part of the answer. Mertens (1991) suggests that cats perceive humans as a member of their colony, while Leyhausen (1979) suggests that cats are actually more friendly to humans than they are to members of their own species. This is possibly because the cat-human relationship is mutualistic, or sometimes commensalistic, whilst the cat-cat relationship is often more competitive.

Brown (1993) suggests that the fact that Feaver *et al* (1986) found separate dimensions (using principal components analysis) for "equable with cats" and "sociable with people", might indicate that the cat-human relationship is subtly different to that of the cat-cat relationship. Hediger, cited in Mertens (1991), suggests that a cat's socialisation with conspecifics and with humans are independent of one another. These two findings may indicate a difference between the conspecific and intraspecific relationship (Brown, 1993).

1.5.2 Undomesticated cats and man

There are many accounts of a variety of undomesticated species being tamed by man, from all lineages (*e.g. F.s.lybica, P.rubiginosa P.viverrinus, H.yaguarondi, P.concolor, O.geoffroyi* (Guggisberg, 1975); *F.s.lybica* (Smithers, 1987); *F.margarita* (Hemmer, 1976); *F.nigripes* (Armstrong, 1977); *L.wiedii* (Petersen, 1979); *L.pardalis* (Leyhausen, 1979). There are also accounts of *free-ranging* individuals living in close proximity to humans, or being unfearful of man (*e.g. F.s.lybica* (Guggisberg, 1975); *F.chaus* (Guggisberg, 1975); *F.margarita* (Hemmer, 1976)), which are all from the domestic cat lineage. Other references cite examples of certain species' intractability (*e.g. F.s.silvestris*, (Pitt, cited in Guggisberg, 1975); *F.nigripes* (Smithers, 1987); *O.colocolo* (Guggisberg, 1975); again, from a mixture of lineages. A list of publications mentioning references of different species' behaviour towards humans is tabulated in *Table 1.3*.

The above citings demonstrate that most felid species have the ability to become tame, if brought up in the correct conditions (*e.g.* with humans from a young age). However, the species that were quoted as being **naturally** unfearful of man (*i.e.* wild-living individuals which had not been tamed) were all from the domestic cat lineage (and were also all living in Africa). This is an interesting finding, as it provides evidence for the theory that the domestic cat lineage is more naturally unfearful of man than the others. However, it is difficult to extract any definite evidence from this due to the fact that the majority of these accounts are anecdotal.

Several published accounts suggest that undomesticated cats communicate with man in a similar way to domestic cats. Social rubbing appears to be the main affiliative signal used by undomesticated cats towards humans (*e.g. L.pardalis* (Leyhausen, 1979); *F.s.lybica* (Smithers, 1968); *L.wiedii* (Petersen, 1979), though Leyhausen (1979) also mentions that his ocelot used to hold its tail upright when greeting a human. These examples, though anecdotal, suggest that the ancestral species of the domestic cat may have a similar behavioural repertoire of social communication as their descendants.

Table 1.3 References mentioning the behaviour of felid species towards humans.

Species	**Author**	**Reference of behaviour towards humans**
Domestic cat lineage		
Felis silvestris silvestris, European wildcat	Guggisberg, 1975	Generally shuns man & cites example of Pitt attempting to tame them and not succeeding, finding them to continue to be very vicious towards man.
Felis silvestris lybica, African wildcat	Smithers, 1983	Reports of a tame African Wild cats being very affectionate; being free to go out but coming back of their own accord.
	Guggisberg, 1975	Does not shun man as much as *F.s.silvestris*. Often lives close to villages and farms. Kittens are easily reared in captivity. Mummies of these cats have been found in Egypt which implies that they have been kept as pets.
	Schwein in Guggisberg, 1975	Describes how *F.s.lybica* is often tamed in African villages in order to keep back the rats.
F.chaus, jungle cat	Guggisberg, 1975	Does not shun man; is often seen in the immediate neighbourhood of villages & farms, and is sometimes even found taking shelter in buildings. Often raids poultry yards. Kittens become tame very quickly and purr like domestic cats.
F.manul, Pallas' cat	Guggisberg, 1975	There are reports of this cat being kept in a semi-domestic state in parts of central Asia. There is a difference of opinion about its behaviour in captivity; some people say that it remains wild and vicious in captivity, other say that it can become tame.
F.margarita, sand cat	Hemmer, 1976	Reports that free-living individuals are not very frightened of man. Also reports that captive individuals are easily tamed.
F.nigripes, black-footed cat	Smithers, 1987	Reports it to be very difficult to tame.
	Armstrong, 1977	Describes the behaviour of 2 hand-reared cats. Reports them to be very friendly, and that they seek out human contact, although are unfriendly to strangers.
***Panthera* lineage**		
H. serval, serval	Smithers, 1987	Will take poultry if not penned.
	Guggisberg, 1975	Takes well to life in captivity. There is surprisingly no evidence for man taming this species for hunting purposes, as they did with the caracal.
Profelis aurata, African golden cat	Guggisberg, 1975	Preys on poultry near villages, and settles down easily in captivity.

P.bengalensis, leopard cat	Stroganov, in Guggisberg, 1975	Has often been said to be fierce and untameable, although some people have reported that they can become tame.
P.rubiginosa, rusty-spotted cat	Guggisberg, 1975	Cites 2 reports of them becoming very tame.
P. viverrinus	Guggisberg, 1975	Cites one report of it being tameable.
H. yaguarondi, jaguarundi	Rengger, in Guggisberg, 1975	Becomes tame and affectionate in captivity. Some individuals in South America have been kept as tame pets.
P. concolor, puma	Guggisberg, 1975	Has the reputation of being gentle towards man. Does well in captivity and becomes tame easily.
ocelot lineage		
L.wiedii, margay	Petersen, 1979	Describes the behaviour of 2 tame margays; they rubbed and groomed humans but social contact was always brief.
L.pardalis, ocelot	Rengger, from Guggisberg, 1975	Generally shuns human habitation, but will occasionally raid chicken houses.
L.guigna, kodkod	Philippi, in Guggisberg, 1975	Frequently raids chicken houses.
P.colocolo, pampas cat	Guggisberg, 1975	Frequently raids hen houses but has the reputation of being difficult to tame.
O.geoffroyi, geoffroy's cat	Guggisberg, 1975	Captive individuals are said to become tame.

1.6 SIGNALLING THEORY

There has been a large amount of literature on the theory of signal evolution. One of the main principles is that signalling movements have most commonly evolved from movements which originally had a separate function. Tinbergen, (1952), named them *derived activities*. This theory does not rule out the possibility that signals can be derived from other signals used in different contexts, but ultimately, the ancestral behaviour must have been a non-signal movement. The process of evolution from a non-signal movement to a signal is called ritualisation. It is the process by which the non-signal movement becomes more exaggerated (either bigger or maintained for longer, for example) and is used in its own context without the original function being present (Krebs & Dawkins, 1984).

The evolutionary pressures causing the non-signal to develop into a ritualised signal, or for signals to develop into slightly different signals has been discussed by Krebs & Dawkins, (1984). They suggest that there are two mechanisms that may cause a signal to be ritualised; 'mind-reading' and 'manipulation'. The terms 'signaller' and 'receiver' have been used to explain this, as signals do not evolve between individuals, but between roles. **Mind-reading** is the mechanism by which a receiver uses his knowledge of the sequence of behaviours usually elicited by the signaller to predict what will occur next. The receiver can then, if necessary, alter his behaviour accordingly. For example, before a dog bites, he bares his teeth (example from Krebs & Dawkins, 1984). The receiver dog may use this knowledge to run before he gets bitten. **Manipulation** is the mechanism by which the signaller changes the receiver's behaviour. Going back to the dog, the signaller may bare his teeth, without intending to bite, purely in order to make the receiver run away. Thus from this example it can be seen that mindreading and manipulation may run hand in hand, and co-evolve together.

Signals: An evolutionarily stable strategy?

The evolution of signals poses a problem, however, because it is difficult to see how signals that give **accurate** information can be evolutionarily stable because a population that used accurate signals would not be stable against an invasion by mutants which cheated and gave inaccurate signals (Maynard Smith, 1982). At first it therefore seemed that only 'assessment signals' could be reliable (*i.e.* Signals which accurately reflected size or fighting ability; Maynard Smith & Parker, 1976). However, Zahavi's handicap principle demonstated that signals could be reliable and evolutionarily stable if they were also costly (Zahavi, 1975, 1977); for example, a low-quality individual, or one with a low motivation, would not be able to make an inaccurate signal because it would cost too much. However, Maynard-Smith (1991, 1994) has since shown that it is possible for a non-costly signal to be an evolutionarily stable strategy (ESS) if there is no conflict of interest between the two individuals involved (*i.e.* if it is in both individuals' interests to have a reliable signal in that situation, then that reliable signal will be evolutionarily stable.) He also demonstrated (Maynard-Smith, 1994) that a non-costly signal would also be an ESS if the two communicating individuals had the same rank order of preference of the outcome of the situation.

Affiliative signals often occur in situations where there there is no conflict of interest. In particular this may occur within animal colonies, because affiliative signals are often advantageous to both interacting individuals. It is therefore not necessary for these types of signals to be costly in order to be honest and therefore evolutionary stable. It is likely that many of the affiliative signals elicited within cat colonies will be of this type (*i.e.* non-costly and honest). However, there is more likely to be a conflict of interest amongst mating interactors and between parents and offspring.

Cat-human signals may also involve a conflict of interest (*e.g.* cat wants more food than human wishes to give). The same conditions apply to interspecific signals as they do for intraspecific signals; where there is a conflict of interest it is necessary for the signal to be truthful in order for it to be an ESS. Therefore we might also expect some cat-human signals to be costly in order to be truthful.

The design of signals

The fact that evolutionarily stable signals must be costly unless there is no conflict of interests has produced an interesting effect on the design of animal signals. Signals that co-evolved to be mutually beneficial, (*i.e.* co-operative communication), can be cost-free, and evolutionarily stable. This should lead to the evolution of cost-minimising, muted signals, or 'conspiratorial whispers' (Krebs &Dawkins, 1984). On the other hand, non-cooperative signals should give rise to repetitive and conspicuous signals. This agrees with Kerby and Macdonald, (1988), who suggested that subtle behavioural cues may be more important in maintaining the social system than loud repetitive aggressive signals.

1.7 AIMS OF THE STUDY

The fundamental aim of this study was to investigate how the change of niche caused by the domestication of the cat, *Felis silvestris catus*, has affected the social communication and signalling methods of this species. Domestication has caused the domestic cat to be social towards (a) humans, and (b) members of its own species.

The domestic cat is known to be directly related to the undomesticated African and Asian forms of *Felis silvestris* (subspecies *lybica* and *ornata*). One of these species (*Felis silvestris ornata*) will therefore be used as a model for the ancestral domestic cat (*i.e.* before domestication), whilst other naturally solitary living felids will be used as models of different points in the evolutionary line.

It is not known whether the domestic cat's social ability is simply a function of the Felidae's flexible behavioural nature (*i.e.* learning during the lifetime of an individual), or whether the domestic cat has actually evolved behaviourally during domestication. If the former is true, we would expect that undomesticated species would exhibit similar social behaviours and signals (and develop similar systematic social systems) if placed in conditions which would allow group-living (such as in zoos, where cats are placed together, and where food is plentiful, so that the need for competition is reduced). Under these conditions we would expect that any social behaviour that does exist in the genetically-determined repertoire, but which does not normally occur in solitary free-living individuals, will be manifested.

By using the captive wild cats as models for the behaviour of the ancestor of the domestic cat, it is therefore possible to investigate how signalling behaviour in the domestic cat has evolved through domestication.

Specific aims of each chapter:

1.*(Chapter 3)*

To investigate how the social signalling methods of the domestic cat differ from those of undomesticated felids living in groups in captivity. This will be used to suggest whether the domestic cat has evolved any different intraspecific signals during domestication.

2.*(Chapter 4)*

Domestic cat colonies have a systematic social system with sub-groups of cats belonging to a different rank (Liberg, 1983, Kerby & Macdonald, 1988, Natoli & de Vito, 1991), possibly maintained by the social rubbing signal (Macdonald *et al*, 1987). In this chapter, I investigate whether there is any evidence for the presence of a similar social system in captive groups of undomesticated felids.

3.*(Chapters 5 & 6)*

To investigate whether the domestic cat uses its tail as a visual signal in intraspecific social interactions, and if so, for what function?

4.*(Chapters 7 & 8)*

To investigate how similar human-directed cat signals are to intraspecific cat signals in the domestic cat (*Chapter 7*). I also aim to investigate how undomesticated felids communicate with humans, and whether they use the same signalling methods as the domestic cat (*Chapter 8*). The answers to these questions will be used to suggest whether the domestic cat has evolved to communicate in a different way with humans as it does with conspecifics.

Chapter 2:

STUDY SITES, SUBJECTS AND METHODOLOGY

2.1 FELID CLASSIFICATION

There has been some contention as to the appropriate generic divisions in the Felidae. The small cat species are often found lumped into one genus, *Felis*, and the large cats into the *Panthera* genus (*e.g.* see Kitchener, 1991, Bradshaw, 1992). However, recent molecular evidence (Collier & O'Brien, 1985, Wayne *et al*, 1989) has shown that this method of classification runs contrary to what is known about felid phylogeny. I have therefore chosen to adopt the system of classification which has been recently adopted by the Felid Taxon Advisory Group (TAG), following a meeting in which a revised felid taxomony was officially agreed (http://www.cathouse-fcc.org/catsinfo.html). This classification system is the same as that given in Wilson & Reeder (1993), and splits the former *Felis* genus into 13 genera and the former *Panthera* genus into 4 genera. This method of classification is supported by a variety of evolutionary molecular and morphological studies (Collier & O'Brien, 1985, Wayne *et al*, 1989, Slattery *et al*, 1994, Werdelin, 1981, 1983, Susuki *et al*, 1994, Masuda *et al*, 1996, Masuda & Yoshida, 1995, Janczewski *et al*, 1995; see *Chapter 1, Section 1.2*). I have followed this classification system throughout this thesis.

Wilson & Reeder (1993) do not include subspecies. This is important when dealing with the taxonomy (and evolution) of *Felis silvestris*, as it has various sub species, one of which is the domestic cat, *Felis silvestris catus*. I have taken the subspecies classification for this species from Kitchener (1991). This is based on the evidence of Ragni & Randi (1986) and Randi & Ragni (1991).

2.2 STUDY SITES AND SUBJECTS

2.2.1 Domestic cats

There are a variety of terms for different types of domestic cats, referring to their very different ways of life; house cats, farm cats and feral cats. Importantly, however, all three belong to the same domestic species, *Felis silvestris catus*, regardless of their life history. There is no other domestic cat species. The definitions of house cats, farm cats and feral cats are frequently confused. Liberg and Sandell (1988) make it clear that a house cat is a domestic cat that lives in close association with a household which assumes most of the responsibility for its feeding, whereas a farm cat is merely a house cat that lives on a farm and which may spend more of its time roaming outside. A feral cat is not attached to any household, though it may still live close to humans on a more anonymous basis, and can range freely. It is able to hunt for itself and can live entirely in this predatory manner, but may also subsist on food obtained directly from humans (Cats Protection League, 1993).

In the course of this thesis I studied both house and feral domestic cats. I also studied domestic cats kept in group catteries. I classed these as a type of house cat, as they are dependent on humans for their food, live indoors and have a lot of human contact, similar to house cats. The colonies and individuals studied are outlined below.

Feral cats: Fir Tree Farm Colony

This colony was originally established in 1989 by Brown (1993), who removed them from a school where they were causing a nuisance, and subsequently neutered and vaccinated them before re-establishing them at a local farm. Brown (1993) refers to them as the 'Chilworth' cats, while I refer to them as the 'Fir Tree' cats, (due to the fact that they were moved to a different location), but the individuals involved are the same as those described in Brown (1993). At the time of my observations this colony consisted of 5 cats; 3 females and 2 males. No information on the relatedness of the cats is available, but they were thought to be about 6 or 7 years old when I carried out my observations. All five cats had lived in the colony together for at least 5 years (since 1989). We do not have any data about the length of time the cats were living at the school together before being rehomed, but they had been a growing problem at the school for some time; it is likely therefore that the cats had been together for longer, and probable that they are at least slightly related.

At Fir Tree Farm, the cats were free-ranging. They tended to centre their activity around 2 sheds; one in which they were fed, the other providing extra shelter. These were locked, but a catflap enabled access by cats 24 hours a day. Proprietory food was provided three times a week, usually in the morning. It is not known how much of their own prey they were catching. Resting boxes were available in both sheds, though the cats often preferred to sleep in the farm barn. The farm was quiet, surrounded by woodland and fields. There was little human activity for most of the day, and there were rarely more than 2 humans present at one time.

Cats tended to aggregate about the 2 sheds in the few hours before feeding and varied in their attendance. Being feral cats, their extent of socialisation towards humans was variable. HONEY (female) was as friendly as a domestic house cat, SID (male) was less so, rarely allowing humans to touch him, though he would approach humans of his own accord. The remaining three cats (GERTIE, PENNY and DUSTY (male)) rarely allowed humans to approach.

Cattery cats: Southampton University Colony

All cattery individuals had been born and lived all their lives in the indoor environment. I classified these cats as indoor house cats because they were totally dependent on humans for food, and because they would readily seek out the company of humans for play and contact. They are all neutered, and are kept for behavioural studies; no invasive work is ever carried out. The cats are accustomed to regular human contact, and are more socialised to humans than the feral cats.

When originally set up in 1989, the colony consisted of 26 neutered domestic cats (14 male and 12 female), all of a similar age (average about 9 years old in 1997). Since then, however, some cats have died, and others have been rehomed. Cat numbers have therefore varied through different studies in this thesis. The cats have lived together as a colony for about 8 years, for many, since they were born. Some of the cats are related to one another (for lineage diagram see Brown, 1993).

The cats' living quarters changed half way through the project. Some studies therefore took place in a different area to others. Both conditions are outlined here: Initially, the cats lived in two indoor rooms ($23m^2$ & $28m^2$), and a connecting indoor corridor for 24 hours a day ($14m^2$), as well as a paved outside enclosure ($96\ m^2$), which they had the run of during daylight hours only. All the rooms, including the outside enclosure, contained climbing frames, toys and logs for scratching in order to enrich the quality of the cats' environment. The two indoor rooms are shelved on several of the walls, on which sleeping boxes are provided.

The cats' living quarters were changed when the number of cats in the colony had decreased to 12. The cats had the run of two rooms during the day ($23m^2$ & $29m^2$), but only of one of these during the night ($29m^2$). The rooms were similarly enriched with toys, logs and shelves. Under these conditions, the cats had increased human contact as one of the rooms was also used as an office for humans.

Proprietory food is provided daily. Most cats (with one exception) are well socialised and will voluntarily seek out human contact. These cats were also studied by Brown (1993).

2.2.2 Undomesticated cats

The undomesticated species that I studied were all captively maintained in zoological parks or feline collections. Several groups or pairs were observed for each of four species (*Oncifelis geoffroyi*, *Felis chaus*, *Caracal caracal*, and *Felis silvestris ornata*). Each group or pair was contained in a separate enclosure. The details of each group is given in *Chapter 3, Table 3.1*. Some cats were related to one another, both within and between different groups (see *Appendix II* for details).

Cats were observed in six different institutions; the Cat Survival Trust, Howletts Zoo, Port

Lympne Zoo, Chester Zoological Gardens, Marwell Zoological Park, and Riber Castle Wildlife Park. Though the conditions varied from zoo to zoo, and even within zoos, some aspects of the cats' maintenance were constant: All cats were fed once a day, on fresh carcasses such as whole rabbits, chickens, chicks, mice, rats, or sometimes on lumps of meat from larger animals. The majority of cats had an outer enclosure, non-heated, and an inner enclosure which was heated either by central heating or by an infra red light. A few cats in the Cat Survival Trust had only an inner enclosure (2 groups of *O.geoffroyi* and 1 group of *F.chaus*); all other cats had access to both an inner and an outer enclosure. The inner enclosures always contained bedding material and sometimes bedding boxes. The outer enclosures tended to be enriched with shelving or logs for climbing. Keepers entered the cages (whilst the cats were there) in all zoos, in order to clean the cages and feed the cats.

2.3 METHODOLOGY

The techniques used in this thesis encompass both manipulative (experimental) and non-manipulative (field observation) methods. Both techniques involved the observation and measurement of single behaviour acts, referred to subsequently as "behaviours".

2.3.1 Ethogram of cat behaviour

The ethogram that I used was based on that used in Brown (1993), and that described by the U.K. Cat Behaviour Working Group (1995), both of which concern only the domestic cat. There is no published ethogram of the behaviour of small wild felids. However, as the behaviour of undomesticated cats is very similar to that of the domestic cat, these two references were also helpful in defining the behaviour of undomesticated cats. Mellen, (1988, 1993), describes some captive wild felid behaviours, as does Petersen (1977, 1979), and Peters (1984), although it was necessary to add additional behaviours myself.

The ethogram of cat tail positions was compiled by myself, though Bernstein & Strack (1996) describe some tail positions in their paper on domestic cats. The exact ethogram used for all five species of cat studied is given in *Appendix I.*

In the domestic cat it was also necessary to compile an ethogram of cat-human behaviours. In fact there were few behaviours which were additional to the cat-cat ethogram. These are also given in *Appendix I.*

2.3.2 FIELD OBSERVATION TECHNIQUES

Field observation techniques were used for data collection of both domestic and undomesticated cats. Colonies of cats of various species were observed to investigate social interactions between cats. The same methods were used for all five species.

I conducted daily ad-lib sampling sessions (Altmann, 1974), which lasted from between 1 and 24 hours. Within this ad-lib period, I recorded only the social interactions; any solitary behaviour that occurred in between interactions was not recorded, although in practise I did take some supplementary behavioural observations. Altmann (1974) terms this 'sequence sampling';

> *"A sample begins when an interaction begins. During the sample, all behaviours under study are recorded, in order of occurrence. The sample continues until the interaction sequence terminates or is interrupted, and the next sample begins with the onset of another sequence of interactions".*

Amongst felids, a 'sequence of interactions' tends to be, in fact, one interaction between two cats. There were rarely any interactions between more than two individuals.

Ad-lib sampling has various disadvantages if one intends to look at daily rhythms of behaviour (Altmann, 1974); however, as I intended to look only at temporal links *within* social interactions, this effect was not an important consideration. Nevertheless, I attempted to spread observation sessions as evenly as possible through the day, from dawn to dusk, in order to avoid any other possible biases which may have occurred. Data collected at night was collected by closed circuit video in the inner enclosure, which was often lit by an infra-red light. However, it was not always possible to collect night time data due to a lack of facilities. I generally found that the cats I observed were more active during the day, despite these species' nocturnal nature in the wild. Night observations showed very little activity occurring in any of the species. It seems likely that cats vary the timing of their activity according to their prey's activity cycle, as described for ocelots in Emmons (1988). Cats in captivity are fed during the day; this may have led to a shift in their circadian rhythm.

I defined a social interaction as *a sequence of behavioural elements occurring between two cats.* I defined the start of an interaction as *whenever one cat approached another cat within one metre,* with the exception of watching or staring, which I included as part of an interaction, even if the cats were further apart than one metre. Each interaction was recorded until one of the cats had moved away to a distance of over one metre, or until 5 minutes had passed and no subsequent social behaviour had occurred. This latter occurred if the cats were resting together.

Interactions were recorded in a similar way to that of Brown (1993), with the cat that appears to initiate the interaction being termed the INITIATOR, and the cat to whom the behaviour is directed being termed the RECIPIENT. The cats maintained this status throughout that interaction, but could have a different status in a subsequent interaction.

The identity of the initiator and recipient were recorded for each separate interaction so that individuals could be identified on analysis. Both colonies of domestic cats had a wide variety of coat colours which enabled the cats to be distinguishable from one another. Some of the undomesticated cats were more difficult to identify due to very similar coat colours and patterns. However, after a period of familiarisation, the identification of each cat was just about possible, although a few cat identities remained elusive. Fortunately, however, cat identities were not fundamental to the study.

Data collection

Interactions were recorded using a number of different methods, depending on the time of the observation and the colony which was being observed.

- *Video:* either a portable video camera (Philips VKR6850, lens: 9-54mm, 1:1.2, 0.3" CCD, wide angle lens converter x 0.45) placed on a tripod or a closed circuit T.V. camera (Panasonic WV-CL502, lens 3.6mm, 1:1.6, 0.5"CCD), monitor and video recorder. The closed circuit method was particularly useful as the camera could be installed in the inner enclosures of the undomesticated cats and left there overnight for the collection of night-time recording.

- *Dictaphone:* behaviours occurring were spoken into a dictaphone (Olympus Pearlcorder S921) by the observer (*i.e.* the author). This had the disadvantage that it brought the observer to the cat's attention. It was necessary to speak in a low voice.
- *Pen and paper:* Behaviours occurring were written down as they occurred using abbreviations.

The observer was present when the latter two methods were used. Brown (1993) discovered that a car acted as a hide in which the cats did not appear to be aware of the observer's presence. I therefore used this method for observing the feral cats. However, it was not possible in the case of the undomesticated cats which were in zoos. I therefore had to place myself in an as unobtrusive a position as possible, causing the minimum of disturbance, whilst still affording the maximum view of individuals and, additionally, being near enough for me to be able to identify the individual cats. There were often bushes and undergrowth present in which I could hide. Although the cats were initially affected by my disturbance they soon either forgot about my presence or became used to me.

All recorded behaviour was subsequently transcribed into an analysable form on computer, using The Observer package (Noldus Information Technology b.v.).

2.3.3 Manipulation (Experimental) Techniques

Manipulation experiments took the form of cats being observed under a variety of controlled conditions, in contrast to the field observations which were uncontrolled. The data collected was behavioural and the same ethogram was used as for the field observations. Experiments were only possible with one species, the domestic cat.

Behaviours were observed using video or Dictaphone and were transcribed using The Observer package (Noldus Information Technology b.v.), as above. The exact details for each experiment are given in the relevant chapters.

2.4 STATISTICAL TECHNIQUES

A variety of parametric and non-parametric tests were used to test hypotheses, according to the type of data being analysed. Multivariate statistics was also used to describe the behavioural data.

2.4.1 Independence of data

Most statistical tests assume that the data points being tested are statistically independent of one another (Martin & Bateson, 1993). The treatment of repeated measurements from one subject as if they were independent replicates is known as pseudoreplication (Hurlbert, 1984). This may result in Type I errors (Kramer & Schidhammer, 1992). Much of the data described here was collected repeatedly from the same subject; it was therefore necessary to use a repeated measures ANOVA (see *Section 2.4.2.*) in order to avoid pseudoreplication.

2.4.2 Analysis of Variance (ANOVA): Parametric

An analysis of variance tests for the effects of one or more independent variables on a dependent variable. It relies on the assumptions that the data is normally distributed, and that the variances are homogeneous. The data in this thesis was rarely found to be normal, and the variances were usually dependent on the mean, which is not unexpected for behavioural data. Data was therefore transformed before carrying out the ANOVA, using either a square root transformation or, in some cases, a logarithmic transformation. Where the data included zero scores, 1 was added to the value before logging (Sokal & Rohlf, 1981). The correct transformation for each data set was chosen by checking the homogeneity of the variances using the F_{max} test (see Fowler & Cohen, 1994), and by looking at graphs of the distribution of means and variances.

A repeated measures design was used in all cases to account for data dependence (see *Section 2.4.1*). This accounts for inter-subject differences by calculating the F ratio using the subject*treatment interaction term as the error term, rather than the residual.

2.4.3 Nonparametric tests

The following nonparametric tests were used. I have not gone into details about standard tests (see Siegel & Castellan, 1988, for more information):

Chi-squared test for 2 or more independent samples
Spearman's Rank Correlation
Kruskal-Wallis one-way analysis of variance by ranks

Kendall's rowwise (K_r) matrix correlation coefficient (see de Vries, 1993)

Rowwise matrix correlation compares two entire matrices, comparing row by row, and using a weighted sum of the correlations between pairs of rows to calculate the final coefficient (de Vries, 1993). The main feature of rowwise correlation is that it only involves the comparison of pairs of cells within the same row. It can therefore be applied in cases where the data cannot be compared between rows, such as conditional proximity matrices. This is in contrast to other matrix correlation methods, such as Mantel's Z test (see Schnell *et al*, 1985, van Dierendonck *et al*, 1995), which compares all pairs of cells in the entire matrix.

Rowwise matrix correlation also calculates the individual weighted correlations for each pair of rows. This shows up which rows are driving the final correlation coefficient, which is helpful when making conclusions from the statistical results.

There are three types of rowwise correlation, based on the indices associated with Pearson (parametric), Spearman, and Kendall (both non-parametric, using rank-order), all of which can be used with both square and rectangular matrices. I used Kendall's rowwise (K_r) matrix correlation because (i) my data was non-parametric, and because (ii) it has been proved that K_r (Kendall's) is slightly more powerful than R_r (Spearman's) in cases where there are a lot of ties (Hemelrijk, 1990a). Examples of the use of these tests can be found in Hemelrijk & Ek, (1991) and de Waal (1991).

The raw index used for Kendall's rowwise matrix correlation is known as K_r, which can range between any minimum and maximum value, depending on the size of the matrix. The normalised correlation coefficient (T_{rw}) is also used and is more comparable, as it ranges between -1 and 1.

When this test is calculated on symmetric frequency matrices (*i.e.* rather than distance/proximity matrices where each cell would contain a value from 0 to 1), it is advisable to dually normalise the data by fitting homogenous margins to both the matrices involved (de Vries, *pers.comm.*, MATMAN manual, 1996). This results in the marginal totals all being equal to the same number. This process is called Iterative Proportional Fitting (Bishop *et al*, 1975). For examples of its use, see Freeman *et al*, (1992) and van Dierendonck *et al*, (1995). This process is only appropriate for symmetric frequency matrices.

The statistical significance of the test was calculated using Mantel's (1967) permutation procedure which respects the interdependencies of the values within rows amd columns of these matrices (de Vries, 1993). In all cases the probability level was based on 10,000 permutations.

All of the procedures described above were carried out using the MATMAN programme, Version 3.2 (1996, Ethology & Socio-ethology, Utrecht University): See de Vries *et al* (1993). This programme is designed specifically for the manipulation and analysis of matrices derived from behavioural data.

2.4.4 Multivariate analysis (on matrix data)

Multivariate statistics was used in order to visualise and describe the behavioural data collected from field observations. The multivariate statistics was carried out on matrix data which were based on the temporal associations between behaviours, the aim being to describe temporal links between behaviours and groups of behaviours. The types of matrices used are described below:

a) First Order Transition matrix: The value in each cell describes the number of times that one behaviour follows another, with the first behaviour being on the rows, and the subsequent behaviour on the columns. It is a square matrix, containing the same behavioural events in both rows and columns. Transitions between behaviours were counted regardless of the time lapse that might occur between the two, provided that they occurred within the same interaction.

b) Co-occurrence matrix: The value in each cell describes the number of times that each behavioural event (*i.e.* sniff, paw) occurred within each behavioural state (*i.e.* during the time that the cat was sitting, or during the time that the cat held a certain tail position). This matrix is asymmetrical, containing behavioural states on the columns and behavioural events on the rows.

c) Sequence-linked matrix: Matrix of the number of times each behaviour is exhibited in the same behavioural sequence as every other behaviour. Note that a behavioural sequence is here defined as a sequence of behaviours exhibited by *one* cat in an interaction (See *Glossary*). This is also a square matrix, containing the same behavioural events in both rows and columns.

The statistical technique that I used to analyse these matrices is described below.

Chi-squared residuals

This technique can be used to highlight non-random cells in a matrix. (Note that a matrix is a type of contingency table). The standardised residual is a measure of the residual difference between the expected and observed frequencies (as defined by the chi-squared test) for each cell of a matrix. It is calculated as:

$$\text{Observed value- Expected value}/\sqrt{\text{Expected value}}$$

and can be calculated for each cell of a matrix (Fagen & Young, 1978, Fagen &

Mankovich, 1980, MATMAN manual, 1996).

A more precise analysis can be gained by the use of the adjusted residual which takes account of the standard deviation of all the standardised residuals in the matrix. The adjusted residual is calculated as:

$$\frac{\text{Observed value- Expected value}/\sqrt{\text{Expected value}}}{\text{Standard deviation of all the standardised residuals}}$$

(Haberman, 1973, MATMAN manual, 1996). This value can also be calculated for each cell of a matrix.

The significance of each residual can then be calculated by comparison with any table showing the probabilities associated with the upper tail of the normal distribution (*e.g.* Table A in Siegel & Castellan, 1988). This gives the critical values as $1.96 = p < 0.05$, $2.57 = p < 0.01$, $3.30 = p < 0.001$, $3.90 = p < 0.0001$. (See also Fagen & Mankovich, 1980, MATMAN manual, 1996.) In this way, a pair of variables (*i.e.* a particular cell in a matrix) can be labelled as significantly more likely or less likely to occur together than expected. A significant positive value indicates that the observed value is higher than expected; a significant negative value indicates that it is lower.

This technique is usually used in analyses of sequences of behaviour, to investigate significant transitions from one behaviour to another. In practice, it can be used to highlight any cell which is significantly aberrant from the expected, and therefore can be used on any of the three matrices described above:

(a) On the transition matrix: Highlighting two behaviours that are significantly likely to follow one another.

(b) On the co-occurence matrix: Highlighting a behavioural event that is significantly likely to occur during a behavioural state.

(c) On the sequence-linked matrix: Highlighting behaviours that are significantly likely to occur in the same behavioural sequence together.

The residuals thus indicate how dependent two behaviours are upon one another; *i.e.* whether the presence of one significantly increases or decreases the likelihood of the presence of another. A diagram of association can then be drawn, visually linking those behaviours which were significantly likely to occur together (see *Fig.3.1* for example).

The diagonal values in matrices *(a)* and *(c)*, were, in this study, structural zeros, because I did not include auto-transitions. It was therefore necessary to use imputed values for the diagonal when calculating the residuals. This method is described in the MATMAN manual (1996). The residuals of the imputed values are naturally zero and therefore do not contribute to the final χ^2 value of the matrix. *Matrix (b)* was rectangular and therefore the diagonal values were already defined.

There are, however, complications with this method of analysis. These are outlined below:

- *Outliers influence residuals*

If this method is used to identify more than one significant cell, each test is not independent of the others (Fagen & Mankovich, 1980). As a result of this, outliers (*i.e.* cells with extremely high or extremely low values) will influence the residual values of other cells via their marginal totals (MATMAN manual, 1996). Thus behaviours that occur often may mask the associations of infrequent behaviours. This may lead to some Type I and Type II errors occurring within a large matrix.

In order to lessen this effect, I carried out three analyses of each set of data, with each matrix containing different numbers of behaviours:

- All behaviours included.
- All behaviours except those that occurred at high frequency.
- All behaviours except those that occurred at a very low frequency.

The comparison showed that there was actually very little difference between the three types of results. The absence of low frequency behaviours made practically no difference at all. However, the absence of some very high frequency behaviours did cause some middle frequency behaviours to become significant. This effect was caused by very high frequency behaviours such as locomotory behaviours (*e.g.* Approach). In *Chapter 3*, these high frequency locomotory behaviours were not included in the analysis for other reasons (see *Section 3.3.1.2*). In the cases where these behaviours were included, (such as in *Chapter 5*), I carried out three analyses for each set of data, as described above, in order to take this into account.

- *Numerous tests cause some Type I errors.*

If the matrix contains many behaviours there is the possibility of a Type 1 Error occurring (*i.e.* the overestimation of significance) due to the large numbers of tests that are being carried out (at $p<0.05$, one in 20 tests will be wrongly labelled as significant). It is possible to eliminate this problem using the Dunn-Sidak or Bonferroni methods (Sokal & Rohlf, 1981), which involves reducing the significance level depending on the number of tests being carried out.

- *Pseudoreplication* (See *Section 2.4.1* above)

Each matrix contains data pooled from different animals. However, it would be impossible to collect testable quantities of independent data of this type: Due to the constraints of chi-squared (it has been suggested that none of the expected values must be less than 1, and that there must be no more than 20% of expected values under 5; Cochran, 1954, Chatfield and Lemon, 1970, Fagen and Young, 1978), it is necessary to have relatively large frequencies in the contingency table. In *Chapter 3* I analysed 135 *F.s.ornata* interactions and 947 *O.geoffroyi* interactions. If I had collected independent data on this number of interactions, I would have had to observe 135x4 *F.s.ornata* cats and 947x4 *O.geoffroyi* cats (!), as every interaction involves two cats, and no one cat can be recorded twice under the rule of independence. This is clearly impossible.

Slater & Ollason (1972) attempt to avoid massing individual data by repeating the analysis for each separate individual. However, the constraints of chi-squared as described above mean that large quantites of data would be needed for each individual, particularly when large matrices are being tested. Lemon & Chatfield (1971) advocate simple visual inspection of data. I, in fact, used this statistical test, but also visually inspected the results in order to check for any individual cat effects which may have been manifested in the significant results.

As a result of these problems, it is best to use chi-squared residuals as an exploratory type of analysis; to provide a description of the behaviour, and to spark off the generation of testable hypotheses. In this study I have used it for both these reasons. In *Chapter 3* the temporal structure of behaviour of the five different species is described using this method. In *Chapter 5* this method is used to explore behavioural associations with tail positions, from which a hypothesis is subsequently generated. (This is then subsequently tested in *Chapter 6* using a repeated measures ANOVA (see *Section 2.3.2* above), which accounts for lack of independence.)

Chapter 3:

SOCIAL COMMUNICATION IN CAPTIVE GROUPS OF [SOLITARY] UNDOMESTICATED FELIDS:

A comparison with the social domestic cat.

3.1 INTRODUCTION

Many of the small felids[1] have been reported to lead a solitary life. For example, *Felis silvestris silvestris,* European wildcat (Corbett, 1979, Stahl *et al,* 1988); *Felis silvestris lybica,* African wildcat, (Smithers, 1983); *Oncifelis geoffroyi,* Geoffroy's cat (Johnson & Franklin, 1991); *Caracal caracal,* caracal (Grobler, 1981, Guggisberg, 1975); *Lynx rufus,* bobcat (Bailey, 1974, Fendley & Buie, 1986), and *Prionailurus iriomotensis,* Iriomote cat (Izawa *et al,* 1989, Yasuma, 1981). There are also various anecdotal accounts of small cats being seen in social pairs or groups (see *Chapter 1, Section 1.4.2, Table 1.1*), but in general it is assumed that small felid species are solitary, even in species where there is actually no supportive evidence either way (*e.g. Felis margarita,* sand cat, Bennett & Mellen, 1983). It is not surprising that these species live solitarily; theories of resource dispersion (Resource Dispersion Hypothesis, Macdonald, 1983; Ideal Free Distribution, Milinski & Parker 1991; see *Section 1.3.1*) predict that a solitary lifestyle would be the most advantageous way of life for a predator feeding on small prey (see also Kleiman & Eisenberg, 1973). This is the case for most small felids. Solitary species such as these would be expected to exhibit very little closely interactive behaviour, with the exception of sexual and mother/young behaviours. The direct (undomesticated) ancestor of the domestic cat is thought to have led a solitary life very similar to that of the undomesticated species which exists today.

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[1] I have arbitrarily categorized these as cats of a Lynx size and smaller, as there is no objective grouping available. This includes cats of the following genera: *Prionailurus, Lynx, Oncifelis, Caracal, Felis, Catopuma, Herpailurus, Leopardus, Leptailurus, Oreailurus, Otocolobus, Profelis, Neofelis.*

The domestic cat, however, is frequently found living gregariously, with group sizes varying from between 2 to over 50 (reviewed in Liberg & Sandell, 1988). Studies of the free-ranging domestic cat have established that the domestic cat varies its spatial organisation according to the distribution of resources available (see *Section 1.3.1* for details). Social groups form when resources are clumped and at high density. This is frequently the situation around human settlements because the presence of humans causes the clumping of resources. It is therefore thought that domestication may have initiated the group living of the domestic cat.

Macdonald *et al* (1987) documented the social interactions occurring in a domestic cat farm colony. He found that cats interacted with one another more often than would be expected by chance, and states that cat colonies are "not merely asocial, structureless aggregations of individuals around a common food resource, but instead are actively communicating social groups". However, this statement is perhaps to be expected as 'asocial aggregations' of carnivores without any form of sociality are likely to be aggressive, and therefore evolutionarily unstable. It seems likely that social signalling has evolved in areas where there are a high density of cats (because of the high density of food) in order to reduce aggression (see *Section 1.3.1*). This has been documented in groups of primates where affiliative behaviours (such as allogrooming) help to diffuse aggression or reconciliate 2 individuals after an agonistic encounter (Terry, 1970, Carpenter, 1942).

Social signalling in domestic cat colonies has been widely documented (Macdonald *et al*, 1987, Macdonald & Apps, 1978, Brown, 1993). Colony cats live closely together and exhibit many close social signals of both affiliative and agonistic kind (*e.g.* Social Rub, Allogroom, Ears back, Stare; see *Appendix I*). These behaviours have been clustered into functional groups by various authors using different methods (Cluster analysis (Brown, 1993, Bradshaw & Brown, 1992); factor analysis (van den Bos & de Vries, 1996); subjective categorization (Kerby, 1987)). Brown (1993) found 6 constant clusters in her three groups of neutered cats, which she termed *Affiliative* (includes Social Rub and Tail Up), *Approach/Sit* (includes Allogroom, Sniff, Touch Nose), *Aggressive* (includes Stare, Fight, Bite), *Defensive* (includes Run Away, Crouch, Hiss), *Investigatory* and *Play*. Van den Bos & de Vries (1996) investigated groupings of behaviours in entire cats of mixed sex and finds the following categories: *Sexual* (includes Social Rub, Roll), *Inspection/Affiliative* (includes Allogroom, Sniff, Touch Nose), and *Defensive* and *Offensive*, (in which distinct behaviours were not given).

These studies have shown that the domestic cat has a wide repertoire of adult-adult social signals. The origins of these signals is not known. There are various possibilities:

- The undomesticated (solitary-living) ancestor of the domestic cat may have had the same behavioural repertoire, but may not have used its social abilities due to its solitary life. Leyhausen, (1988), cited examples of advanced species of bumble bees, under unusual conditions, falling back on behaviour patterns normally only exhibited by the primitive species (Haas, 1962, 1965, cited in Leyhausen, 1988), thereby implying that a species has the entire behavioural repertoire of a genus in store and is able to fall back upon normally unused components of the repertoire under stressful conditions. Haas called these components 'generic behaviour'. Leyhausen suggests that the range of social communication of the domestic cat might, similarly, be generic behaviour which, in undomesticated cats, is not manifest because it is unnecessary in the habitats which they presently inhabit. It has been previously shown that present day felids have a flexible behavioural repertoire (Macdonald, 1983, Kruuk, 1975, Leyhausen, 1988).

- These social signals may have been utilised in the ancestral domestic cat under specific circumstances (*e.g.* sexual/mother-young interactions).

- The domestic cat's repertoire of social signals may have evolved through domestication, with the formation of social colonies. This could also have occurred in combination with the above two possibilities.

Ewer (1974), used current knowledge of the behaviour of the viverrids to give clues about how wild felid behaviour evolved. The viverrids are the family that have diverged least from the ancestral animal from which the Feloidea emerged; thus their behaviour is expected to be similar to that of the ancestral felid. I intend to make use of a similar relationship between the domestic cat and the undomesticated small felids, to generate clues about how domestic cat social behaviour evolved. This is under the premise that the undomesticated felids will have evolved slower than the domestic cat which has undergone a drastic change in niche during domestication. I will therefore use the undomesticated forms of felid as a model for the ancestral domestic cat (*i.e.* before domestication), in particular, *Felis silvestris ornata*, which is considered to be a direct ancestor of at least some breeds of the domestic cat (Kratochvil & Kratochvil, 1976).

Captive undomesticated felids are usually kept in pairs or small groups, and as food is plentiful under these conditions, this provides an artificial situation in which the food is of a high density clumped distribution, similar to the situation of social-living domestic cats. By investigating the social behaviour of undomesticated felids under captive conditions it is therefore possible to consider how domestic cat social signalling has evolved during domestication. The shortcoming of this method is that cats are being forced to live in a group by the confines of the cage. Space is therefore limited, and these cats cannot roam as freely as domestic cats.

The overall aim of this chapter is therefore to investigate the evolution of social signalling in the domestic cat, through a comparative study, using the undomesticated forms of today's small felids as models for the undomesticated ancestor of the domestic cat. Specific questions to be answered are as follows:

- Have any 'new' social signals evolved through domestication?
- Have any 'old' signals re-evolved so that

  (a) they are changed physically?, or

  (b) they are performed in a different context (this may indicate that they have a different meaning).

This chapter will therefore describe and compare visual and tactile social behaviours in five species of evolutionarily diverse felids, one domestic and four undomesticated.

3.2 METHODS

3.2.1 Species, Subjects and Study Sites

I chose four evolutionarily diverse species to observe. The *Felis* genus is known to have diversified from three lineages (Collier & O'Brien, 1985, Wayne *et al*, 1989; see *Chapter 1, Fig 1.1* for evolutionary tree); one that led to the evolution of the domestic cat, one that led to the evolution of the *Panthera* genus, and one from which the ocelots emerged (ocelot lineage), which contains many of the South American cats. I chose one species each from the *Panthera* and ocelot lineages (*Caracal caracal: Panthera* lineage, *Oncifelis geoffroyi:* ocelot lineage), and two from the domestic cat lineage (*Felis chaus* and *Felis silvestris ornata*). *Felis silvestris ornata* is, of the four, the most closely related to the domestic cat, as it is thought to be one of the direct ancestors of the domestic cat along with *Felis silvestris lybica* (Kratochvil & Kratochvil, 1976, Ragni & Randi, 1986).

Observations were taken of as many individuals as was practically possible for each species, in a variety of zoos. I was limited by the numbers of individual cats available, and by time.

Caracal caracal n=13 (6 groups)
Oncifelis geoffroyi n=14 (6 groups)
Felis silvestris ornata n=7 (3 groups)
Felis chaus n=12 (5 groups)

Species descriptions (see *Plates 3.1-3.4* for pictures)

Oncifelis geoffroyi (Geoffroy's cat) See **Plate 3.2.**
There are 4 subspecies of the Geoffroy's cat (Ximenez, 1975), whose distribution ranges from the Bolivian Andes and the mountains of northwestern Argentina, to Uruguay and Southern Brazil, and throughout Argentina to Patagonia. It is slightly smaller than the average domestic cat, with a stripey grey coat, rather similar to a small tabby (Kitchener, 1991). They are solitary (Johnson & Franklin, 1991), and live in forested areas (Yanosky & Mercolli, 1994, Ximenez, 1975), and in open bush country (Guggisberg, 1975), up to an altitude of 3300m (Kitchener, 1991). They are nocturnal, with the highest activity occuring at dawn and dusk, when they feed on hares, rodents and small birds. (Johnson & Franklin, 1991). Guggisberg (1975) reported that captive individuals are easily tamed.

Plate 3.1 *Felis silvestris ornata* (Indian desert cat).

Plate 3.2 *Oncifelis geoffroyi* (Geoffroy's cat).

Plates 3.3a&b *Caracal caracal* (caracal)

(a)

(b)

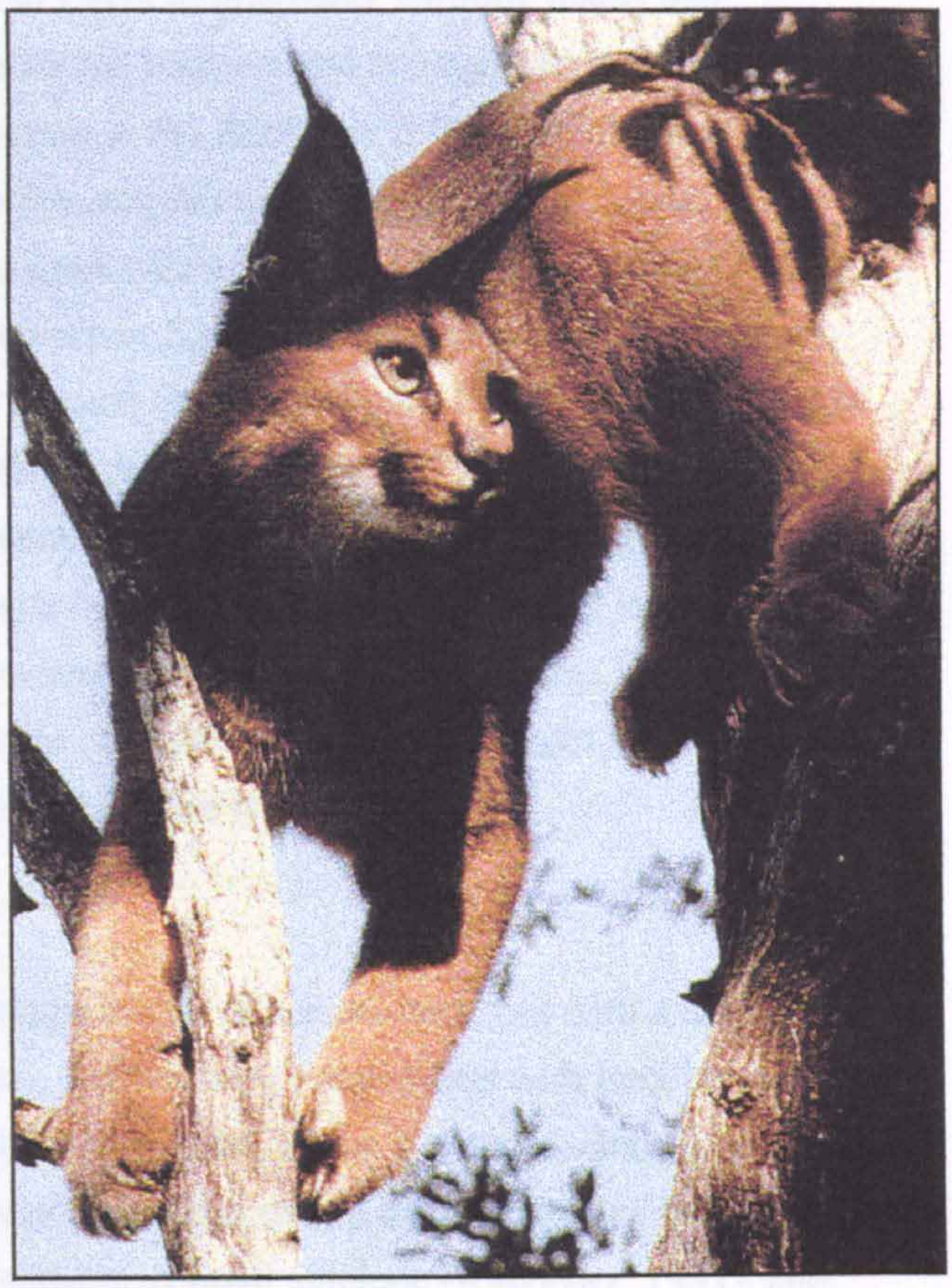

Plate 3.4. *Felis chaus* (jungle cat).

Felis chaus (Jungle cat) See **Plate 3.4**.
This cat is about 0.6m long, of a uniform sandy colour, with long legs and a relatively short tail. It ranges from the south of Egypt, through Sri Lanka & South India, to the east of Vietnam. It inhabits a variety of habitats, from swamps and reed beds in Egypt to grassland, shrubby plains and woodlands, in India, making its dens in disused mammal burrows and amongst reeds or bushes (Guggisberg, 1975). It is sometimes called the Swamp or the Reed Cat. It feeds primarily on small mammals, particularly gerbils, but also birds, reptiles, amphibians, and insects (Kitchener, 1991, Ishunin, 1965, Litvinov, 1981). Ancient Egyptian mummies have been found of *F. chaus*, (though the majority were of *F.s.lybica*), implying that the ancient Egyptians must have kept them as pets, and thus that they must have been relatively easy to tame (Morrison-Scott, 1952). They are thought to have been used for hunting wildfowl in Ancient Egypt (Guggisberg, 1975), and are frequently found in the vicinity of villages. Kittens become tame very easily and purr like domestic cats (Guggisberg, 1975). There is little data on the social behaviour of this species, but it is generally thought to be solitary, like all small wild cats. However, Schaller (from Guggisberg, 1975), observed congregations of jungle cats on open meadows in the cool season, which he thought may have been part of their mating behaviour. No further information on this is available.

Caracal caracal (Caracal) See **Plates 3.3a&b.**
The caracal is about 0.9m long, and of a similar shape to that of a small lynx, but with a longer tail and slimmer body. It is a uniform red-brown colour, and has long pointed ears with long black tufts. It is fairly common in Africa, but also extends into central India, where it is approaching extinction. The caracal is able to live successfully in virtually every habitat within its range except rain forest. Its diet varies as a result, ranging from birds and rodents to small antelope (Kitchener, 1991), and occasionally domestic sheep or goats (Pringle and Pringle (1979). Adult cats are solitary (Grobler, 1981, Guggisberg, 1975, Kingdon, 1977), and associate only during the breeding season, (Pringle & Pringle, 1979), when they make dens in burrows, often taken over from porcupines or foxes (Sapozhenkov, 1961), or in dense bushes. The caracal is mainly nocturnal (Grobler, 1981, Guggisberg, 1975), and is the fastest and best jumping cat of its size (McNeely, 1981, Guggisberg, 1975). As it is easily tamed, it has been trained for hunting in the past (Guggisberg, 1975, Kingdon, 1977). Ancient Egyptian mummies have been found of this cat (Kingdon, 1977), implying that they, too, must have been kept as pets.

Felis silvestris ornata (Indian or Arabian Desert Cat) See **Plate 3.1**
This cat is thought to be the direct ancestor of the Asian breeds of domestic cat (Kratochvil & Kratochvil, 1976). It lives in the semi-deserts and steppes of southwestern Asia, reaching as far east as Northern India. It is about the same size or slightly smaller than the domestic cat, and has a sandy, or grey coloured coat, covered in dark spots (Kitchener, 1991) or stripes, and sometimes totally unmarked (Guggisberg, 1975). Its diet consists of rodents (mainly gerbils in the desert), squirrels, hares, birds, snakes, geckos, scorpions, and insects such as beetles. In the breeding season they make

dens in hummocks hidden by vegetation with several openings (Sharma, 1979). Nothing has been published on this cat's reaction to man, although its close relative, the African Wild cat (*F.s.libyca*) is renowned for its tameness. As far as I am aware, there is no data on the social behaviour of this species; Tonkin & Kohler (1981) report on some aspects of its behaviour in captivity but give no account of any social behaviour.

The study was conducted at six separate sites; Port Lympne Wild Animal Park, Chester Zoo, The Cat Survival Trust (Welwyn), Marwell Zoological Park, Riber Castle Wildlife Park, and Howletts Zoological Park. Cats in captivity tend to be kept either in small groups or pairs; I was therefore unable to find any that were kept in groups of more than 3/4 individuals. It was thus necessary to keep several study groups for each species, in order that the sample size was large enough for each species. Furthermore, this was advantageous because separate groups are statistically independent from one another whilst individuals within a group are not. An attempt was made to observe each species in at least two different sites, to ensure that a behavioural difference caused by site was not attributed to a species difference. (See *Table 3.1* for details on each group.). The relatedness of cats varied (See *Appendix II* for details).

3.2.2 Data Collection (details described in *Chapter 2, Section 2.3.2*)

Data was collected during daily ad-lib sessions, in which sequence sampling was undertaken (Altmann, 1974). Sequence sampling can be described as the recording of every social interaction (for definition see *Chapter 2, Section 2.3.2*) that occurs within the ad-lib session. The following were recorded:

- the **identity** of the initiator and of the recipient (for definitions see *Chpt 2, Section 2.3.2*).
- all **behavioural elements** exhibited by both individuals involved in the interaction (as defined in the ethogram; see *Chapter 2, Section 2.3.1, & Appendix I*)
- **tail postures** of both individuals throughout the interaction (defined in tail positions ethogram, *Fig. 5.1*).

Data was recorded either by dictaphone or video, and individuals were identified using coat colours and patterns. Thus the data consisted of a series of recordings of social interactions.

Domestic cat data

The domestic cat data used in this chapter was collected and collated by Brown (1993), using the same techniques as described for the wild felids (*i.e.* ad-lib sequence sampling, recording via dictaphone, pen & paper, and video). I re-analysed some of her data for the purposes of this study, in order that the data was analysed in the same way as for the wild felids. This enabled direct comparison between the two. Three groups were analysed, all of which were neutered:

Site	*Numbers & Sex*	*No. of interactions observed*
Knowle (free-ranging)	3♀, 2♂	404
Chilworth (free-ranging)	7♀, 4♂	574
University (confined)	12♀, 14♂	1066

(See *Chapter 2* for details of University group)

3.2.3 Data Analysis

Frequency data were organised into sequence-linked matrices (see *Chapter 2, Section 2.4.4*), which formed the basis of the analysis for *Section 3.3*. In some cases the analysis required the calculation of the **rate** of a behaviour (*i.e.* no. of times a behavioural element occurred per unit time), rather than the frequency of a behaviour, in order to be able to compare the different groups and dyads. Rates were calculated using the number of **active hours** observed in each dyad. This value was defined as the number of observed hours when at least one of the two cats of the dyad was not sleeping. Interactions frequently occurred when one cat was sleeping and the other was awake, so it was felt necessary to include the time when one cat was sleeping in the active hours for that dyad. *Table 3.1* gives a summary of the total time, and total active time that each group was observed for, along with the number of interactions which were observed during this period.

Statistical methods used are described in more detail in *Chapter 2*, and will also be described briefly in each separate results section.

Table 3.1 **Details of groups observed for each species, total time in hours (with active time in parentheses), and total no. of interactions observed. In cases where the group contains three individuals, I have given an average active time for the three possible dyads, for ease of tabulation; in reality each dyad had slightly different active times, so for statistical purposes these more accurate times have been used. CST= Cat Survival Trust**

SPECIES	LINEAGE	GROUP	NUMBERS & SEX	SITE	TOTAL HOURS OBSERVED (ACTIVE TIME)	Total no. of interactions observed
F.chaus	Domestic cat	A	3♀	CST	19.46 **(18.46)**	147
	Domestic cat	B	2♂	CST	14.68 **(14.68)**	192
	Domestic cat	C	2♀	Howletts	25.8 **(25.8)**	166
	Domestic cat	D	2♂	Howletts	61.83 **(37.59)**	81
	Domestic cat	E	2♀, 1♂	Riber Castle	26.0 **(26)**	57
F.s.ornata	Domestic cat	A	2♀	Port Lympne	105.43 **(79.03)**	60
	Domestic cat	B	3♀	Port Lympne	112.86 **(58.96)**	58
	Domestic cat	C	1♀, 1♂	Howletts	27.5 **(19.33)**	17
O.geoffroyi	Ocelot	A	1♀, 1♂	CST	18.5 **(18.5)**	129
	Ocelot	B	2♀,1♂	CST	14.02 **(14.02)**	190
	Ocelot	C	1♀, 1♂	CST	20.82 **(20.82)**	250
	Ocelot	D	2♀,1♂	CST	15.58 **(13.55)**	163
	Ocelot	E	2♀	Chester	52.75 **(45.72)**	101
	Ocelot	F	1♀, 1♂	Chester	71.5 **(50.27)**	114
C.caracal	*Panthera*	A	2♂	CST	21.2 **(21.2)**	107
	Panthera	B	3♀	CST	12.25 **(12.25)**	70
	Panthera	C	2♀	CST	11.25 **(11.25)**	111
	Panthera	D	1♀, 1♂	Marwell	22.42 **(22.42)**	50
	Panthera	E	1♀, 1♂	Marwell	18.75 **(18.75)**	101
	Panthera	F	1♀, 1♂	Chester	23.55 **(16.07)**	68

A total of 696.33 hours was spent observing the cats in total (see *Table 3.1* for breakdown). This includes both video and direct observation. The total number of interactions observed during this period were as follows: *F.chaus* (643), *O.geoffroyi* (947), *C.caracal* (507), *F.s.ornata*, (135).

3.3 RESULTS

3.3.1 Diagrammatic representation of temporal behavioural links in each species

The aim of this section was to investigate temporal associations between behaviours (*i.e.* which behaviours are likely to occur together in time?) in each species. Analysis was based on frequency matrices which contained values of: *The number of times each behaviour occurred in the same sequence as every other behaviour*, where a 'sequence' implies a string of behaviours used by the same cat in the same interaction. (I refer to these as 'sequence-linked matrices'; see *Chapter 2, Section 2.4.4*).

Previous studies investigating temporal links between behaviours have traditionally used the frequency of *transitions* from one behaviour to another as the raw data, based on a First/Second Order Markov Chain. However, these models assume that the probability of a given behavioural act depends only on the one/two behavioural acts which have immediately preceeded it (Fagen & Young, 1978). In practise it is more likely to depend on all the behaviours occurring within the sequence, particularly in the higher organisms such as mammals, where the order of behavioural elements within a sequence is very much interchangeable. I have therefore chosen to use a method which uses sequence links between behaviours rather than transitional links.

The word 'link' is used throughout this section to mean a temporal association between two behaviours. *e.g.* One behaviour is significantly likely to occur in the same behavioural sequence as a second behaviour.

3.3.1.1 Statistical techniques

Brown (1993), in her work on the domestic cat, used the temporal positioning of behaviours with one another, in order to classify them objectively, assuming temporal linkage to suggest either a motivational or functional linkage (this assumption is discussed further in *Section 3.4.1*). She used cluster analysis as a statistical method of doing this. However, this method should only be employed on hierarchical data (Morgan *et al*, 1974). Behavioural patterns are extremely unlikely to be hierarchical, particularly amongst mammals, and therefore the clusters produced are likely to be somewhat artificial; they imply cleaner divisions between behaviour types than is really the case.

Thus, in an attempt to compare the domestic cat with its wild cat counterparts, I have re-analysed Brown's (1993) data, using a method (chi-squared residuals; see *Chapter 2, Section 2.4.4*) which does not give clean clusters or categories of behaviours, but instead gives a significance value for each possible pair of behaviours, implying how likely two behaviours are to occur together. The result is more chaotic than the neat clusters produced by cluster analysis, but I would argue that it is also more representative. As Cormack, (1971), states, "when the data have not been forced into clusters, the observer can assess better whether clusters exist".

The statistical method used is based on the chi-squared test, and uses adjusted residuals produced as a result of this test as a basis for significance values (for details see *Chapter 2, Section 2.4.4*). This method is not perfect, but other methods attempted appeared to have similar or different problems. It was therefore a matter of choosing arbitrarily between them. The main problem was pseudoreplication, due to the fact that the data was pooled from different animals. However, this would have been a problem in any of the analyses available (*i.e.* cluster analysis, multi-dimensional scaling, chi-squared residuals). As it would not have been possible to collect testable quantites of independent data of this type (see *Section 2.4.4* for explanation), it was not possible to avoid pseudoreplicating. Fagen & Young (1978) therefore suggested that this type of analysis is best used to **describe** behaviour, rather than to **test hypotheses** about behaviour; I have therefore used it only to serve the function of describing the behaviour of each species.

Multi-dimensional scaling was attempted but the linkage patterns for this data are so complex that it was not possible to produce a viable solution (*i.e.* with a Kruskal's 'Stress Formula 1' of <0.1, as suggested by Kruskal & Wish, 1978, in Manly, 1995)), even in 5 dimensions. Cluster analysis was not used for the reasons described above. Thus in the absence of a perfect statistical test I used chi-squared residuals (See *Section 2.4.4*) to give significance results for whether a pair of behaviours is significantly likely to occur in the same sequence together. Diagrams demonstrating the results are drawn in 2D (*Figs. 3.1-3.5*). These diagrams give a symbolic representation of the temporal patterns within the ethogram of each species.

3.3.1.2 Methodological notes on statistical techniques:

1. The chi-squared test acts on frequency data, and therefore the probability of there being a significant association between two behaviours increases as the total frequency of interactions observed increases. This is important because I am attempting to compare various different matrices (*i.e.* a different matrix for each species), with very different total interaction values. *e.g.* Total interactions: *F.s.ornata* = 135, *C.caracal* = 507, *F.chaus*, = 643, *O.geoffroyi* = 947, *F.s.catus* = 2044. Thus the number of significant links in *F.s.ornata* (*Fig. 3.3*) is far fewer than in any of the other species. This does not necessarily imply that behaviours in *F.s.ornata* are less linked to one another than in the other species, but that, given the low number of observed interactions, it was only possible to establish a few significant links. The number of interactions observed in the

domestic cat was twice as large as any of the other species (n= 2044). Therefore the number of significant links which could be identified in the domestic cat was higher than in any other species. This made it difficult to compare to the other species. The frequencies in the domestic cat matrix were therefore all corrected to a lower level of interaction (to the same level of interaction as *O. geoffroyi*, n=947), by dividing all cells in the matrix by 947/2044. It must be stressed that the matrix pattern was not changed in any way by doing this.

2. Certain behaviours were found to be significantly linked to many behaviours from virtually all categories. This indicates that these behaviours are unlikely to have a function in a particular behavioural context. I termed these 'neutral behaviours'. They include:

Approach (without Tail Up)	Tail Curved
Move Away (without Tail Up)	Tail Down
Walk Past (without Tail Up)	

Three of these behaviours are locomotory behaviours; it is therefore not surprising that these should be found to be occurring in a neutral capacity (*i.e.* in no specific behavioural context). The other two behaviours are tail positions. In *Chapter 5* these two tail positions (amongst others) are investigated to see which other behaviours they occur simultaneously with. *Chapter 5* finds that they tend to occur simultaneously with locomotory behaviours, rather than with behaviours of any specific context or function (see *Table 5.1*, & *Section 5.4*). This suggests that they may be acting to improve balance, or may simply be the most comfortable holding positions when locomoting. I therefore feel that it is correct to exclude these 'neutral' locomotory behaviours from the analysis.

3. The majority of species, with the exception of *O.geoffroyi*, exhibited very little sexual behaviour. For comparison purposes, I have therefore included an extra diagram of behavioural links for *O.geoffroyi*, analysed only from interactions which did not contain any copulatory behaviours (*Fig. 3.5b*). Interactions that included any of the following behaviours were excluded: Mount, Lordosis, Copulation, and Yowl. The comparison of *Figs. 3.5a* and *3.5b* demonstrates that this actually makes very little difference to the positioning of the behaviours in the remaining categories; *e.g.* Bite, Pounce and Crouch are associated with the *Aggressive* category in both cases, whether or not the copulatory interactions were included.

3.3.1.3 Description of categories

The results from the chi-squared residual analysis are diagrammatically shown in *Figs. 3.1 to 3.5* (raw data is given in matrices in *Appendix IV*). The diagrams illustrate all the links between behaviours which are significantly likely to occur at $p<0.05$. These diagrams *(Figs. 3.1 to 3.5)* show that the behaviours do not always fall into neat clusters. Many behaviours are ambiguous as to the group which they may belong to[2], though others fall more obviously into specific categories. As it is useful for descriptive purposes to be able to classify behaviours into groups, I have attempted to do this subjectively (see *Table 3.2*). In order that the more ambiguous behaviours are not forced into categories which they may only partially belong to, behaviours may be classified into more than one group; it is hoped that this reflects the true complexity of the behavioural links involved. As a general guide, behaviours were included in categories if they were highly significantly attached (at least $p<0.01$) to at least one behaviour which was highly significantly attached (at least $p<0.01$) to at least two behaviours of that category. However, sub-categories were more subjective. The categories chosen are not intended to represent a complete behavioural classification system for that species, but instead to summarize what I found in the groups and species that were observed.

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[2] This indicates that my earlier assumption that this type of data was non-hierarchical, and therefore unsuited to a cluster analysis, was therefore correct.

Figure 3.1 **<u>Significant behavioural links: *Felis silvestris catus* (The domestic cat).</u>** Data reanalysed from Brown (1993). Values were corrected to a lower level of interaction (see *Section 3.3.1.2*). Behaviours that were observed but which occured in <10 interactions and which were therefore not included in the diagram are: Arch back, Growl, Mount, Fight. Behaviours that occured but which were not linked to any other behaviour: Tail Jerk. Behaviours which may have been linked to other behaviours, but which were not recorded in this species (study carried out at different time and by different observer): Back Off, Self-Groom, Spray, Tail Half-Up, Tail Under.

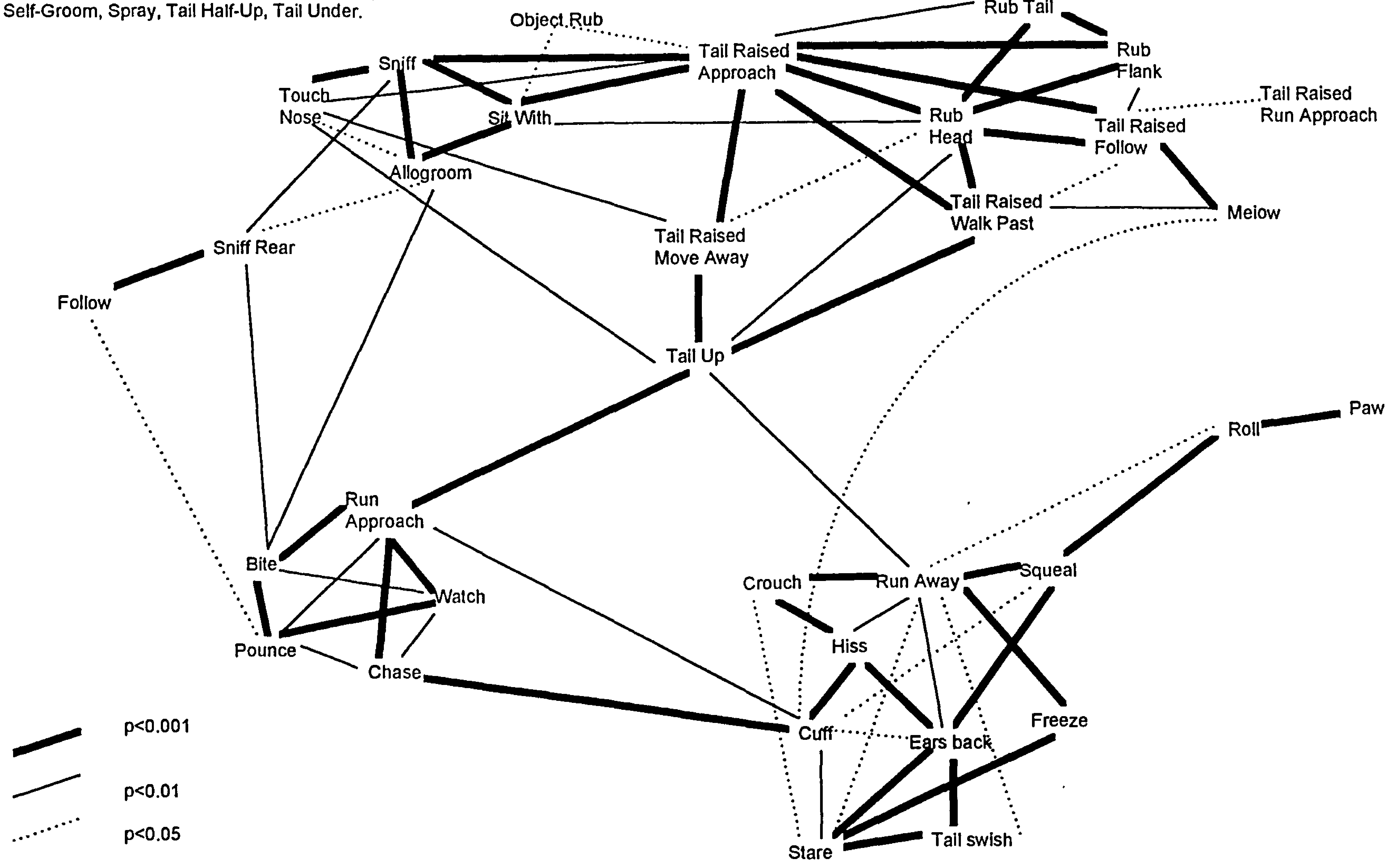


Figure 3.2 **Significant behavioural links: *Felis chaus.***
Behaviours that were observed but which occured in <10 interactions and which were therefore not included in the diagram are:Tail Half-up, Rub flank, Tail Jerk, Chase, Mount, Ow, Fight.
Behaviours that occurred but which were not linked to any other behaviour: None

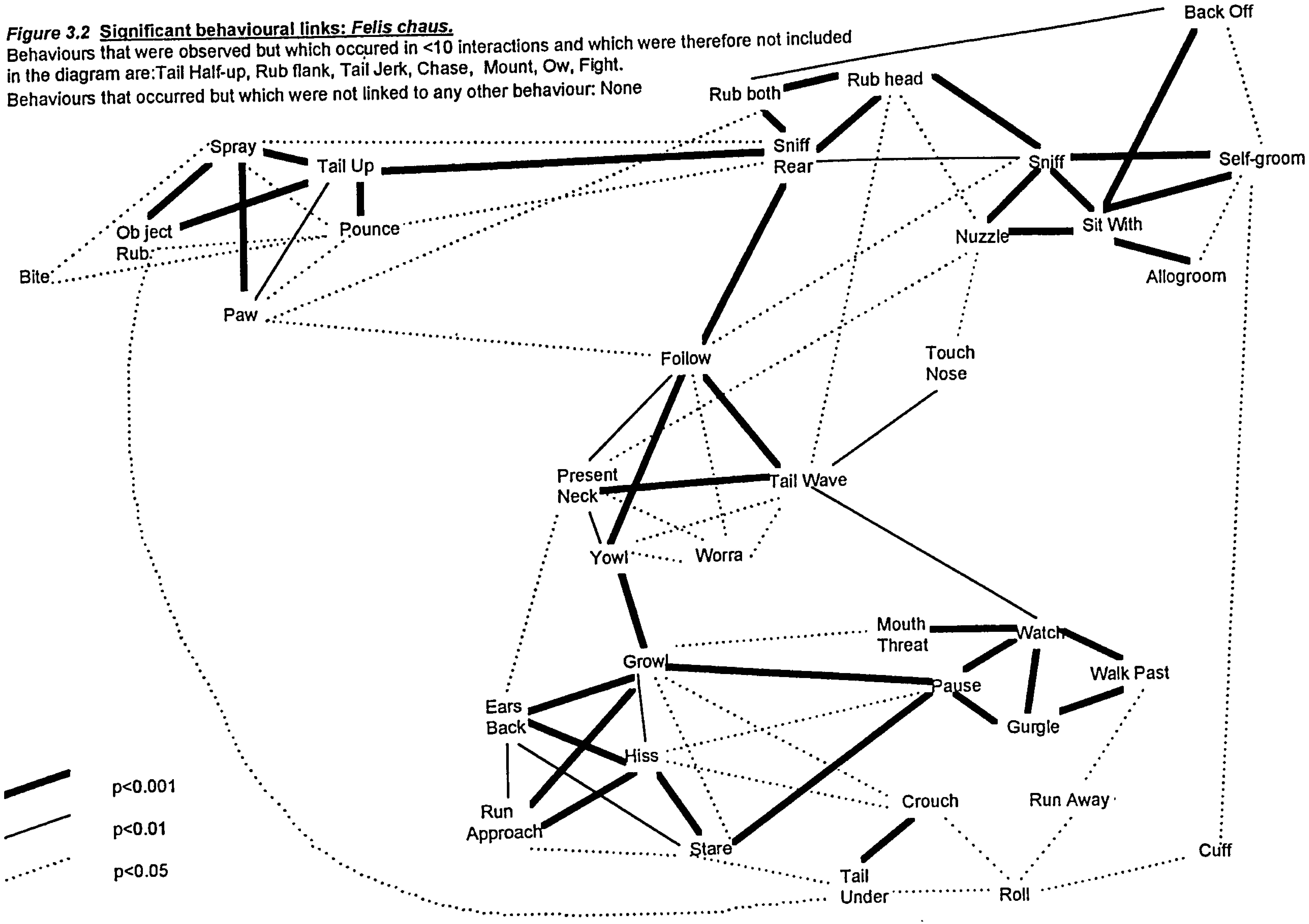


Figure 3.3 **Significant behavioural links: *Felis silvestris ornata.*** Behaviours which were observed but which occured in <10 interactions which were therefore not included in the diagram are Tail Half-Up, Melow, Tail Jerk, Tail Quiver, Pounce, Paw, Ow, Mouth threat, Krrr.
Behaviours that occurred but which were not linked to any other behaviour: None

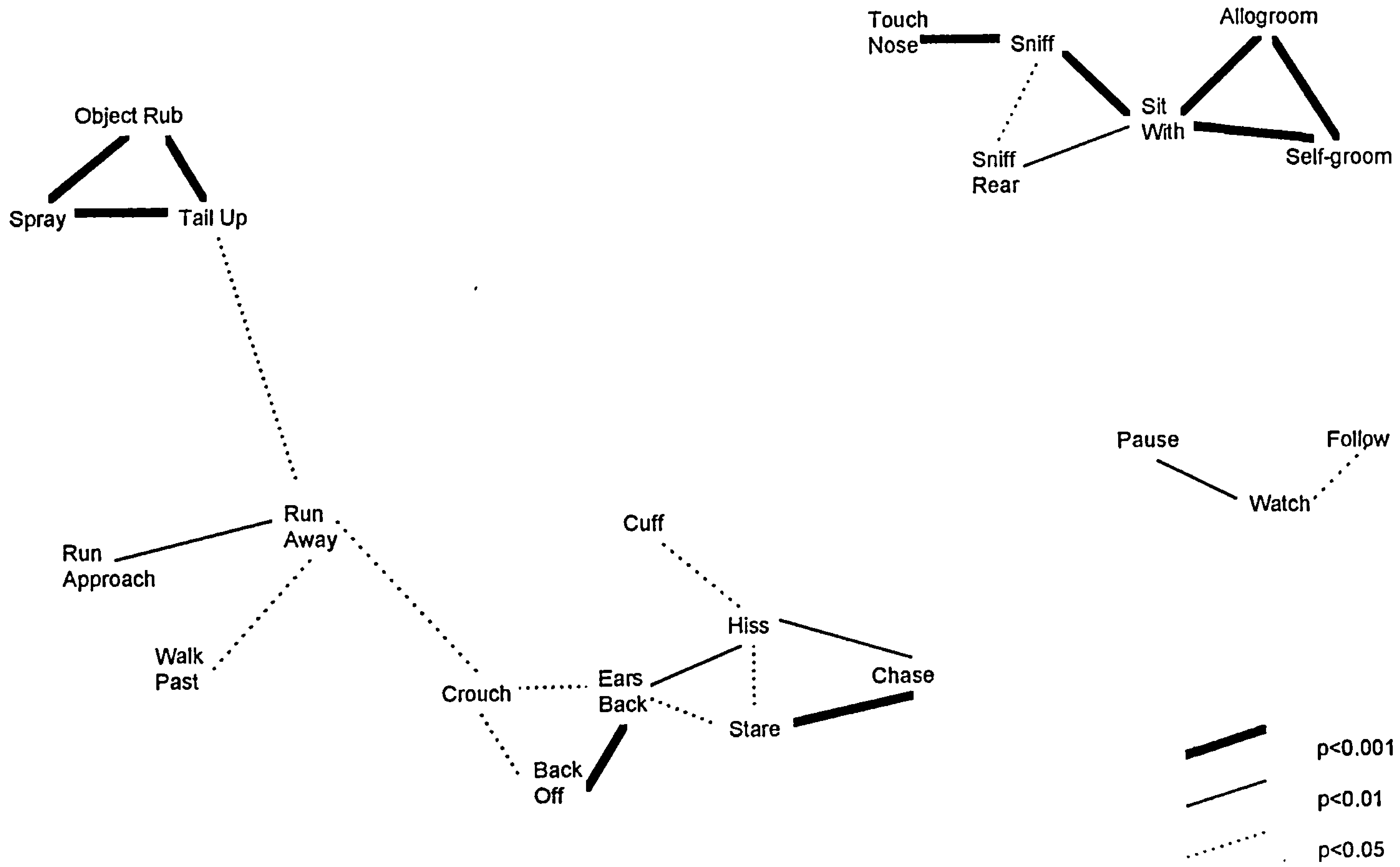


Figure 3.4 **Significant behavioural links: *Caracal caracal.*** Behaviours that were observed but which occured in <10 interactions, and which are therefore not included in the diagram are: Jostle Play, Meiow, Fight, Krrr, Tail Half-Up, Mount.
Behaviours that occurred but which were not linked to any other behaviour: Tail Under.

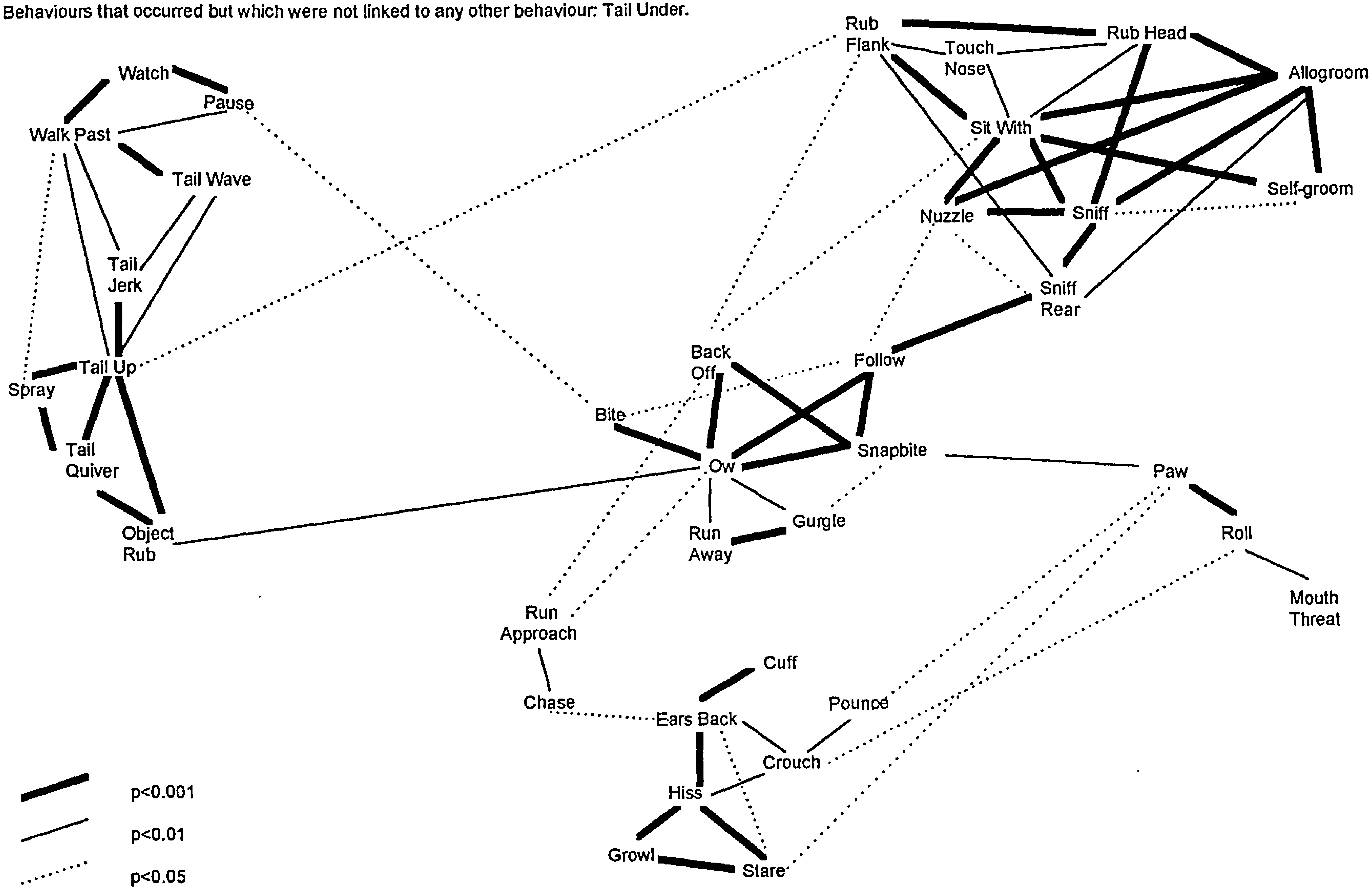
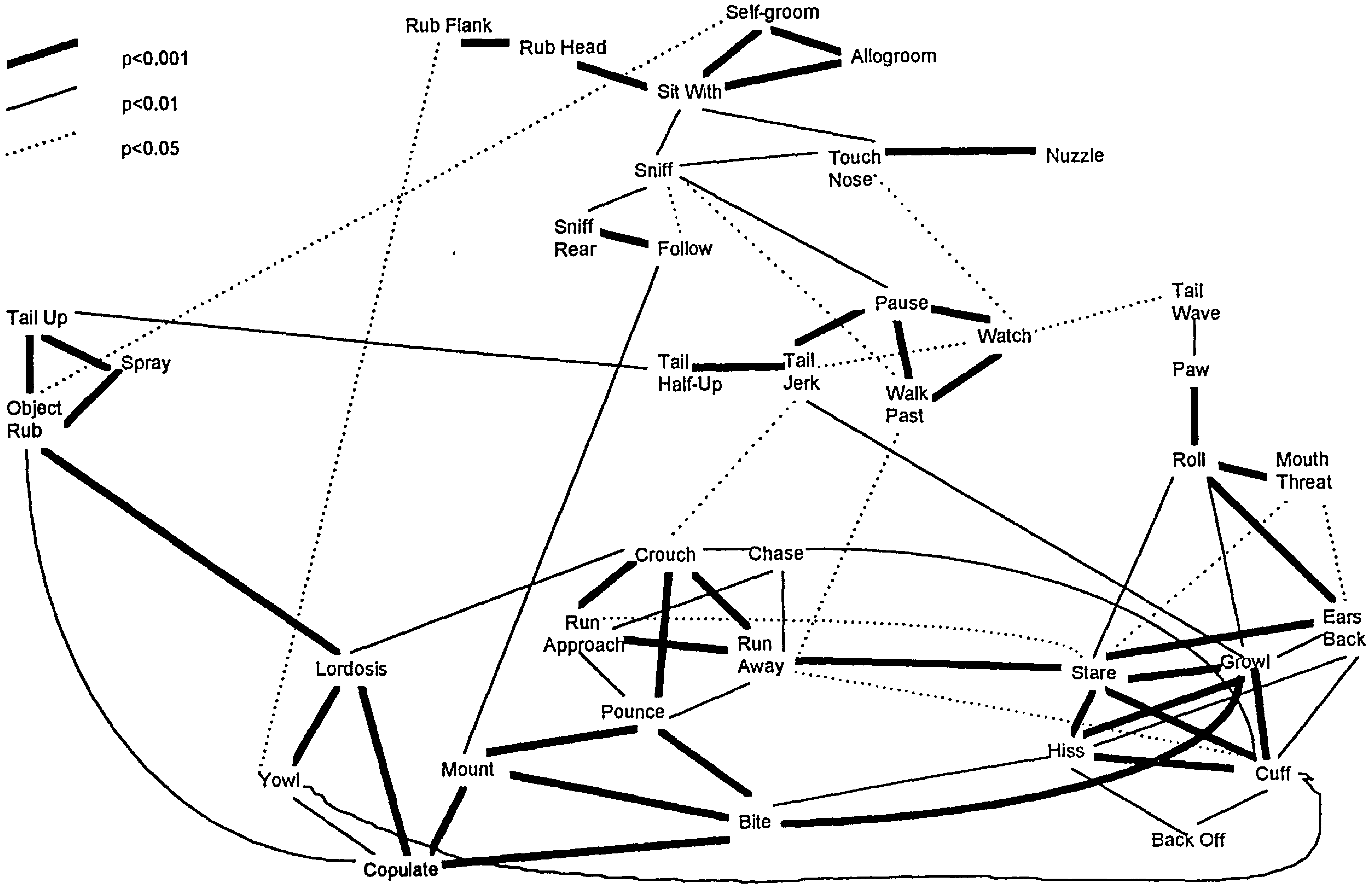


Figure 3.5a **Significant behavioural links: *Oncifelis geoffroyi.*** Behaviours that were observed but which occured in <10 interactions and which were therefore no included in the diagram are: Tail Under, Rub Tail, Jostle Play, Meiow, Tail Quiver, Arch back, Gurgle, Fight, Ow, Snapbite, Tail Curved-Up, Beep.
Behaviours that occured but which were not linked to any other behaviour: Rub both.



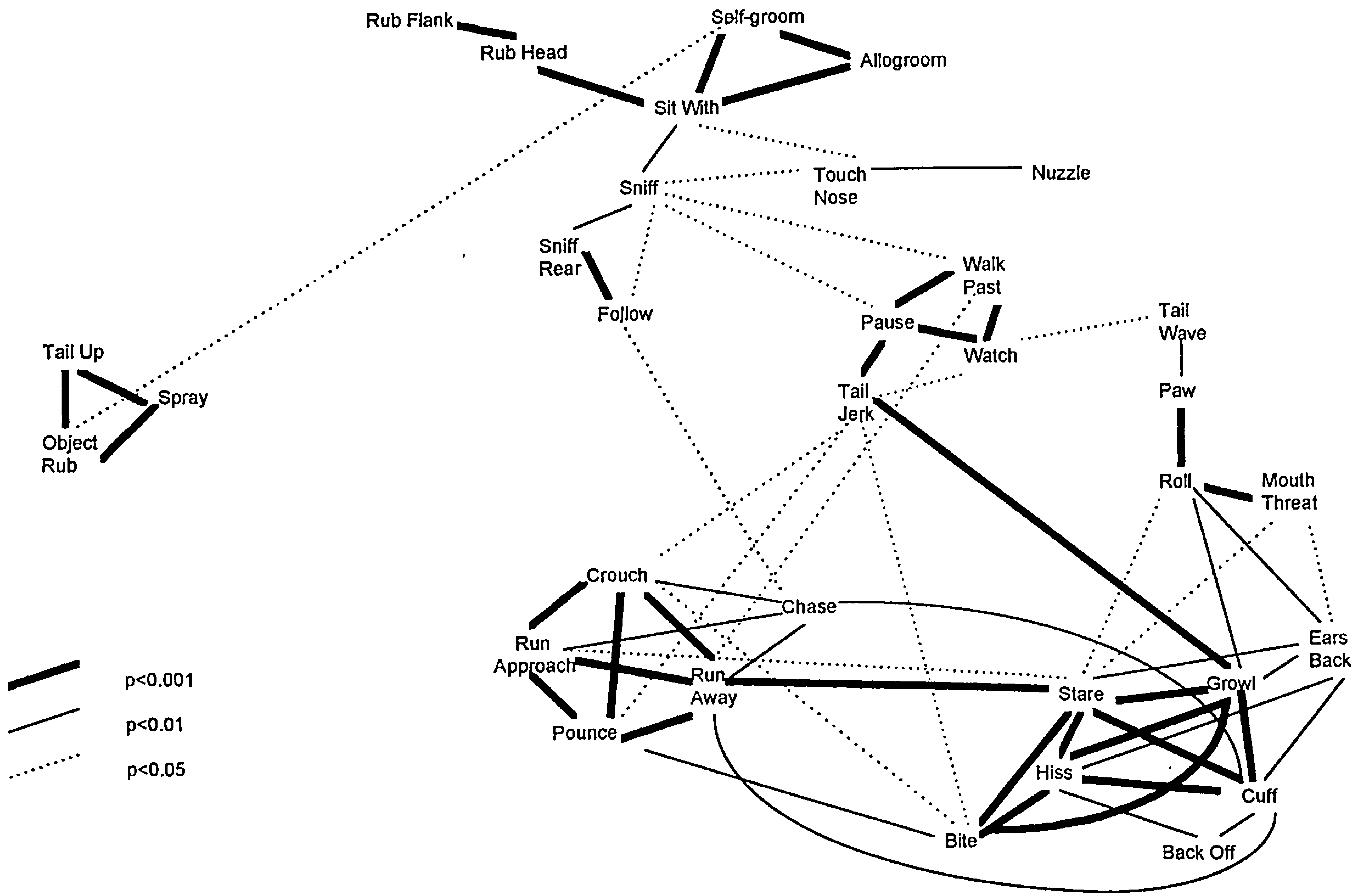


Figure 3.5b Significant behavioural links: *Oncifelis geoffroyi*, excluding copulatory interactions (*i.e.* interactions which contained any one or more of: Copulate, Mount, Lordosis, & Yowl). Behaviours that were observed but which occurred in <10 interactions and which were therefore not included in the diagram are: Tail Under, Rub tail, Jostle Play, Meiow, Tail Quiver, Arch back, Gurgle, Fight, Ow, Snapbite. Behaviours that occured but which were not linked to any other behaviour: Rub both.

Table 3.2* Classification system for the behaviours in each species, based on temporal groupings found in *Figs. 3.1- 3.5. Behaviours may be found in more than one category in cases where there is overlap. Some behaviours were not categorized at all if they did not belong strongly enough to any one category. Behaviours that are found in more than one group are in bold. Sub-categories are indicated by numbers. ††† Indicates that behaviour was not recorded in that species. †† Indicates that behaviour was not recorded in sufficient numbers to be included (*i.e.* in <10 interactions). Behaviours in parentheses are only weakly linked with that category. A **'TU' prefix** implies that the behaviour occurs with tail upright: *e.g.* TU Approach= Tail Up Approach. Sub-categories have only been given titles where they can be used with constancy across several species.‡ This sub-category (in *F. chaus*) is repeated in two categories (*Investigative* and *Aggressive*), because it did not fall clearly into either.

Category	*F. s. catus*	*F. s. ornata*	*F. chaus*	*O. geoffroyi*	*C. caracal.*
Affiliative	*(1) Rub sub-category* Rub Head Rub Tail Rub Flank **TU Approach** TU Follow **(TU Move Away)** TU Walk Past Tail Up Meiow *(2) Groom sub-category* Allogroom **Sniff** Touch Nose **Sniff Rear** Sit With **TU Approach** **(TU Move Away)**	*(1) Groom sub-category* Allogroom Selfgroom **Sit With** *(2)Touch Nose sub-category* Touch Nose Sniff Sniff Rear **Sit With**	*(1) Rub sub-category* **Rub Head** Rub Both **Sniff Rear** **(Sniff)** *(2) Groom sub-category* Sit With **Sniff** Nuzzle Allogroom Selfgroom Back Off **(Rub Head)**	*(1) Rub sub-category* Rub Head Rub Flank Rub Tail **Sit With** *(2) Groom sub-category* **Sit With** Allogroom Selfgroom *(3) Touch Nose sub-category* Touch Nose **Sit With** Nuzzle **Sniff**	Rub Head Rub Flank Touch Nose **Sit With** Sniff Nuzzle Allogroom Selfgroom **Sniff Rear**
Investigatory	Follow **Sniff Rear** **(Sniff)** (Bite)	Follow Pause Watch	*(1)* Follow **Sniff Rear** (Tail Wave) (Present Neck) (Yowl) (Worra) *(2) Investigate/ Aggressive* ‡ Watch Walk Past **Pause** Gurgle Mouth Threat (Tail Wave)	*(1)* Follow Sniff Rear **Sniff** **(Pause)** *(2)* Watch **Pause** Walk Past (Tail Wave) Tail Jerk Tail Half-Up **(Sniff)**	*(1)* **Follow** **Sniff Rear** **Sniff** *(2)* Watch Pause **Walk past** **Tail Wave** **Tail Jerk** **(Tail Up)**

Category	*F. s. catus*	*F. s. ornata*	*F. chaus*	*O. geoffroyi*	*C. caracal.*
Spray	†††	Tail Up Object Rub Spray	Tail Up Object Rub Spray Pounce Paw (Bite) **(Sniff Rear)**	Tail Up Object Rub Spray	Tail Up Object Rub Spray Tail Quiver **Tail Jerk** **Tail Wave** **Walk Past**
Copulatory	††	††	††	Copulation Mount Yowl Lordosis Bite **Pounce** **(Object Rub)** **(Follow)**	††
Agonistic	*(1) Aggressive* Run Approach Chase Bite Watch Pounce Cuff *(2) Defensive* Stare Cuff Hiss Ears Back Crouch **Run Away** **Squeal** Freeze Tail Swish *(3)Play/ Aggressive* Roll Paw **Squeal** **(Run Away)**	*(1) Aggressive* Run Approach Run Away **Crouch** Walk Past *(2) Defensive* Stare Cuff Hiss Ears Back Back Off **Crouch** Chase	*(1) Aggressive* Run Approach Stare Growl Ears Back Hiss **Pause** *(2) Defensive* Crouch Tail Under Roll Cuff **Run Away** **(Walk Past)** *(3)Investigate/ Aggressive* ‡ Gurgle Mouth Threat Watch **Walk Past** **Pause** **(Run Away)** (Tail Wave) **(Growl)** **(Stare)**	*(1) Aggressive* Run Approach Run Away Chase **Pounce** **Crouch** **Stare** *(2) Defensive* **Stare** Cuff Hiss **Ears Back** Back Off (Tail Jerk) **Growl** *(3)Play/ Aggressive* Roll Paw Mouth Threat **Ears Back** **Growl** **(Stare)** Tail Wave	*(1) Aggressive* **Run Approach** Run Away Snapbite Back Off Bite Ow Gurgle **Follow** **Chase** *(2) Defensive* Stare Cuff Hiss Ears Back Growl Crouch **Chase** Pounce **Run Approach** *(3)Play/ Aggressive* Roll Paw Mouth Threat Snapbite

Table 3.2 demonstrates more clearly the differences between species than the diagrams (*Figs. 3.1-3.5*), though in doing so, some of the more detailed information is lost. The important aspects of the comparisons between species in each category are summarized below:

3.3.1.3.1 Affiliative category

The *Affiliative* category contains generally the same behaviours across all the species; with the core behaviours in all species being Social Rub, Touch Nose, Sit With, Sniff and Allogroom. In three out of the four species which do exhibit social rubbing (*F.s.ornata* did not), Social Rub and Allogroom are classed into two distinct sub-categories, which I named the *Rub* sub-category, and the *Groom* sub-category. *C.caracal* is the only species in which these two behaviours are found in the same category.

Touch Nose was found in a separate category again (in two out of the three species in which it occurred, *i.e. O.geoffroyi* & *F.s.ornata*). This category did not contain Social Rubs or Allogrooms, but does contain Sniff and Sit With. However, in *F.s.ornata*, this sub-division could be due to the few number of significant links present in total (See *Section 3.3.1.2* (1), above); this may lead to a false sub-division being shown up).

In *F.s.catus*, the *Rub* and *Groom* sub-categories contain additional behaviours which do not exist in any of the wild species: the Tail Up behaviours. These include: Tail Up Approach, Tail Up Walk Past, Tail Up Move Away, Tail Up Follow, and simply Tail Up. These two behavioural categories *(Rub* and *Groom)* were also found by Brown (1993) in her cluster analysis (although she termed them the *Affiliative* cluster, and the *Approach/Sit* cluster, respectively). Her cluster analysis classed the Tail Up behaviours as members of solely the *Rub* category. However, I found that Tail Up Approach and Tail Up Move Away were actually members of both the *Rub* and *Groom* categories. This difference is likely to be a result of the drawback of the cluster analysis which requires behaviours to be in either one or the other.

Other brief points to make are as follows:

(i) The behaviour 'Nuzzle' was found only in *F.chaus, O.geoffroyi*, and *C.caracal*.
(ii) Meiow did not occur substantially in any species, although it occurred marginally more in the domestic cat than in any other. Average no. of meiows per interaction: *F.s.catus* = 0.014), *O.geoffroyi* = 0.007, *F.s.ornata*, = 0.007, *C.caracal* = 0.002, *F. chaus*, = 0).

3.3.1.3.2 Investigatory behaviour

This category was variable, though in most species it consisted of Follow, Sniff Rear, Watch and Pause; and of Tail Jerks and Tail Waves in the species where these were observed. The sub-categories that these were placed in were variable. *F.s.ornata* was the only species not to have Sniff Rear in its *Investigatory* category: It was placed in the *Affiliative* category only. In the majority of the other species Sniff Rear was placed in both *Affiliative* and *Investigatory* categories. This could be because so few behaviours were observed in *F.s.ornata* that there were very few significant links. It is therefore difficult to say whether this is a true split or whether it is simply an artefact of the few number of total behaviours observed.

The presence of Tail Jerk and Tail Wave in this category is interesting. This will be discussed in detail in the discussion, in the light of other work on tail movements in cats.

3.3.1.3.3 Spray behaviour

The pattern of spraying in the four undomesticated felids is very standardized, with all species putting their tail up whilst spraying, and Object Rub also being closely linked. The comparison between the domestic cat and the undomesticated cats for this behaviour is made difficult by the fact that Brown (1993) never observed spraying[3] . However, in the domestic cat, it is generally accepted that the tail is raised, and usually quivered during spraying (U.K. Cat Working Group, 1995, Bradshaw, 1992, Wemmer & Scow, 1977, Feldman, 1994a: For specific observational reports see Dards, 1979, Corbett, 1979). The

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[3] I only recorded spraying when it occurred as part of a social interaction, not when it occurred solitarily. Brown (1993)'s methods were the same; however, she never observed spraying to occur as part of a social interaction. Behaviours linked with spraying can therefore not be established from Brown's study.

occurrence of 'Tail Quiver' as part of spraying in domestic cats is interesting because I found this to occur in *C. caracal*, but not in any of the other species (*Figs.3.1-3.5*, *Table 3.2*). Wemmer & Scow (1977) also found the tail quiver absent in most of the small felids that they observed (genera as follows: *Felis, Otocolobus, Catopuma, Prionailurus, Leopardus*, and *Herpailurus*), with the exception of the domestic cat and *Lynx canadensis.*

The possible association of Object Rub with spraying in the domestic cat is less well documented. None of the reports above mention any temporal link between Object Rub and Spray in the domestic cat, but Macdonald (1987), reports that out of 79 sprays, a male cat object rubbed in 22.8 % of cases, and object rubbed in 41% of occasions when it both sprayed and sniffed. The percentage value is relatively low, but it does indicate that there is some association between these two behaviours. It therefore seems likely that the Object Rub/Spray association does exist in the domestic cat, as least to some extent, although it could not be documented in this study. Object Rub has also been reported as being associated with spraying in other species, (*Panthera leo* (Schaller, 1972), *Neofelis nebulosa* (Wemmer & Scow, 1977), *Panthera tigris* (Smith *et al*, 1989).

The connection between Tail Up and Spray is ubiquitous across the four undomesticated felids. Tail Up is generally acknowledged as an obligatory part of the definition of spraying in all cat species, (*e.g. Neofelis nebulosa,* (Wemmer & Scow, 1977), *Acinonyx jubatus*, (Eaton, 1970b). It is likely that Tail Up in in the spray situation is a facilitating movement, aiding the spray action.

3.3.1.3.4 Copulatory behaviour

The domestic cats were neutered, and very little copulatory behaviour was observed in three out of the four undomesticated species. It is therefore impossible to make any comparisons. *O.geoffroyi* was the only species to exhibit enough copulatory behaviour for analysis. The behaviours linked in the copulatory category are as expected for Felidae copulation; Mount, Lordosis, Copulation, Bite, Pounce, Crouch, Follow and Object Rub (see *Section 1.4.3*). Rolling was not connected to this category, despite it being recorded as part of the courtship/oestrous behaviour in other cat species (*Uncia uncia* (Freeman, 1977), *Acinonyx jubatus* (Foster, 1977), *F.s.catus* (Michael, 1961; see *Section 1.3.3*).

3.3.1.3.5 Agonistic behaviour

Though there is a large discrepancy in the groupings of the agonistic behaviours between species, there are some behaviours that always remain together, namely; Stare, Cuff, Hiss, Ears Back, and Growl (with the exception of *F.chaus*, where Cuff is in a separate category). These behaviours are generally utilised in a defensive role; for this reason I have named this the *Defensive* sub-category. There also seems to be a general vein running through all five species in a second sub-category. This generally contains the behaviours Run Approach, Chase, Run Away, though it is less well defined across the species than the *Defensive* sub-category. Generally it includes the behaviours which initiate aggression; thus I have named this the *Aggressive* sub-category. There is, however, some overlap between the *Aggressive* and *Defensive* sub-categories; in *F.chaus*, Run Approach belongs to the *Defensive* sub-category, whilst in all other species it belongs to the *Aggressive* sub-category.

3.3.1.3.6 A Note on Play

Play is a difficult behaviour to categorize because it generally includes many of the aggressive behaviours. It is therefore difficult to objectively separate play behaviour from aggression, though subjectively it appears intuitive (Barrett & Bateson, 1978). On a subjective note, social play was infrequent in all the wild cat species studied, but prolific in both the domestic cat groups studied, possibly as a result of their neutering. In the two groups of domestic cats which I observed as part of *Chapters 4 & 5*, I observed play to be, as recorded, no different from aggression, including, in particular, Run Approach, Chase, Tail Up, Roll, Paw, and Squeal, amongst others. Looking at *Fig 3.1*, and *Table 3.2*, I have classifed these behaviours mostly as *Aggressive*; however, I acknowledge that most, if not all, of the behaviours I have categorized as *Aggressive* may also be used during play.

3.3.2 Quantitative comparison of core behavioural links in each species

It is difficult to objectively evaluate the similarity of the behavioural linkage diagrams (*i.e. Figs. 3.1-3.5*), due to the uniqueness of each species' ethogram. This section thus attempts to quantitatively compare the temporal behavioural links in each species. This was done using Kendall's rowwise (K_r) matrix correlation test (de Vries *et al*, 1993, de Vries, 1993, Schnell *et al*, 1985; See *Chapter 2, Section 2.3.4*). This test calculates a correlation coefficient which indicates how similar two matrices are to one another. The matrices used were sequence-linked matrices (see *Section 2.4.4*), one for each species, as in the previous section (*3.3.1*). Kendall's rowwise correlation coefficient was calculated for each pair of matrices, where each matrix corresponded to one species.

3.3.2.1 Methodological notes on statistical techniques:

Core behaviours only were included in this analysis, in order that the matrices of two species would be the same size (*i.e.* contain the same number of behaviours). A core behaviour was defined as a non-locomotory behaviour that occurred in 4 out of the 5 possible species. A matrix was constructed for each species, containing values for *the number of times each core behaviour occurred in the same sequence as every other core behaviour* (*i.e.* a sequence-linked matrix, as used in the previous section (*3.3.1*), but containing fewer behaviours). Most of the core behaviours occurred in all the species, with the exception of Rub Head, Roll, Growl, and Bite, which did not occur in *F.s.ornata*. All the other core behaviours occurred in all five species. Matrices which were compared against the *F.s.ornata* matrix therefore did not include these five behaviours. In addition, behaviours that only had values in less than 4 rows of the matrix cannot be analysed, as it is impossible for these behaviours to attain significance (Hemelrijk & Ek, 1991, Hemelrijk, 1990). This was the case for Pounce, Paw, and Touch Nose in *F.s.ornata*, and Growl in *F.s.catus*. I did not include Rub Flank as well as Rub Head because the two are so closely associated in all the species (see *Figs 3.1-3.5*).

Table 3.3 **Core behaviours:** *i.e.* Behaviours which occurred in at least 4 out of 5 species.
†= Behaviour occurred in less than 4 rows of the matrix in *F.s.catus*, and therefore was not included. ††= Behaviour occurred in less than 4 rows of the matrix in *F.s.ornata*, and therefore was not included.
†††=Behaviour did not occur at all in *F.s.ornata*. All other behaviours occurred in 5 out of 5 species, with values in at least 4 rows of each species matrix.

Tail Up
Rub Head †††
Sniff
Sniff Rear
Cuff
Ears back
Stare
Pounce ††
Crouch
Roll †††
Allogroom
Touch Nose ††
Sit With
Object Rub
Hiss
Growl ††† & †
Chase
Bite †††
Watch
Paw ††

The rowwise matrix correlation coefficient is based on a weighted sum of the correlations between all pairs of corresponding rows of the two matrices (de Vries, 1993). Before correlating the matrices, it was necessary to fit homogenous margins to each matrix (Iterative Proportional Fitting (Freeman *et al*, 1992, Bishop et al, 1975)), to control for the differences among the row and column totals (de Vries, *pers. comm.*, see *Section 2.4.3*).

The statistical significance of the correlation coefficient was calculated by using Mantel's (1967) permutation procedure which respects the interdependencies of the values within rows and columns of these matrices. The Matman programme (de Vries *et al*, 1993) was used to perform these permutations.

3.3.2.2 Results of overall correlation of matrices

Kendall's rowwise correlation coefficient was calculated for each pair of matrices, where each matrix corresponded to one species. *Table 3.4* gives the normalised coefficient (τ_{rw}) for each possible species pair.

Table 3.4 Kendall's (rowwise) correlation coefficient, (τ_{rw}), for each pair of species. Values quoted are the normalised correlation coefficient (τ_{rw}), which may range between -1 and 1, rather than the raw index (K_r), which may range between any minimum and maximum value, depending on the size of the matrix (See *Chapter 2, Section 2.4.3* for details)
$P_{r/l}$ = one tailed probability value in the right or left tail of the permutation distribution.
The probability level is based on 10,000 permutations.

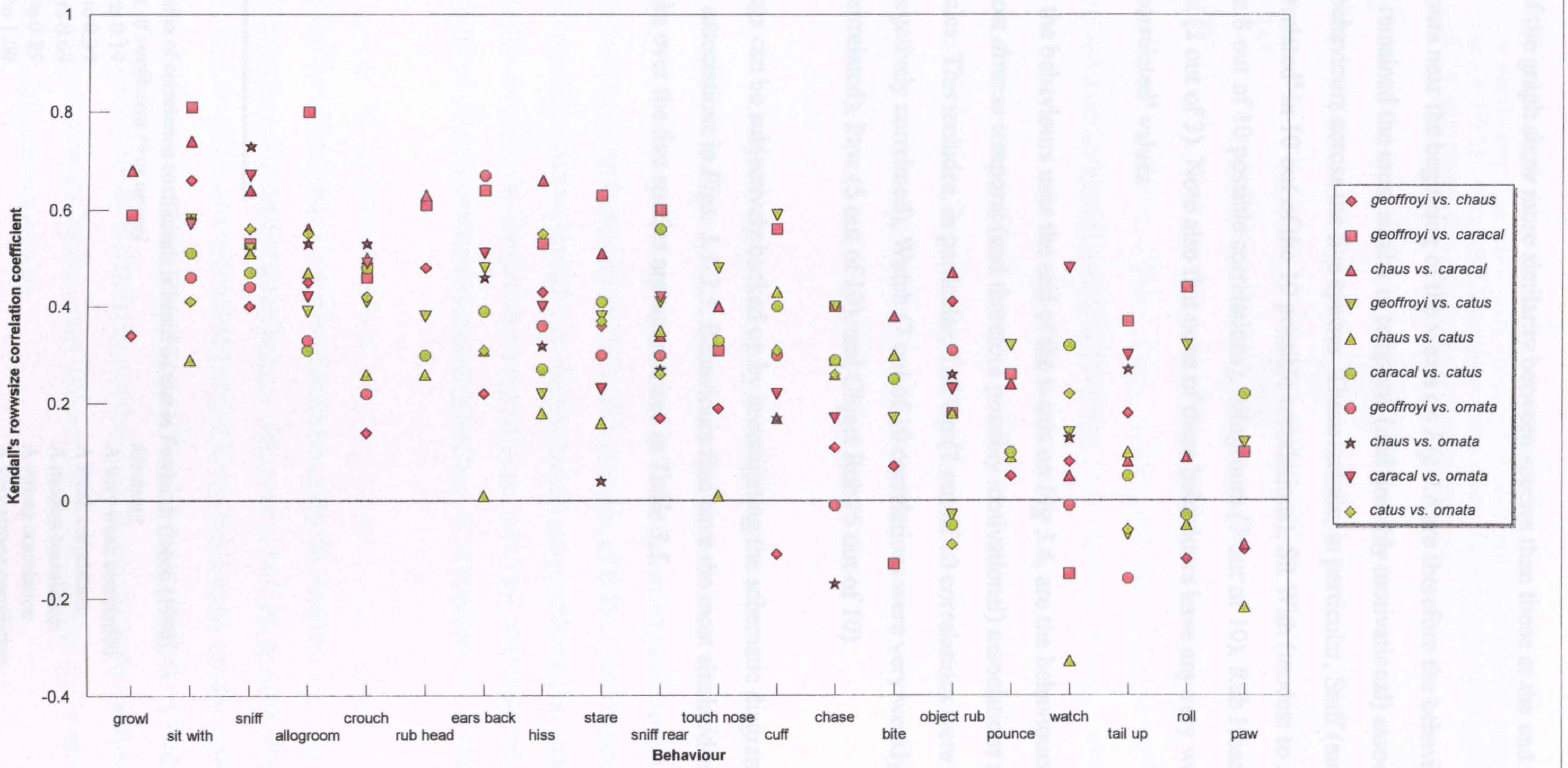
	C. caracal	*O.geoffroyi*	*F.chaus*	*F.s.ornata*	*F.s.catus*
C.caracal		τ_{rw}=0.425 P_r= 0.0001	τ_{rw}=0.380 P_r= 0.0001	τ_{rw}=0.367 P_r= 0.0001	τ_{rw}=0.292 P_r= 0.0001
O.geoffroyi			τ_{rw}=0.231 P_r= 0.0001	τ_{rw}=0.247 P_r=0.0017	τ_{rw}=0.327 P_r= 0.0001
F.chaus				τ_{rw}=0.288 P_r= 0.0001	τ_{rw}=0.173 P_r= 0.0027
F.s.ornata					τ_{rw}=0.298 P_r= 0.0001
F.s.catus					

All pairs of matrix correlations were highly significant, implying that the core behaviour structure has changed little from species to species. One cannot attach too much importance to the *exact* significance levels for each comparison, because the number of behaviours that are included in the analysis affects the probability level, although the values always remain significant. For example, if Watch is not included in the core behaviour matrices, the probability levels do change, but remain significant. The same occurs if different behaviours are removed. Thus the important point from these statistics is the fact that all species comparisons are positively correlated to $p<0.05$, not the fact that, for example, *F.s. ornata* is less similar to *O.geoffroyi* than it is to *F.chaus*.

3.3.2.3 Rowwise correlation of specific behaviours

The advantage of a rowwise matrix correlation is that it allows the examination of the correlation coefficients for each separate row. Thus one can see which rows (or behaviours, in this instance), are more or less correlated than others. The graph in *Fig. 3.6* gives the rowwise correlation coefficients for each behaviour, and for each species comparison. Behaviours were placed in order of their medians; thus behaviours near the

Figure 3.6 Rowwise correlation coefficients for each behavior, and for each species comparison
Green points show domestic/undomesticated comparisons; Red points show undomesticated/undomesticated comparisons.



beginning of the graph show more similarity between species than those at the end.

The behaviours near the beginning of the x-axis on *Fig.3.6* are therefore the behaviours which have remained the most similar in temporal (and possibly motivational) association with other behaviours across the five species. These include, in particular, Sniff (modest to strongly correlated[4] in 10 out of the 10 possible correlations), Sit With (modest to strongly correlated in 8 out of 10 possible correlations), Allogroom (7 out of 10), Rub Head (3 out of 6), Growl (2 out of 3). Note also that none of these behaviours have any very weakly or negatively correlated[4] values.

In contrast, the behaviours near the end of the x-axis on *Fig 3.6*, are the behaviours which show the most *diverse* temporal (and therefore possibly motivational) associations across the five species. This includes, in particular, Tail Up (7 out of 10 correlations were very weakly or negatively correlated), Watch (7 out of 10 correlations were very weakly or negatively correlated), Paw (5 out of 10), and Object Rub (5 out of 10).

These findings can be subjectively backed up by investigating the schematic diagrams of behavioural associations in *Figs. 3.1-3.5*. Behaviours that have the most similar/dissimilar temporal links over the five species are summarised in *Table 3.5*.

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[4] This classification of correlation coefficients is based on that in Fowler & Cohen (1990).

i.e.	*Value of coefficient (+ve or -ve)*	*Meaning*
	0.00 to 0.19	A very weak correlation
	0.20 to 0.39	A weak correlation
	0.40 to 0.69	A modest correlation
	0.70 to 0.89	A strong correlation
	0.90 to 1.00	A very strong correlation

Table 3.5 Summary of *Fig.3.6*:
Similar behaviours were classed as behaviours which had at least half their values as modest to strong correlations (*i.e.* >0.39). **Dissimilar** behaviours were classed as having at least half their values under 0.19 (*i.e.* very weak), and at least 2 negative correlations.

Similar	Dissimilar
Growl	Tail Up
Sit With	Roll
Sniff	Paw
Allogroom	Object Rub
Rub Head	Watch
Crouch	
Ears back	
Hiss	

3.3.2.4 Domestic/Undomesticated species differences

Species specific differences are also demonstrated by *Fig 3.6*. Particularly interesting is the difference between the domestic cat and the undomesticated felids. Comparisons between the domestic cat and undomesticated felids are shown by the green points. The red points show the correlations between two species of undomesticated felids.

The behaviour of Object Rub shows a dichotomy in correlation coefficients, with three of the domestic cat comparisons showing a negative correlation, and the fourth being only very weakly positive[4], whereas the comparisons between the undomesticated species show much higher values (ranging from 0.18 to 0.47, with a median of 0.29). Tail Up also shows this dichotomous pattern, though to a slightly lesser extent, with the correlation coefficients of the domestic cat comparisons ranging from -0.07 to 0.10 (median of -0.005), and those of the undomesticated cats ranging from -0.16 (outlier) to 0.37 (median of 0.23).

The behaviour of Rub Head shows a similar distribution with the domestic cat comparisons having lower correlation coefficients (values of 0.38,0.29, & 0.30; all weak correlations), than the comparisons involving only the undomesticated species (values of 0.48, 0.61 & 0.63). However, all the correlations of Rub Head are relatively strong. This suggests that though the temporal distribution of Rub Head in the domestic cat is more dissimilar to the undomesticated species than the undomesticated species are to each other, there is still an overall general similarity.

In summary, the temporal distributions of these three behaviours in the domestic cat are different to those in the four undomesticated species, more so with Tail Up and Object Rub than with Rub Head. This can be explained by looking at the behavioural linkage diagrams in *Section 3.3.1* (*Figs. 3.1-3.5* & *Table 3.2*): In the **undomesticated** species, Tail Up is classed in the *Spray* category, along with Spray and Object Rub. In the **domestic** cat, however, it is classed in the *Affiliative* category. It is likely that this difference has caused the correlation coefficient dichotomy in all three aforementioned behaviours (Object Rub, Tail Up and Rub Head), due to the fact that Tail Up is significantly associated with Object Rub in the undomesticated species, and with Rub Head (and other social rubs) in the domestic species. This has the effect of causing a dichotomy in Rub Head, even though Rub Head itself exists in the same category in all four species which exhibited it.

3.3.3 Species comparison of the rates and percentages at which different types of interactions occur.

It is difficult to compare the rate at which behaviour types occurred across the species, because the groups varied so widely in composition of age, relatedness, and gender. These factors are likely to affect **the rate of behaviour** much more than they are likely to affect the **fundamental links between behaviours** (*i.e.*the links that have been described in the previous two sections, *3.3.1* & *3.3.2*). I have therefore included this current section in order to describe the social behaviour of the particular groups watched, and not because I wish to make overiding conclusions about particular species.

For the purposes of this section, interactions were divided into 3 types; *Affiliative, Aggressive* (based on the categories established in *Section 3.3.1*;see *Table 3.2*), and a more general category (*Neutral*) which includes all behaviours that were not classed as either *Affiliative* or *Aggressive* in *Table 3.2*. The classification of these is included in the legend of *Fig.3.7*. Interactions were not classed into the more detailed behavioural categories described in *Table 3.2*, because an interaction frequently involves behaviours from more than one behavioural category.

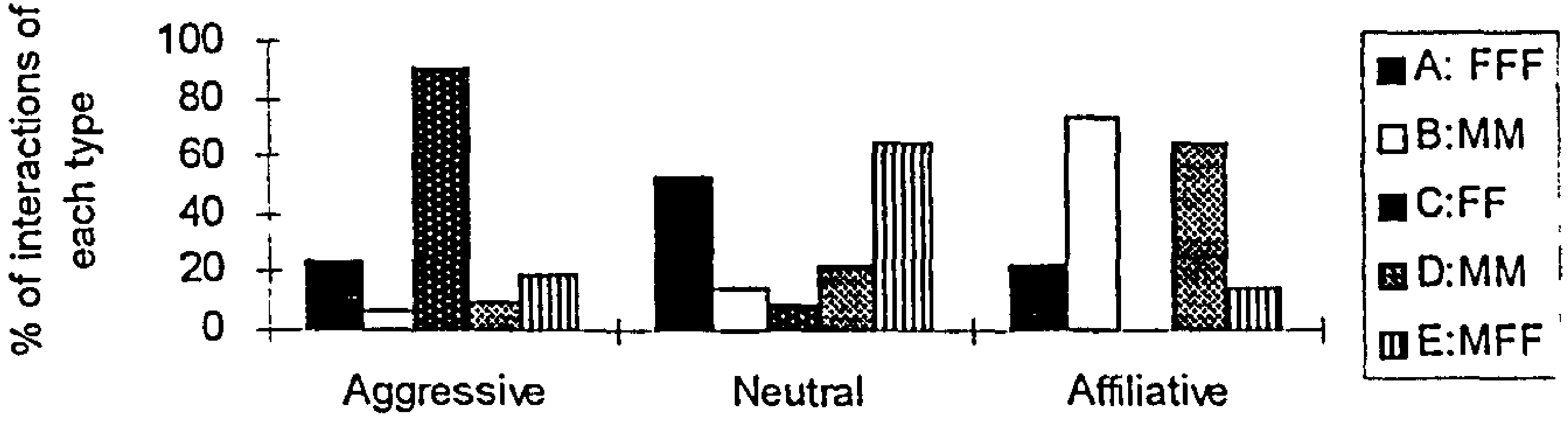
Fig 3.7 shows a graph for each species, giving the proportion of interactions of each type (*Aggressive, Neutral* and *Affiliative*) shown in each group of cats. The different groups of *O.geoffroyi* and *F.s.ornata* follow a consistent pattern for their species, with very little difference between groups. The mean values (±SD) for each species are given in *Fig 3.9*. *O.geoffroyi* shows much higher numbers of *Affiliative* interactions than it does *Aggressive*. *F.s.ornata* shows low numbers of both *Aggressive* and *Affiliative* interactions, and much higher levels of *Neutral* interactions. The three *F.s.catus* groups also follow vaguely consistent patterns, with all three groups showing highest numbers of *Affiliative* interactions. *F.chaus* and *C.caracal* show more variation between cat groups, so that a general pattern for the species cannot really be suggested.

Fig. 3.8 shows the **rates** of interactions of each type occurring per active hour, per dyad (See *Section 3.2*). These show broadly similar patterns to those exhibited by the proportion graphs (*Fig 3.9*). The rate of *Affiliative* interactions of *O.geoffroyi* is almost on a par to that of the domestic cat, with means of 2.02 ± 1.49 and 3.19 ± 1.62 per active hour, per dyad, respectively. Other species show lower rates of *Affiliative* interactions, particularly *C.caracal* (0.53 ± 0.51) and *F.s.ornata* (0.04 ± 0.02).

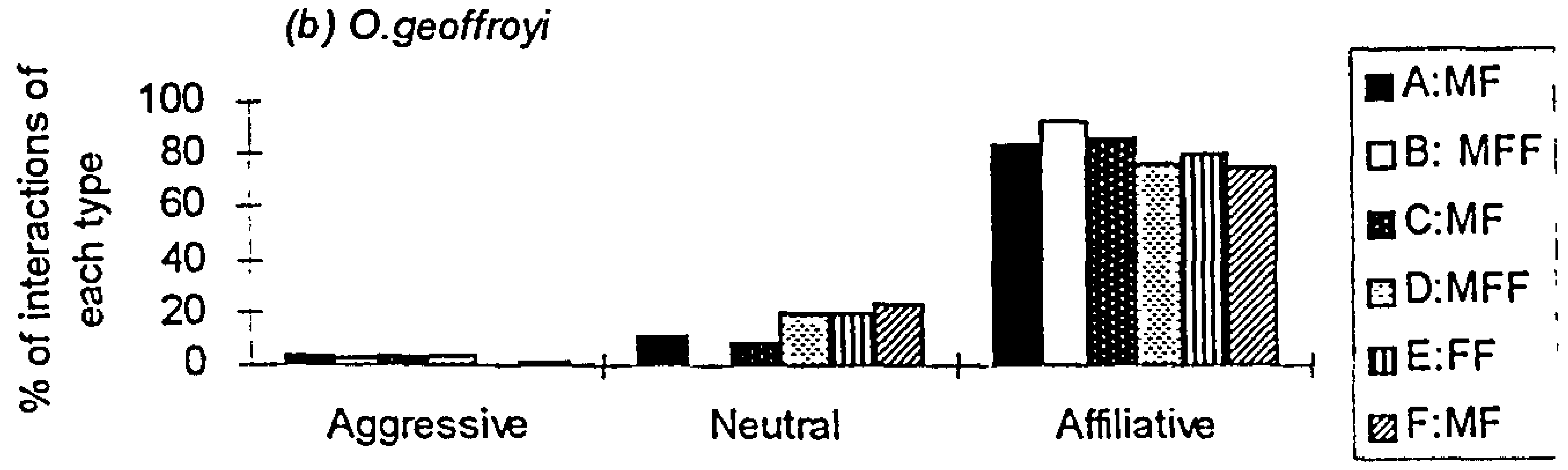
O. geoffroyi has the most similar proportions and rates of *Affiliative* interactions to the domestic cat. The domestic cat showed more *Affiliative* interactions in total, but *O.geoffroyi* showed proportionally more *Affiliative* interactions. *O.geoffroyi* also had the most similar temporal links to the domestic cat; it therefore seems to be the species showing the most similar social behaviour to the domestic cat, out of the four studied. This is surprising considering that it is only remotely related to the domestic cat, in contrast to *F.s.ornata* which is considered to be one of the ancestors of the domestic cat, and yet which was found to exhibit little social behaviour.

Figure 3.7 Percentage of interactions of each type, for each species, *(a) F.chaus, (b) O.geoffroyi, (c) C.caracal, (d) F.s.ornata*, and *(e) F.s.catus*. Each group for each species is plotted separately (See *Table 3.1* for sample sizes (*i.e.* total number of interactions observed) for each group). Standard errors are not given because the majority of groups consist of only one dyad. Affiliative interactions were taken to be interactions which contained any one or more of the core affiliative behaviours, as classified in *Table 3.2*. Agonistic interactions were taken to be interactions which contained any one or more of the core agonistic behaviours, as classified in *Table 3.2* Interactions containing both types were very few and were left out altogether. Interactions containing copulatory behaviours were also left out altogether, as the numbers of copulatory interactions were so few. All other interactions were classed as neutral. The sex composition of each group is given in the legend by the group letter.

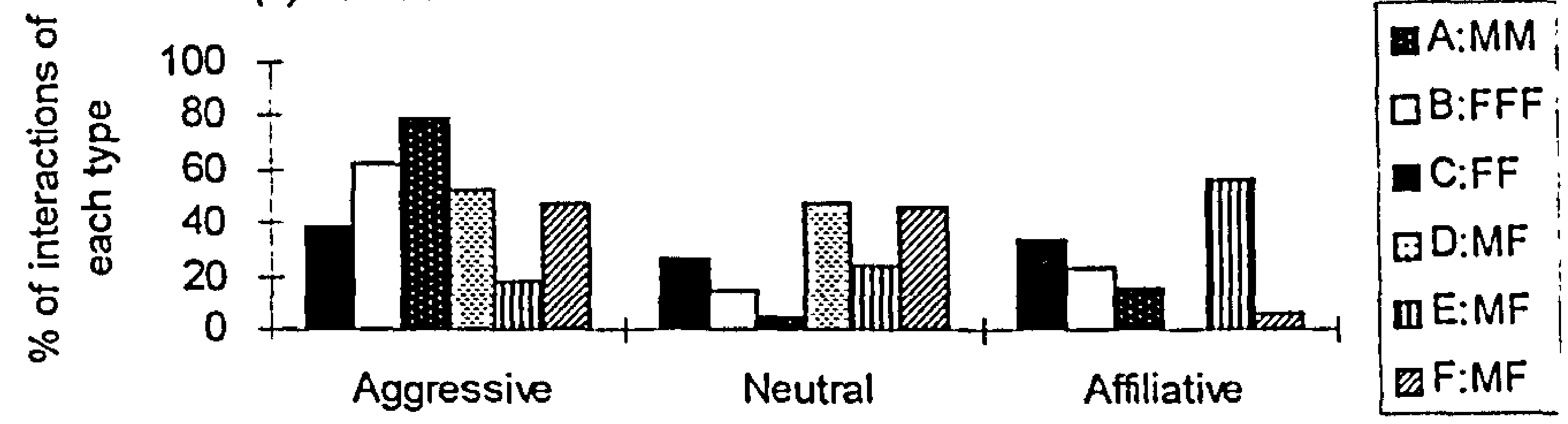
(a) F.chaus



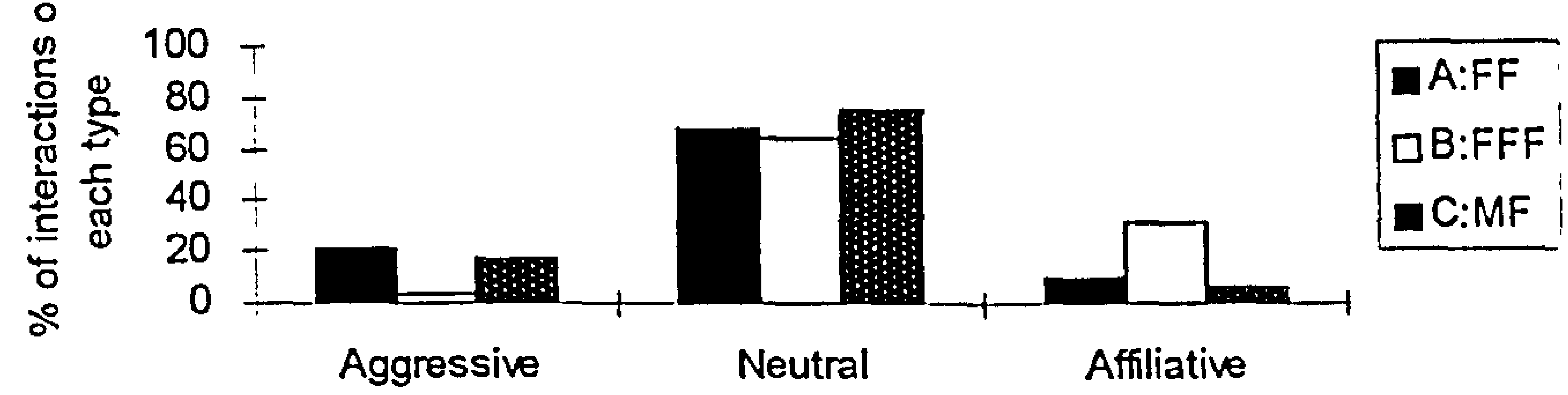
(b) O.geoffroyi



(c) C.caracal



(d) F.s.ornata



(e) F.s.catus

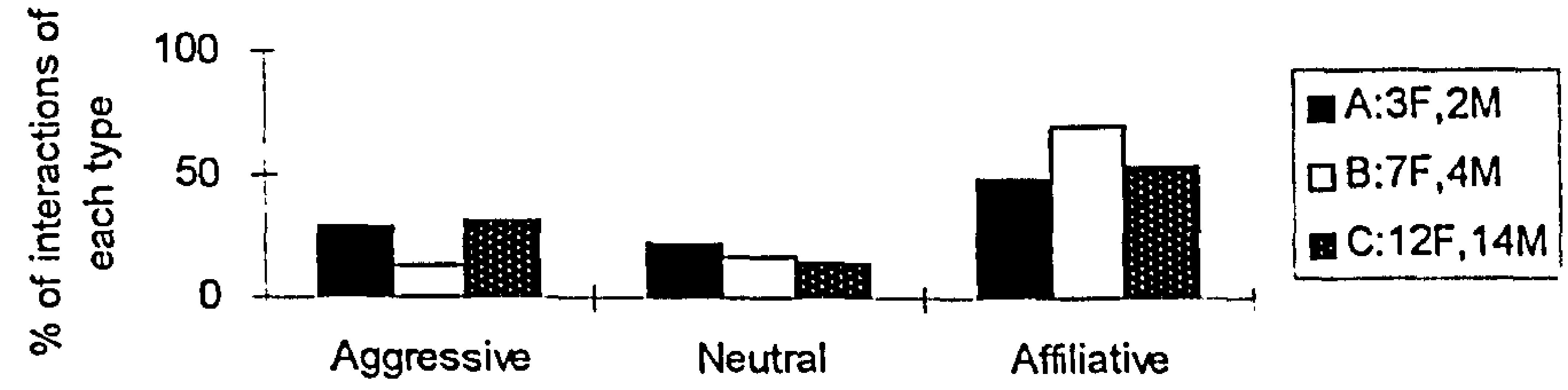
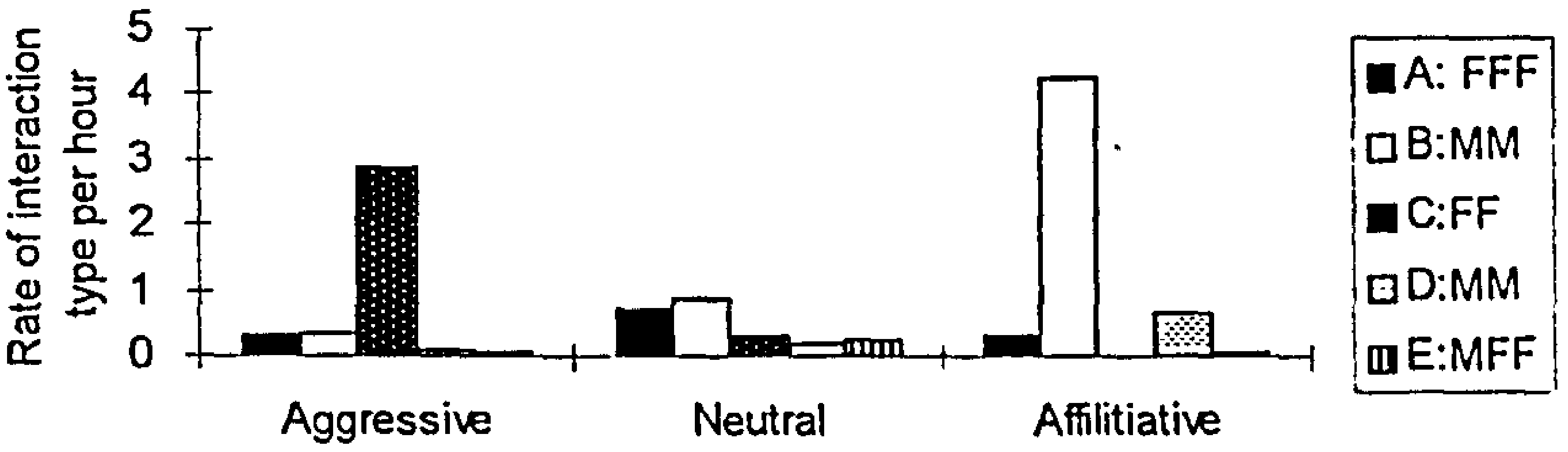
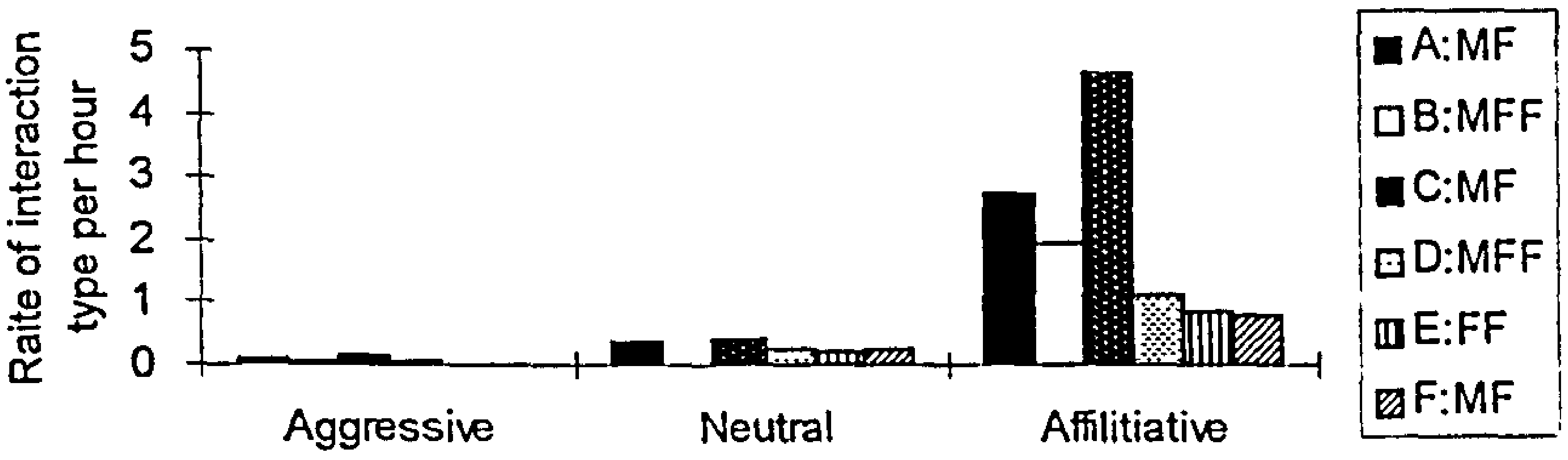


Figure 3.8 Rates per active hour, per dyad, for different types of interactions for each species: *(a) F.chaus, (b) O.geoffroyi, (c) C.caracal, (d) F.s.ornata,* and *(e) F.s.catus.* See *Table 3.1* for sample sizes (*i.e.* total number of interactions observed) for each group. See Section 3.2 for explanation of an active hour. The number of dyads in a group is taken into account by this figure. Standard errors were not given because most groups existed of one dyad, so that it was not possible to calculate a standard error. The sex composition of each group is given in the legend by the group letter. The system of classification of interactions as *Affiliative, Neutral,* or *Aggressive* is given in the legend of *Figure 3.7.*

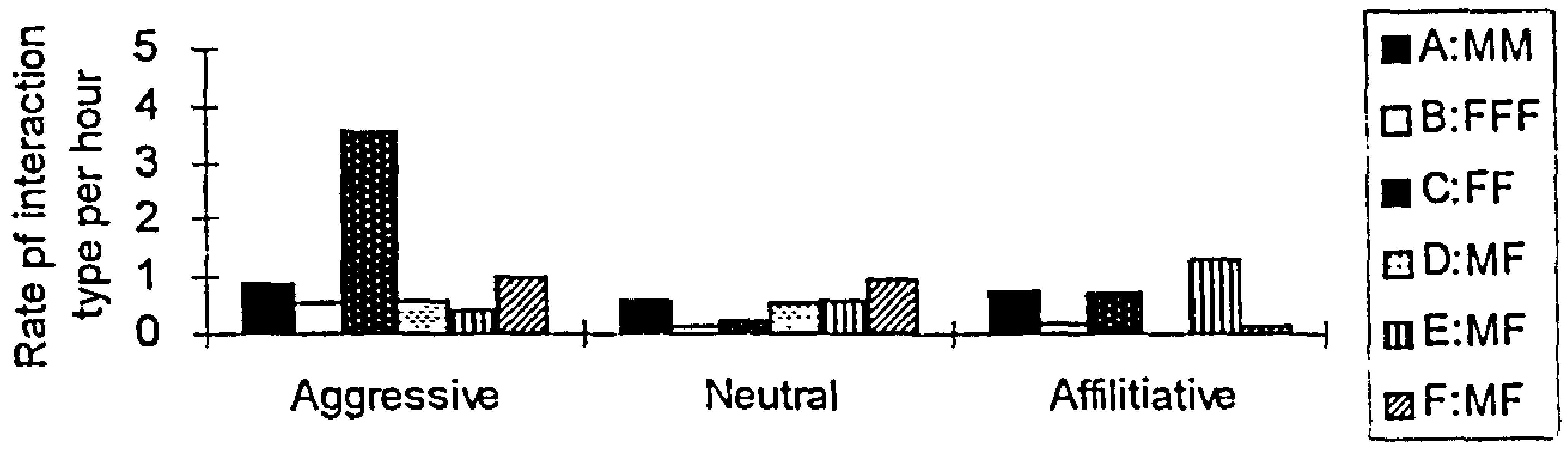
(a) F.chaus



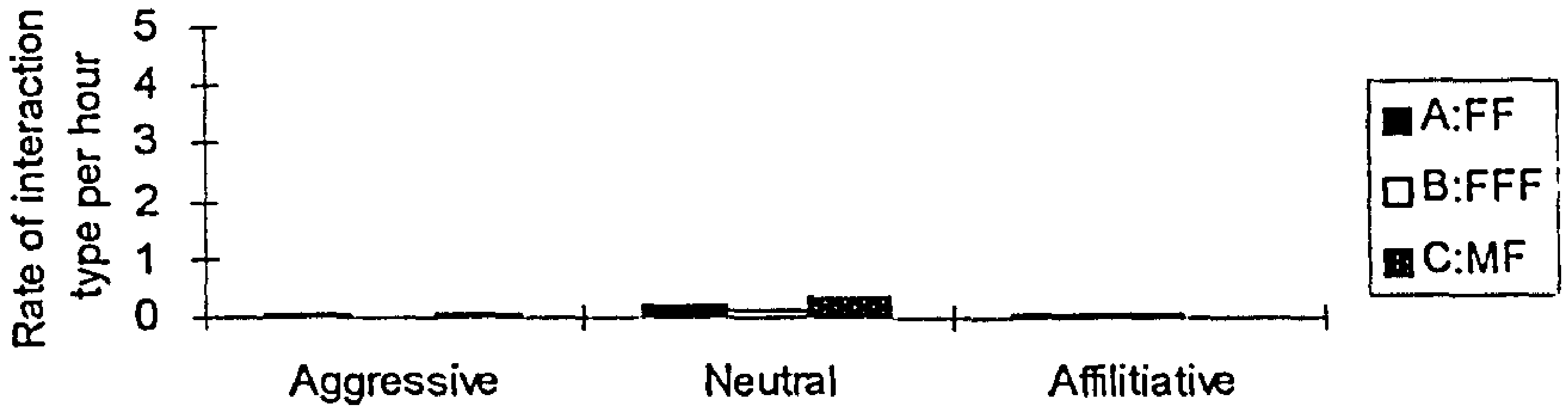
(b) O.geoffroyi



(c) C.caracal



(d) F.s.ornata



(e) F.s.catus

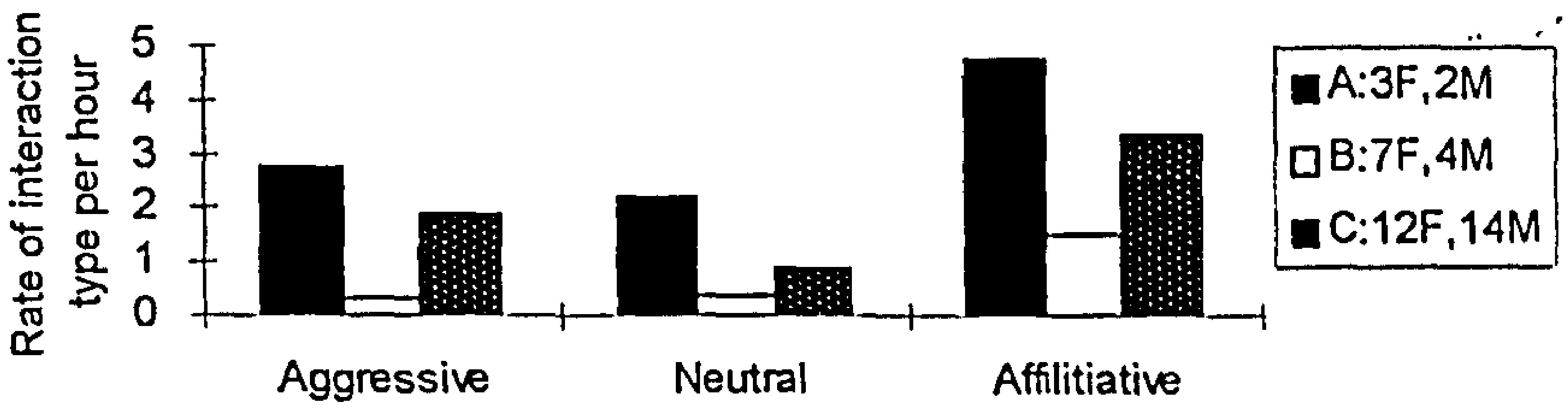


Figure 3.9 Mean percentage of each interaction type (as a percentage of the total number of interactions). Error bars give the standard deviation for each species. The method of classification of interactions as *Affiliative, Neutral*, or *Aggressive* is given in the legend of *Figure 3.7*.

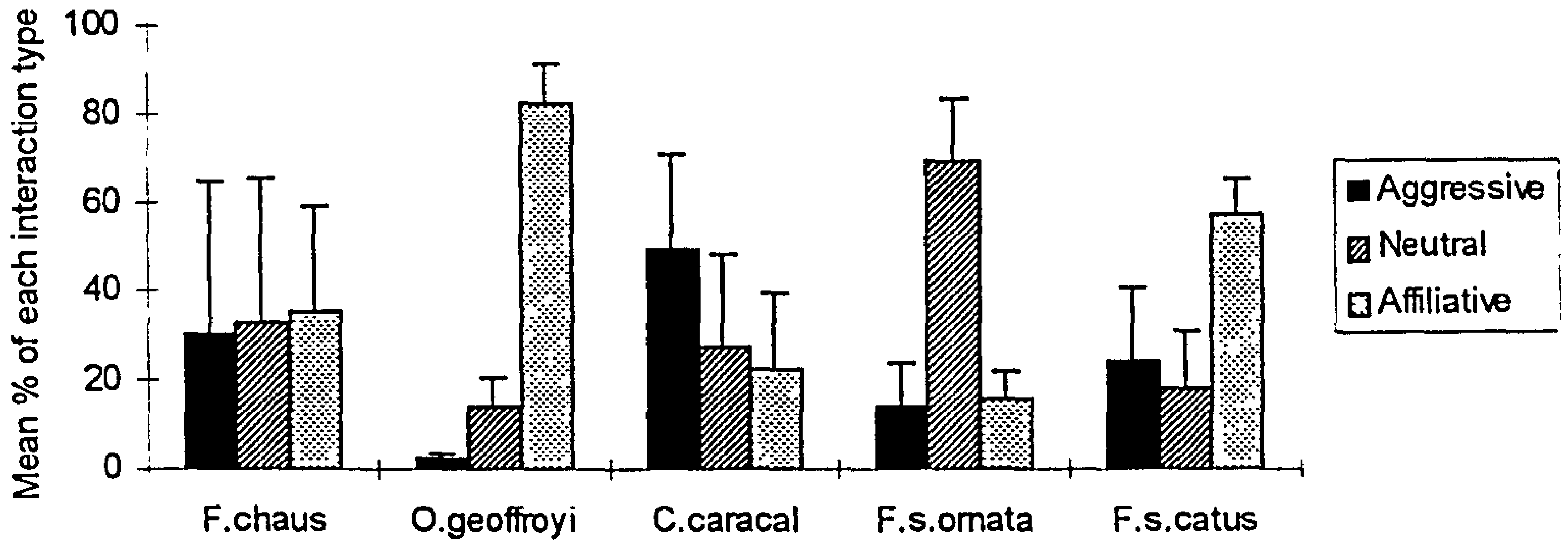
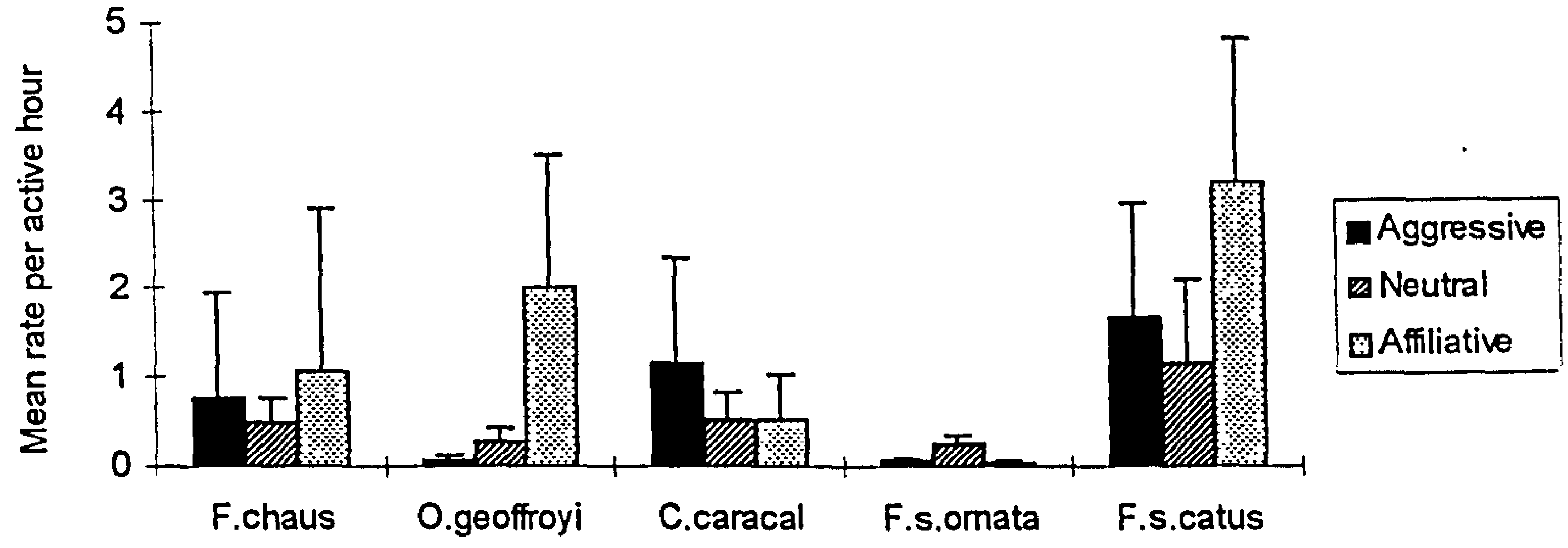


Figure 3.10 Mean rate of interactions of each type for each species. Rate is given per active hour of a dyad. The number of dyads in a group is therefore taken into account by this figure. Error bars give the standard deviation for each species. The method of classification of interactions as *Affiliative, Neutral*, or *Aggressive* is given in the legend of *Figure 3.7*.



3.4 DISCUSSION

3.4.1 The inference of causation and function

The repeated occurrence of two behaviours close together in time generally indicates that they have some causal factors in common. This is not always the case; it may be that one of the behaviours results in a change of situation, which results in the second behaviour then becoming appropriate (Slater, 1973), but it is generally a plausible explanation. The causal factor shared by the two behaviours may be either internal (*e.g.* hormones), or external (*e.g.* external stimuli) (Slater, 1973). Either way they are in some way motivationally linked.

It follows that the two behaviours may also be similar in function. However, because behaviour is so affected by external factors, this is not always so. For example, if two behaviours always occur when food is present, the observer might assume that they are similar in function because they occur together temporally. But the reason they occur together temporally is only because both occur when food is present. In this case there is a motivational link, but no functional link. Thus this assumption that temporal association indicates a functional association must be used cautiously.

Slater (1973) states that "One should not make causal inferences based solely on sequence analysis"; by sequence analysis he means any method which investigates temporal associations between behaviours. In this chapter I have used a type of sequence analysis to group behaviours that occur together in time. By doing this I aim to describe the structure of the behaviour rather than to make causal or functional inferences. However, I have used broad functional definitions to describe the behavioural categories (*e.g.* Affiliative/ Agonistic/ Investigatory). The aim of this was to describe the situation in which a behaviour or group of behaviours is used, rather than to infer a distinct function to a behaviour. Therefore, by entitling a category *'Affiliative'* I do not mean to ascribe a distinct function; but merely to point out that the behaviours within that category are used in an affiliative situation. Thus the behaviours within these categories may have specific functions whilst still occurring in an *Affiliative* context.

3.4.2 Ethogram similarities

All four species of undomesticated felid have a very similar ethogram to that of the domestic cat. All species exhibited the key affiliative behaviours of Sniff, Allogroom, and Sit With, although only four out of the five species exhibited Social Rub (*i.e.* Rub Head, Rub Flank, Rub Tail). All five species were also observed to exhibit the key agonistic behaviours of of Cuff, Stare, Hiss, Ears back, Pounce, Crouch, Chase (See *Appendix V* for presence/absence table).

The exception in each case was *F.s.ornata*, which was not observed to exhibit either social rubbing or growling. However, as none of the observed groups of *F.s.ornata* were very social, and because only 7 individuals of this species were observed, it is impossible to say whether this difference is a species difference or merely a quirk of the individuals involved. In fact, Tonkin & Kohler (1981) included growling in their acoustic ethogram of *F.s.ornata*, thus proving that the absence of this behaviour in the individuals observed is not due to a species effect. It seems unlikely that social rubbing would be absent from the genetic behavioural repertoire of this species, considering that it was found to be present in all three of the evolutionary lineages, including its own. In addition, the zoo keeper of these cats (*F.s.ornata*) anecdotally reported that he had seen them rubbing socially. Therefore given the evidence that all the other four species (*C.caracal, O.geoffroyi, F.chaus, F.s.catus*) did exhibit social rubbing, and considering that many other wild cat species have also been observed to exhibit it (Mellen, 1993), it seems likely that the absence of Social Rub (in *F.s.ornata*) from the behavioural observations of this study is an artefact of the individuals observed, rather than a characteristic of the species as a whole.

The main difference between the ethograms of the domestic cat and the undomesticated felids was the presence of Tail Up locomotory behaviours (*e.g.* Tail Up Approach) in the domestic cat. These were not observed at all in any of the undomesticated felids. This will be discussed further in *Section 3.4.4*.

3.4.3 Behavioural Categories

The behavioural linkage diagrams proved to be a successful method of investigating temporal associations between behaviours. The subsequent placing of behaviours into categories (as in *Table 3.2*) provided a visual, albeit subjective method of comparing the temporal behavioural links across species. Behaviours from all species could be placed into one of five categories: Affiliative, Investigatory, Spray, Copulatory, and Agonistic.

Kendall's rowwise matrix correlation coefficient demonstrated that the temporal linkages between **core** behaviours differed little from species to species. Behaviours that were found to be highly correlated between all five species were: Allogroom, Sit With, Sniff, Rub Head, Crouch, Ears Back, and Hiss. The fact that the temporal linkages surrounding these behaviours were very similar through all the species may imply that these behaviours have changed little in context (and therefore possibly function) through evolution or domestication; possibly these behaviours were already mapped out in this way in the ancestral felid.

Other behaviours were less correlated between species (Tail Up, Roll, Paw, Object Rub, and Watch). This indicates that the temporal linkages surrounding these behaviours must differ from species to species. This may be due to one of two reasons; either that these behaviours have evolved to exist in a slightly different context (and therefore possibly function) in a different species, or that they are simply not very specific to a particular context in any species. Out of these less correlated behaviours, Object Rub and Tail Up were found to be less correlated in domestic cat/undomestic cat comparisons than they were in undomesticated/undomesticated comparisons. The reasons for this will be discussed in the following section (*3.4.4*).

3.4.4 Tail Up and Object Rub: Evolved through domestication?

Tail Up

The behaviour 'Tail Up' is defined as 'the action of putting the tail into an upright position' (see *Appendix I*). Note that this does not include any **prolonged** activity whilst the tail is in the upright position as these are defined by other behaviours; notably, any of the following- Tail Up Approach, Tail Up Move Away, Tail Up Walk Past, Tail Up Run Approach, Tail Up Run Away and Tail Up Follow. In the undomesticated species, the only tail upright behaviour to be observed was 'Tail Up' (*i.e.* the action of putting the tail upright); no prolonged activities whilst the tail was upright were ever observed. In the domestic cat, however, the tail was observed upright for far longer periods of time; thus the Tail Up locomotory behaviours (*i.e.* Tail Up Approach, Tail Up Move Away *etc.*) were observed in the domestic cat (and can be seen in its behavioural linkage diagram, *Fig. 3.1*), but were never observed in any of the four species of undomesticated species.

The fact that the domestic cat has these tail upright locomotory behaviours in its ethogram whereas the undomesticated species do not implies that the Tail Up position has come to be more significant in the domestic cat than in its wild counterparts. This possibility is supported by the discovery that the Tail Up behaviour (*i.e.* the action of putting the tail upright) is classed in different categories in the domestic cat (*Affiliative* category & *Spray*[5] category) than it is in the undomesticated species (*Spray* category only). When a cat (domestic or undomesticated) sprays, the sequence of behaviour is generally as follows: Cat backs up to prominent object, puts tail up, sprays out urine, puts tail down, and then walks away. Thus the action of putting the tail up simply facilitates the spraying action. It is a brief action, and lasts barely longer than the spray itself. This is in contrast to its use in the *Affiliative* category, which is prolonged, as described in the above paragraph. Thus the structure of the Tail Up behaviour differs according to the context in which it belongs (*Affiliative* context= prolonged Tail Up behaviours; *Spray* context= brief Tail Up).

The temporal links surrounding Tail Up in the domestic cat were quantitatively compared to those in the undomesticated felids using Kendall's rowwise correlation coefficient. This supported the qualitative differences described in the above paragraph; there is a

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[5] The domestic cats in this study were not observed to spray. However, Tail Up is known to be very tightly associated with Spray in all species of felid, including the domestic cat, so much so that it is part of the definition of spraying (see *Section 3.3.1*). We can therefore be certain that Tail Up is associated with the Spray category in the domestic cat. This is explained in more detail in *Section 3.3.1.3.3*.

dichotomous effect, with temporal associations of Tail Up being less correlated in the domestic cat/undomesticated comparisons than in the undomesticated/undomesticated comparisons (domestic cat values range from -0.07 to 0.10 (median of -0.005); undomesticated cats range from -0.16 to 0.37 (median of 0.23). (See *Fig. 3.6*)

These results therefore indicate that the Tail Up position in the domestic cat differs from that in the undomesticated felids in two important ways:

- **Differs in context:** Tail Up in the domestic cat is linked both to *Affiliative* behaviours (this study), and to *Spray* behaviours[5]. In undomesticated felids, however, it is linked only to *Spray* behaviours. This difference is supported statistically by the Kendall's rowwise correlation coefficients for Tail Up, which were lower for domestic/undomesticated cat correlations than for undomesticated/undomesticated correlations.
- **Differs in structure:** Tail Upright behaviours in the domestic cat includes Tail Up, Tail Up Approach, Tail Up Move Away, Tail Up Run Away, Tail Up Run Approach, Tail Up Follow, Tail Up Walk Past, *etc.*). These locomotory Tail Up behaviours are prolonged, by their very nature. However, in the undomesticated felids, the only Tail Upright behaviour to be observed was the Tail Up itself (*i.e.* 'the action of putting the tail upright'); no prolonged Tail Up behaviours were observed.

From this twofold evidence, it seems likely that Tail Up has evolved a second function in the domestic cat, as part of the *Affiliative* category, in addition to its facilitating role in spraying.

None of the four undomesticated species (from diverse lineages) used the Tail Up in this manner, not even *F.s.ornata* which is known to be one of the direct ancestors of the domestic cat. Thus it is tempting to suggest that this behaviour must have evolved during domestication. However, anecdotal evidence from *F.s.ornata* indicates that we cannot rule out the possibility that some change may have occurred earlier than domestication: One individual of *F.s.ornata* was seen displaying Tail Up in a locomotory capacity on two occasions, though never as part of a social interaction. In addition, though *F.s.ornata* was never observed to Social Rub during the observations of this study, the cat keeper of these individuals reported that he had seen them social rubbing with their tail upright. As this is only anecdotal evidence, it is not possible to establish whether *F.s.ornata* perform Tail Up *always* when social rubbing, or only *occasionally* when social rubbing. All other undomesticated species were seen social rubbing **without** Tail Up (and never with). As a result of these factors, we cannot rule out the possibility that a change in use of Tail Up may have occurred earlier than domestication.

Object Rub

Object Rub showed similar differences between domestic and undomesticated species; it occured in the Spray category in all five species of cats, domestic[6] and undomesticated, whilst in the domestic cat it was additionally found *very loosely* linked to the *Affiliative* category. Kendall's correlation coefficient showed a dichotomy whereby the domestic/ undomesticated cat comparisons were less correlated than the undomesticated/ undomesticated comparisons. These findings possibly suggest that Object Rub may also have evolved to be used in a second context (*i.e. Affiliative*) in the domestic cat, as was suggested above for Tail Up.

However, another explanation may be that Object Rub is loosely attached to the *Affiliative* category because it is not attached to any other behaviour very strongly (*i.e.* as an artefact of the statistics). This explanation cannot be used to explain the Tail Up results, however, because (a) new Tail Up behaviours exist in the form of the prolonged Tail Up locomotory behaviours, and (b) Tail Up (and its locomotory derivitives) are very strongly attached to many behaviours in the *Affiliative* category. This is in contrast to Object Rub which is only *very loosely* attached to one *Affiliative* behaviour.

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[6] Spraying behaviour was not recorded in the domestic cat in this study but evidence from Macdonald (1987) indicates that Object Rubbing does often occur close in time with Spray (see *Section 3.3.1.3.3*).

3.4.5 Rates of interaction

Three out of four of the species of undomesticated cats studied appear to be very social; with overall interaction rates of these species being only slightly lower than for domestic cats. This is with the exception of *F.s.ornata* (See *Fig 3.10*), whose overall interaction rates were far lower. *O.geoffroyi* had the highest ratio of affiliative:aggressive interactions of all the species (see *Fig 3.9*), even more so than the domestic cat. This may be due to the fact that there were more MF pairs than in the other species (copulation attempts were also higher). However, the MF pairs of the other species do not show this pattern, whilst the FF *O.geoffroyi* pair does; this indicates that it is a function of the species rather than the sex combination.

These results indicate that *C.caracal, O.geoffroyi,* and *F.chaus* interact with one another frequently, and do not simply avoid one another within the confines of the cage. This is in contrast to *F.s.ornata* which did appear to avoid the other individuals in its cage, temporally and spatially, and which exhibited little close contact social behaviour (*i.e. Affiliative* or *Aggressive*); thus it scores highly in rate and percentage of neutral behaviours which tended to include behaviours such as Watch, Pause and Walk Past. This is surprising, considering that it is the species most closely related to the domestic cat, out of the four undomesticated species observed. However, many of the individuals of this species were related. This may therefore be an individual genetic disposition rather than a species characteristic. The sample size was also smaller than for the other species, as it was not possible to find any more *F.s.ornata* at any other sites.

3.4.6 Tail Jerks and Tail Waves

The only previous work done on tail movements in the cat is by Kiley-Worthington (1976). She did some observations on tail 'wagging', by which I presume she means a combination of both Tail Jerk and Tail Wave, as they are sometimes difficult to tell apart. She reports that tail wags tend to occur in situations involving conflict or frustration, not only in the cat but in many other species as well. In particular, in the cat, she reports it to occur during the violation of another's individual distance, during situations of sexual frustration, a mother's isolation from young, between play bouts, and when there is an obstacle preventing the cat from obtaining its goal. She also found experimentally that cats were significantly likely to have a higher frequency of tail wagging during a food-frustration period than during a control period. Her results also show that tail wagging is a transitional type of activity that occurs between bouts of ongoing behaviour, rather than with it.

The results from this chapter back up this hypothesis; I found that Tail Jerk and Tail Wave were attached mainly to Pause, Follow and Walk Past (in the *Investigative* category), in all the species where tail movements were observed in enough frequency to be analysed. The set of behaviours involving Pause, Walk Past and Watch are a transitional set of behaviours, generally occuring when the cat is investigating and unsure as to what to do next; they often occur in between bouts of other activity such as eating or interacting. Thus this fits in with Kiley-Worthington's idea that tail wags occur in a frustration situation, and with her suggestion that it is a transitional type of activity that occurs between bouts of ongoing behaviour, rather than with it.

Kiley-Worthington also reports tail movements to occur during aggression, in particular as part of the threat display and between fighting bouts, (frustration situation). Both *F. chaus* and *O. geoffroyi* show Tail Waves and Tail Jerks as part of their aggressive repertoire, though they are not linked to this category as strongly as they are to the *Investigative* category.

3.4.7 Criticisms of the study

The main restriction was the lack of control of zoo conditions; the size and type of cage varied from zoo to zoo, sometimes even within zoos. The size of groups was not constant, nor was the sex content of groups. All of this produces effects difficult to control for.

Despite these problems, the fundamental behavioural links (*Section 3.3.1 & 3.3.2*) should be relatively robust across different conditions, due to the fact that the links themselves are caused by underlying motivational links in the animal. I would therefore expect the diagrams of temporal behavioural links (*Section 3.3.1*) to be good indicators of what one would expect to observe in any group/pair of animals of that species. In comparison, however, the **proportions and rates** of interactions of different types (*i.e. Affiliative/ Neutral, Aggressive*; *Section 3.3.3*), and of behaviours of different types (*i.e.* Aggressive/ Defensive/ Affiliative/ Play), may change according to independent factors. Nevertheless, I reported these proportional results as a basis for future studies on the subject.

A third problem was caused by the fact that I used social data on neutered domestic cats as a comparison for entire undomesticated cats. Unfortunately this could not be avoided as this was the only data available to me. Comparisons of my neutered domestic cat data with that of published data on entire domestic cat data do imply, however, that there is little difference in behavioural temporal links between entire and neutered domestic cats: The categories of behaviour which I found in neutered domestic cats (See *Table 3.2*) are very similar to those found by van den Bos & de Vries (1996), who investigated temporal categories of behaviour in entire domestic cats (the one difference being that there is obviously no copulatory behaviour in neutered cats). This similarity implies that motivational **links** between behaviours change little as a result of neutering, although the type of motivation that occurs will (*e.g.* no copulatory motivation). As I was looking specifically at **links** between behaviours (rather than at rates of types of behaviours), I believe that the domestic/undomesticated comparison is still valid, although the use of entire domestic cats would have provided a more robust comparison.

3.5 CONCLUSIONS: The origins of adult domestic cat social behaviour

Three possibilities for the origins of the intraspecific social behaviour of the domestic cat were outlined in the introduction:

(a) Behaviours were present in the behavioural repertoire of the direct ancestor of the domestic cat but not utilised due to the solitary way of life.

(b) Behaviours were present in the behavioural repertoire of the direct ancestor of the domestic cat but used in specific situations (*e.g.* sexual/mother-young interactions).

(c) Behaviours evolved through the process of domestication (this may have occurred in conjunction with the above two possibilities).

All four of the undomesticated species were found to exhibit the majority of domestic cat social behaviours (*Section 3.3.1*). Indeed, looking at the core behaviours, and comparing the temporal links between these core behaviours (*Section 3.3.2*), there is a strong correlation between all four undomesticated species and the domestic cat (See *Fig 3.6*). Thus it seems likely that the social signals used by the domestic cat, and the motivational links surrounding these signals have not changed a great deal during domestication, nor through the evolution of the entire Felidae, considering that the four species observed were very evolutionarily diverse. This suggests that the majority of visual and tacile social signals are present in the behavioural repertoire of all undomesticated felids. It also indicates that these behaviours must have been present in the repertoire of the direct ancestor of the domestic cat, and therefore that no evolution of these signals has occurred through domestication, although, from this data, it is not possible to distinguish between possibilities (a) and (b) above.

Tail Up is the only behaviour which did not fit this general pattern. The data suggests that the use of Tail Up as an *Affiliative* social behaviour evolved relatively recently, possibly during domestication. The function of this behaviour will be investigated in *Chapter 6*, and the reasons for its evolution discussed in the general discussion (*Chapter 9*). The use of Tail Up in a Spray context by all cat species indicates that this is may have been the origin for the Tail Up Affiliative behaviour. This will also be discussed in *Chapter 9*.

Social rubbing was the one important social signal which was not observed in all the species (not observed in *F.s.ornata*). However, the fact that it was observed in species from all three lineages, and in two other species from the same lineage as *F.s.ornata*, indicates that the absence of social rubbing is unlikely to be a species characteristic. The fact that a keeper anecdotally reported having seen this species socially rub supports this.

Three out of the four species of undomesticated cat (*O.geoffroyi, C.caracal* and *F.chaus*) were found to exhibit a surprising amount of social affiliative behaviour, considering their solitary lifestyle. These results suggest that these species could adapt very easily to a group-living life if conditions allowed. This finding agrees with the generally accepted view that felids have an innate behavioural flexibility (Macdonald, 1983, 1987, Kruuk, 1975, Leyhausen, 1988).

Chapter 4:

INVESTIGATING THE SIGNALLING SYSTEM OF CAPTIVE FELIDS: EVIDENCE FOR A SYSTEMATIC STRUCTURE?

4.1 INTRODUCTION

A social system is defined as the system of rank and dominance which often forms within social colonies (Alexander, 1974). A variety of separate studies on dominance came to the same conclusion that dominance is maintained more by low key threat signals than by overt signs of aggression (Cole & Shafer, 1966, Podberscek *et al*, 1991, Leyhausen, 1965b; see *Section 1.3.1.2*). Macdonald *et al* (1987) suggested that 'subtle behavioural cues' would be more likely to be important in maintaining the social system than loud repetitive aggressive signals, which would be more detrimental to the individuals involved (See *Chapter 1, Section 1.3.1*).

Macdonald *et al* (1987) studied in detail some specific behaviours which he considered to be key social behaviours; social rubbing, allogrooming, sniffing, aggression, and playing, on a colony of free-ranging entire farm cats. He looked at the directional flow of these behaviours between two individuals. He found that the flow of social rubbing was asymmetrical in the majority of dyads, being skewed from (a) adult females to males, (b) within adult females, (c) from adult daughters to mothers, (d) from kittens to adult females, and (e) from previously dominated cats to previously aggressive ones. The flow of aggression, and the 'net flow of initiations' were also found to be assymmetrical, though less so than social rubbing. Other behaviours, (particularly allogrooming), were found to be more reciprocal.

Macdonald *et al* (1987) suggested that the fact that these behaviours (social rubbing, aggression, and the 'net flow of initiations') are asymmetrical, implies that they act to maintain social hierachy in some way, in particular social rubbing, which he suggested could be an example of the 'subtle behavioural cue' that acts to maintain social hierarchy. The 'net flow of initiations' involves so many different types of behaviours that it may be inappropriate to lump them together when their function is so diverse (aggressive to affiliative). His data does not **conclusively** support the hypothesis that social rubbing acts to maintain social hierarchy, but no other data has been published on this subject to confirm or reject the hypothesis. If this is the case, it may be an indication of a systematic signalling structure acting to maintain a social system.

However, another possible way of explaining the finding that social rubbing is particularly asymmetrical from females to males is that object rubbing (which is the same pattern of behaviour as social rubbing) is conclusively known as an oestrous behaviour in felids (see *Section 1.4.4*). Possibly this background of rubbing makes the females more likely to rub than males, even when out of season. However this does not explain the finding that younger cats rub more on older cats, nor that previously subordinate cats rub more on previously dominant ones. Within this chapter, I have therefore assumed that Macdonald's hypothesis is correct; it was not possible to test it because I only had access to neutered domestic cats, and the fact that the cats had been neutered may have affected the behavioural system.

In this chapter I therefore investigated the asymmetry of various social behaviours (Social Rub, Allogroom, Sit With & Agonistic behaviour) amongst groups of undomesticated felids in a captive situation. *Chapter 3* established that the four undomesticated species studied have much the same adult-adult social behavioural repertoire as adult domestic cats. However, it has not been established whether they use these behaviours in a random way as a result of being forced to live together, or whether they also have the ability to use these signals in a systematic way, to maintain a hierarchy, as has been suggested with domestic cats by Macdonald *et al* (1987).

* *If social rubbing is asymmetrical* in undomesticated felids, this would indicate one

of two possibilities: Either that this social signalling system is a genetic component of all felids, or that Macdonald's hypothesis is unfounded; probably the latter, because it seems unlikely that solitary felids would have a genetic ability to perform signals in such a way to maintain a social system.

* *If social rubbing is not asymmetrical* in undomesticated felids, (and providing that Macdonald's hypothesis is correct), this would indicate that undomesticated felids do not have the ability to use these behaviours in a way to maintain the social system. This would indicate that this method of maintaining the social system has evolved through domestication as cats began to live in groups (See *Chapter 1, 1.3.1*). It may additionally give support for Macdonald's hypothesis.

The null hypothesis to be tested is therefore: Directional flows of various affiliative and aggressive behaviours are reciprocal between the two individuals involved.

4.2 METHODS

The data set used was as *Chapter 3.*

Data analysis

The frequency of occurrence of four different behaviours (Social Rub, Allogroom, Sit With, & Aggressive behaviours) was calculated for each dyad, and in each direction within the dyad (*e.g.* Minnie ➔Sam and Sam ➔ Minnie). A chi-squared goodness-of-fit test (to 1:1) was subsequently used to determine whether the direction of flow of a behaviour was significantly asymmetrical. By 'asymmetrical', I mean that the behaviour is more likely to flow in one direction than in the other (*e.g.* more likely to flow from Minnie to Sam than from Sam to Minnie). In this chapter I have used the term "percentage asymmetry" to mean the percentage of dyads of that species for which a behaviour was asymmetrical.

4.3 RESULTS

4.3.1 Asymmetries within dyads

Table 4.1 shows whether or not each behaviour was significantly asymmetrical, for each possible dyad of undomesticated felids, (based on a chi-squared goodness-of-fit test). *Table 4.2* shows a summary of the data in *Table 4.1*, and of data published in two other studies on domestic cats (Brown, 1993, & Macdonald *et al*, 1987). The sample sizes for the undomesticated cats were generally low because not all cats exhibited these behaviours, and because many dyads exhibited these behaviours at a low frequency (<10), so that it was impossible to statistically test these dyads. However, I have included the percentage values in *Table 4.2* for reference.

There were very few behavioural asymmetries within dyads of undomesticated cats, probably no more than would be expected by chance. Macdonald found high percentages of asymmetries in the behaviours of Social Rubbing (83.3%) and Aggressive behaviours (66.6%). However, in undomesticated cats, Social Rubbing and Aggressive behaviours showed low percentages of asymmetry (**Social rubbing:** *O.geoffroyi*, 10%, *F.chaus*, 25%, *C.caracal*, 33%; **Aggression:** *O.geoffroyi*, 0%, *F.chaus*, 13%, *C.caracal*, 38%). Amongst neutered domestic cats (2 groups studied by Brown, 1993), there was also low percentage of asymmetry in Social Rubbing and Aggression (Social rubbing; 25% and 17%; Aggression; 20% & 11%).

The percentage of dyads exhibiting asymmetry of Social Rubbing and Aggression was therefore higher in the entire domestic cats than in any of the other groups or species investigated. Other behaviours (Allogroom and Sit With) showed low percentage of asymmetry amongst all groups and species, although Sit With was not recorded for Macdonald *et al*'s cats.

Table 4.1 Table showing the significant asymmetries in each possible dyad, for each of the four behaviours. Significance levels are based on chi-squared goodness-of-fit tests on the frequencies at which a behaviour is shown from one cat to the subsequent cat. The direction of the arrow implies the direction of the highest flow. The probability levels are symbolised as: $p<0.05$=*, $p<0.01$=**, $p<0.001$=***. X = behaviour did not occur in that dyad.‡ = the expected values for that dyad behaviour did not exceed 5 and therefore could not be tested (*i.e.* observed frequency was <10). ns = non-significant.

(a) Felis chaus.

		Rubs	*Allogrooms*	*Sit With*	*Aggressive*
F-F	NI-TH	‡	X	‡	‡
	NI-SH	X	X	‡	
	TH-SH	X	X		
	FS-LZ	X	X	X	←★
	ST-BI	X	X	X	ns
M-M	PB-MM	★★→	ns	★→	ns
	IK-IN	ns	ns	ns	ns
MF	MN-FS	X	X	X	X
	MN-LZ	‡	X	X	‡

(b) Oncifelis geoffroyi

		Rubs	*Allogrooms*	*Sit With*	*Aggressive*
F-F	AN-BW	‡	ns	ns	X
	CE-CL	‡	‡	ns	‡
	EV-AM	X	★→	←★	X
M-F	BI-TI	ns	ns	ns	‡
	SM-AN	★★★←	★★★→	★★→	‡
	SM-BW	ns	‡	‡	X
	AR-CI	ns	←★★★	ns	‡
	SB-CE	‡	‡	ns	X
	SB-CL	ns	‡	ns	‡
	CH-ST	ns	ns	ns	‡

(c) Caracal caracal

		Rubs	Allogrooms	Sit With	Aggressive
F-F	FK-MP	‡	ns	ns	
	SP-MP	X	X	X	★→
	SP-FK	X	X	X	★★→
	EA-FK	X	★★→	ns	←★★
M-M	RD-SD	‡	ns	ns	ns
M-F	BO-RU	X	X	X	ns
	BG-SM	ns	★★→	ns	ns
	MU-NF	X	‡	X	ns

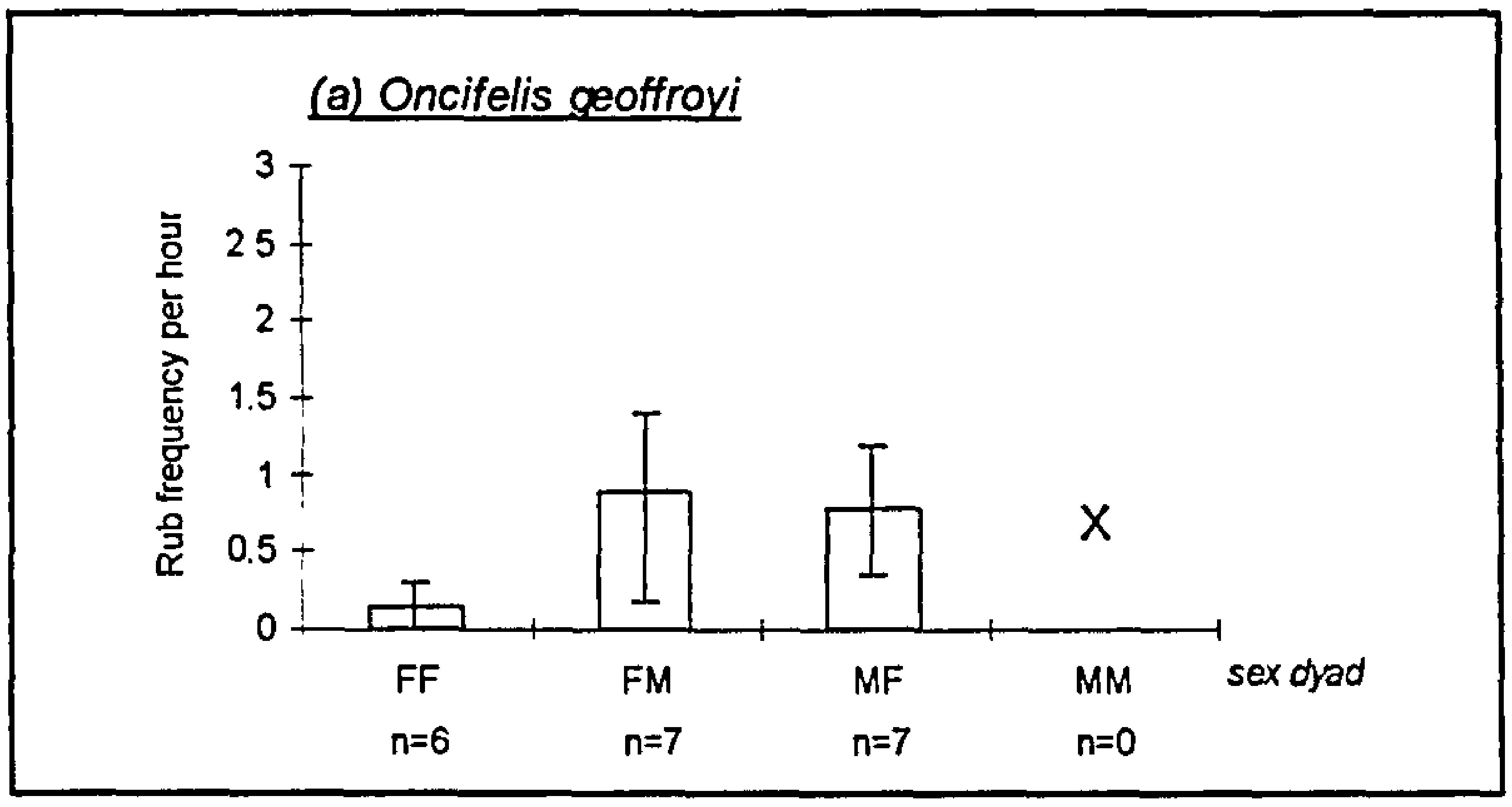
(d) Felis silvestris ornata

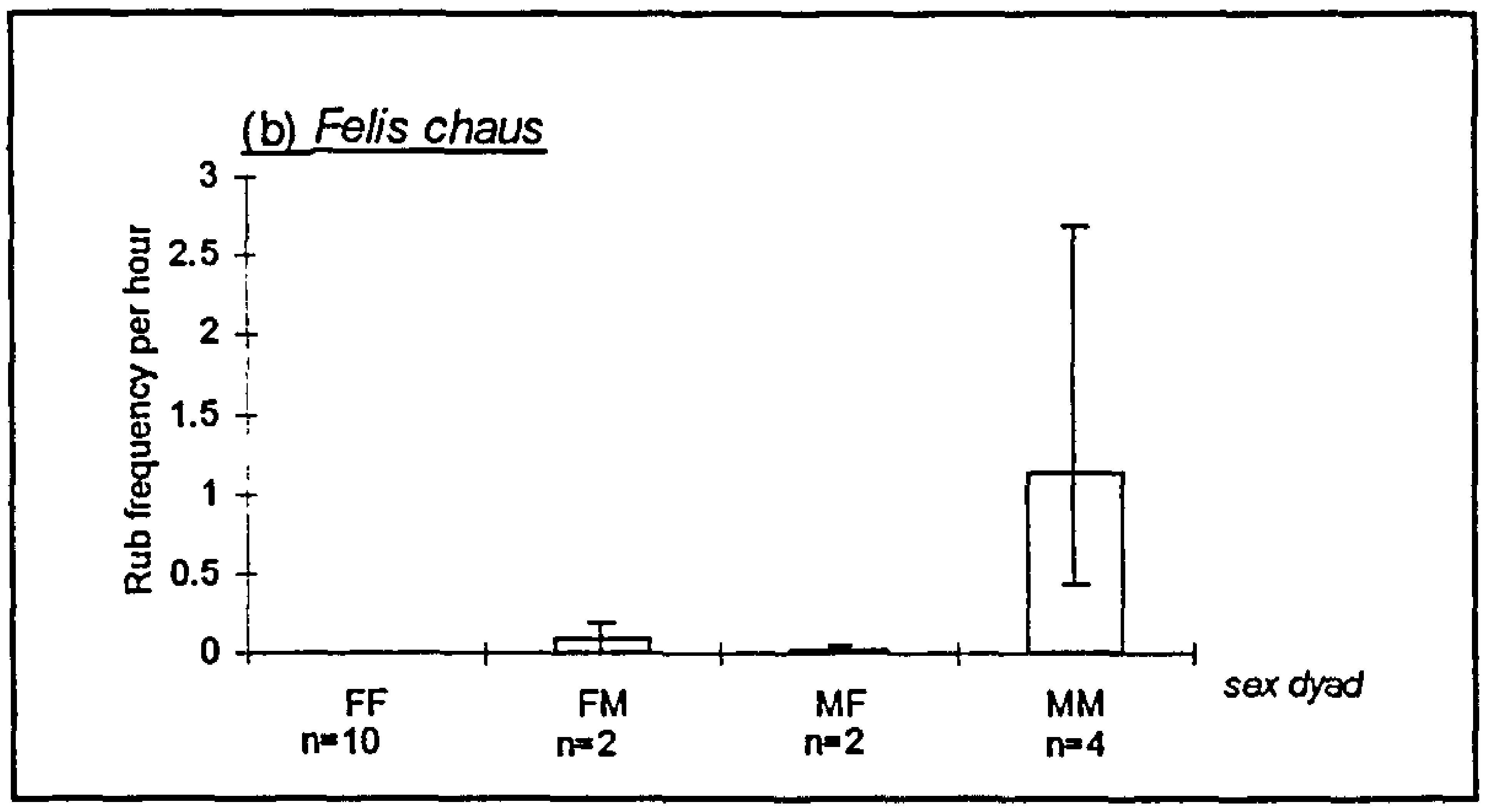
		Rubs	Allogrooms	Sit With	Aggressive
F-F	BL-PE	X	X	X	←★
	BR-PU	X	‡	ns	X
	BR-NA	X	X	‡	‡
	NA-PU	X	X	X	‡
M-F	JH-KH	X	X	X	‡

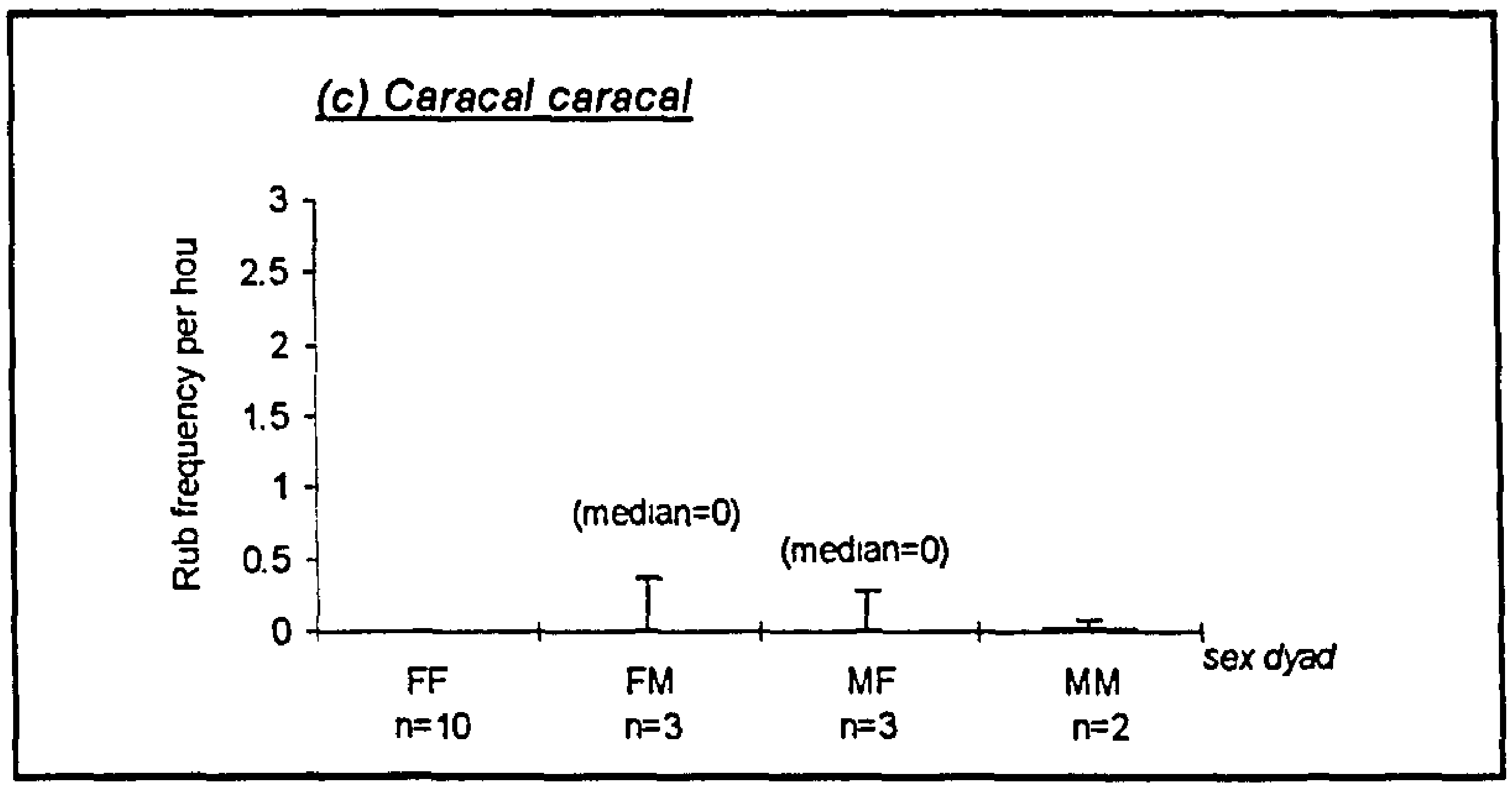
Table 4.2 The number of dyads (non-directional) which exhibited each type of behaviour, followed by the percentage of dyads whose behaviour of that type was asymmetrical (See figures above for more detail). In cases where n<3, the percentage value has not been included. NB. The figures from Macdonald's paper were taken over a longer period of time (April to December) than mine (various depending on the species). The domestic cat data was in each case corrected for the time that each cat spent in the observation area. (It was not necessary to do this for the wild cats, which were constantly in each others presence.)

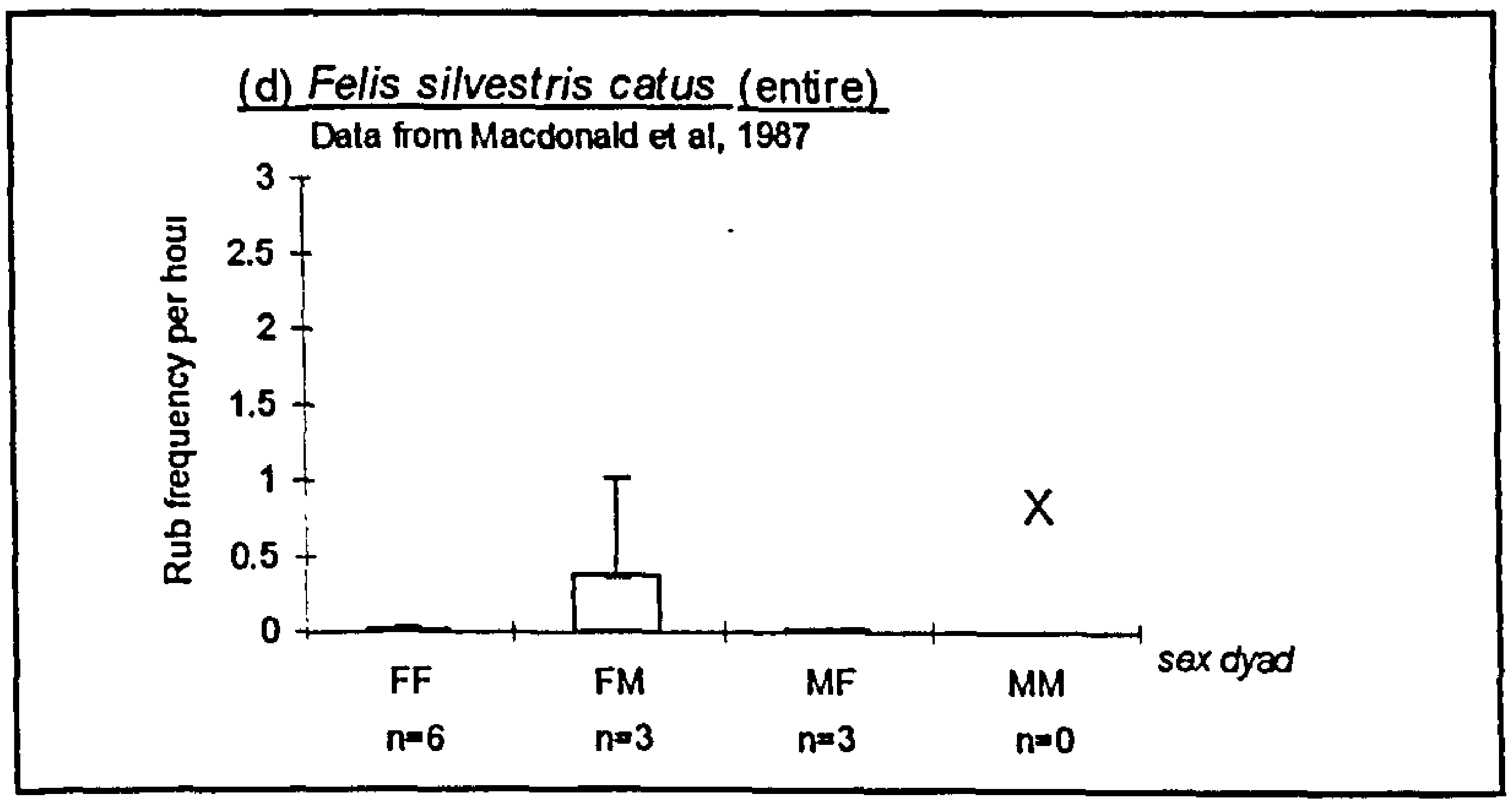
Species	*Social Rubs*	*Allogrooms*	*Sit With*	*Agonistic behaviours*
F.s.catus (entire) (Macdonald, 1987)	n=6, 83.3%	n=6, 33.3%	-	n=6, 66.6%
F.s.catus, Group C (neutered) (Brown, 1993)	n=8, 25%	n=1	n=10, 20%	n=10, 20%
F.s.catus, Group A *(neutered)* *(Brown, 1993)*	n=24, 17%	n=6, 0%	n=23, 0%	n=35, 11%
O.geoffroyi	n=9, 10%	n=10, 30%	n=10, 20%	n=6, 0%
F.chaus	n=4, 25%	n=2, 0%	n=5, 20%	n=8, 12.5%
F.s.ornata	n=0	n=1	n=2	n=1
C.caracal	n=3, 33.3%	n=5, 40%	n=4, 0%	n=8, 37.5%

Figure 4.1 **Median social rub frequency per active hour, per dyad, for each of the three undomesticated species that were found to rub; (a) *Oncifelis geoffroyi*, (b) *Felis chaus*, (c) *Caracal caracal;* and for the domestic cat (*F.s.catus*), from entire cats ((d); data from Macdonald *et al*, 1987). Error bars show the upper (75%) and lower (25%) quartiles. The sample size indicates the number of dyads in each category.**


(a) *Oncifelis geoffroyi*


(b) *Felis chaus*


(c) *Caracal caracal*


(d) *Felis silvestris catus* (entire)
Data from Macdonald et al, 1987

4.3.2 Sex combination differences in social rubbing

Fig. 4.1 shows the frequency of social rubbing between each sex dyad (directional). Statistics were not applied as the dyads were not independent of one another, but graphs give an overall descriptive view of the data. Medians and quartiles were used as the data was not normal due to the low sample sizes.

The domestic cat data (*Fig. 4.1d*) has been taken from Macdonald *et al* (1987). It demonstrates the high incidence of rubbing from female to male, and the low incidence from male to female, as demonstrated previously in Macdonald *et al* (1987). *O. geoffroyi* showed a similar tendency to *F. s. catus*, in that the female-male pairs showed the highest tendency to rub, although *O. geoffroyi* also showed a high tendency to rub from male to female, in contrast to the domestic cat data. *C. caracal* exhibited social rubbing at such a low frequency that a pattern could not be established. In *F. chaus* the male-male pairs rubbed on each other more than all the other possible sex combinations. But again this graph is difficult to evaluate because only 4 out of 9 dyads rubbed at all, with 2 of those dyads being male-male pairs. *O. geoffroyi* showed a far higher incidence of rubbing than either *C. caracal* or *F. chaus*, with 9 out of 10 pairs exhibiting rubbing behaviour, whilst all dyads of *F.s.catus* (Macdonald *et al* 1987 data) exhibited rubbing. It was not possible to calculate values of rub frequency per active hour for neutered domestic cats, so this pattern could not be investigated in neutered cats (Brown, 1993).

4.4 DISCUSSION

4.4.1 Asymmetries within dyads

The *F.s.catus* entire colony (data from Macdonald *et al*, 1987) showed far higher incidences of asymmetry in Social Rubbing and Aggression than the undomesticated species and the neutered domestic cats. Macdonald *et al* suggested that asymmetry may indicate that a behaviour acts to maintain the social hierarchy. The data outlined in this chapter indicates that

(a) Undomesticated cat dyads are no more asymmetrical in these behaviours than would be expected by chance, and that

(b) Neutered domestic cat dyads are also no more asymmetrical in these behaviours than would be expected by chance.

Other behaviours such as Allogroom and Sit With were also found not to be very asymmetrical in any group or species.

Assuming that Macdonald's hypothesis is correct (See *Section 4.1*), these findings suggest that groups of undomesticated cats do not have the ability to use social behaviours to maintain hierarchy (if a hierarchy exists at all). However, the fact that neutered domestic cats also only show very low percentage asymmetries in these two behaviours (see *Table 4.2*) suggests that Macdonald's hypothesis may, in fact, not hold anyway. However, as these cats were not entire it is not possible to definetely conclude either way, because neutering may have affected the usual formation of social hierarchy.

4.4.2 Sex combination differences in Social Rubbing

No overall pattern can be described for the pattern of social rubbing with gender. Mixed pairs rubbed more than female-female pairs in *O.geoffroyi.* This may be due to the fact that this behaviour was noticed to occasionally occur during courtship, although was not always exhibited in this context. None of the undomesticated species exhibited a gender pattern similar to that shown by the entire colony of domestic cats. None of the undomesticated cats exhibited the predominant female to male pattern which is exhibited by entire domestic cats. This finding indicates that Macdonald's results cannot be explained by the oestrous behaviour of the female, as suggested in *Section 4.1*; this finding may therefore provide support for Macdonald *et al*'s hypothesis.

4.4.3 Critisms of the study

The problems with the methods of data collection have been dealt with in *Chapter 3* (*Section 3.4.7*), because the methods were the same for both chapters. There were some statistical problems encountered in this chapter, however. Firstly, social rubbing occurred at a very low frequency in all cats. As a result, some dyads could not be tested for asymmetricality because the expected values were below 5, and many dyads did not rub at all. This resulted in low sample sizes.

The second statistical problem was that the data was not independent which meant that it was not possible to carry out ANOVA's on the sex direction data. Data was not independent in a variety of different ways; firstly, data was taken several times from one individual, and secondly, the same dyad was used twice, one in each direction (this was necessary in order to split up male-female, and female-male differences). Statistics could therefore not be used due to this problem of pseudoreplication.

It would have been interesting to continue this work on social rank and hierarchy in undomesticated cats, by finding out whether a social hierachy exists in artificial groups of captive cats. However, it is notoriously difficult to measure hierarchy, because hierachies can be found when none actually exists (*e.g.* through a feeding order). Furthermore, the fact that the cats were in zoo conditions ruled out this type of study, as manipulation of feeding regimes would have been necessary.

4.5 CONCLUSIONS

Rubbing is less asymmetrical in the undomesticated species than has been previously found in entire domestic cats. Macdonald *et al* (1987) suggests that asymmetries in behaviour may indicate that that behaviour maintains social hierachy in some way. Macdonald *et al* also found that Social Rubbing was predominantly asymmetrical between females and males, flowing from females towards males. This pattern was also not observed in any of the undomesticated species. The finding that undomesticated species do not follow these two patterns described for domestic cats (by Macdonald *et al*, 1987) suggests that the role of social rubbing in maintaining social structure has not evolved in the **undomesticated** species. This is not unexpected, considering that undomesticated species are solitary in the wild. Undomesticated cats therefore do not have a genetic ability to use social rubbing in this systematic way. We can therefore conclude that the use of social rubbing to maintain social hierarchy must have evolved during domestication, after the formation of social colonies of domestic cats.

However, Brown's (1993) data on the domestic cat do not back up Macdonald's ideas on the asymmetry of rubbing. Her data shows very few asymmetrical flows, and the predominant direction was not from females to males. This throws doubts on Macdonald *et al*'s hypothesis, although it does not totally rule out the possibility that rubbing may have a role to maintain social hierarchy, due to the fact that these cats were neutered. In contrast, the finding that undomesticated cats do not predominantly rub from females to males indicates that Macdonald *et al's* findings cannot be explained by female oestrous rubbing behaviour; this may therefore provide support for Macdonald *et al*'s hypothesis. It is not possible to make any definite conclusions as to whether this hypothesis should be rejected or accepted.

Chapter 5:

THE BEHAVIOURAL CONTEXT OF TAIL POSTURES IN THE DOMESTIC CAT: EVIDENCE OF A SIGNALLING FUNCTION?

5.1 INTRODUCTION

The tail has evolved a signalling function many times over in different vertebrate families. For example, birds often use their brightly coloured tails as sexual advertisement (*e.g. peacocks*, Petrie *et al*, 1990); canids indicate dominance or submission by the height of carriage of the tail (for review see Bradshaw & Nott, 1995, Fox, 1969); tail flagging in some ungulates acts as an alarm signal, and sometimes to promote social cohesiveness (*e.g. white-tailed deer*, Bildstein, 1983, Hirth & McCullough, 1977; *pronghorn*, Kitchen, 1972), and tail flagging in Californian ground squirrels induces nearby animals to maintain an increased level of snake vigilance (Hersek & Owings, 1993, 1994). There is also some evidence that otters may use their tail in social communication (Watson, 1984); many reptiles have also evolved a tail display which is exhibited on encounter with predators (*salamander*, Ducey & Brodie, 1991; *iguanid lizards*, Dial, 1986; *snakes*, Greene, 1973, and tail position acts as a predictor of actions in vervet monkeys (Bernstein, 1978). Guilford & Dawkins (1991) suggested three components which are necessary in order for a behaviour to be selected for as a signal; signals must be both detectable and memorable for the receiver, and, above all, discriminable from the usual pattern of life in that species. It therefore comes as no surprise that the tail has been selected for as a signal so profusely; in many species, the tail is not involved in any locomotory apparatus, and as a result has a high likelihood of fulfilling all three requisites in a great number of species. Ears, similarly, are not involved with locomotion and are also very popular as signal conveyors.

Kiley-Worthington (1976) described tail positions in a variety of mammals, and gave suggestions for their causation and function. For the domestic cat, she characterised six tail positions (Tail Up, Tail Half-Up, Tail Parallel, Tail Down, Tail Bent-Up, and Tail Under, although she only gave pictures of the positions; the terms were devised in this thesis (see *Fig 5.1* for ethogram)), though in reality they form a continuum. She investigated the use of different tail positions at different speeds of locomotion. At a walking and trotting pace, any tail position could be used, with the exception of Tail Under and Tail Bent-Up. At faster paces, however, she found that it was necessary for the tail position to be Tail Parallel or thereabouts, presumably for balance. I observed that the commonest tail positions at any speed of locomotion are Tail Parallel and Tail Down. From this we can predict that the intermediate tail positions (*i.e.* Tail Parallel and Tail Down), which are obligatory at a fast speed of locomotion (Kiley-Worthington, 1976), and also commonly used at slower speeds (*pers. obs.*), would be less discriminable as a signal than the more extreme tail positions, which are less frequently used in locomotion.

Kiley-Worthington (1976) also investigated the use of tail positions under different situations. She found Tail Under (with Crouch) to be used in defensive threat, in 'submission', and on aggressive approach. However, she does not explain how she defined these categories. With all the other tail positions she found very little specificity in function or use; most of the tail positions were interchangeable amongst situations, with the exception of Tail Up which was particularly associated with greeting situations, and during tactile stimulation. However, she investigated mainly general situations, and not the specific behavioural context[1] of the situation involved. For example, she looked at 'tactile stimulation' and 'greeting' as different situations, but did not ascertain whether these interactions were occurring under affiliative or aggressive situations (the familiarity of the cat with the other cat/ human may have affected the behavioural context). My aim in this

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[1] By behavioural context I mean the behaviours which the tail position is temporally associated with (as investigated in *Chapter 3*). From this we can ascribe the situation in which the behaviour may occur (*i.e.* Affiliative/ Agonistic/ Investigatory), though we cannot ascribe a specific function necessarily. Thus I have avoided calling this a 'functional context' for this reason.

section is to look more at the behavioural context[1] of the interaction (*i.e.* whether it used in an Affiliative or Agonistic context), rather than the general social context ((*i.e.* whether it occurs in sexual behaviour/ greeting behaviour/ mother-young behaviour *etc.*).

Bernstein & Strack (1996) studied the behaviour of a colony of 14 domestic cats and included in it a brief description of the 6 types of tail positions they observed. They suggest that "tail positions may play a key role in the community by "tagging" individuals as being more or less likely to interact and/or be aggressive"; that is, signifying the mood and possibly the intentions of the cat. If this is so, then the behavioural context[1] would be more likely to correlate with tail position than the general social context.

The aim of this chapter is therefore to give a broad overview of the behavioural context in which each tail position is exhibited. It is hoped that this will give some idea as to which tail positions, if any, are acting as signals; if a tail position is specifically linked to one or more particular contexts, then this implies that it may have a some kind of function within that context. This correspondingly implies that it may have a signalling function, as there is no other function that a tail position can have with respect to a specific *behavioural* context.

Behavicural context will be investigated by looking at the temporal association between tail posture and other behavioural events to which a functional category has already been assigned in *Chapter 3* (*Table 3.2*). Thus by investigating the temporal association of tail positions to behaviours, we can establish whether or not certain tail positions are more or less associated with, for example, *Affiliative* behaviours or *Agonistic* behaviours. It is hoped that this will help us explore the various possibilities for their function.

5.2 METHODS

Ethogram of tail postures

Preliminary observations were carried out to establish what categories of tail postures existed. Observed tail positions ranged from the tail pointing directly upwards (Tail Up) to being tucked under or by the side of the body (Tail Under). Some of these categories stood out as being more distinct than others. However, distinct categories had to be made in order to carry out the observations, and so the range of positions was divided into 7 subsets, some of which were more clearly delineated than others. The ethogram used therefore contained 7 postures, which are defined in *Fig. 5.1*. Three of the tail positions described (Tail Bent-Up, Tail Under, & Tail Over) occurred so rarely that it was not possible to include them in any analysis, so they will not be discussed at all here. I have, however, included them in the ethogram for completeness. Three non-standing stances (Sit, Crouch, Lie Down) were also included in the ethogram, in addition to the tail positions, because I wanted the ethogram to be not only mutually exclusive, but also exhaustive (*i.e.* all recorded time is accounted for as a posture of some sort).

Colonies used

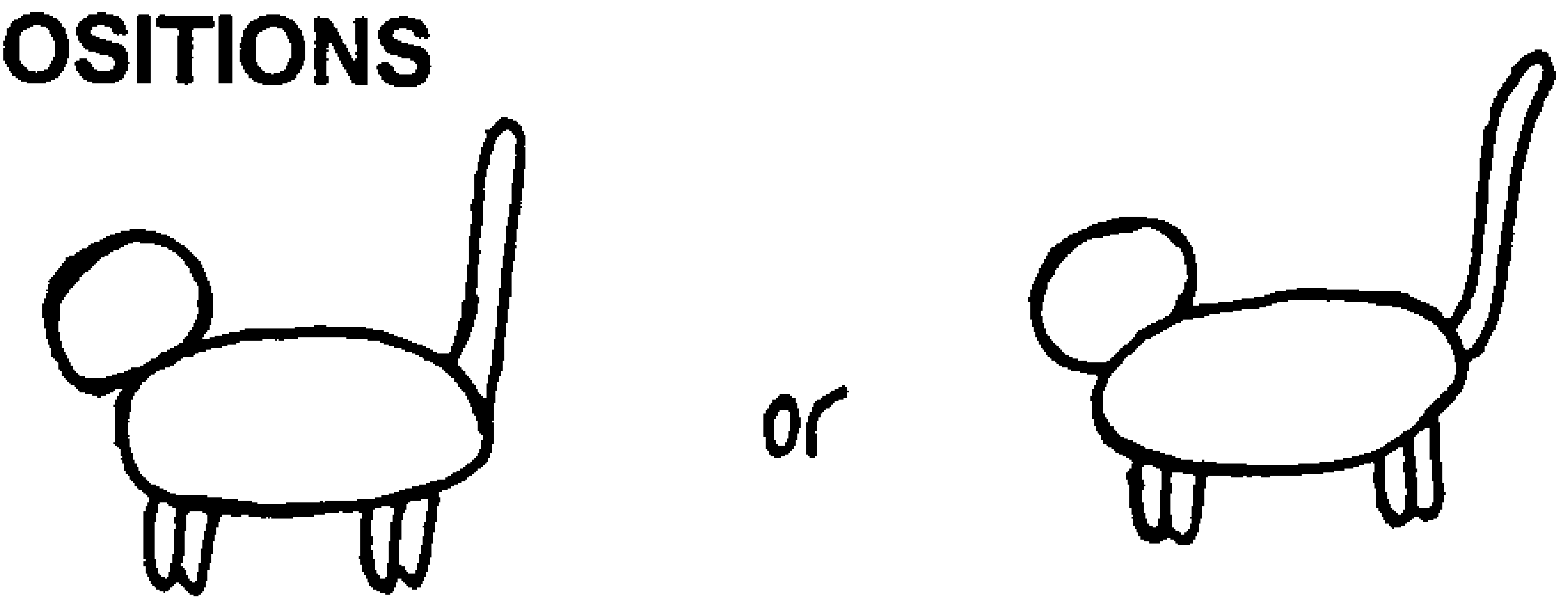
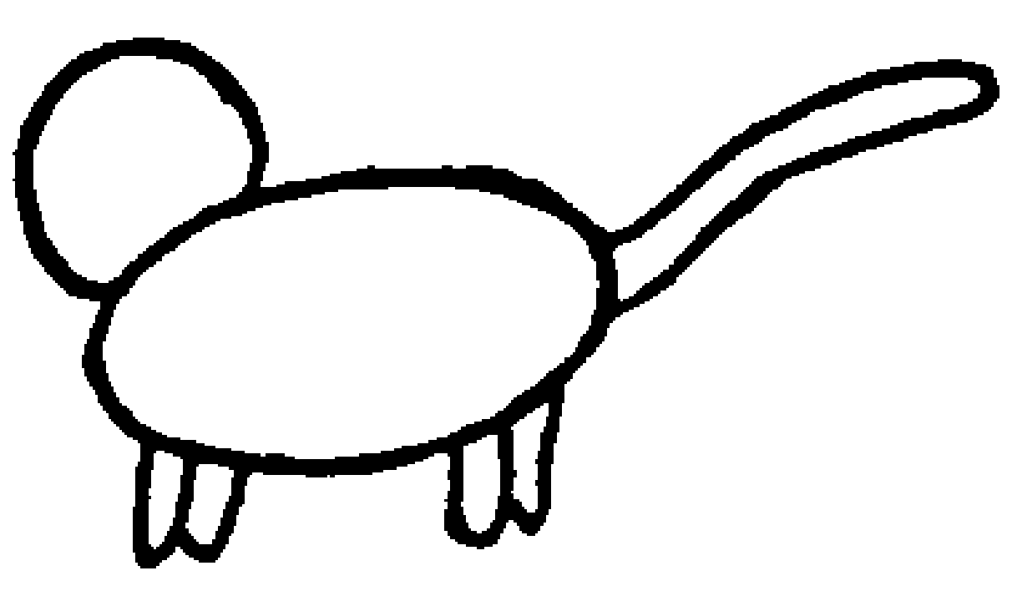
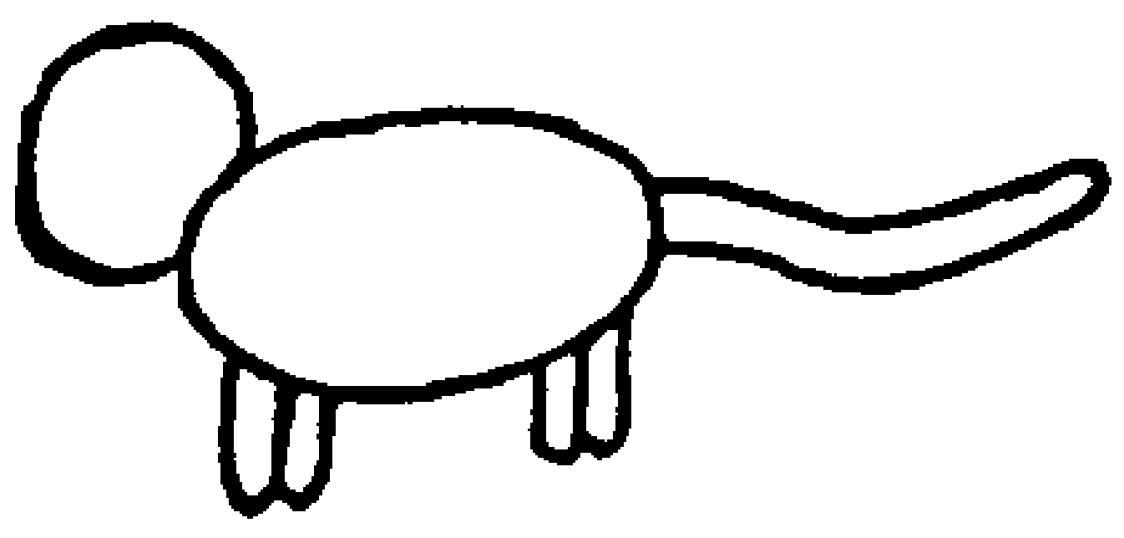
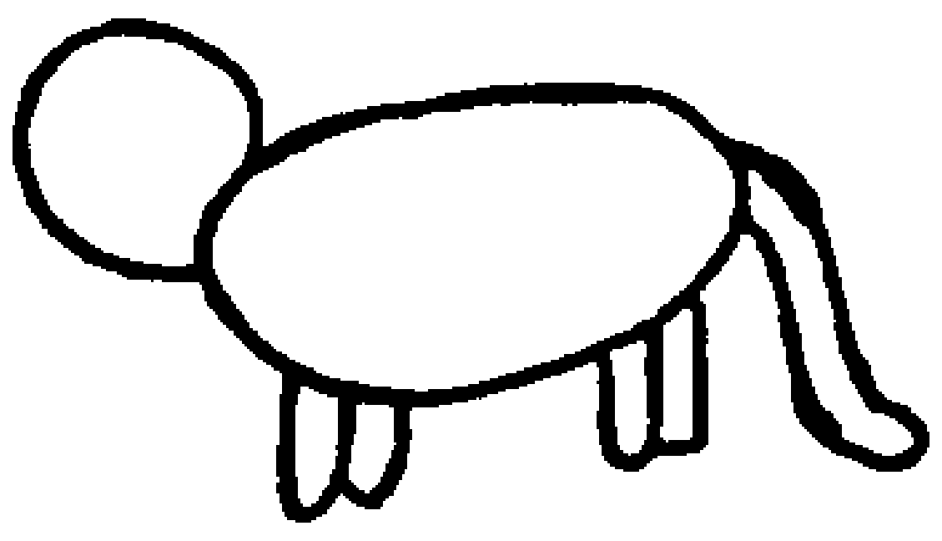
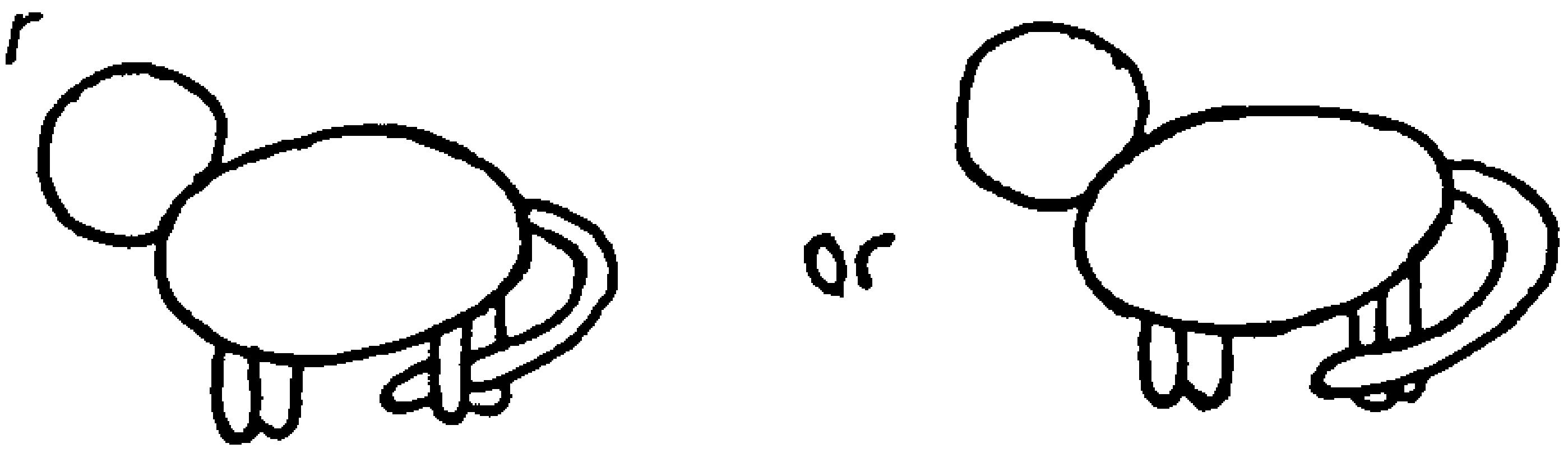
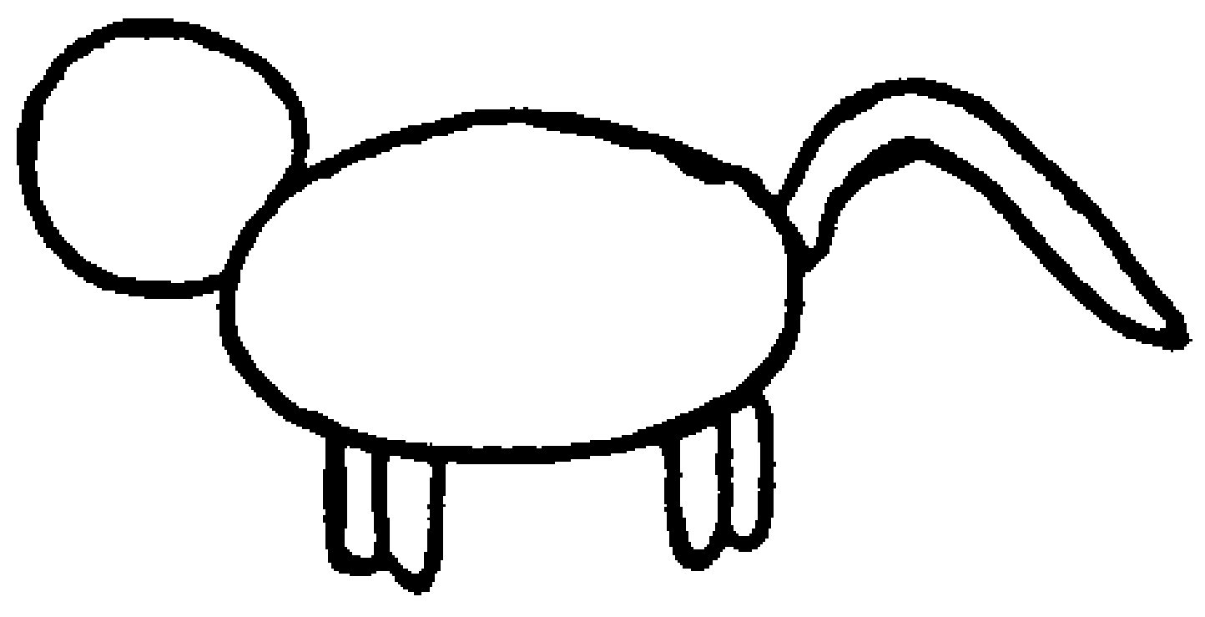
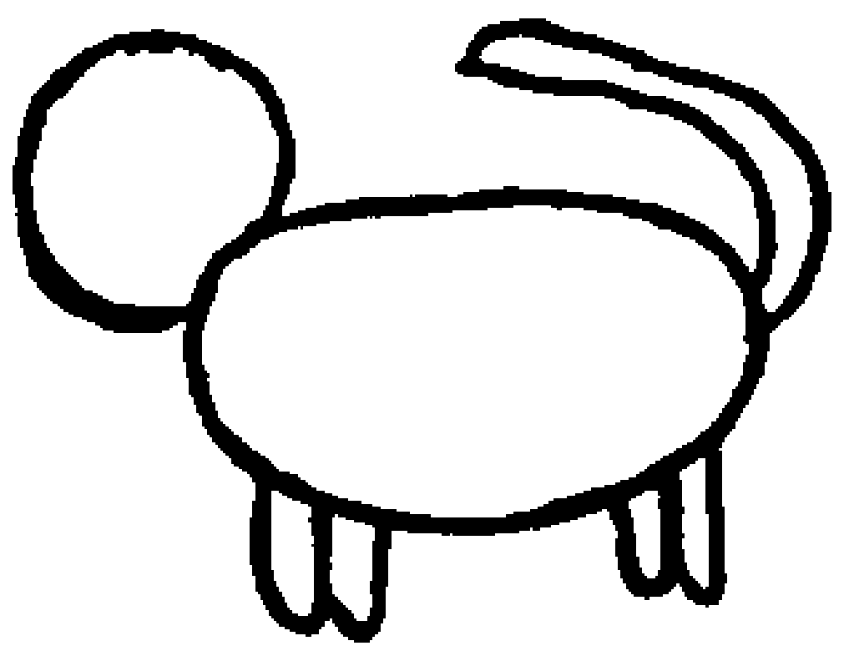
1. Fir Tree Farm Colony (Feral cats):

for details see Chapter 2

This colony consisted of 5 free-ranging feral cats (3♀, 2♂), which had been living together for at least 5 years. They were fed 3 times a week and tended to aggregate about the feeding shed in the few hours before feeding. They varied in their attendance. These cats were previously part of the 'Chilworth' colony observed by Brown (1993) but at a different location.

Figure 5.1 **Ethogram of tail positions and other stances in the domestic cat.**
† These tail positions occurred so infrequently that it was not possible to analyse them, and so they are not mentioned in this chapter again. They have been included here for completeness of the ethogram.

TAIL POSITIONS

Tail Up		Tail held in upright position.
Tail Half-Up		Tail held at 45° to the tail up posture or thereabouts.
Tail Parallel		Tail parallel to the ground, sometimes slightly curved.
Tail Down		Tail held down, with the end kinked out.
Tail Under		Tail curled under, or to the side of the body.
Tail Bent-Up †		Tail is bent in an upward curve.
Tail Over †		Tail bent directly over the body

NON-STANDING STANCES:

These were included in the ethogram in order that it was mutually exclusive and exhaustive.

Sit Cat sits on its haunches.

Crouch Cat crouches with all four feet underneath its body.

Lie Down Cat reclines with its legs to the side.

2. University Colony (Indoor domestic cats):

for details see Chapter 2

This colony was an indoor colony with strict boundaries, though they have total freedom within the enclosure. At the time of recording, the colony consisted of 26 cats (14 ♂, 12♀). They were totally dependent on humans for food, and are fed every day. The majority of the cats had been together for 7 years, and many of the cats are related. These cats were also observed by Brown (1993).

Procedure

(Techniques are explained fully in Chapter 2, 2.3.2)

Social interactions between cats in both groups were recorded *ad lib*, taking account of both tail postures and behavioural events exhibited by both cats throughout the interaction. The aim of this was to produce data of temporal associations between specific tail postures and specific behavioural events. The ethogram of behavioural events is discussed in *Chapter 2, 2.3.1*, and can be found in *Appendix I.*

The *Fir Tree feral cats* were observed during the months of April and May, 1994, for two or three days a week, using a Dictaphone to record data. The days and the times at which they were observed varied, but observations were mostly recorded on feeding days. Single observation sessions lasted between 30 minutes and 2.5 hours. A total number of 186 interactions were recorded.

The *University indoor cats* were re-observed from videos previously recorded by Brown, (1993), in order to include analysis of tail positions. The cats were recorded in the outside enclosure (96m^2) when no humans were present. The video was placed on a tripod, and the cats recorded for 2 to 3 hours a day. A total number of 365 interactions were recorded.

Statistical Techniques

Initially, I used conditional probabilities[2] to describe the data. These probabilities show up the behavioural transitions which occur the most. Conditional probabilities are a good way of describing the data because the extent of temporal association between **every pair of behaviours** can be seen. However, these probabilities will not always be the most significant ones (Bakeman & Gottman, 1986), because of differences in the total frequencies of each behaviour. It is therefore necessary to also carry out some form of statistical test. I used chi-squared residuals to do this (see *Chapter 2, 2.4.4.*). Chi-squared residuals were calculated for both (a) a co-occurrence matrix (see *Chapter 2, 2.4.4)* of the number of times each behavioural event occurred during each tail position (as a duration) and for (b) a transition matrix (see *Chapter 2, 2.4.4*) which calculated the number of times a *change* in tail position was preceded or followed by another behaviour (this used the change in tail position as a frequency rather than the whole duration of a tail position).

5.3 RESULTS

The distribution of the tail postures amongst behavioural events was investigated. This was done in two ways:

(i) An investigation of *co-occurrences* of behavioural events and tail positions.

(ii) An investigation of behavioural transitions involving a tail position (*i.e.* the behavioural events which precede and follow a change in tail posture.

5.3.1 Co-occurrences of tail postures and behavioural events.

Tail postures occur as durations rather than as single frequencies in time, and are mutually exclusive from one another. Behavioural events, on the other hand, (such as 'Sniff'), are single events in time. It is therefore possible to calculate the number of times that each

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[2] A conditional probability value can be calculated for each pair of behaviours. It can be described as the probability of one behaviour occurring, assuming that another behaviour has already occurred.

behavioural event was exhibited during each type of tail posture. By looking at the frequency distribution of each behavioural event across the different possible tail postures, we can establish whether certain behavioural events or categories of behavioural events are linked with certain tail postures. (*e.g.* Are the defensive behaviours mostly exhibited whilst the cat has a 'Tail Under' posture?). I also recorded events which occurred during the non-standing stances (*i.e.* Sit, Crouch, Lie Down). These reclining postures will not be discussed, as I was only interested in the data for the tail positions.

A frequency matrix was constructed for each group of domestic cats to show the total frequency of each behavioural event occurring in each tail posture category (Defined as a *co-occurrence matrix*; see *Chapter 2, 2.4.4*). This included both initiator and recipient behaviours.

Table 5.1 shows the conditional probability of each behavioural event occurring during each tail posture. Percentages were calculated for each behavioural event. Thus, in the feral cats, 84% of the Rub Head events occurred whilst the cat was holding a Tail Up posture, 16% occurred with a Tail Half-Up posture, and Rub Head never occurred at all with a Tail Parallel or Tail Down posture, nor was it exhibited when the cat was in a reclining position. Tail Under occurred too rarely to be included (feral cats: only observed to occur 6 times, University cats: only observed to occur once).

Table 5.1 Conditional probabilities (expressed as a percentage) of the co-occurrence of each tail position with various behavioural events. All behavioural events were included which occurred over 10 times. ***Bold*** ● indicates over 40%. † Behaviour occurred less than 10 times in this colony. *'Fir'* = Fir Tree Colony data; *'Uni'* = University colony data.

(a) Affiliative behaviours

		Rub Head	*Rub Flank*	*Rub Tail*	*Object Rub*	*Sniff*	*Sniff Rear*	*Allo-groom*	*Touch Nose*
Tail Up	Fir	***84*** ●	***84*** ●	***72*** ●	18	***82*** ●	***64*** ●	†	***100*** ●
	Uni	***73*** ●	†	†	***44*** ●	15	2	4	13
Tail Half-Up	Fir	16	16	28	27	12	0	†	0
	Uni	3	†	†	33	2	0	0	3
Tail Parallel	Fir	0	0	0	9	6	28	†	0
	Uni	6	†	†	11	14	2	15	7
Tail Down	Fir	0	0	0	9	0	0	†	0
	Uni	0	†	†	0	***57*** ●	***53*** ●	***43*** ●	37
Sit/ Crouch/ Lie Down	Fir	0	0	0	36	0	9	†	0
	Uni	18	†	†	11	12	8	38	39

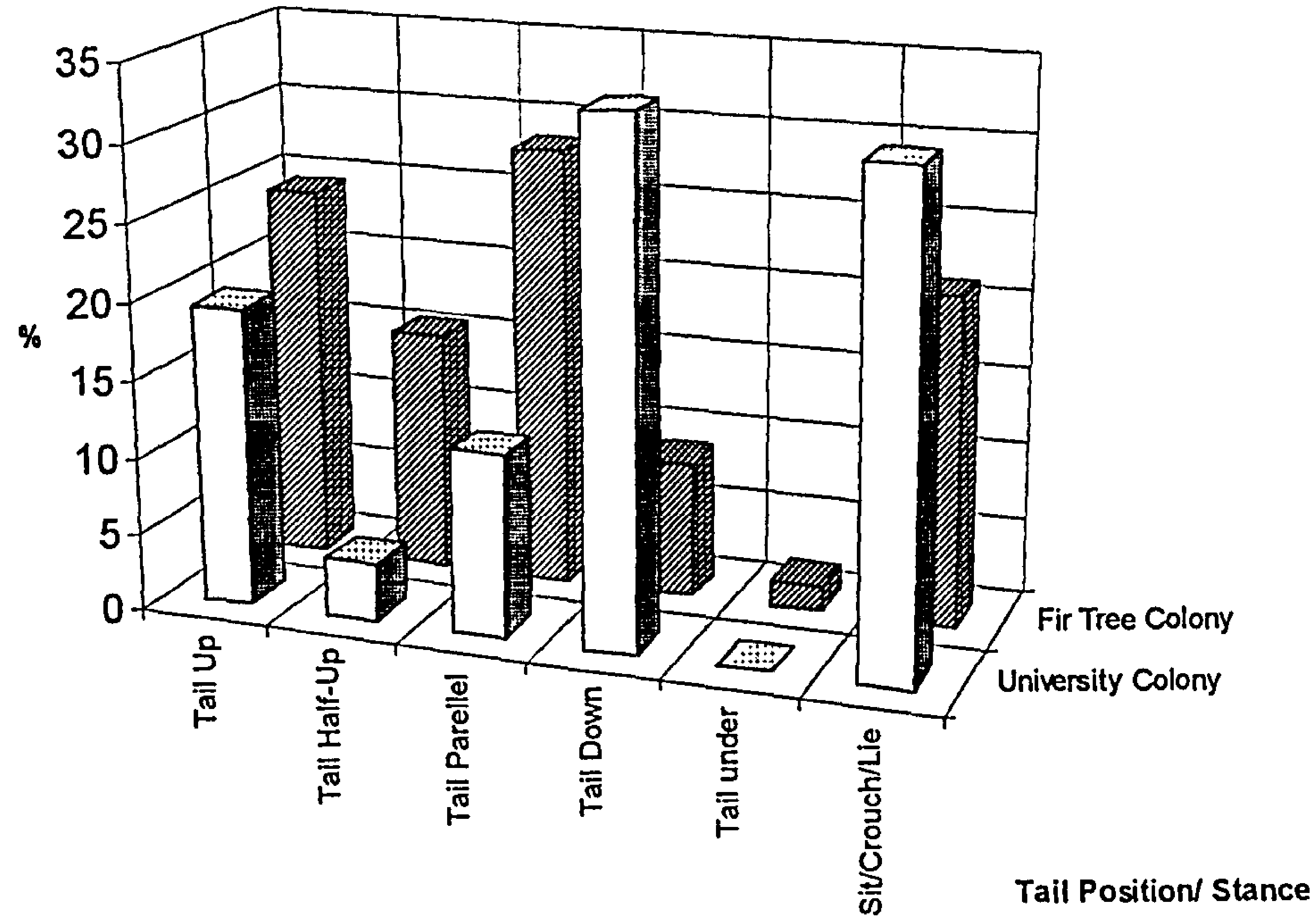
(b) Neutral behaviours and tail movements

		Approach	*Move Away*	*Watch*	*Walk Past*	*Follow*	*Tail wave*	*Tail jerk*
Tail Up	Fir	***58*** ●	28	16	16	†	†	20
	Uni	19	19	19	35	***42*** ●	24	31
Tail Half-Up	Fir	17	20	5	8	†	†	27
	Uni	4	6	3	10	0	8	7
Tail Parallel	Fir	25	***44*** ●	24	37	†	†	36
	Uni	15	18	11	3	0	14	20
Tail Down	Fir	0	8	12	6	†	†	12
	Uni	***60*** ●	***55*** ●	***40*** ●	***51*** ●	***58*** ●	33	39
Sit/ Crouch/ LieDown	Fir			***43*** ●			†	5
	Uni			36			21	3

(c) Agonistic behaviours

		Bite	*Cuff*	*Stare*	*Back Off*	*Run Approach*	*Run Away*
Tail Up	Fir	†	22	4	12	†	***56 ●***
	Uni	9	20	4	28	39	33
Tail Half-Up	Fir	†	22	9	8	†	0
	Uni	3	3	2	3	2	8
Tail Parallel	Fir	†	11	18	37	†	33
	Uni	13	13	10	11	17	12
Tail Down	Fir	†	33	9	12	†	11
	Uni	34	34	***40 ●***	***42 ●***	***40 ●***	***47 ●***
Sit/ Crouch/ Lie Down	Fir	†	11	***43 ●***	31	‡	‡
	Uni	9	30	***43 ●***	17	‡	‡

Figure 5.2 Percentage frequency of tail postures used during social interactions for both colonies. (NB. These values therefore do not necessary reflect the proportions used out of social interactions.) Frequency was calculated as each transition to a tail position (feral colony, N=386, University colony, N=1580).



The tail position which predominates amongst the *Affiliative*[3] behaviours is the Tail Up posture (***Table 5.1a***), as we would expect from the analysis visualised in the previous chapter (*Table 3.2*). ***Table 5.1b*** tabulates the *Neutral*[4] behaviours. In the University cats, the tail position which predominates here is the Tail Down posture. In the feral cats there is no predominant tail posture, though Tail Parallel appears to be in use the most, with the exception of Approach. In general there is more of an even distribution of tail postures here than in the *Affiliative* behaviours. ***Table 5.1c*** demonstrates the *Agonistic*[5] behaviours. *Tail Down* again appears to be the most predominant amongst the University cats, whilst in the Fir Tree Cats there is no predominant behaviour. Many of the *Aggressive* behaviours were also used as play, which complicates the interpretation, as it is difficult to objectively separate play behaviour from aggressive, though subjectively it appears intuitive (see *Chapter 3, 3.3.1.3.6*).

In order to understand these patterns it is necessary to know the percentage use of tail posture in the two colonies (*Fig. 5.2*). The two colonies show broadly similar percentage use for Tail Up (24% &19%), Tail Under (1.6% & 0.06%) and Sit/Crouch/Lie Down (20% & 27%). However, Tail Down is used in far lower quantity in the feral colony (8.8% as against 33.6% in the University colony). This pattern is reversed for Tail Parallel (28.5% ferals, 11.8% University). Tail Half-Up also occurs more frequently in the feral colony (16%, ferals, 4% University).

The results shown in *Table 5.1* will now be discussed for each tail position separately.

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[3] These were classed as behaviours that had been classified in the *Affiliative* category for domestic cats in *Chapter 3* (*Table 3.2*).

[4] These were classed as behaviours which were not classified into any particular category in *Chapter 3* (See *Table 3.2*). The locomotory behaviours have already been classified as 'Neutral', in *Chapter 3, Section 3.3.1.2, Methodological notes*).

[5] These were classed as behaviours that had been classified in the *Agonistic* category for domestic cats in *Chapter 3* (*Table 3.2*).

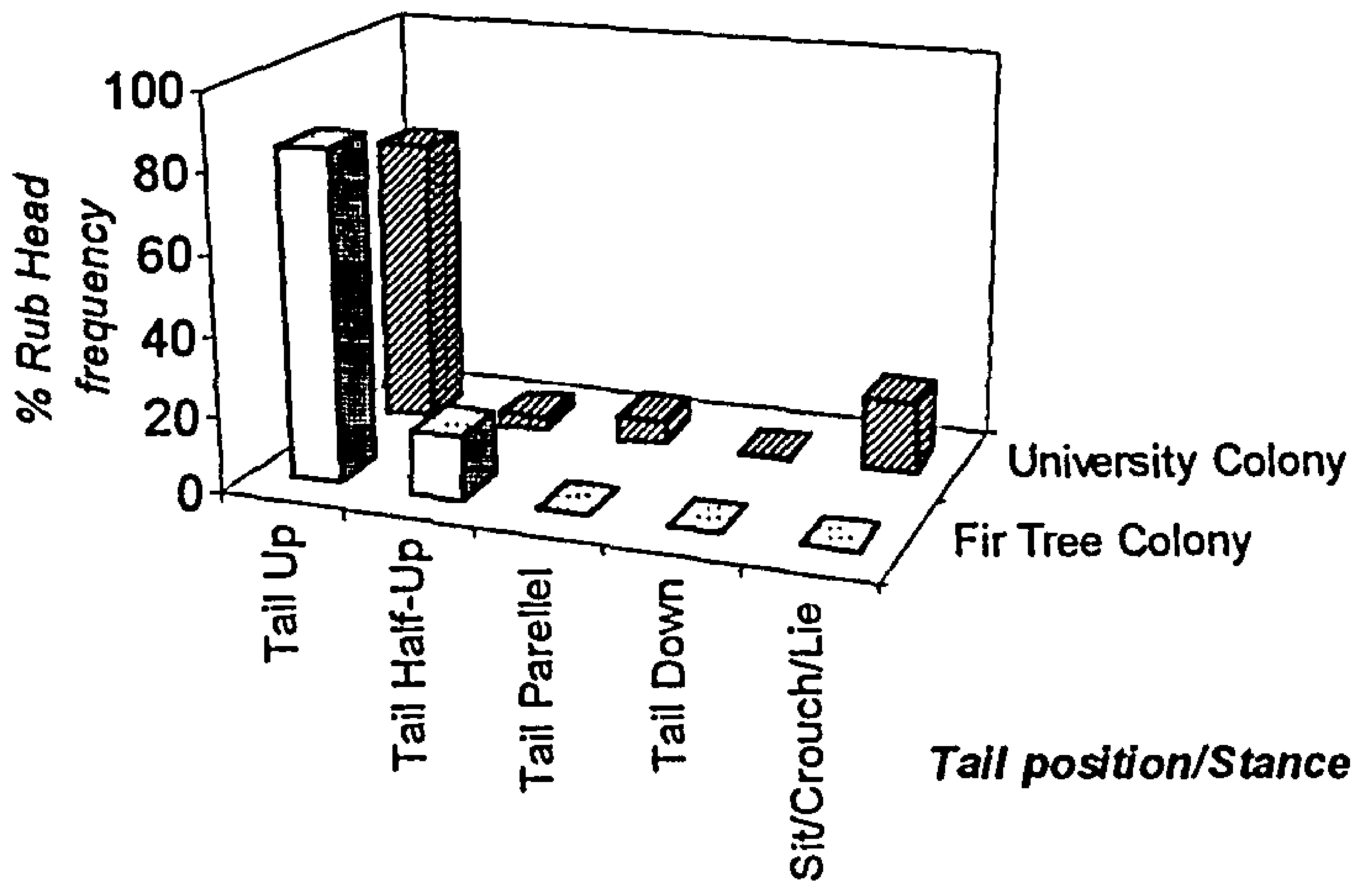
Tail Up

The 'Tail Up' position appears to predominate among the *Affiliative* behaviours. Specifically, Tail Up is most closely connected with Social Rubs, both in the feral and indoor colonies. In the feral colony Tail Up is also highly likely to occur with the other *Affiliative* behaviours of Sniff and Sniff Rear, though not, surprisingly, Object Rub, which is more likely to occur with Tail Half-Up or whilst in a reclining position. In the indoor colony, Tail Up is connected to both Social and Object Rubs, though not to Sniff, Sniff Rear, Allogroom or Touch Nose, all of which are more likely to occur with Tail Down, or, in some cases, a reclining position.

This general connection between the Tail Up position and the *Affiliative* behaviours reinforces the analysis of *Chapter 3*, which has already demonstrated that Tail Up belongs to the *Affiliative* category in domestic cats (*Table 3.2*)

More specifically, the extremely close temporal connection between Social Rubbing and Tail Up occurred in both colonies: 84% (ferals) and 73% (indoor) of Rub Head incidences occurred with Tail Up. A further 16% (ferals) and 3% (indoor) occurred with Tail Half-Up; the other tail positions were used at very low frequencies in comparison to this. This is demonstrated graphically in *Fig. 5.3*.

Figure 5.3 Percentage Distribution of Rub Head across all possible tail postures.



In summary, Tail Up occurs in a distinct behavioural context (*Affiliative*; *Table 5.1a*). It occurs at much lower frequencies during *Neutral* behaviours (*Table 5.1b*), with the possible exception of Approach in the feral cats (58%), and Follow in the indoor cats (42%)[6]. Tail Up also occurs at low frequencies during *Agonistic* behaviours (see *Table 5.1c*), with the exception of Run Away in the feral cats (56%), and Run Approach in the indoor cats (39%). These two behaviours are often associated with play as well as aggression, and Tail Up is frequently used in play (*pers. obs.*). This will be discussed further in *Chapter 6.*

Tail Half-Up

This tail posture is not performed in great quantity by either colony (*Fig. 5.2*). As a result its percentages are generally low. It occurs most in the *Affiliative* context, and occurs at particularly low frequencies amongst the *Aggressive* behaviours. It is not tightly associated with any specific behaviour.

Tail Down

University Cats:

Tail Down shows relatively high percentages in all three types of behaviours (*Affiliative:* 57% Sniff, 53%, Sniff Rear, 43% Allogroom, 37% Touch Nose; *Neutral:* 60% Approach, 55% Move Away, 40% Watch, 52% Walk Past, 58% Follow, 33% Tail Wave, 39% Tail Jerk; *Agonistic*: 34% Bite, 34% Cuff, 40% Stare, 42% Back Off, 40% Run Approach, 47% Run Away. However, these percentages are much lower than those involved with the Tail Up association (*e.g.* 84%,73%, 84%, 72%, 82%, 64%); it is therefore likely that the relatively high values for Tail Down merely reflect the

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[6] These two relatively high proportions of Tail Up in the *Neutral* category may have been caused by the fact that I defined *Neutral* behaviours as behaviours that were not associated with any one category (in *Chapter 3, Table 3.2)*. Thus behaviours that occur in all types of interaction (*i.e.*. in both *Affiliative* and *Agonistic* interactions), such as locomotory behaviours, were classed as *Neutral.* The reasonably high values for Tail Up in the *Neutral* section may therefore be a by-product of the temporal link to the affiliative interactions which these three behaviours (Approach, Follow, Move Away) sometimes occur in.

high overall percentage for the use of Tail Down in this colony (33.6%; see *Fig. 5.2*). Its distribution is relatively even across the three behavioural contexts.

Tail Down was also the most common tail position to occur during locomotion in the University cats (58% Follow; 52% Walk Past; 55% Move Away; 60% Approach; 40% Run Approach, 47% Run Away).

Fir Tree Cats:

Tail Down is performed far less often in this colony (8.8% as against 33.6% in the University colony). This pattern is reversed for Tail Parallel (28.5% ferals, 11.8% University). There are no high percentage values for Tail Down in the Fir Tree colony.

Tail Parallel

University cats: Tail Parallel is not performed at high percentage with any of the behaviours described, and is evenly distributed amongst the three behavioural contexts, as was Tail Down. (*Affiliative*: 6% Rub Head, 11% Object Rub, 14% Sniff, 2% Sniff Rear, 15% Allogroom, 7% Touch Nose; *Neutral:* 15% Approach, 18% Move Away, 11% Watch, 3% Walk Past, 0% Follow, 14% Tail Wave, 20% Tail Jerk; *Aggressive*: 13 % Cuff, 10% Stare, 11% Back Off, 17% Run Approach, 12% Run Away).

Fir Tree cats: Though Tail Parallel occurs at higher frequency in this colony, there is still little specificity in its use. It is used at its highest frequencies amongst the *Neutral* behaviours (25% Approach, 44% Move Away, 24% Watch, 37% Walk Past, 36% Tail Jerk), and is used little during *Affiliative* behaviours or *Agonistic* behaviours, the exceptions being Sniff Rear (28%), Run Away (33%), and Back Off (37%).

Tail Parallel was the most common tail position performed during locomotion in the Fir Tree cats (37% Walk Past; 44% Move Away, 25% Approach), although Approach was actually more commonly performed with Tail Up (58%).

In summary, patterns which held for both colonies were as follows:

(i) *Tail Up* occurred at higher percentages amongst the *Affiliative* behaviours than in the other two categories.
(ii) *Tail Half-Up* occurred little, but appeared to have a similar distribution to Tail Up.
(iii) *Tail Parallel* showed a relatively even distribution across the behavioural contexts.
(iv) *Tail Down* showed a relatively even distribution across the behavioural contexts.
(v) The majority of *Social Rubs* occurred whilst a *Tail Up* was being performed.

This co-occurrence data was also statistically analysed using chi-squared residuals (see *Chapter 2, Section 2.4.4*) to enable a diagram to be drawn showing those co-occurrences which are significantly likely to occur (*Fig. 5.4*). The chi-squared residuals statistical method is more limited than the conditional probabilities, but the main co-occurrences can be seen to be (a) Tail Up with Social Rubs (*i.e.* any one of Rub Head, Rub Flank, and Rub Tail), (b) Tail Curved with locomotory behaviours (Walk Past, Move Away) in the feral cats, (c) Tail Down with locomotory behaviours (Approach) in the University cats. This is in agreement with the results from the conditional probabilities.

5.3.2 Transitions between tail positions and behavioural events

First order transition matrices (See *Chapter 2, 2.4.4*) were compiled to show the frequency of transition from one behavioural element to another, where the transition involved a change in tail posture. Chi-squared residuals (See *Chapter 2, Section 2.4.4*) were calculated for each colony matrix.

The results are shown diagrammatically in *Fig. 5.5.* The results are in agreement with *Section 5.3.1* above; (a) Tail Up (and Tail Half-Up, to a lesser extent) is significantly likely to be followed by Social Rubbing (*i.e.* Rub Head and Rub Tail), and (b) Tail Down (in the University colony) , and Tail Parallel (in the feral colony) are both most likely to be followed by some kind of locomotory activity. In the feral colony, Tail Curved is

Figure 5.4 Tail postures and behavioural events; behaviours significantly likely to occur simultaneously. All associations are significant at p<0.01.

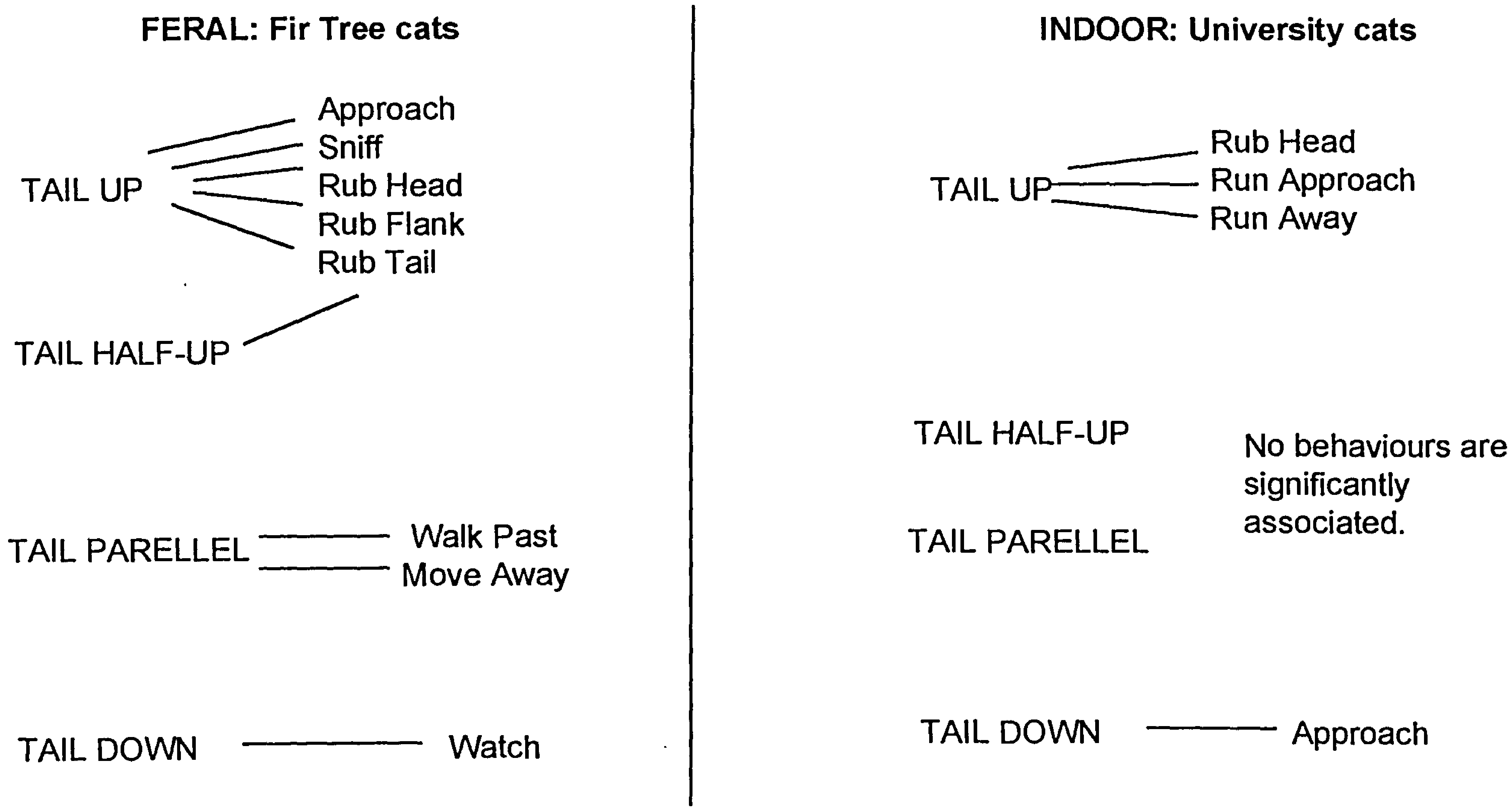
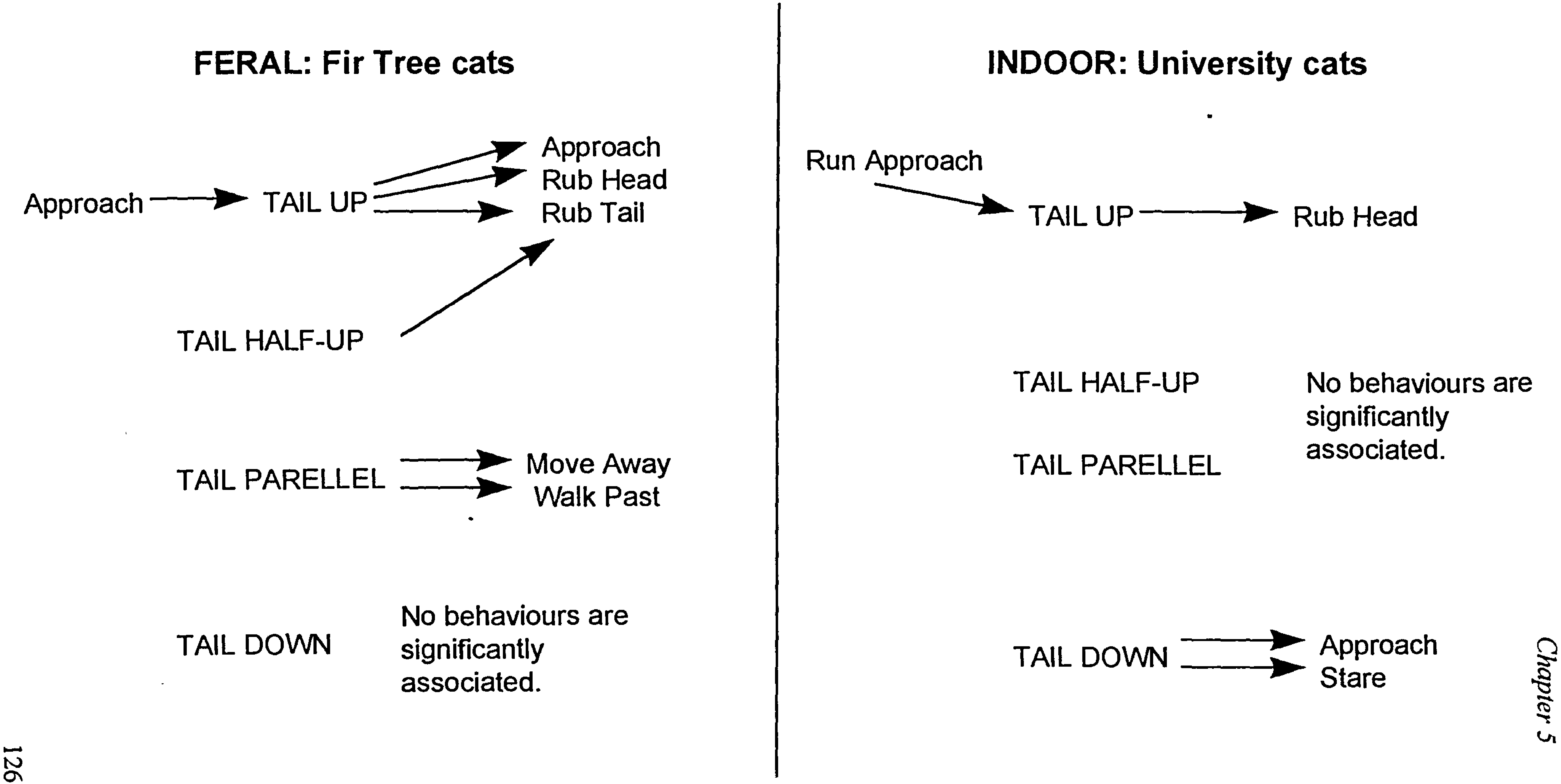


Figure 5.5 Significant transitions involving tail positions.
Behaviours used for this analysis were identical to those displayed in *Table 5.1*, but only significant transitions (p<0.01) are displayed here.



significantly likely to be followed by Move Away & Walk Past, whilst in the University colony, Tail Down is significantly likely to be followed by Approach in the University colony.

5.4 DISCUSSION

Tail Down and Tail Parallel are performed relatively evenly across all three behavioural contexts. From this we can conclude that they have no function in any particular behavioural context. Kiley-Worthington (1976) also found that Tail Down and Tail Parallel had little specificity to general *social* context (*i.e.* whether it occurs in sexual behaviour/ greeting behaviour/ mother-young behaviour *etc.*). These findings suggest that Tail Down and Tail Parallel are unlikely to possess a signalling function.

However, both these tail positions were found to be strongly linked to a variety of locomotory behaviours. Tail Down was the tail position most likely to be performed with all the possible locomotory behaviours (*i.e.* Approach, Move Away, Follow, Walk Past, Run Approach, and Run Away) in the University cats. Tail Parallel was the tail position most likely to be performed with some, though not all, of the locomotory behaviours in the feral cats (*i.e.* Move Away, Walk Past). The association found between these two tail positions and locomotion (based on conditional probabilities) is backed up by the significant links demonstrated by the chi-squared residual analysis. Thus both these tail positions are often performed during locomotion. This may be either because these positions are the best for balance, or simply that these positions expend the least energy without dragging the tail along the floor. The fact that the feral cats perform Tail Parallel during locomotion, whilst the University cats perform Tail Down, implies that there must be a genetic or learned element or involved as well (*e.g.* ferals may learn to hold their tails higher to keep them from getting caught/wet/dirty). As Tail Down forms a close continuum with Tail Parallel, it is not surprising that the two positions may be acting similarly in two different colonies.

Tail Up was found to be associated with the *Affiliative* context in both the feral and

University cats (though less so with the University cats), and, more specifically, with Social Rubbing behaviour (*i.e.* Rub Head, Rub Flank, Rub Tail) in both colonies (See *Table 5.1*). The connection between Tail Up and the *Affiliative* category has already been demonstrated in *Chapter 3*. The presence of this link between the *Affiliative* context (particularly Social Rubbing) and Tail Up suggests that Tail Up has a specific function in that context. As mentioned in *Chapter 4, Section 4.1*, the most likely function is that of a signal, as there is little else that a tail position can be used for with respect to one particular behavioural context. The signalling function of Tail Up will be investigated further in *Chapter 6*.

Kiley-Worthington (1976) found that Tail Up was performed in greeting situations and during tactile stimulation. The evidence from this chapter suggests that this is because both these situations are generally *Affiliative*, rather than because Tail Up is specific to those situations in particular. (*i.e.* Tail Up has a '*behavioural* context' function rather than a '*social* context' function; see *Section 5.1*).

Kiley-Worthington (1976) found that Tail Under was also specific to a particular behavioural context; she found that it was used in defensive or submissive situations. I rarely observed this behaviour, and therefore was unfortunately unable to analyse it. However, the few observations that I did make of this behaviour did back up Kiley-Worthington's suggestions. I observed this behaviour to be commonly used at feeding time (when I did not record), when cats were feeding from the same bowl, and were thus in defensive mode.

5.5 CONCLUSIONS

From the data in this study, and from previous data from Kiley-Worthington (1976), it seems likely that the only two tail positions to have a signalling function are the Tail Up and Tail Under postures. These are the two most extreme positions. These findings fit with the prediction made in *Section 5.1*; that the intermediate tail postures (*i.e.* Tail Parallel and Tail Down) are unlikely to have evolved as signals due to their indiscriminability from the usual carriage of tail held in locomotion, particularly in fast locomotion, when Tail Parallel is the necessary position (Kiley-Worthington, 1976). The use of Tail Down and Tail Parallel in locomotion is supported by data from this chapter. Tail Up and Tail Under are thus the two positions which are visually most discriminable from the usual tail position held in locomotion. Discriminability is an important factor in signal selection (Guilford & Dawkins, 1991); it therefore seems likely that the reason that the other tail positions are not utilised as social signals is because they are not discriminable enough from one another, nor from the "usual pattern of life" (Guildford & Dawkins, 1991) in the domestic cat.

Chapter 6:

THE SIGNALLING FUNCTION OF THE TAIL UP POSTURE

6.1 INTRODUCTION

The previous chapter has shown that there are only two tail positions in domestic cats which are reliably associated with other behavioural elements and which may therefore act as signals: Tail Up and Tail Under, the two most extreme positions. Tail Under was elicited only very rarely in the domestic cats that I observed, whereas Tail Up was very common. In this chapter I therefore investigate the signalling function of the Tail Up posture.

The results of *Chapter 5*, and the data reanalysed from Brown (1993) in *Chapter 3*, show the strong temporal association between Social Rub (*i.e.* Rub Head, Rub Flank, Rub Tail) and Tail Up. 84% and 73% of Rub Heads (feral cats and indoor cats respectively) were exhibited during a Tail Up position (*Chapter 5, Table 5.1a*), and the behaviours found to make up the *Affiliative* (*Rub*) sub-category in *Chapter 3* (*Table 3.2*) included almost without exception only rubbing and tail upright behaviours *(see Table 6.1* for summary). Brown (1993) described a practically identical temporal group by the cluster analysis method, which she termed the *Affiliative* cluster (See *Table 6.1*).

Table 6.1 List of behaviours found to be in the *Affiliative* category (*Rub* sub-category) in Chapter 3 (data reanalysed from Brown (1993). † indicates that these behaviours were also found to be part of the Affiliative cluster described by Brown (1993)

Rub Head †
Rub Flank †
Rub Tail †
Tail Up †
Tail Upright Approach †
Tail Upright Move Away †
Tail Upright Walk Past †
Tail Upright Follow †
Meiow

Although the results from *Chapters 3* and *5* have shown that rubbing almost always occurs during Tail Up, it does not hold that Tail Up must occur with Rubs: In *Chapter 3* the tail upright behaviours were shown to be components of, not only the *Affiliative* (*Rub*) sub-category, but also the *Affiliative* (*Allogroom*) sub-category (see *Table 6.2*; see also *Chapter 3, Table 3.2*). The data in *Chapter 5* supports this; in the feral cat colony, Tail Up was highly utilised with several Affiliative behaviours other than rubbing (82% of Sniffs, 64% of Sniff Rears, and 100% of Touch Noses occurred whilst the cat was holding a Tail Up position).

Table 6.2 List of behaviours found to be in the *Affiliative* category (*Allogroom* sub-category) in Chapter 3 (data reanalysed from Brown, 1993).

Allogroom
Sniff Rear
Touch Nose
Sit With
Tail Up Approach
Tail Up Move Away
Sniff

Bernstein & Strack (1996) studied the behaviour of a colony of 14 domestic cats and suggest that tail positions may "tag" individuals as being more or less likely to interact and/or be aggressive; that is, signifying the mood, and/or the intentions of the cat. I have established in the previous chapter that the majority of tail positions do not appear to have a signalling function. However, Bernstein & Strack's hypothesis may still hold for Tail Up. Bernstein & Strack did not test their hypothesis, but I intend to do so in this chapter.

The fact that tail postures may signify the intentions of the cat has also been suggested but not directly tested by Brown (1993), who studied the communication between members of a neutered feral cat group. She suggests that the position of the tail may be important in determining what happens in the rest of the interaction. She analysed the ordering of all the behavioural elements that she observed during interactions, and investigated common transitions from one behaviour to another. This data showed that there are patterns of behaviour that are significantly likely to follow the Tail Up posture, all of which are of an affiliative nature. She found that the Tail Up posture affected, not only the subsequent behaviour of the initiator of the interaction, but also the behaviour of the recipient. Thus the recipient may be adapting its behaviour according to the tail position of the initiator.

The aim of this chapter is therefore to test the hypothesis which is based on the suggestions of Bernstein & Strack (1996) and Brown (1993); that *the Tail Up posture acts as an intention indicator in cat-cat interactions.*

This chapter will be divided up as follows:

- *Section 6.2:* Initial investigation of field observational data to see if the suggestions of Bernstein & Strack (1996) and of Brown (1993) hold for this data. I have done this by investigating the relationship between Tail Up and social rubbing, looking at the effect of the tail position of both the initiator and the recipient on the likelihood of the occurrence of social rubbing.
- *Section 6.3:* Experimental manipulation which directly tests the hypothesis that the Tail Up is an intention signal.

6.2 FIELD OBSERVATION DATA: DOES THE TAIL UP POSTURE AFFECT THE FOLLOWING INTERACTION?

6.2.1 Methods

The data used was identical to that described in *Chapter 5*, but analysed in a different way.

Data analysis

Tail positions were not sub-divided into such detail as the last chapter. *Chapter 5* established that Tail Down and Tail Parallel were acting neutrally and do not have any signalling function. They were therefore combined together for the purposes of this study, and termed the 'Tail Neutral' position. Results from the previous chapter suggest that Tail Half-Up acts similarly to Tail Up, but as this was not totally certain, the data for Tail Up and Tail Half-Up were kept separate. The three tail sub-divisions that were investigated in this section are therefore: Tail Up, Tail Half-Up and Tail Neutral. Tail Half-Up occurred only at very low frequencies (*Fir Tree Cats*, n=19; *University Cats*, n=13), and, for most cats, not at all. This skewed the data in a way that was difficult to normalise. The Tail Half-Up data was therefore not included in the ANOVA. However, I have included the data for Tail Half-Up in legends by the graphs to give an idea of how this tail position is acting in comparison to the other two possible tail position groups.

All recorded interactions between two cats were divided into one of 2 groups: Those containing rubs (RUB interactions) and those without rubs (NO-RUB interactions).

Behavioural interactions analysed in *Sections 6.2.2.1* and *6.2.2.2* include only interactions beginning with a *Walking Approach* (not a *Run Approach*) because I found that the Run Approach interactions in the University cats followed a different pattern to that of Walking Approach interactions. The majority of approaches began by *Walking Approach* in both sets of cats (Fir Tree Cats, 97.3%; University cats, 84.4%); the results sections *6.2.2.1* and *6.2.2.2* are therefore concerned only with interactions that began with a Walking Approach. Run Approach interactions are dealt with in *Section 6.2.2.3*.

Data was analysed using a repeated measures ANOVA, which eliminates any individual bias which may affect the result. The main effects calculated were: Initiator cat, Tail position (Tail Up position or Tail Neutral position), and type of interaction (either Rub or No Rub). However, I was only interested in the interaction[1] effect of tail position x type of interaction[2]. Data was transformed using LOG10(x+1). Cats which interacted less than 5 times in the observation period were removed from the data prior to the analysis.

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[1] as in the statistical sense

[2] as in the behavioural sense

6.2.2 Results

6.2.2.1 Initiator tail posture: Does the tail posture of the initiator on approach affect the nature of the following interaction?

For each interaction, in both cat colonies, the tail position of the *initiator* on first approach was noted. The distribution of the **initiator approach tail position** across the 2 types of interaction could then be investigated. This data is shown in *Fig. 6.1.*

The interaction effect[1] (tail posture x type of interaction[2] (Rub/NoRub)) was significant in both groups of cats (*Fir Tree Cats:* $F_{1,4}$ =22.72, p<0.01; *University Cats:* $F_{1,16}$ =110.32, p<0.0001). The same pattern was observed in both groups: *A RUB interaction is significantly likely to have been preceded by a Tail Up Approach by the initiator, rather than by a Tail Neutral Approach, but a Tail Up Approach by the initiator is not significantly likely to be followed by a RUB interaction; it is equally as likely* (Fir Tree Cats), *or even more likely* (University Cats) *to be followed by a No Rub Interaction.*

What prevents rubbing from occurring in the cases where the initiator approaches with Tail Up but a Rub interaction does not ensue? In order to investigate this, I looked at the effect of recipient tail posture.

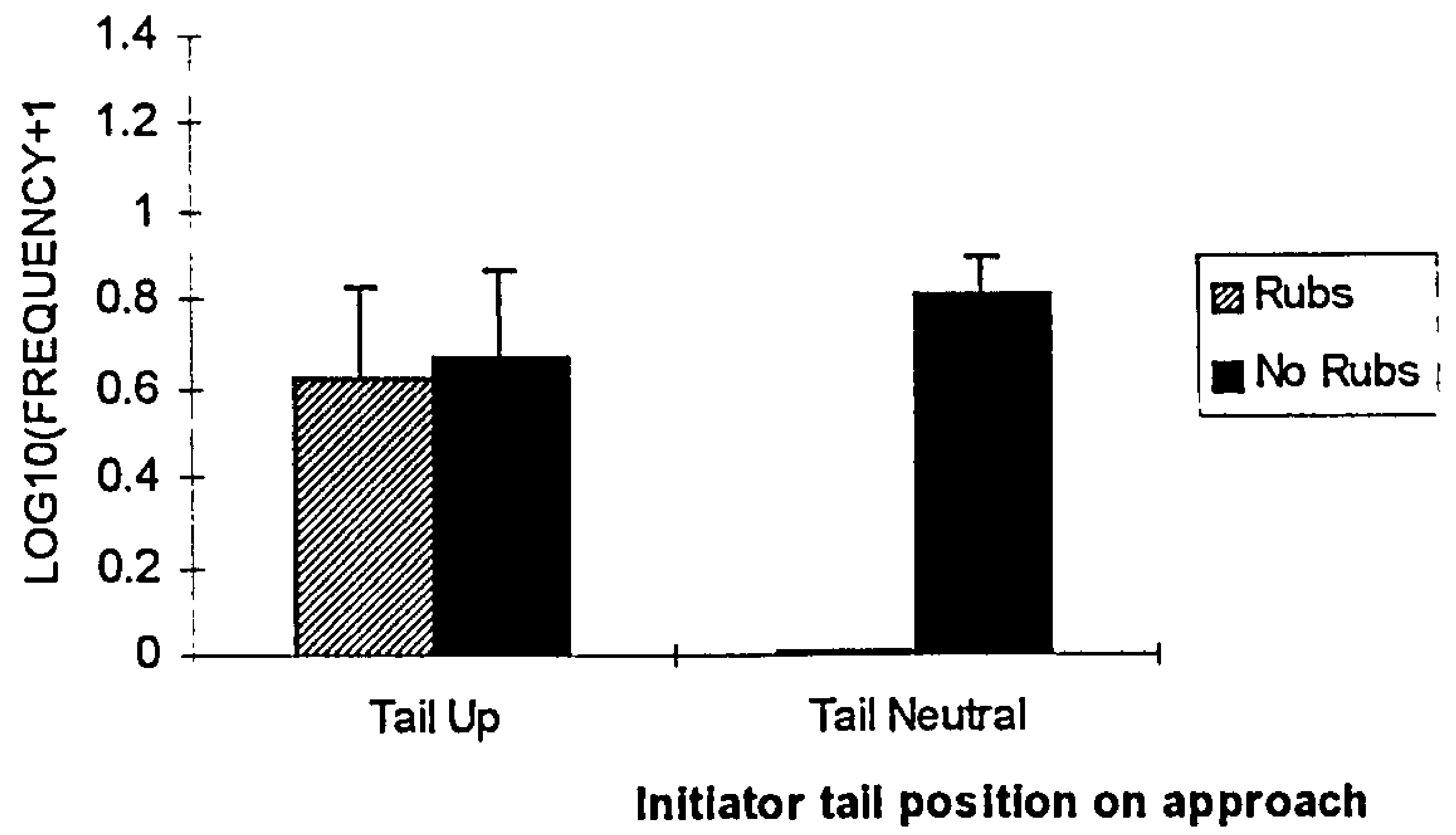
6.2.2.2 Recipient tail posture: Does the recipient tail posture affect the nature of the following interaction?

In order to investigate this it was necessary to look only at interactions that began with a Tail Up Approach by the INITIATOR (so that this variable was then controlled for). The tail posture of the recipient in reaction to the initiator's Tail Up Approach was noted, and the interaction effect for recipient tail posture (Tail Up or Tail Neutral) x type of interaction (Rub or No Rub) was calculated as above.

The interpretation of these results was slightly more complicated due to the fact that the two colonies showed different patterns:

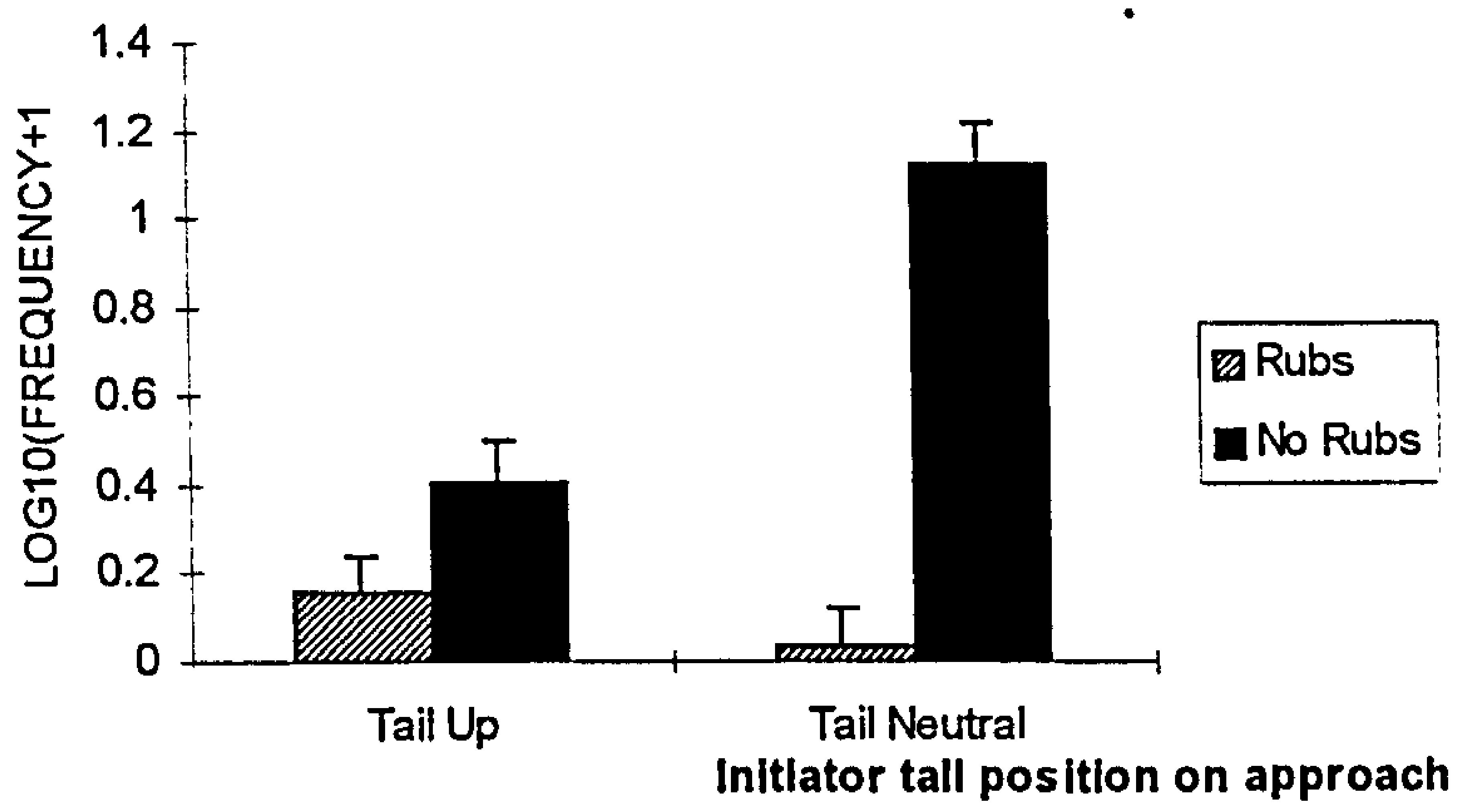
Figure 6.1 **Plot of interaction effect between tail posture of initiator (Tail Up or Tail Neutral) in a Walking Approach, and subsequent type of behavioural interaction (Rub or No Rub);** mean frequency (log10(x+1)) of occurrence in each category (+SE). Tail Half-Up was not included in the ANOVA because it did not occur frequently enough to be analysed (*Fir Tree Cats*, n=19; *University Cats*, n=13). However, its mean values are included in a legend by the graph.

(a) Fir Tree feral cats. Interaction effect (tail position x type of interaction), $F_{1,4} = 22.72$, $p < 0.01$.



Tail Half-Up data (means only): Rubs, 0.24, No Rubs, 0.38.

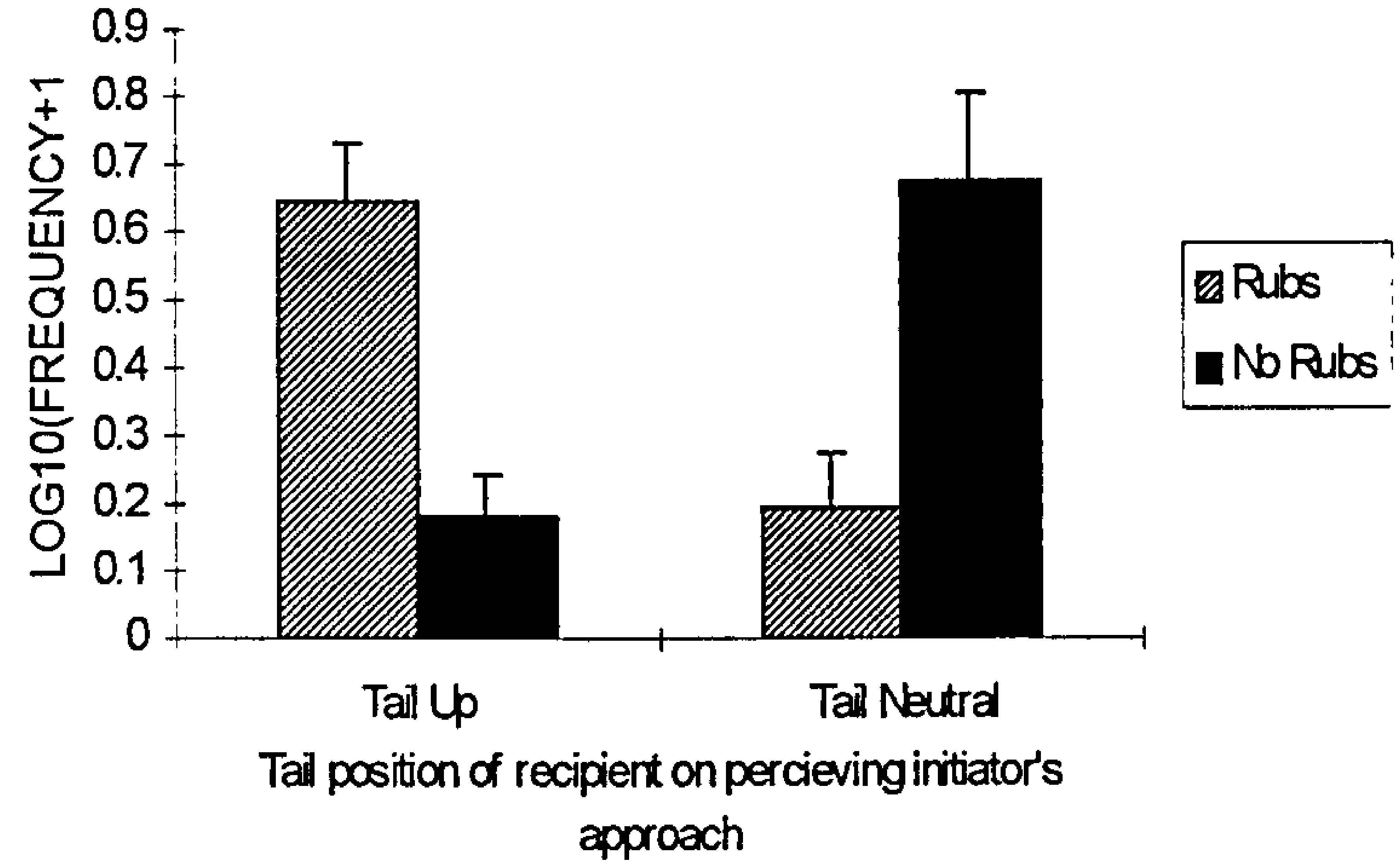
(b) University indoor cats. Interaction effect (tail position x type of interaction) $F_{1,16} = 110.32$, $p < 0.0001$.



Tail Half-Up data (means only): Rubs, 0.028, No Rubs, 0.06.

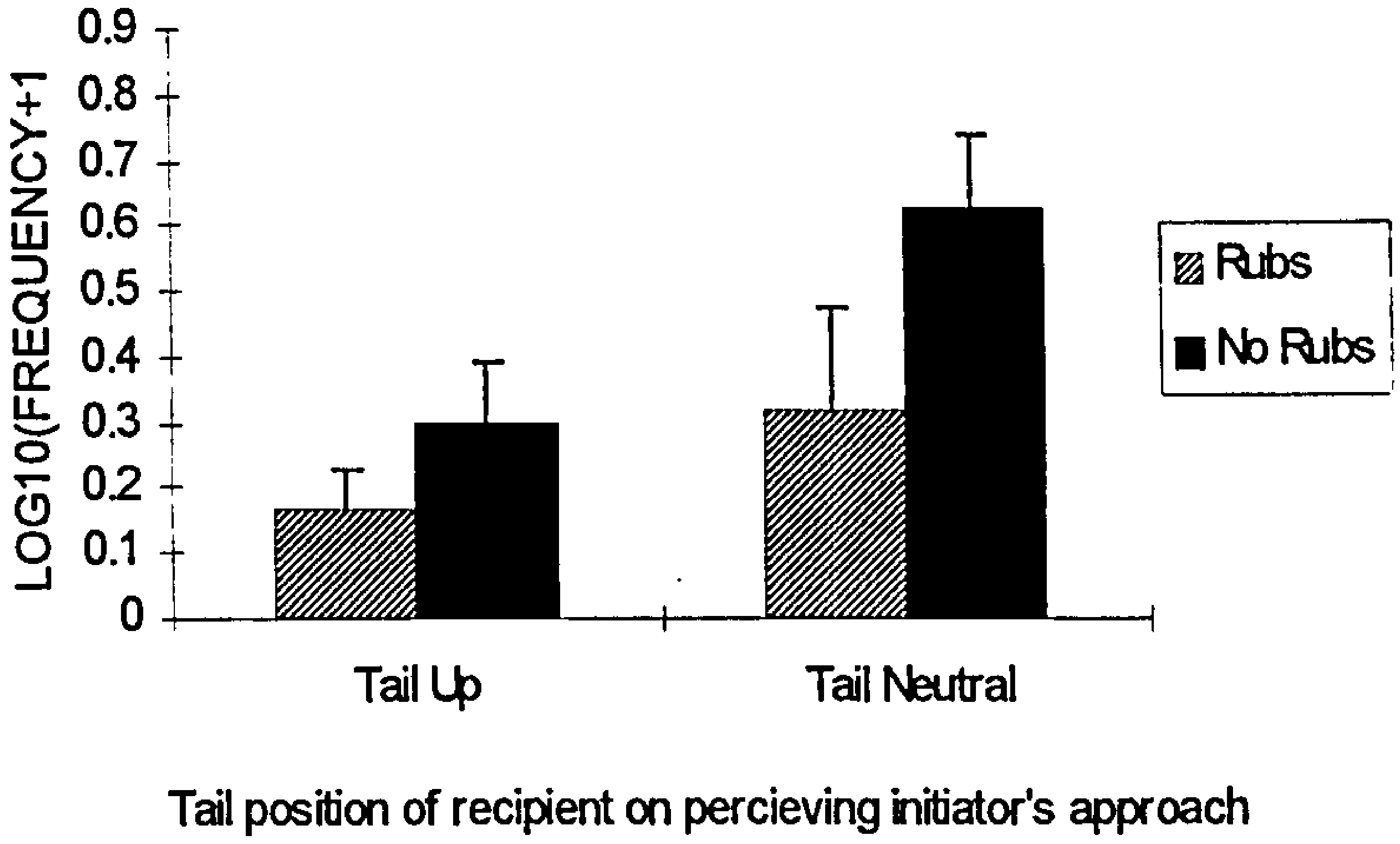
Figure 6.2 **Tail posture of the recipient in response to a TAIL UP INITIATOR APPROACH (Walking).** Plot of the interaction effect between recipient tail position and type of behavioural interaction (Rub or No Rub); mean frequency (log10 (x+1)) of occurrence in each category (+SE). Tail Half-Up was not included in the ANOVA because it did not occur frequently enough to be analysed (*Fir Tree Cats*, n=13; *University Cats*, n=3). However, its mean values are included in the legend below the graph.

(a) Fir Tree feral Cats. Interaction effect (tail position x type of interaction) $F_{1,4}$ =32.23, p<0.01.



Tail Half-Up data (means only): Rubs, 0.095, No Rubs, 0.24.

(b) University indoor cats. Interaction effect (tail position x type of interaction) $F_{1,6}$ =1.33, ns.



Tail Half-Up data (means only): Rubs, 0.00, No Rubs, 0.10.

Fir Tree feral colony: The recipient tail position had a strong effect on the nature of the subsequent interaction: A Tail Up posture by the RECIPIENT in response to a Tail Up INITIATOR Approach is more likely to be followed by a RUB interaction, while a Tail Neutral response by the recipient (in reaction to the same initiator approach) is more likely to be followed by a No Rub interaction (tail position x type of interaction, $F_{1,4}=32.23$, $p<0.01$).

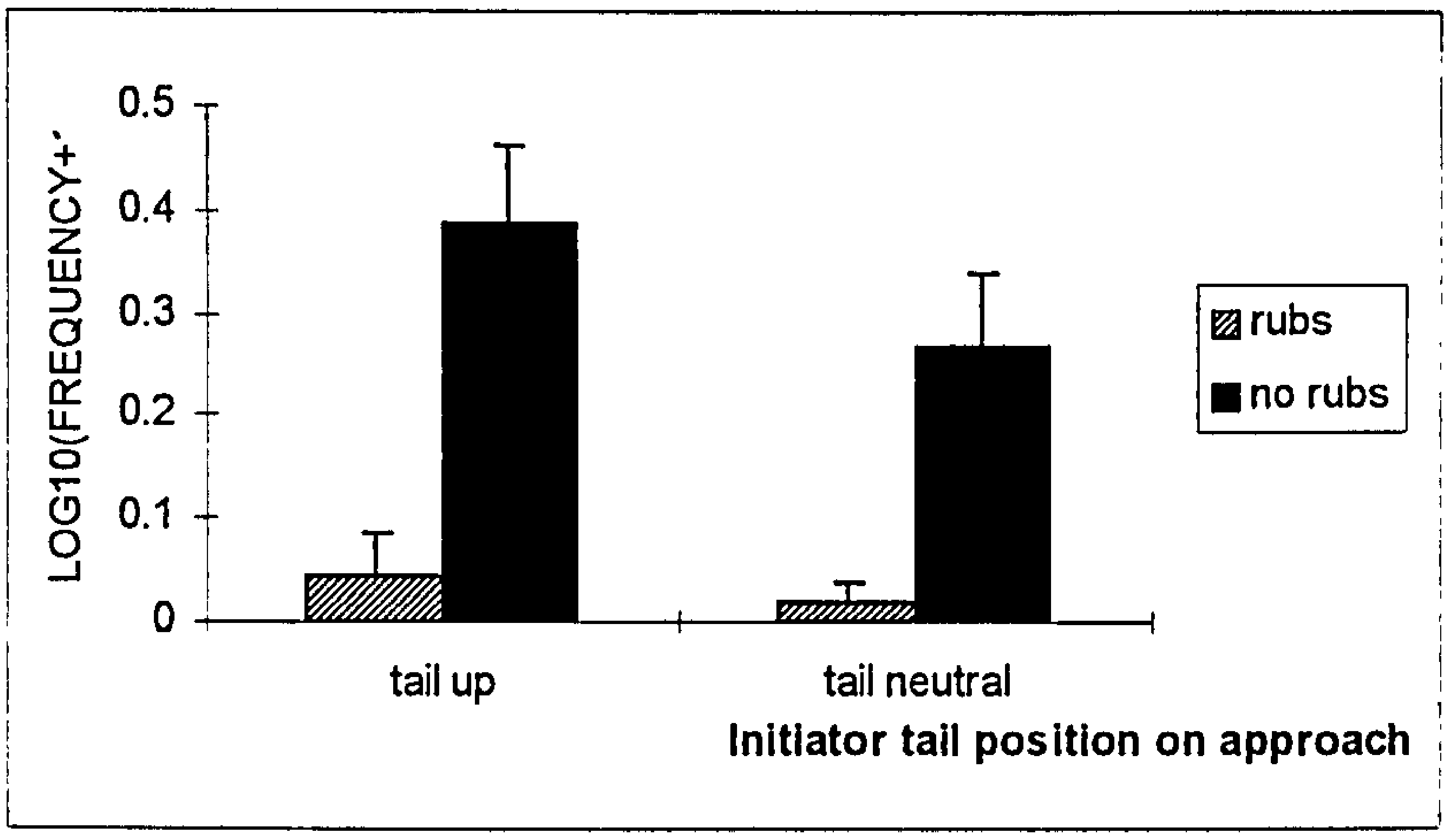
University indoor colony: The recipient tail position has **no effect** on whether or not the following interaction will contain a Rub (tail position x type of interaction, $F_{1,6}=1.33$, ns.). Every tail posture showed more NO RUB interactions than RUB interactions. There was no difference in distribution between different tail postures.

6.2.2.3 Run Approach Interactions: University cats and play

In the University colony, many interactions which began with a Run Approach appeared to be playful. However, this is difficult to prove, as it is almost impossible to classify play interactions objectively by the behaviours contained in them (Barrett & Bateson, 1978; see also *Chapter 3, Section 3.3.1*). The University cats showed a higher frequency of interactions beginning with a Run Approach than did the feral cats (University cats, n=57; feral cats, n=5). In the University cats the Run Approach interactions showed a different distribution across the tail positions than Walking Approaches. For this reason, the results sections *6.2.2.1* and *6.2.2.2* above were only concerned with interactions which began with a Walking Approach.

Fig. 6.3 shows the effect of tail position x type of interaction (Rub/No Rub) for behavioural interactions beginning with an initiator Run Approach (in the same way as was done for Walking Approach interactions in *Fig 6.1)*. This is given for University cats only, as the number of feral cat Run Approach interactions was too low (n=5). In the University cats, too few Run Approach interactions were performed by individual cats to allow analysis by repeated measures ANOVA (Total no of interactions= 57).

Figure 6.3 University indoor cats: **Run Approach Interactions only.**
Plot of the interaction effect between tail posture of initiator (Tail Up/ Tail Neutral) and subsequent type of interaction (Rub/ No Rub).



(i) Rub interactions are rare following a Run Approach. This is not surprising if a Run Approach does indeed occur in the majority of play interactions, as Rub is rarely associated with play (see *Chapter 3, Table 3.1*).

(ii) Tail Up on approach on the other hand is proportionally very common; more common than during Walking Approaches (21% of Walking Approach interactions began with a Tail Up Approach; 51% of Run Approach interactions began with a Tail Up Approach).

(iii) Very few Tail Up Approaches are followed by rubs. This is in contrast to the Walking Approach interactions described in *Sections 6.2.2.1* and *6.2.2.2*. The Tail Up - No Rub category is larger *in proportion* to the other three categories than it is in Walking Approaches (compare *Figs. 6.1b* and *Fig 6.3*).

6.2.3 Discussion

6.2.3.1 Interpretation of results

The results for both colonies show that RUB interactions are more likely to be preceded by a Tail Up Approach by the initiator than by an approach with any other tail position.

In the *feral colony*, a RUB interaction is also more likely to occur if the approach of the initiator is reciprocated by a Tail Up signal from the recipient. Thus, in the feral colony, RUB interactions are most likely to occur if preceded by a *Tail Up Approach from the initiator and a subsequent Tail Up signal from the recipient.*

In the *indoor colony*, however, the tail position of the recipient in response to the initiator's approach has no effect on the subsequent interaction.

My interpretation of this is as follows:

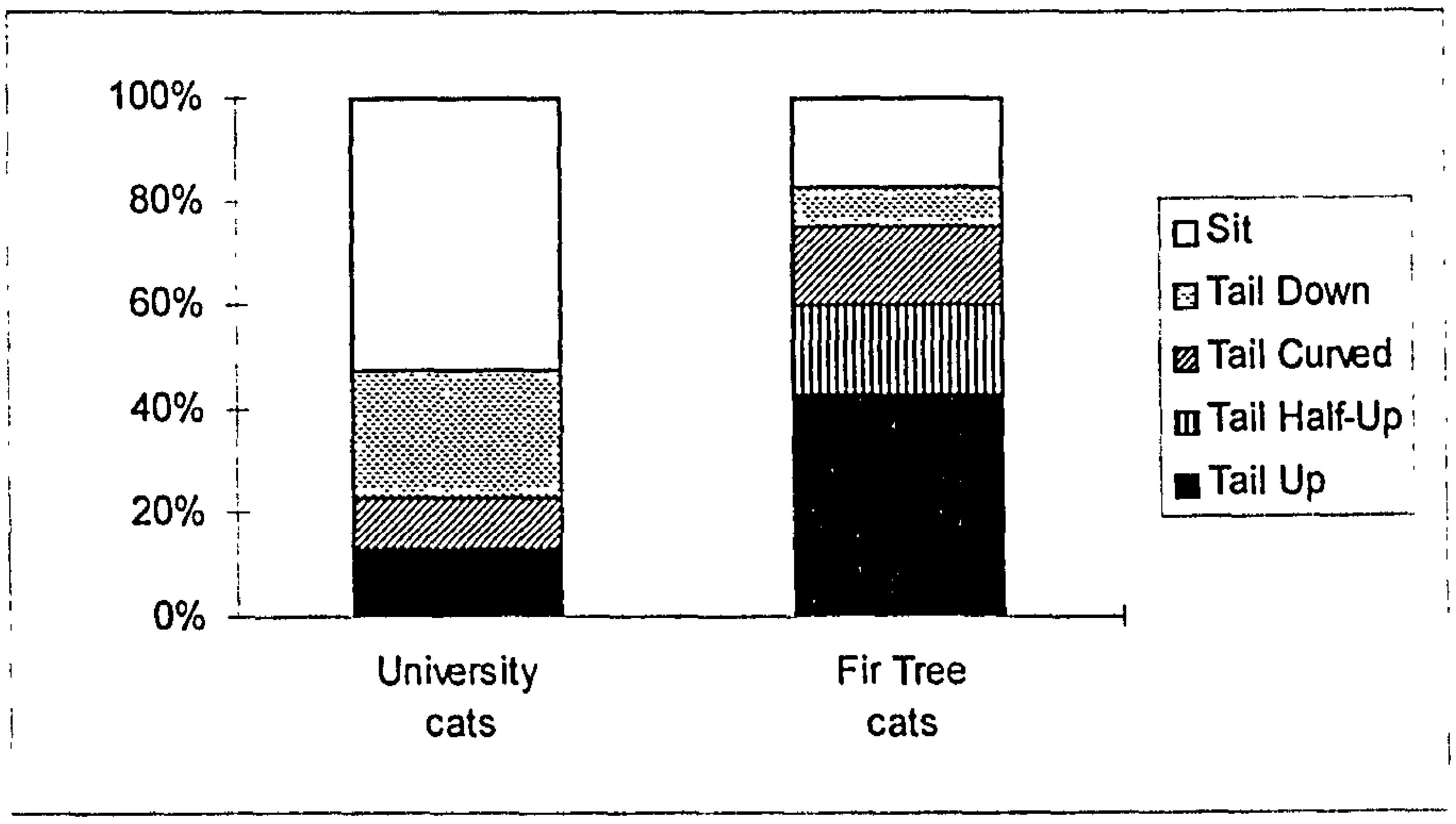
Feral colony: The Tail Up signal is acting as an intention indicator: The initiator signals a Tail Up to imply an intention to rub and be affiliative. This usually occurs as soon as the initiator begins to approach the recipient so that the recipient has the maximum time to catch sight of the signal. For example, I observed approaches in which the initiator was up to 15 metres away from the recipient at the time it began the Tail Up signal.

When the recipient sights the signal, it signals to the initiator with either a Tail Up or no Tail Up (*ie.* any other tail position). This tail position then affects the initiator's subsequent behaviour; the initiator is significantly more likely to rub if the recipient has reciprocated with a Tail Up signal. Thus *the tail up signal in the recipient acts as a intention indicator, implying that it is likely to be receptive to the initiator's affiliative advances (and therefore will not be aggressive).* This signalling of intention would be beneficial in a colony because it would reduce the possibility of aggression caused by unwanted advances.

University indoor colony: A Tail Up Approach by the initiator predicts a RUB Interaction, in the same way as it does in the feral colony. However, the distance at which the signal was emitted was shorter, typically occurring when the cats were less than one metre apart. Initiators were observed approaching with Tail Neutral, and then changing to a Tail Up at the very last second before rubbing, whereas in the feral cats the initiators signalled with a Tail Up as soon as they began to approach. This difference cannot be attributed to the size of the enclosure, because the outside enclosure was 94m^2.

The recipient tail posture has no effect on the subsequent interaction. This may be because the recipient has no time to give a signal, given the evidence that initiator's begin to signal Tail Up at less than 1 m away from the recipient. Or it may be that the initiator is ignoring signals provided by the recipient. Which of these two possibilities is most likely? It seems to be mainly that the recipients are not signalling: *Fig. 6.4* shows the percentage of each recipient posture displayed in response to a Tail Up Approach by the initiator, compared between the 2 colonies (RUB and NO RUB interactions are combined). It shows that for the majority of interactions, the University cats **did not respond** to an initiator Tail Up Approach; they merely remained in their reclining position (Sit/Lie Down/Crouch: 55.3% of interactions). The Fir Tree recipients, in contrast, most commonly reacted to a Tail Up Approach by displaying the Tail Up position (43.9% of all interactions).

Figure 6.4 Percentage of recipient postures displayed in response to a Tail Up Approach by the initiator.



In the indoor colony, therefore, the signalling mechanism does not exist: The initiator tends not to display the Tail Up posture until the very last second of approach, while the recipient tends not to signal at all.

Chapter 5 showed that Tail Up is motivationally linked with rubbing in the domestic cat as domestic cats practically never rub without holding their tail erect (see *Chapter 5, Table 5.1*); 84% (feral cats) and 73% (indoor cats) of Rub Heads occured with a Tail Up. Thus I suggest that in the indoor colony, the Tail Up position which is emitted by the initiator just before rubbing is not a signal, but a behaviour which is physically linked to rubbing. The differences in distances at which the Tail Up position is emitted between Fir Tree cats and University cats give evidence for this.

6.2.3.2 Reasons for the evolution of an intention signal

Intention movements in *aggressive* encounters rarely evolve via ritualisation into signals, due to the fact that it is not in the initiator's interest for its intention movement to be 'read' (Caryl, 1982), and because such a non-costly signal would not be evolutionarily stable, being liable to invasion by cheats (Maynard-Smith, 1974, 1982).

The Tail Up signal, however, is not an aggressive signal, but an affiliative signal. In this case it is actually in both individuals' interest that the intentions of the other cat are known. It is in the initiator's interest to know the mood of the recipient in order that it can avoid the encounter if there is any chance that the recipient might be aggressive; it is in the recipient's interest to know the intentions of the initiator so that it may subsequently signal that the encounter is unwanted. As unwanted encounters may lead to aggression, during which either cat may get injured, it is thus in both cats' interest to communicate their intentions to the other. Maynard-Smith (1991, 1994) showed that non-costly signals may evolve if there is no conflict of interest between signallers. This is often the case in affiliative interactions between members of a colony.

The evolution of this signal is discussed in further detail in the general discussion at the end of this chapter.

6.2.3.3 The relationship between Tail Up and other affiliative behaviours

If, as I hypothesize, the function of the Tail Up signal is to indicate an intention to be affiliative, then the Tail Up signal should be predictive of, not only social rubbing, but also of other affiliative behaviours, such as Sniff, Sniff Rear, and Touch Nose. Allogroom is a separate entity because it generally occurs after two cats have been sitting with one another for a while (*pers.obs.*, van den Bos, *pers.comm.*). Thus the Tail Up Approach does not generally occur immediately before or during allogrooming, since the fact that the two cats are receptive to each other's close presence has been established *before* allogrooming occurs.

It was not possible to test the predictive value of Tail Up for other affiliative behaviours in a similar way to that already carried out for social rubbing, because the behaviours were more infrequent. However, the results quoted in *Chapter 5* do suggest that Tail Up may be predictive of other social behaviours in the feral colony, but not in the indoor colony (results quoted in *Table 6.3*; see also *Chapter 5, Fig. 5.1*)

Table 6.3 **Percentage occurrence with Tail Up for various behaviours.**
† = behaviour occurred less than 10 times.

	Sniff	*Sniff Rear*	*Touch Nose*	*Allogroom*
Feral cats	82%	64%	100%	†
Indoor cats	15%	2%	13%	4%

In the *feral cats,* the affiliative behaviours Sniff, Sniff Rear, and Touch Nose occured mainly during Tail Up, as would be expected if Tail Up is occuring as an intention indicator. In the indoor cats, in contrast, these same behaviours occurred more commonly with Tail Down (*i.e.* neutral tail position). This is as I would expect if the Tail Up is not acting as a signal in this colony.

This data on the other social behaviours therefore backs up the hypothesis that in feral cats the Tail Up acts as an intention and mood indicator, but that in indoor cats Tail Up does not act as a signal at all. This hypothesis is tested experimentally in *Section 6.3.*

6.2.3.4 Run Approach Interactions (University cats only)

In the University cats, interactions beginning with a Run Approach frequently involved play (See *Section 6.2.2.3*). About half of Run Approach interactions began with a Tail Up Run Approach by the initiator. In addition, the graph showing the effect of initiator tail position x type of interaction (RUB/NO RUB) (*Fig 6.3*) showed a different pattern to that produced by Walking Approaches (*Fig 6.1b*), with the Tail Up - No Rub category occuring *proportionally* more often in Run Approach interactions than during Walk Approach interactions. Rubs were rare in Run Approach interactions.

One suggestion for the interpretation of these results is that Tail Up is used as a signal of intention of affiliation in play. This would be particularly important in play where the associated behaviours are often similar to agonistic behaviours, leaving room for ambiguity in interpretation; recipients may interpret a Run Approach as aggression, and respond aggressively when the initiator is, in fact, playing. However, as I could not objectively categorize play interactions as distinct from aggressive interactions it was impossible to test this hypothesis. Alternatively, it may be that Tail Up is linked to motivational "excitement", as defined by Kiley-Worthington (1976) and thus is exhibited in play (this hypothesis is discussed in detail in *Chapter 8, Section 8.4.1*).

6.2.3.5 Interpretation of the absence of signalling in the indoor cats

These indoor cats live in a closed system, with fixed boundaries and without any possibility of meeting unfamiliar cats. They have lived together for a minimum of 6 years, and are almost constantly in sight of one another. It may be that the relationships between the cats in each possible dyad are so well defined after several years of living in close proximity to one another, that the situation has led to a cultural slip in signalling. Signalling of intention may be unimportant because the individuals know one another so well that they are aware of what one anothers' reactions are likely to be. There may, therefore, be a lower risk of aggression due to an unexpected or unwanted advance. However, there may be a higher risk during play, where the behaviours exhibited are ambiguous (see *Section 6.2.3.4*, above). This could explain the high proportion of Tail Up Approaches in Run Approach interactions.

The Fir Tree feral cats are also very familiar with one another, and have lived with one another for at least 5 years. The important difference is that they live in an open system, where there is constantly the possibility of meeting unfamiliar or non-colony cats, with which it would be important to maintain the signalling system in order to avoid unnecessary aggression. There is therefore less chance for cultural change due to the presence of external individuals. In addition, the feral cats spend less of their time with each other than do the indoor cats. This makes it more difficult for the feral cats to track the mood of the other cats in their colony, (*e.g.* by observing their behaviour to other colony cats), making a signal displaying intention more important than in the indoor colony.

In addition, the University cats have come from generations of cats that have been reared indoors. If the Tail Up signal is a culturally learnt signal, as seems likely, (though the actual temporal and motivational connection with rubbing may not be), then it may be that the Tail Up signalling method broke down several generations previously and was therefore not passed on. Either of these explanations would give evidence for cultural differences in signalling in cats.

Overall, the Fir Tree feral cats have maintained a precise mechanism for signalling intention and/or mood in order to reduce aggression. The University indoor cats, however, appear to have undergone a cultural change which has resulted in a decrease in the use of signals. The hypothesis that the Tail Up signal is used as an intention indicator in outdoor cats is tested experimentally in the following section.

6.3 THE REACTIONS OF HOUSE CATS AND INDOOR COLONY CATS TO SILHOUETTES OF CATS WITH DIFFERING TAIL POSITIONS

The following hypotheses were created by the field observation data in the previous section:

(i) In free ranging cats the Tail Up signal is a signal of intention to be affiliative

(ii) In indoor cats the Tail Up position does not act as a signal of intention to be affiliative, (though may indicate an intention to play).

In this section, these hypotheses will be tested experimentally.

There is evidence that cats initially react to cat-shaped silhouettes as if they were real cats (Leyhausen, 1979, Kolb & Nonneman, 1975). Leyhausen (1979) reports that cats sniff cat silhouettes from front to rear, as they would a real cat. However, he also reports that cats lose interest in them rapidly, usually during the course of a second test. Kolb & Nonneman (1975) compared the reaction of adult cats to (a) real cats, (b) silhouettes of random shape, and (c) silhouettes of cat shape. Cats reaction to the cat-silhouette was similar to that of a real unfamiliar cat: they exhibited pilo-erection, slow cautious approach and occasionally vocalisations. They subsequently would investigate the silhouette, sniffing both head and anal regions (locations of the scent glands), and sometimes pawing at the head region. Cats showed little or no reponse to randomly shaped silhouettes.

A cat-shaped silhouette was therefore used in this experiment as a standardized model for a real cat to investigate the effect of tail position on the behaviour of real cats.

If the Tail Up position is acting as a signal of intention to be affiliative, then the following would be expected to be true:

(1) Cats will approach a TAIL UP silhouette more quickly than a TAIL DOWN (This was the neutral tail position chosen; see *Section 6.3.1*) silhouette.

(2) With the TAIL UP silhouette, cats will exhibit fewer behaviours indicating confusion or internal motivational conflict (*i.e.* Pause, Watch, Tail Wave, Tail Jerk; see *Chapter 3, Section 3.4.6*), than during the TAIL DOWN silhouette.

3) Cats will be more likely to exhibit a Tail Up (*Affiliative*) position in response to the

TAIL UP silhouette, and a neutral (*i.e.* Tail Down or Tail Curved) or defensive (*i.e.* Tail Under) position to a TAIL DOWN silhouette.

6.3.1 Methods

Life-size silhouettes of two cats were constructed, one with the tail in the Tail Up position, the other with the tail in the Tail Down position (*See Plate 6.1a&b* for pictures). Tail Down was chosen as a Tail Neutral position because evidence from *Chapter 5* indicated that Tail Down is a commonly used neutral tail position.

Subjects used.

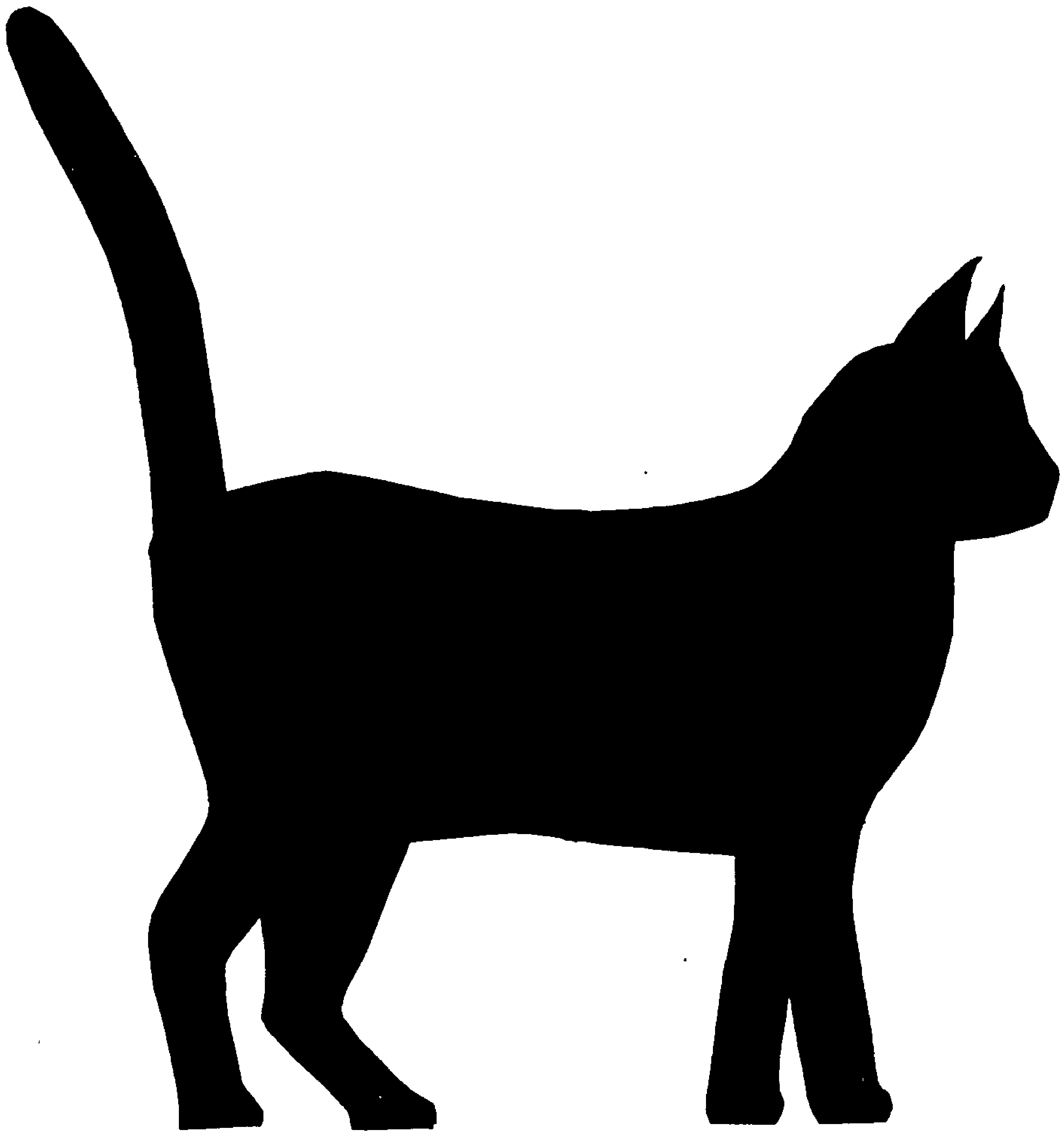
The University cats were again used, of which ten cats were tested. The feral cats could not be used for this experiment due to their timidity towards humans. Individual house cats were therefore used instead (*i.e.* cats individually owned and belonging to a particular household), all of which had regular exposure to unfamiliar cats (and also familiar cats which they do not live with), and which were free ranging. Because they are used to human presence they could be easily handled for the purposes of the experiment. Twelve house cats were tested.

Procedure

The University cats were all tested separately in a room which they are accustomed to (visiting it for approximately 1 hour, 4 times per week), but which is not their habitual quarters. The behaviour of the cat was monitored by two video cameras set into the wall and roof of the room, without a human being present in the room. The procedure for each cat was as follows:

The cat was taken into the room and placed 2 metres away from one of the silhouettes, which was stuck to the wall (cream-coloured), with its feet touching the ground. The cat was videoed for one minute and then taken back to its living quarters. Cats were only observed for one minute because in preliminary trials I found that their interest in the silhouette declined rapidly after about 30 seconds or so.

Plate 6.1 The TAIL UP silhouette (actual silhouette used was life size).
The TAIL DOWN silhouette had the same body with a TAIL DOWN position.



The domestic house cats could not be tested in this observation room because they were not familiar with it. Each cat was therefore tested in a suitable room, in its own home, and its reaction to the silhouette filmed by video on a tripod positioned in an elevated place in the room. The procedure was otherwise exactly as for the University cats.

The order in which the two silhouettes were presented was allocated randomly to each cat, and a month was left between each treatment. Half the cats from each group were allocated TAIL DOWN (Treatment A) first; the other half TAIL UP (Treatment B) first. I defined the first session for every cat as the *first trial*, regardless of the treatment given, and the second session as the second trial. The effect of *trial* was looked at to investigate whether an order effect was occurring (*i.e.* Whether the cats' reaction to a silhouette was affected by whether they had had a previous experience of one).

Various measures were extracted from the videotapes:

- *Measures of the tail position of the target cat:*
  Tail position after first sighting silhouette
  Tail position whilst approaching silhouette
- *Measures of the speed of approach of the target cat:*
  Latency from initial emplacement to approaching within 0.5m from silhouette
  Latency from first sighting of silhouette to approaching within 0.5m
- *Measures of the internal motivational conflict of the target cat:*
  Frequency of Pauses
  Frequency of Tail Waves/Tail Jerks
  Frequency of Watches
- *Other behaviours that were performed during the minute observation period were also noted.*

Data analysis

A repeated measures multifactor ANOVA (nested) was carried out in order to avoid pseudoreplication (Hurlbert, 1984), as each cat was used twice during the course of the experiment. Data was transformed using $\log10(x+1)$.

The effect of trial could not be tested **directly** due to the nested nature of the experiment. Cats were therefore divided into 2 groups:

Group A: Cats which had TAIL UP treatment first.

Group B: Cats which had TAIL DOWN treatment first.

This group effect was incorporated into the model to account for the effect of TRIAL. A significant value for the treatment x group interaction would therefore indicate that a trial effect was occurring.

For some variables, a one-way ANOVA was also carried out on data from the first trial only. This data was independent. However, this analysis did not account for individual cat idiosyncrasy in reaction to silhouettes (*i.e.* irrespective of tail position).

6.3.2 Results

All cats reacted to the silhouette in a way similar to that described by Leyhausen (1979) and Kolb & Nonneman (1975), initially behaving as if the silhouette was a real cat. Most cats stared at or watched the silhouette on first noticing it. This was followed usually by an approach, and then a sniffing investigation, then a move away, though individual behaviour varied. Some of the more uncommon behaviours exhibited included piloerection, arched back, and cuffing the silhouette. Cats lost interest after the initial approach, some even before this, presumably as soon as they realised that the model was not real.

6.3.2.1 Effect of treatment on the tail position of the target cat

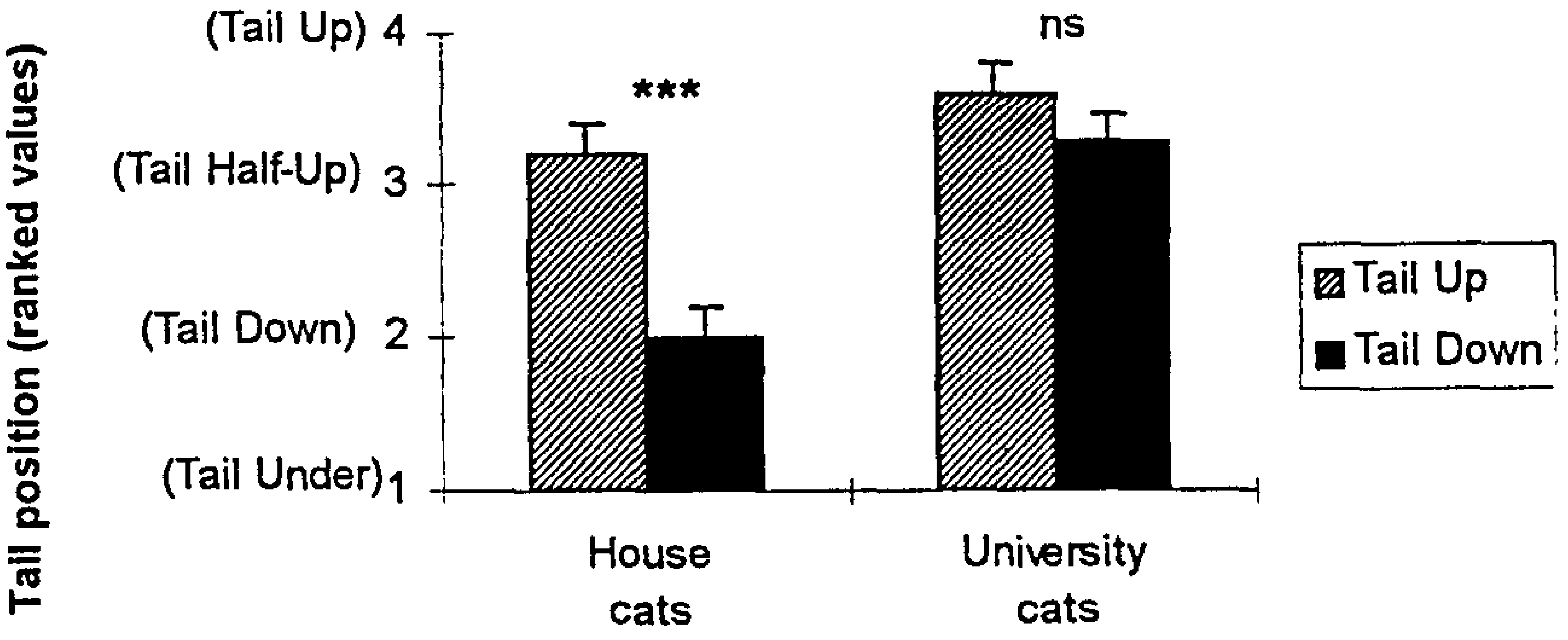
Cat tail postions were ranked into the following classes; 4 (Tail Up), 3 (Tail Half-Up), 2 (Tail Down), and 1 (Tail Under), so that the higher the number, the higher the tail was held. Tail Curved was not exhibited at all during the course of this experiment and so was not included. These ranked values were then used in an ANOVA.

House cats

Treatment significantly affected the target cat tail position. Tail position was held higher (*i.e.* nearer Tail Up, or 4) under the TAIL UP silhouette treatment than under the TAIL

Figure 6.5 Mean ranked tail position (+SE) under each treatment for both cat colonies. (a) gives the mean ranked treatment on first sighting of the silhouette. (b) gives the mean ranked tail position on approaching the silhouette. The tail position corresponding to each rank number is given in parentheses by the number. Significance levels for differences between treatments are given above the pair of bars for each cat colony. $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***.

(a) Mean ranked tail position on first sighting of silhouette.



(b) Mean ranked tail position on approaching the silhouette.

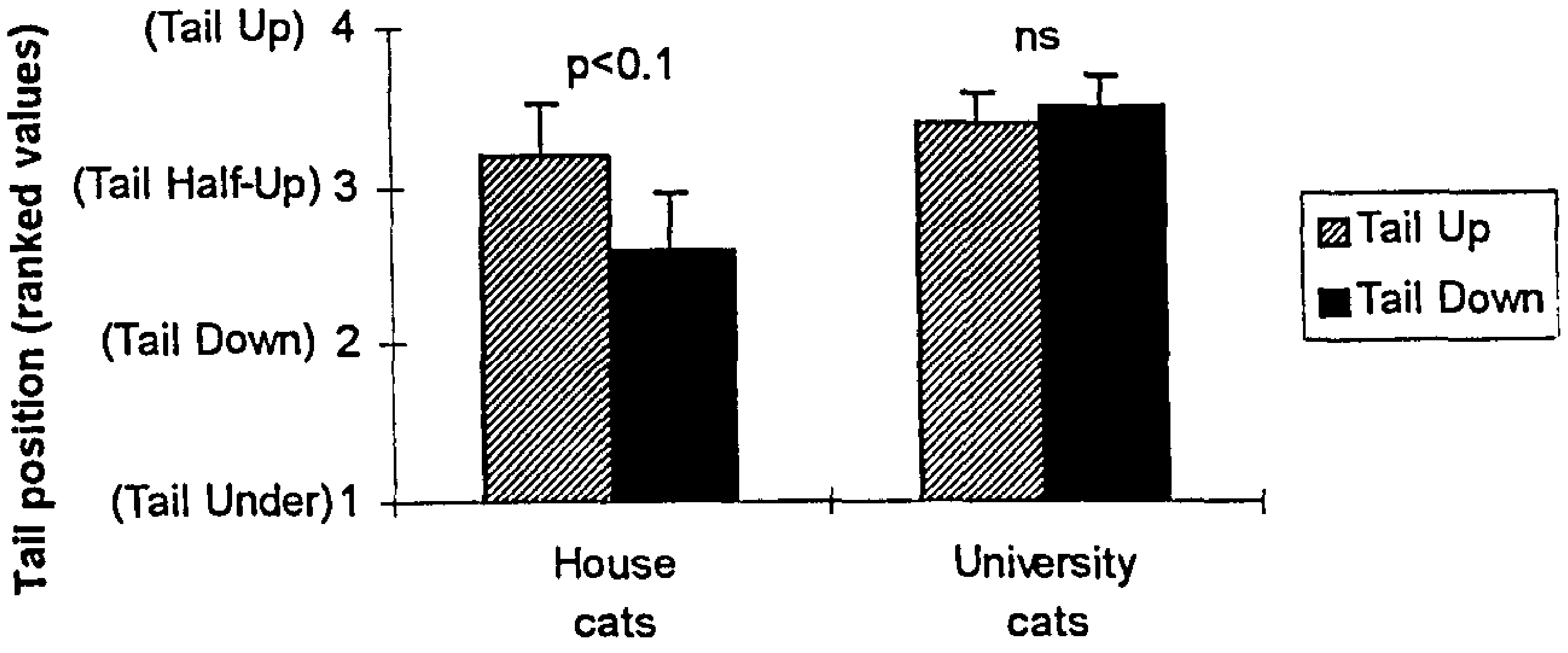


Table 6.4 Table of ANOVA results for (a) House cats and (b) University cats. F values refer to a multifactor nested ANOVA as described in the methods. $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***. P values between 0.05 and 0.2 are quoted. Group main effect looked for differences between groups where Group A cats had TAIL UP silhouette treatment first, and Group B had TAIL DOWN silhouette treatment first.

(a) House cats

Behaviour Variable	Treatment main effect		Group main effect		Treatment x group	
	F	*P value*	F	*P value*	F	*P value*
Tail position on Approach	$F_{1,9}=4.41$	$p<0.1$	$F_{1,9}=2.09$	–	$F_{1,9}=0.00$	–
Tail position on first sighting	$F_{1,10}=17.5$	***	$F_{1,10}=0.36$	–	$F_{1,10}=0.36$	–
Latency fromemplacement to approach <0.5m	$F_{1,10}=4.16$	$p<0.1$	$F_{1,10}=0.27$	–	$F_{1,10}=2.87$	$p=0.12$
Latency from first sighting to approach <0.5m	$F_{1,10}=1.07$	–	$F_{1,10}=0.53$	–	$F_{1,10}=1.27$	–
Pause *frequency*	$F_{1,10}=0.07$	–	$F_{1,10}=1.65$	–	$F_{1,10}=1.07$	*
Watch *frequency*	$F_{1,10}=0.03$	–	$F_{1,10}=2.83$	$p<0.1$	$F_{1,10}=0.05$	–
Tail Wave & Tail Jerk *frequency*	$F_{1,10}=2.07$	$p=0.18$	$F_{1,10}=1.34$	–	$F_{1,10}=2.44$	$p=0.14$

(b) University cats

Behaviour Variable	Treatment main effect		Group main effect		Treatment x group	
	$F_{1,8}$	*P value*	$F_{1,8}$	*P value*	$F_{1,8}$	*P value*
Tail position on Approach	0.13	–	6.13	*	3.13	$p=0.11$
Tail position on first sighting	2.25	$p=0.17$	1.29	–	1.00	–
Latency from emplacement to approach <0.5m.	1.66	–	1.07	–	0.13	–
Latency from first sighting to approach <0.5m	0.03	–	0.35	–	0.22	–
Pause *frequency*	0.11	–	0.13	–	0.00	–
Watch *frequency*	4.50	$p<0.1$	0.44	–	4.50	$p<0.1$
Tail Wave & Tail Jerk *frequency*	0.00	–	0.00	–	2.19	$p=0.17$

DOWN silhouette treatment, and vice versa. This pattern was significant for the variable *tail position on first sighting silhouette* (Multifactor ANOVA, treatment main effect, $F_{1,10}=17.50$, $p<0.001$), but was only almost significant for the variable *tail position on approach* (Multifactor ANOVA, treatment main effect, $F_{1,10}= 4.41$, $p<0.1$). *Fig. 6.5* displays the mean rank tail position value for each treatment, and *Table 6.4* gives the exact F ratios. There was no significant difference between groups, and no significant group x treatment effect (See *Table 6.4* for F ratios). The effect of trial therefore does not appear to be significantly affecting the cats' behaviour.

University cats

Treatment did not affect the tail position of the target cats (*Tail position on first sighting*; $F_{1,8}=2.25$, ns; *Tail position on approach*; $F_{1,8}= 1.13$, ns). 9 out of the 10 cats held the same tail position under both treatments, thus indicating that tail position in these cats is controlled by idiosyncracy. The group effect was significant for tail position of approach ($F_{1,8}=6.13$, $p<0.05$), with Group A having a higher mean tail position ranked value (*ie.* nearer Tail Up) than Group B. However this was not significant for the variable of tail position at first sighting. The treatment x group interaction was almost significant for tail position on approach ($F_{1,8}=3.13$, $p=0.11$), though not for tail position on first sighting, indicating that trial order was not significantly affecting the cats' behaviour.

6.3.2.2 Effect of treatment on latency to approach

House cats appeared to approach the TAIL UP silhouette quicker than the TAIL DOWN silhouette, although this was not totally significant (*Latency from intial emplacement to approaching within 0.5m*; $F_{1,10}= 4.16$, $p<0.1$; See *Fig. 6.6*). The *latency from initial sighting to approach* showed the same pattern but was not significant. It is possible that I may have wrongly judged the cats 'initial sighting' of the silhouette, in which case this may have affected this variable. Latency to approach from initial emplacement is a more objective measure.

This effect was not observed for the University cats at all (See *Fig 6.6* and *Table 6.4* for F ratios)

Figure 6.6 Mean latency to approach within 0.5m of the silhouette (+SE) in seconds from initial emplacement, for each treatment and for both cat colonies. Figures given are back transformed from the log value. Significance levels for differences between treatments are given above the pair of bars for each cat colony. p<0.05 *, p<0.01 **, p<0.001 ***, ns=p>0.1.

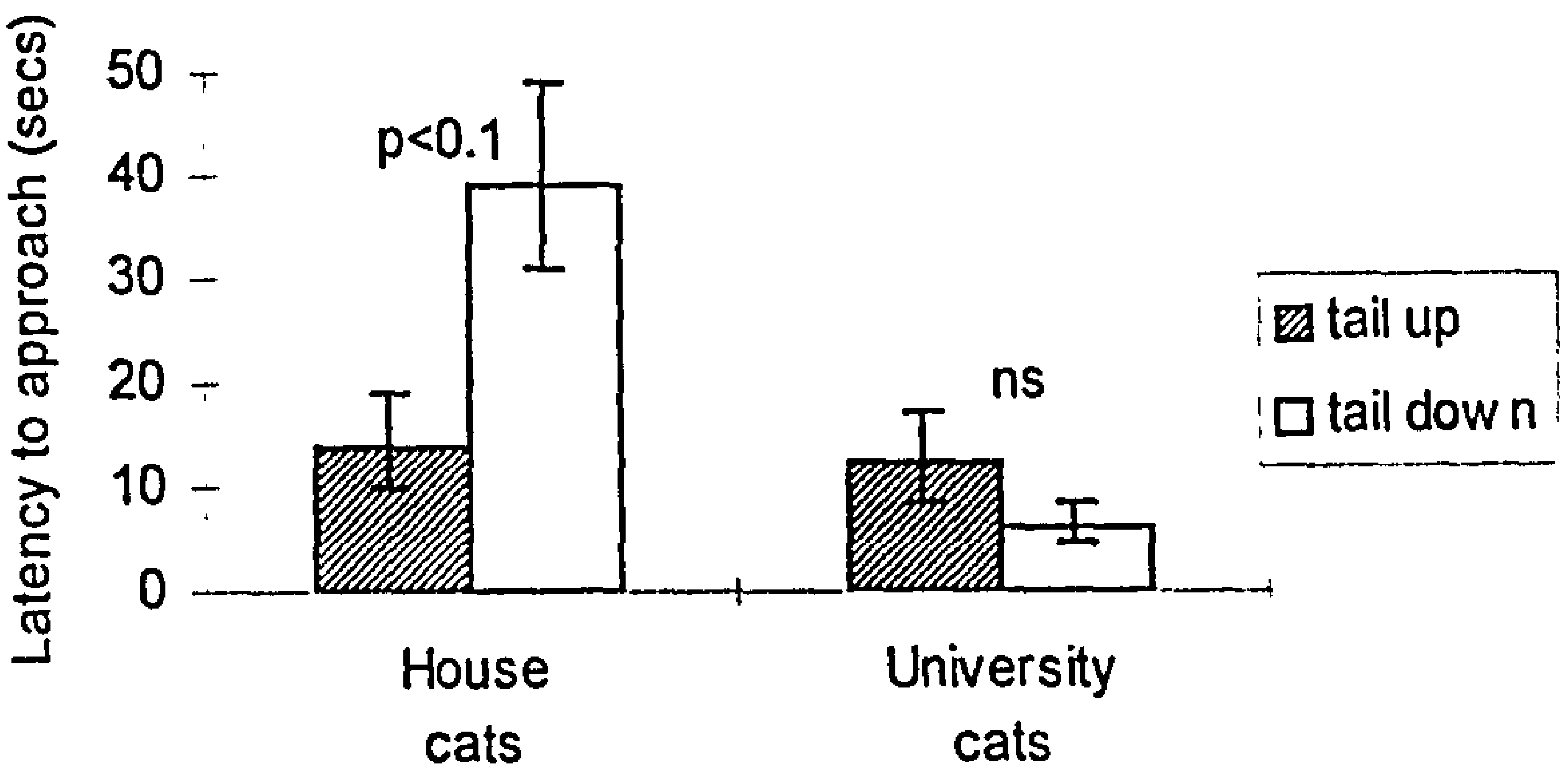
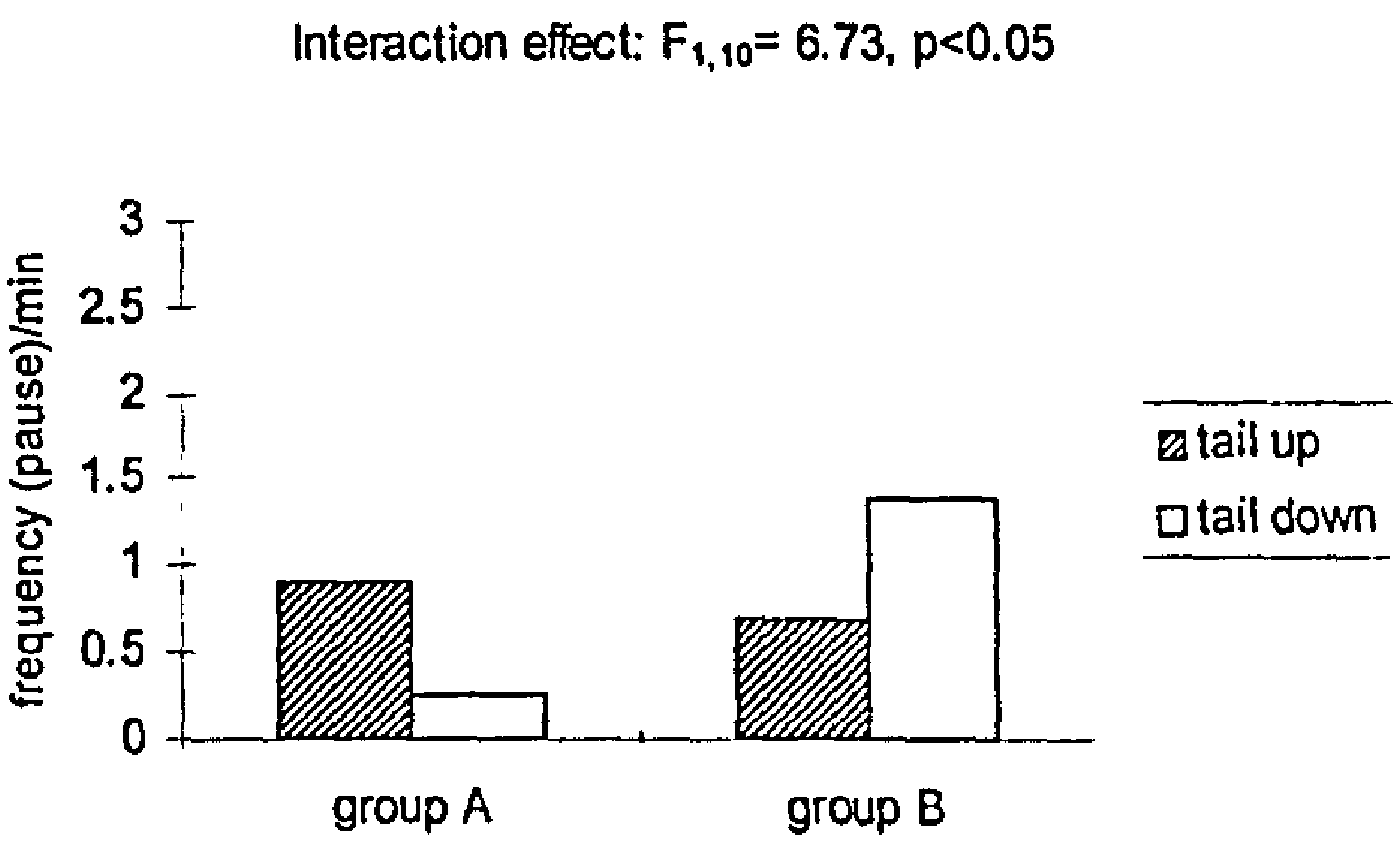
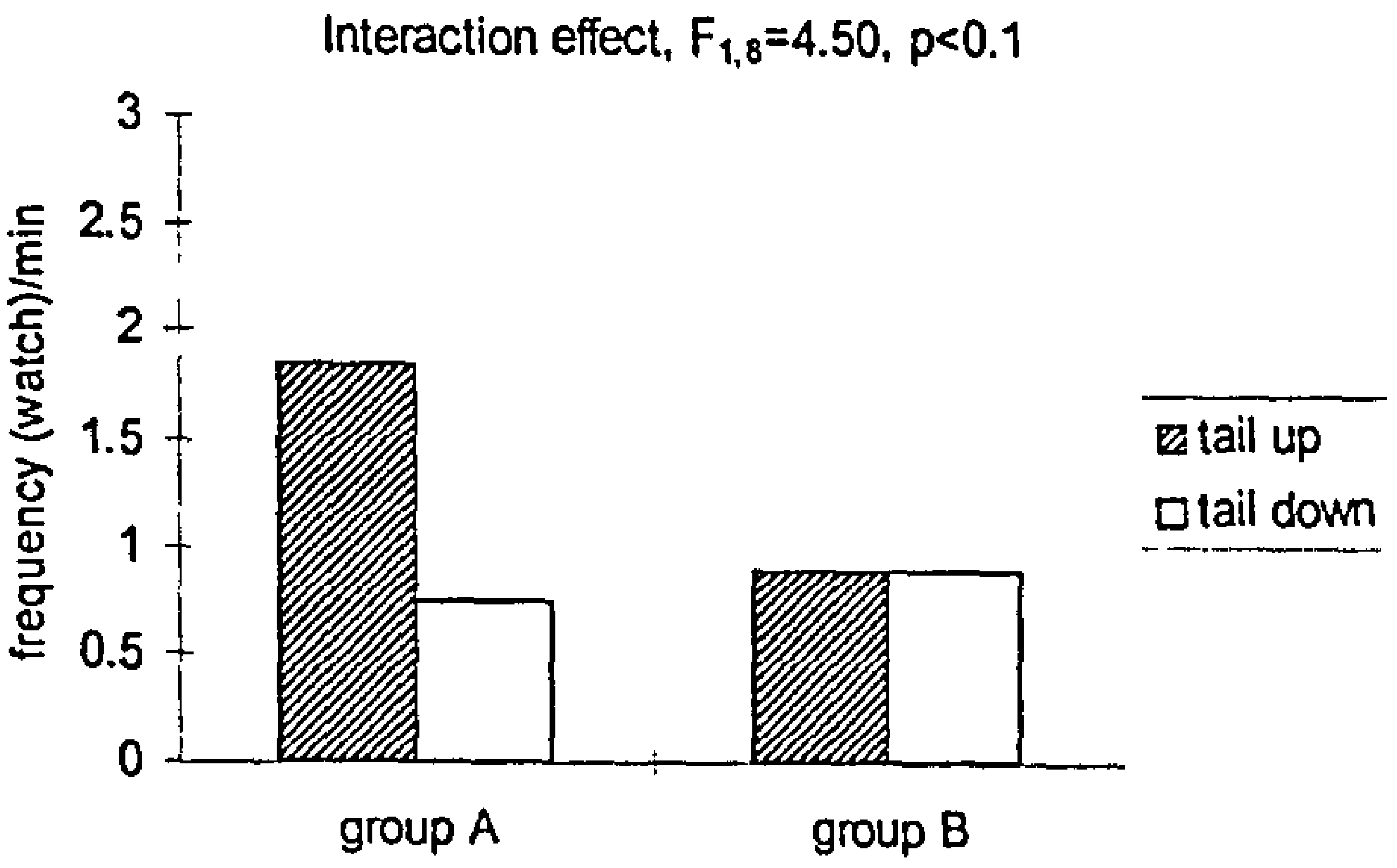


Figure 6.7 Interaction plots (treatment x group) for each variable where $p<0.2$. Graphs show mean frequency of (a) Pauses (House cats only) (b) Watch (University cats only), and (c) Tail Waves&Jerks (University and House cats) per minute (±SE). Group A cats had the TAIL UP silhouette treatment first; Group B had the TAIL DOWN treatment first.

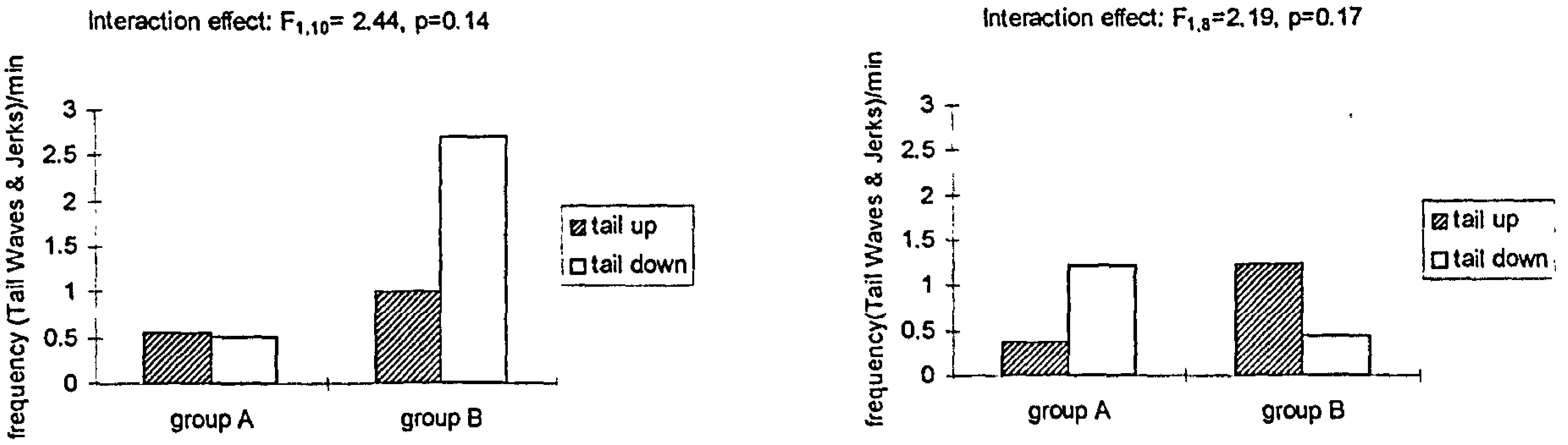
(a) Mean *Pause* frequency per minute in the House cats.



(b) Mean *Watch* frequency per minute in the University cats.



(c) Mean *Tail Waves&Jerks* frequency per minute in both the University and House cats.


House cats

University cats

The group effect and the treatment x group interaction effect were both non-significant in both cat colonies (see *Table 6.4*), indicating that a trial effect was not occurring.

6.3.2.3 Effect of treatment on the frequency of Pause, Watch, Tail Wave & Tail Jerk

None of these behaviours were significantly affected by treatment under a Multifactor ANOVA (House Cats; *Pause*, $F_{1,10}=0.07$, ns, *Watch*, $F_{1,10}=0.03$, ns, *Tail Jerks&Waves*, $F_{1,10}=2.07$, ns ($p=0.18$); University cats; *Pause*, $F_{1,10}=0.11$, ns, *Watch*, $F_{1,10}=4.50$, $p<0.1$, *Tail Jerks&Waves*, $F_{1,10}=0.00$, ns).

Group effect was also non-significant in all variables. However, the treatment x group interaction was significant for variable Pause in the house cats ($F_{1,10}=6.73$, $p<0.05$), and was almost significant in three other cases (House Cats; *Tail Jerks&Waves*, $F_{1,10}=2.44$, ns ($p=0.14$) ; University cats; *Watch*, $F_{1,10}=4.50$, $p<0.1$, *Tail Jerks&Waves* $F_{1,10}=2.19$, ns ($p=0.17$). This indicated that the trial order may have been slightly affecting the behaviour of the cats in these variables, although they are not significant. *Fig. 6.7* shows interaction plots for each of these variables.

Fig. 6.7a, shows the mean *Pause* frequency in the house cats (treatment x group interaction, $F_{1,10}=6.73$, $p<0.05$). Remembering that Group A had the TAIL UP treatment first, and Group B had TAIL DOWN treatment first, it can be seen that *Pause* frequency was higher in the first trial in both cases, regardless of the treatment. The *Tail Waves&Jerks* frequency in the house cats and the *Watch* frequency in the University cats are both more difficult to interpret, but they do seem to be following a similar trend (See *Fig 6.7b&c*). As these three behaviours (Pause, Watch and Tail Waves&Jerks) are expressions of internal motivational conflict, it is not surprising that they occur at a higher level during the first trial, when the situation is new, than during the second. The frequency of Tail Jerks & Waves in the University colony, however appears to be following the opposite trend.

It is difficult to totally eliminate the effect of trial (and any interaction[3] effects involving trial) on these variables because of the nested nature of the experiment. A one-way ANOVA was therefore carried out on the first trial only, in order to totally eliminate the trial effect.

In the *house cats*, the effect of treatment on Tail Jerks&Waves was almost significant ($F_{1,10}$=3.85, p<0.1). *Fig 6.8c* shows the mean frequency of Tail Jerks&Waves, carried out at a higher frequency under the TAIL DOWN treatment than under the TAIL UP treatment. Watch and Pause showed a similar pattern, (See *Figs. 6.8a & b*), occuring at a higher rate under the TAIL DOWN treatment than under the TAIL UP treatment. However, neither of these were significant (House cats; *Watch*, $F_{1,10}$=2.01, ns; *Pause*, $F_{1,10}$=0.69, ns).

There was no effect in the *University cats* for Tail Waves&Jerks ($F_{1,10}$=0.01, ns; see *Fig 6.8c*) or Pause ($F_{1,10}$=0.13, ns; see *Fig 6.8a*). Watch was almost significant ($F_{1,10}$=3.49, p<0.1), but showed a different pattern, being exhibited at a higher frequency in the TAIL UP treatment than the TAIL DOWN treatment (See *Fig 6.8b*).

6.3.2.4 Effect of trial

There were very few significant effects caused by treatment x group interactions (*i.e.* effect caused by trial; see *Section 6.3.1, Data Analysis*). However, trial did appear to be slightly affecting the frequency of some behaviours, (Pause, Watch and Tail Waves&Jerks; see *Figs. 6.7 a,b&c*) although it was not totally significant. It is possible that the method of statistics (multifactor nested ANOVA), which could not test for trial directly (only indirectly via the treatment x group interaction), could not pick up on the trial effect as strongly as it might have done if it had been possible to test for it directly. It was also not possible to test for treatment x trial interactions, which may have been affecting the analysis.

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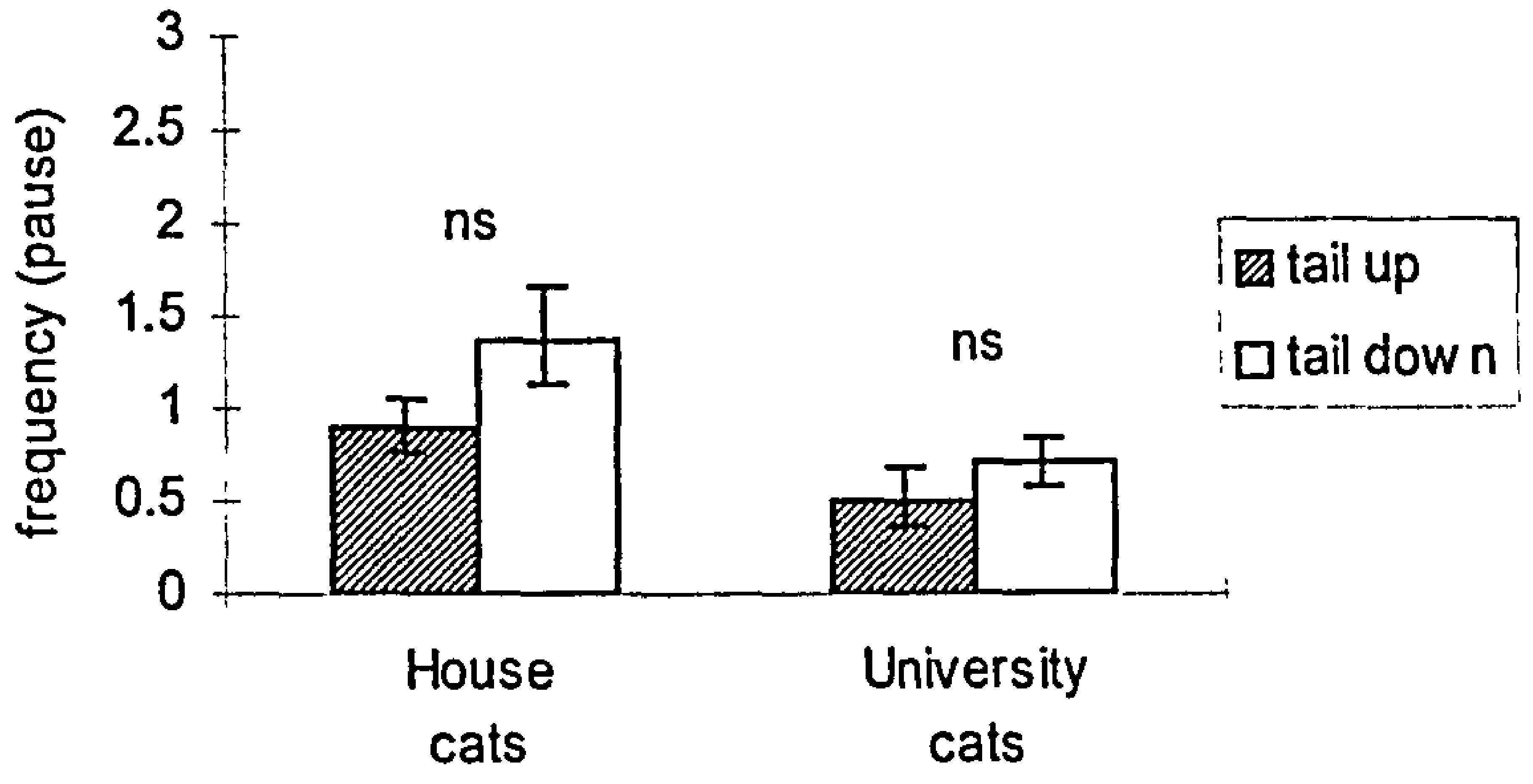
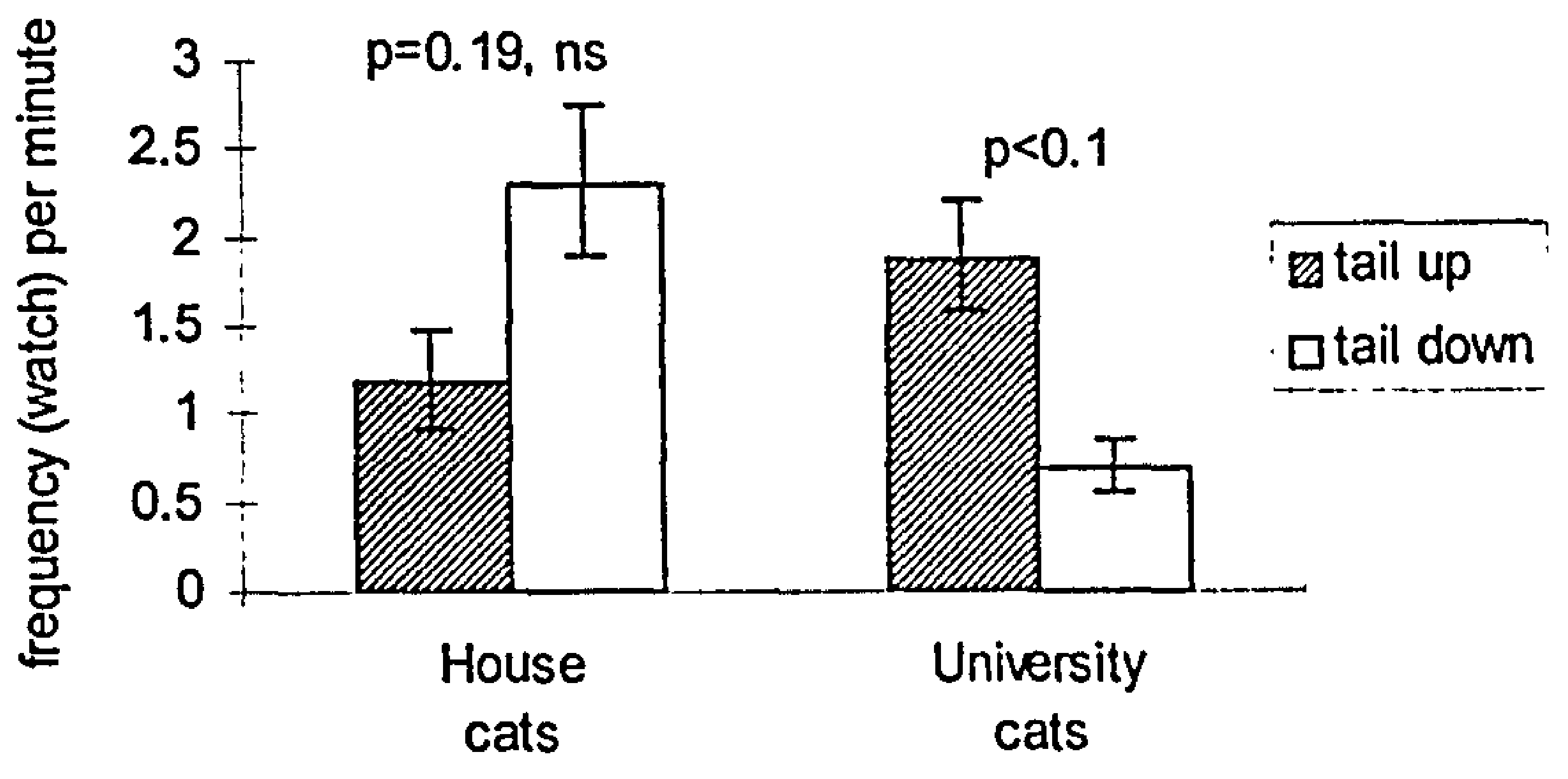
[3] as in the statistical sense

Figure 6.8 One way ANOVA on first trial only for (a) *Pause* frequency, (b) *Watch* frequency, and (c) *Tail Waves&Jerks* frequency. Mean frequencies per minute are given (+SE), for both treatments and for both cat colonies.

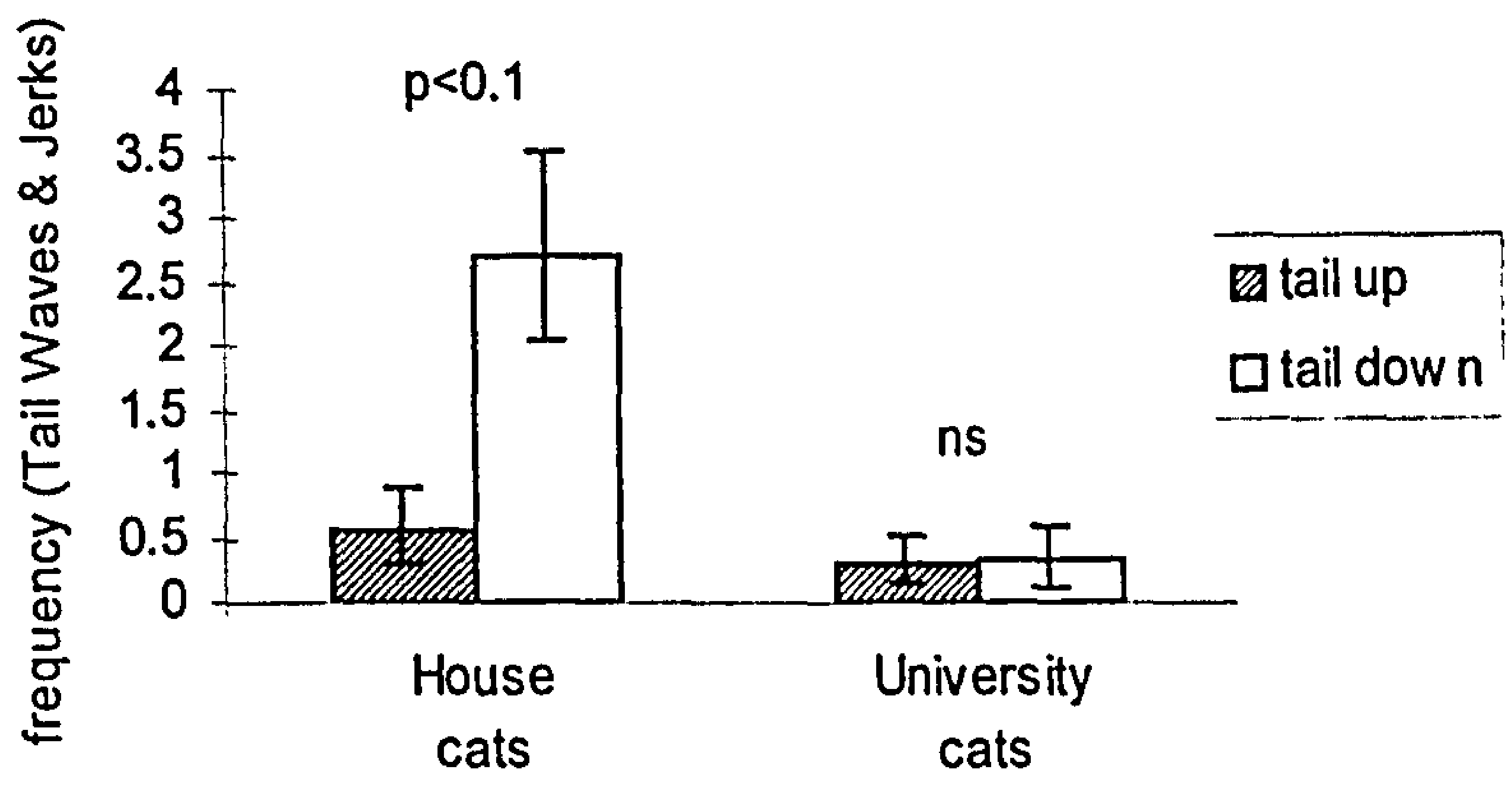
(a) Mean *Pause* frequency per minute.



(b) Mean *Watch* frequency per minute.



(c) Mean *Tail Waves & Jerks* frequency per minute.



In general it appeared that cats did react slightly differently in the second trial than they did in the first, though this effect was not always stronger than the treatment effect and thus was not always significant. It seems most likely that this is a learning effect; in the first trial cats are initially under the impression that the silhouette is a real cat, and react accordingly, though they do soon realise that it is only a model. In the second trial, it is possible that they remember that it is only a model and thus may not be reacting as if the silhouette is a real cat. I left a month between trials in the hope that this would not occur but perhaps this was not long enough.

If this experiment was to be repeated, I would therefore test a larger sample of cats once, as the nested nature of this experiment made the analysis difficult to analyse in cases where the treatment x group interaction was significant.

6.3.3 Discussion

The main results can be summarized as follows: In the *house cats*, the TAIL UP silhouette treatment caused the target cat to be more likely to:
(a) Hold its tail in a high position on first sighting the silhouette,
(b) Hold its tail in a high position on approaching the silhouette.
(c) Approach quicker.
and (d) Exhibit fewer Tail Jerks & Waves,
than they did when exposed to a TAIL DOWN silhouette.
It is also possible that house cats may also Pause less and Watch less before approaching, but these results were not significant.

In the *University cats*, however, none of these effects occurred. Treatment was not found to significantly affect any of the measured variables.

All the target cats appeared to react as if the silhouette was a real cat. These results can therefore be interpreted to suggest how cats react to different tail positions in real cats.

In the *house cats*, the TAIL UP treatment appeared to make the target cat less hesitant in approaching the 'intruding cat' (Approached quicker; and less Tail Jerks & Waves), and less fearful of the 'intruding cat' (Tail Under not exhibited at all during this treatment[4]; Tail Up is more likely to be exhibited[5]; Approached quicker; and possibly watched less before approaching). TAIL DOWN, in comparison, made the target cat hesitate more before approaching (more Tail Jerks & Waves; Approached slower; and possibly[6] an increased frequency of Pause and Watch), and be more fearful of the 'intruding cat' (Tail Under more likely to be exhibited during this treatment[3]; Tail Up less likely to be exhibited[4]).

However, in the *University cats*, the tail position of the 'intruding cat' does not appear to make any difference to the type of reaction received.

This data supports the field observation data described in the previous section; house cats interpret the TAIL UP signal as a signal of intention to be affiliative, and are therefore less fearful when they see the 'intruding cat' with this tail position. A TAIL DOWN 'intruding cat' is more ambiguous; it does not rule out the possibility of aggression, thus the target cat is more hesitant and wary when investigating this silhouette. University cats do not seem to interpret the tail signals in the same way, or else they are simply not responding to the message. This finding is in agreement with the observations that I made in *Section 6.2*, where I observed that University cats did not seem to be using the Tail Up position as a signal; it was merely motivationally connected with rubbing (See *Section 6.2.3.1*). The feral cats, on the other hand, were found to be using the Tail Up as a signal of intention to be affiliative.

In *Section 6.2.3.5*, I speculated on the possibilities for the difference in behaviour between the two groups of cats, and suggested that it may be due to the fact that the University cats live in an isolated area where they never meet stranger cats. They have always lived indoors, and come from a population of cats that were brought up indoors. The feral cats, on the other hand, are constantly exposed to new and stranger cats. For them, therefore,

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[4] Tail Under is a defensive tail position (see *Chapter 5, Section 5.1*)

[5] The presence of Tail Up may indicate that the cat is less fearful than the presence of any other tail position because it is never associated with defensive or offensive behaviour.

[6] This was not significant.

the Tail Up signal is particularly important, especially when a stranger cat invades their territory. All the house cats that I tested had access to the outside. This silhouette experiment therefore indicates that house cats use the Tail Up signal in the same way as the feral cats. This backs up my suggestion that isolation of the University cats has led to a breakdown in cultural transmission of this affiliative signalling system.

Why did the Tail Up signal evolve as a social signal in the domestic cat?

Tail Up does not act as a social signal in groups of undomesticated felids. This indicates that the change in niche and behaviour during domestication may have caused a Tail Up signal of intention to be advantageous when it would not have been previously. It was mentioned in *Section 6.2.3.2* that the main advantage in having an intention signal would be to reduce aggression. This would be expected to be particularly important in *colonies* of cats which in close proximity to one another, and at high densities, but would not be so important in solitary living individuals.

It therefore seems likely that the presence of *Felis silvestris* in *colonies* during and after domestication (around human settlements) caused a signal of intention to be advantageous. However, it should be noted that in this study, free-ranging *house* cats, which were living solitarily or in pairs, but not in groups, were also found to perform Tail Up in this manner. I suggest that this is because, once the Tail Up had evolved amongst colonies of domestic cats, it would not have de-evolved merely because some cats began to live solitarily in households. It is likely that this type of signal would still be advantageous in monitoring the intentions of the other cats in the area, particularly as many house cats live in urban areas where there is a very high density of cats.

In the following section I discuss how this signal may have evolved in free ranging cats, both house cats and ferals.

6.4 PHYLOGENY OF THE TAIL UP SIGNAL

The mechanism of evolution of the 'question and answer' format of the Tail Up signal as a reciprocal intention indicator can be perhaps explained by using Krebs and Dawkins (1984) idea of the co-evolution of mindreaders and manipulators. Signals must be derived ultimately from non-signal movements. These may be, for example, autonomic responses (*e.g.* erect fur of a threatened cat), protective responses (*e.g.* closing of eyes in primates before a fight), or intention movements (*e.g.* crouching and raising of the tail in birds before they take off) (Harper, 1991).

In *Chapter 5* it was established that Tail Up is motivationally connected to rubbing. As rubbing is one of the main affiliative behaviours amongst cats, it seems likely that this may have been the starting point for the evolution of the Tail Up position as a signal of intention to be affiliative. The starting assumption that I have made here is therefore that the evolution of the Tail Up *signal* as an intention indicator was derived from a Tail Up *position* which was motivationally linked with rubbing (*i.e.* that one always occurred with the other). The possible reasons for this motivational link, and the evolutionary point at which this connection may have developed, are discussed in the general discussion, *Chapter 9*.

The following paragraph describes the possible stages of evolution. It must be remembered that mindreaders and manipulators are not necessarily separate individuals; the same individual may occupy different roles at different times. Co-evolution therefore occurs between roles (recipient role and initiator role), not between individuals.

Stage A:

- Tail Up position is motivationally connected with rubbing (see above, & general discussion, *Chapter 9*), and one occurs with the other. Thus the initiator will perform the Tail Up position immediately before rubbing on the recipient. The recipient will react to the initiator's rub, either by being affiliative, in which case it will rub with its tail up, or by being non-affiliative, in which case it will not rub, and therefore its tail will not go up, and it may be aggressive.

Stage B:

- Recipient 'mindreads' the initiator by learning the sequence of behaviours. It reacts to the initiator's Tail Up position which occurs briefly before the rub, rather than waiting until the rub occurs. The recipient will therefore raise its tail in preparation for the rub as soon as it sees the Tail Up position occur in the initiator. As a result of this, the initiator has the chance to see the Tail Up position of the recipient, (meaning affiliative), *before* it has actually reached the recipient.

Stage C

- Initiator 'mindreads' the recipient; The sequence of behaviours is such that a Tail Up by the recipient is followed by an affiliative interaction, and if the Tail Up signal is not performed, an affiliative interaction does not occur, and aggression sometimes does. The initiator uses this to his advantage - in the case where the recipient does *not* give a Tail Up display, the initiator moves away before the recipient can be aggressive. It is to both their advantage that this communication takes place.

Stage D

- Manipulation by the initiator causes ritualization of the Tail Up position into a signal: The initiator causes the recipient to either give or not give the Tail Up signal by displaying a Tail Up signal earlier than he would have before. Again, it is to both their advantages that this manipulation takes place. This causes ritualization of the Tail Up signal which gradually becomes more temporally separated from the rubbing behaviour with which it was originally occured simultaneously.

The word 'manipulation' does not necessarily imply that a cat is being manipulated against his own interest. To the contrary, it is actually to both participants' advantage that the manipulation and subsequent ritualization occurs. The result is an efficient signalling system which results in a decrease of unnecessary aggression between individuals, which is clearly in both their interest. Thus this signalling strategy is evolutionary stable without being costly because there is no conflict of interest between the signalling partners (Maynard Smith, 1991, 1994). The Tail Up signal can therefore perhaps be regarded as one of the 'conspiratorial whispers' of Krebs & Dawkins, (1984) and the 'subtle behavioural cues' of Kerby & Macdonald, (1988) which would be expected to have evolved in a situation where the communication is cooperative.

The Tail Up signal appears to be well-suited for its function. Firstly, it is cost-minimising and subtle, as would be expected from a cooperative signal (See *Chapter 1, Section 1.6*). One would not expect a costly signal to have evolved unless absolutely necessary as this would produce a reduction in fitness. Secondly, being a visual signal, it acts well as an intention indicator because it can be seen from far away. Other modes of communication are not so well-suited to this function; tactile signals involve close interaction and therefore could not act as a signal of intention to interact, while olfactory signals are not immediate and their direction is difficult to control. It may be possible to use vocal signals for this function, but the only possible problem may be that they may have to be relatively loud in order to be heard from a distance, and this may be costly.

Tail positions in general are in fact well designed to be used as signals as part of cooperative communication, mainly because they are cost-minimising (*i.e.* having little effect on overall fitness), easily detectable, and not 'loud', so that they do not attract the attention of a predator (in felids this might be important for the protection of young offspring). It is not surprising, therefore, that they are used co-operatively in so many species: for example, as dominance and subordinance signals in dog and wolf packs, (for review see Bradshaw & Nott, 1995), as a predictor of actions in colonies of vervet monkeys (Bernstein, 1978), as warning signals in antelope herds (*e.g.* white-tailed deer; Smith, 1991), and to increase vigilance in groups of Californian ground squirrels (Hersek & Owings, 1994). The use of tail positions as subtle behavioural cues in colonies of animals where communication is generally cooperative would be expected to be widespread.

Chapter 7:

DOMESTIC CAT-HUMAN SIGNALLING

The domestic cat has lived commensally with humans since around 7000BC and possibly longer (Thorne, 1992, Serpell, 1988). In a human-based niche, a cat that is successful at communicating with humans is likely to gain increased access to food and shelter, via contact with humans. This is likely to have produced positive selection for successful human-directed signals.

Certainly the domestic cats of today are adept at signalling to humans. Where do these cat-human signalling methods originate? Signals rarely originate *de novo*; they more usually originate from behaviour which has some other function (*e.g.* from other signals, from intention movements, or from cues given by autonomic or protective responses; see Harper, 1991). There are therefore various possibilities of origin. However, the most likely source is from intraspecific communciation (*i.e.* from signals that would be used in specific situations such as sexual/mother-young interactions or in territorial disputes).

It may be that intraspecific signals such as these are simply being performed in an interspecific context (*i.e.* towards humans) without any change to the signal having taken place in order for this to occur. Alternatively, the signals emitted by the domestic cat may have evolved such that human-directed signals are distinct from those that are cat-directed.

The next two chapters will therefore investigate the origins and evolution of human-directed behaviour of the domestic cat. This will be done by:

Chapter 7: comparing it to domestic cat-cat communication, and
Chapter 8: comparing it to human-directed undomesticated cat communication.

7.1 INTRODUCTION

Previous studies of cat-human interactions have generally focussed on either the behaviour of the human, or of the cat-human relationship as a whole, rather than specifically on cat behaviour (*e.g.* Mertens, 1991, Mertens & Turner, 1988). Some studies that have been more cat orientated have considered socialisation and the effect of early handling on the cat-human relationship (Karsh, 1983a, 1983b, 1984, McCune, 1995; for review see Karsh & Turner, 1988). Other studies have looked at people's perceptions of cats (Bradshaw & Limond, 1997, Poresky 1989), and at differences in cat personality and temperament within the cat-human relationship (Meier & Turner, 1985, Turner *et al*, 1986, Bradshaw & Cook, 1996, Feaver *et al*, 1986).

There have been few studies purely about the behaviour of the cat in the cat-human situation. Turner (1991) observed natural interactions between cats and humans in the home setting. He describes both cat and human behaviours, and uses a cluster analysis to group these behaviours temporally. However, though his ethogram was broad, it was not detailed in social behaviours, and, in addition, he included human behaviours into the cluster analysis. Podberscek *et al* (1991) investigated the behaviour of laboratory cats and their behaviour towards familiar and unfamiliar people. He classes the cat's behaviour towards the human into three groups: Contact attention (rubbing, clawing), Non-contact attention (Stand & Watch, Jumping to floor, Stretching out head to person, Lying near person), and No attention (Rests, Eats, Jumps to shelf, Object Rub, Walk Away). Unfortunately neither of these studies give an exhaustive ethogram for the study of domestic cat-human interactions. Bradshaw & Cook (1996) give a more detailed ethogram of cat behaviour towards humans, and describe the behavioural sequences that occurred pre- and post-feeding, finding that cats were more likely to interact with their owner pre-meal. This perhaps suggests that one of the main reasons for cat-human signalling is as a food soliciting device.

However, there have been no studies of cat-human behaviour from an evolutionary point of view. In this chapter, therefore, I intended to look only at the behaviour of the cat, with the intention of comparing human-directed cat behaviour to the cat-directed cat behaviour studied in Chapter 3. This will be compared on three levels:

- Comparison of ethograms
- Comparison of temporal behavioural structure
- Comparison of physical structure of signals

7.2 METHODS

Procedure

The reaction of 20 cats to the approach of a human was recorded on video. Each cat was recorded separately in a familiar room (9m x 5m) in a section of their living quarters, at a particular time each morning. The human approach was neutral and standardised. The neutral approach was classified as follows: The human crouched 3m away from the cat, and then approached, in a crouching position, until the human was 0.25m away from the subject cat. Once in close proximity to the cat, the human remained in that position, crouching and still, without talking or reaching out to the cat.

The interaction was recorded on surveillance video from the time that the human began to approach the cat, until the subject cat moved out of proximity from the target human, or, alternatively, if the recording time was more than 60 seconds. 'In proximity' was defined as within a metre of the human. The posture (tail position & stance) and behaviour of the subject cat was noted throughout this period.

Two preliminary experiments were carried out for each cat to accustom the cats to the experimental set up (no recording of data took place).

Subjects

The Southampton University colony was used for this experiment (see *Chapter 2* for details).

Most of these cats have a high tolerance for human presence but there are a few exceptions which will not readily approach humans. At the time of the experiment the colony consisted of 20 cats, including those tolerant and intolerant to human presence. Their different reactions to the presence of a human was important in this experiment as I wanted to record as wide a variety of behavioural reactions as possible; *i.e.* not only affiliative reactions from the more friendly cats, but also defensive, and possibly aggressive reactions from the less tolerant cats. In this way, I attempted to include all possible elements of the cat's interspecific behavioural repertoire in the experiment.

Six target humans were used in this experiment (4♀, 2♂), who were of varying familiarity to the cats. This was important in order that as wide a variety of behavioural elements was elicited from the 20 cats as possible. Each replicate consisted of one human meeting 20 cats, one at a time (thus producing 20 cat-human interactions). This was replicated 3 times for each human. The total number of interactions recorded was therefore 360.

Statistical techniques

Behavioural sequences (see *Glossary*) from every combination of subjects were combined for the analysis, because I wanted to look at temporal links within behavioural sequences, **not at the effect of independent variables or individual cat differences**. Temporal links between types of behaviours either exist or do not exist, and therefore would not be expected to vary depending on the condition of the experiment, though the *type* of behaviour (*e.g.* aggressive/ affiliative/ defensive) would be expected to vary.

The behavioural sequence data was collated into two types of matrices: A *sequence-linked matrix* which shows frequencies for how often each behaviour was performed in the same behavioural sequence as every other behaviour, and a *co-occurrence matrix*, which shows frequencies for how often each behavioural event (*e.g.* sniff) occurred during each behavioural state (*i.e.* tail position or stance). See *Chapter 2, Section 2.4.4* for further description of these matrices.

Chi-squared adjusted residuals were then calculated for both matrices, and the significant behavioural links were established. This method is described in *Chapter 2*, *Section 2.4.4*, and has already been used in *Chapter 3* for cat-cat interactions. *Section 7.3.3* uses a one way ANOVA.

7.3 RESULTS

7.3.1 Cat-human ethogram

The ethogram devised is given in *Fig. 7.1*. This ethogram lists not only the behaviours which were exhibited by the cats towards humans in this experiment, but also behaviours which were not observed in this experiment but which have been previously reported to occur in cat-human interactions (Bradshaw & Cook, 1996, Turner *et al*, 1991), in order that it is as exhaustive as possible.

This cat-human ethogram can be compared to the cat-cat ethogram in *Appendix I* (diagrammatically represented in *Chapter 3*, *Fig. 3.1*). It must be noted that the cat-cat ethogram contains only behaviours that occurred between adult cats; behaviours that occur between adults and kittens are not represented here.

The cat-human ethogram contains slightly fewer behaviours than the cat-cat ethogram (30 human-directed behavioural elements as against 35 cat-directed behavioural elements) This difference is partly because there are many cat-cat behaviours which cannot physically be carried out in a cat-human situation due to either the difference in size (*i.e.* Pounce, Sniff Rear) or the necessity of reciprocation for the behaviour to occur (*e.g.* Touch Nose, Chase, Follow, Jostle Play, Fight,). Similarly, Jump Up can only occur in a human-directed situation, as it is the size difference which makes this behaviour possible.

However, there are differences between the two which cannot be accounted for in this manner:

- Knead Floor occurs only in the human-directed situation.
- Meiow occurs very often in the human-directed situation and only very rarely between adult cats.

Both of these behaviours are known to be particularly important in intraspecific kitten behaviour, usually directed towards its mother (Deag *et al*, 1988, Bradshaw, 1992). (Thus, these behaviours are not included in the cat-cat ethogram because this ethogram contains only adult behaviours.) Purr is also considered to be a kitten behaviour (Deag *et al*, 1988), but some authors have reported its use in intraspecific signalling between adult domestic cats (Kiley-Worthington, 1984, Leyhausen, 1979). I never heard adult cats purr in intraspecific interactions but this is likely to be due to the low amplitude at which it is emitted. Thus, it is not possible to establish whether Purr should be added to the above list of behaviours or not.

Figure 7.1 **Cat-human behaviour ethogram.** See *Appendix I* for description of behaviours.

* Behaviours that were observed but which occurred less than 10 times, and which were therefore not included in the analysis.
† Behaviours that were not observed in this experiment but which have been previously reported to occur in cat-human behaviour (Bradshaw & Cook, 1996, Turner *et al*, 1991).

<u>Behavioural events (as frequencies)</u>

Rub Head
Rub Flank
Rub Tail
Object Rub
Sniff human
Approach human
Move Away from human
Back Off
Knead Floor
Tail Wave
Tail Jerk
Roll
Groom Human
Self Groom
Watch
Walk Past
Run Away from human
Pause
Run Approach*
Stare*
Cuff*
Jump Up to human*
Sit With Human†
Purr †
Arch Back†
Tail Quiver†
Paw†
Hiss†
Ears Back†
Meiow†

<u>Tail posture and non-standing stances (as durations)</u>

Tail Up
Tail Half-Up
Tail Curved
Tail Down
Tail Under
Sit
Lie Down
Crouch

7.3.2 Description of temporal behavioural structure

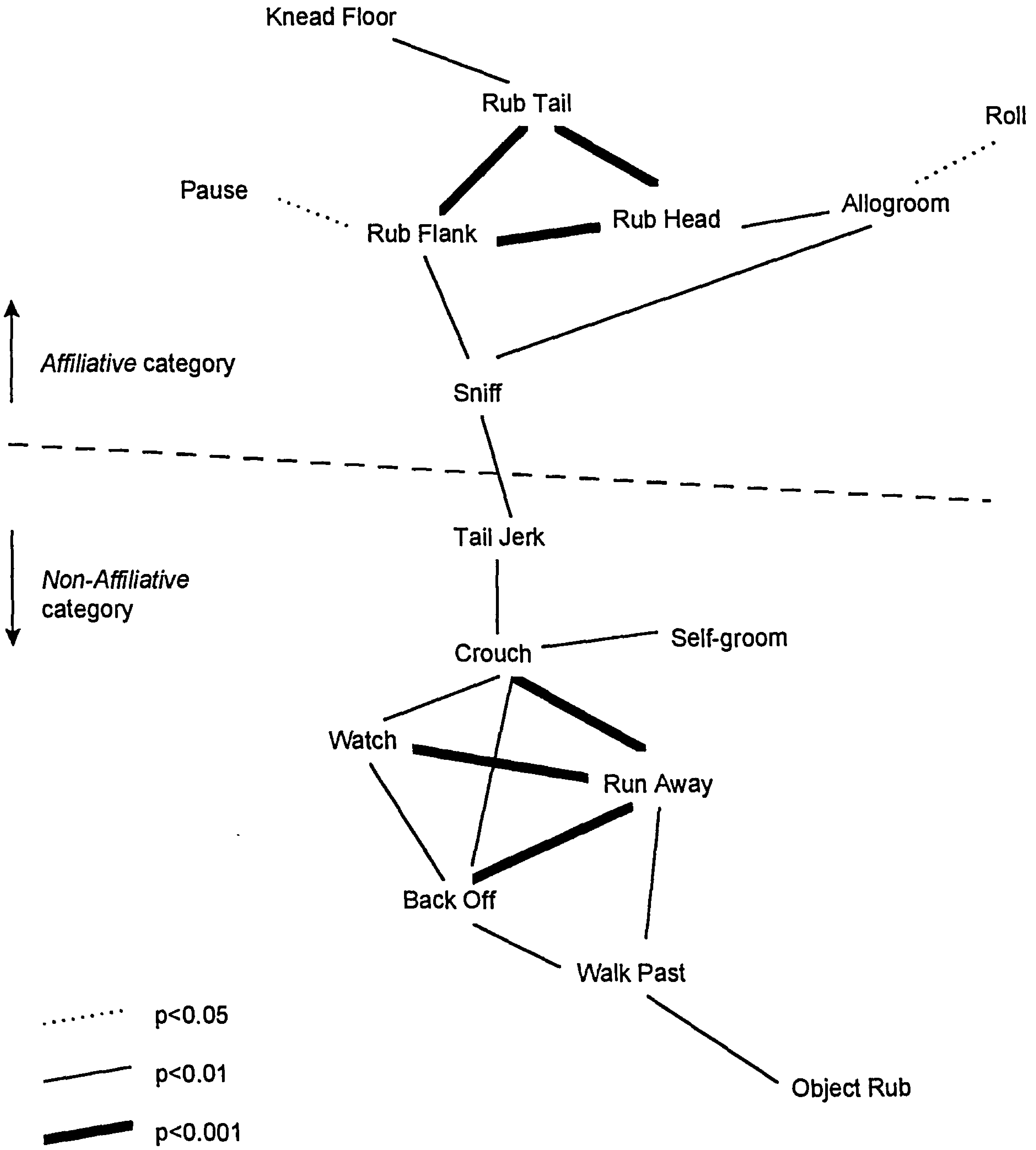
Linkage diagrams, similar to those drawn in *Chapters 3 & 4*, were drawn to represent the temporal structure of the behaviours listed in the ethogram (*Fig. 7.1*). The raw data (in matrix form) can be found in Appendix IV. Two types of diagrams were constructed, to illustrate the results from the two types of matrices described in *Section 7.2*:

- Sequence-linked diagram (*Fig. 7.2*). This shows human-directed behavioural elements that were significantly likely to occur in the same behavioural sequence together. This can be compared to *Fig. 3.1. (Chapter 3)*, which shows the equivalent cat-directed diagram.
- Co-occurrence diagram (*Fig. 7.3*). This shows human-directed behavioural events that were significantly likely to occur during behavioural states (*i.e.* stances or postures). The equivalent diagram for cat-directed behaviour, is given alongside it, for comparison. (The data for the cat-directed behaviour was taken from *Chapter 3)*.

Only behaviours that occurred over 10 times were included in these diagrams. The following behaviours were observed but occurred <10 times: Stare, Cuff, Jump Up, Run Approach.

Fig. 7.2. can be used to divide up the behaviours into temporal categories, in a similar way to that done in *Chapter 3* for cat-cat behaviour. The behaviours group themselves into two categories; one which I defined as the *Affiliative* category, which contains the behaviours that were categorized as *Affiliative* in *Chapter 3*, and the other which I defined as the *Non-Affiliative* category, for the remaining group of behaviours. I have avoided using any functional name for the latter group as it contains defensive behaviours, avoidance behaviours and others which are more difficult to define.

Figure 7.2 Significant behavioural links in *F.s.catus* for behaviours that were directed towards a human. Data from Southampton University colony cats. Meiow & Purr were not recorded in this experiment. Behaviours that occurred but n<10 were Stare, Jump Up, Run Approach and Cuff. Behaviours that occurred but which were not significantly associated with any one behaviour : Tail Up (see text for explanation), and Tail Wave.



These two categories can be compared to the six categories which were found in *Chapter 3* for cat-directed behaviours. A summary of the categories found in both cat-directed and human-directed behaviour can be seen in *Table 7.1 & 7.2.* Briefly, the two affiliative categories in cat-directed behaviour are combined into one in human-directed behaviour. The remaining four categories of cat-directed behaviour appear to be loosely combined again in human-directed behaviour to form the *Non-Affiliative* category. This category contains elements of cat-directed defensive behaviour (Run Away, Back Off, Crouch), and a mixture of behaviours that do not originate from any one cat-directed category. These include Self-groom & Tail Jerk, which may be behaviours which indicate frustration or uncertainty (See *Chapter 3*, *Section 3.4.6*, and Kiley-Worthington, 1976), and Walk Past & Watch which may be avoidance/alert behaviours. The one thing that all of these behaviours have in common is that they are non-affiliative; they represent the behaviours that a cat would exhibit towards a human if it was either fearful (defensive behaviours) or not sure about how to react (frustration/ avoidance/ alert behaviours). There were no directly aggressive behaviours exhibited at all during this experiment. This is probably representative of the friendly nature of all of the cats which took part. It may be that a third category of aggressive behaviours would have emerged if unsocialised cats had been included into the experiment.

Table 7.1 **Cat-directed behaviours**: List of categories. Taken from *Chapter 3* (See *Table 3.2* & *Fig. 3.1*). Behaviours in parentheses are only weakly linked with that category. The categories were established using a linkage diagram drawn from the chi-squared residuals of a sequence-linked matrix.

Name of Category	**Behaviours included**
Affiliative (Rub sub-category)	Rub Head, Rub Flank, Rub Tail, Tail raised Approach, Tail raised Follow, (Tail raised Move away), Tail raised Walk Past, Tail Up.
Affiliative (Groom sub-category)	Groom Cat, Sniff, Touch Nose, Sniff Rear, Sit With, Tail Raised Approach, (Tail raised Move Away).
Investigatory	Follow, Sniff Rear, (Sniff), (Bite).
Agonistic (Aggressive sub-category)	Run Approach, Chase, Bite, Watch, Pounce, Cuff.
Agonistic (Defensive sub-category)	Stare, Cuff, Hiss, Ears Back, Crouch, Run away, Squeal, Freeze, Tail Swish.
Agonistic (Play Aggression sub-category)	Roll, Paw, Squeal, (Run Away).

Table 7.2 **Human-directed behaviours**: List of categories. The categories were established using a linkage diagram drawn from the chi-squared residuals of a sequence linked matrix.
*Tail Up was included in this category after the same analysis (chi-squared residuals) was carried out on the co-occurrence matrix

Name of Category	**Behaviours included**
Affiliative Category	Rub Head, Rub Flank, Knead Floor, Groom Human, Roll, Jump Up, Sniff, Tail Up*.
Non-Affiliative Category	Run away, Watch, Back Off, Walk Past, Object Rub, Crouch, Self-groom, Tail Jerk.

It should be noted that Tail Up was not found to be linked to any particular behaviours in *Fig.7.2*, which showed human-directed behavioural patterns. This is in contrast to its position in cat-cat interactions, in which it is strongly linked to many of the *Affiliative* behaviours. This may be due to a combination of factors:

(a) Tail Up occurs at a very high frequency in cat-human interactions (76% of interactions in this experiment contained Tail Up). In cat-cat interactions it occurs at a far lower level (only 38% of cat-cat interactions analysed in this experiment on the same colony as above contained Tail Up).

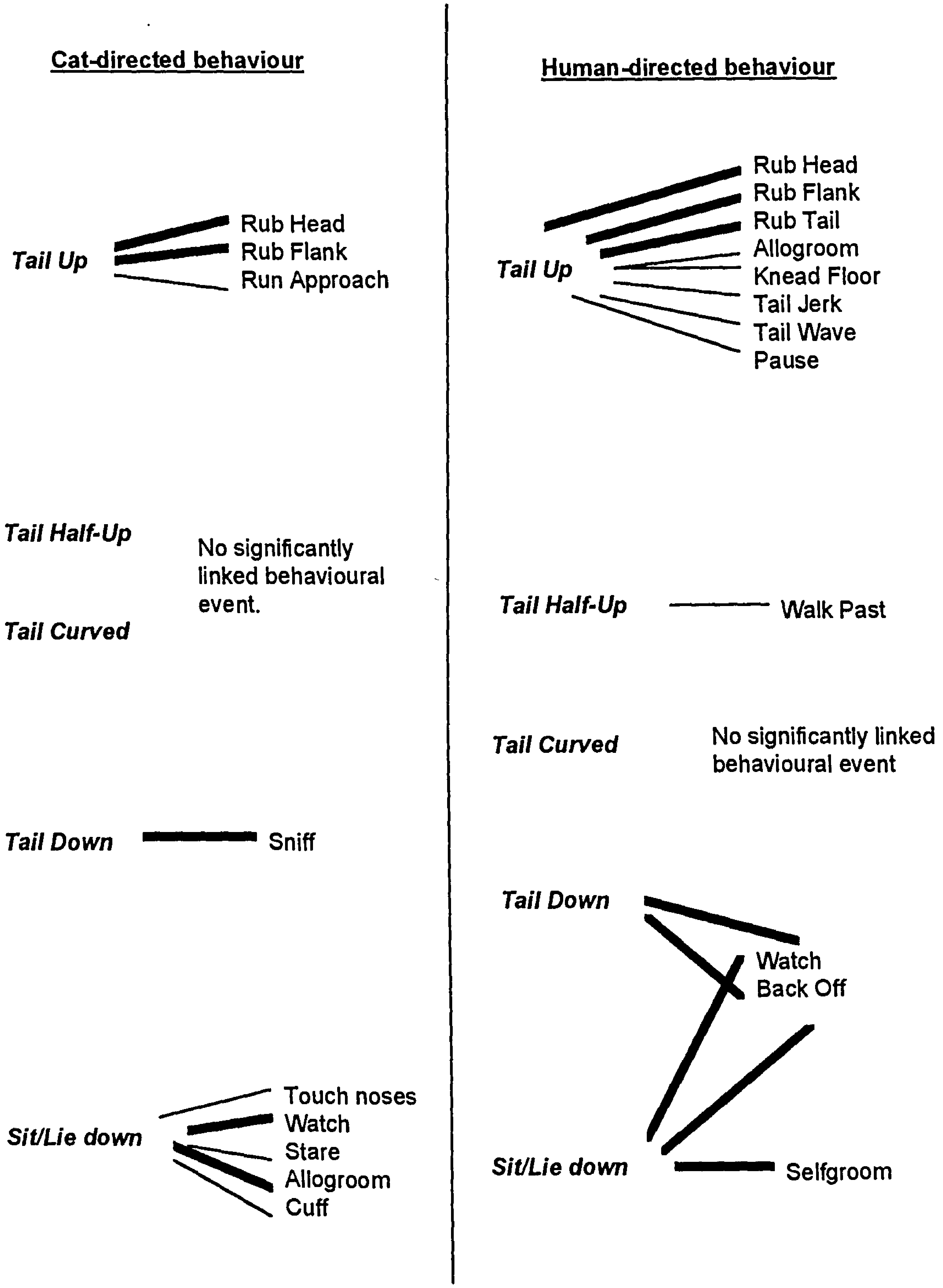
(b) When a behaviour occurs in a very high proportion of interactions, as above, the large scale on which the sequence-linked matrix is based ("the number of times one behaviour occurs in the same behavioural sequence as another") means that its links are not picked up by the test.

It was therefore necessary to carry out the same analysis on a matrix which contained more detailed data (co-occurrence matrix; see *Section 7.2*), but which did not give the broad outlook which the sequence-linked matrix gives.

The linkage diagram produced using this co-occurrence matrix is given in *Fig. 7.3*. (See Appendix IV for raw data matrix.) In the human-directed diagram, it can be seen that Tail Up is associated mostly with behaviours that occurred in the *Affiliative* category (Rub Head, Rub Flank, Rub Tail, Groom Human, Knead Floor, and Pause), although also with Tail Jerk which was part of the *Non-Affiliative* category, and with Tail Wave which could not be placed in any category (See *Table 7.2* for list of behaviours in each category). The strong connection that exists between Tail Up and several behavioural elements from the *Affiliative* category ($p<0.001$) suggests that Tail Up should be included as part of the *Affiliative* category for human-directed interactions.

Figure 7.3 Co-occurrences of postures and behavioural events: patterns significantly likely to occur simultaneously. Data was taken in both cases using the Southampton University colony cats. Meiow & Purr were not recorded in this experiment.

.... $p<0.05$ ——— $p<0.01$ ▬▬ $p<0.001$.



7.3.3 Physical differences in the Rub signal

The Rub signal is a very common affiliative social behaviour which occurs frequently in both inter- and intraspecific interactions. It is a physically diverse behaviour which can be exhibited either in bouts (a bout was classed as a series of rubbing where no behavioural event occurred in between rubs, and there was no pause within the bout for longer than 3 seconds) or in single occurrences. This represents a difference in the number of rubs exhibited in an interaction. It may also be exhibited at differing intensities: A rub sequence is classed as *one movement of rubbing* which may encompass anything from a single Rub Head to an entire rubbing movement down the body which would encompass all of Rub Head, Rub Flank, Rub Tail. Thus the number of single rubs (with a maximum of 3) which occur within a rub sequence gives an idea of the intensity with which the cat is performing the behaviour. A bout of rubbing may consist of several rub sequences.

Rubbing behaviour is therefore suitable for investigating differences in the physical structure of cat-cat and cat-human behaviours, because it is diverse in structure, and common in both interaction types.

Data from the human-directed interactions, recorded as described above, and from cat-directed interactions which were recorded from the same colony by Brown (1993)[1] were analysed to investigate differences in the number of bouts of rubbing per interaction, the total number of rubs per bout (including Rub Head, Rub Flank & Rub Tail), and the number of single rubs per rub sequence (*i.e.* Rub Head, Rub Flank, & Rub Tail). A random sample of 60 *rub interactions* (*i.e.* an interaction that contained at least one rub) from both the cat-directed data and the human-directed data were analysed.

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[1] This data was also used in *Chapter 3*; see *Section 3.2.2*)

Figure 7.4. Mean (±SD) no. of bouts of rubbing per interaction (back-transformed from a square root transformation) (p<0.01)

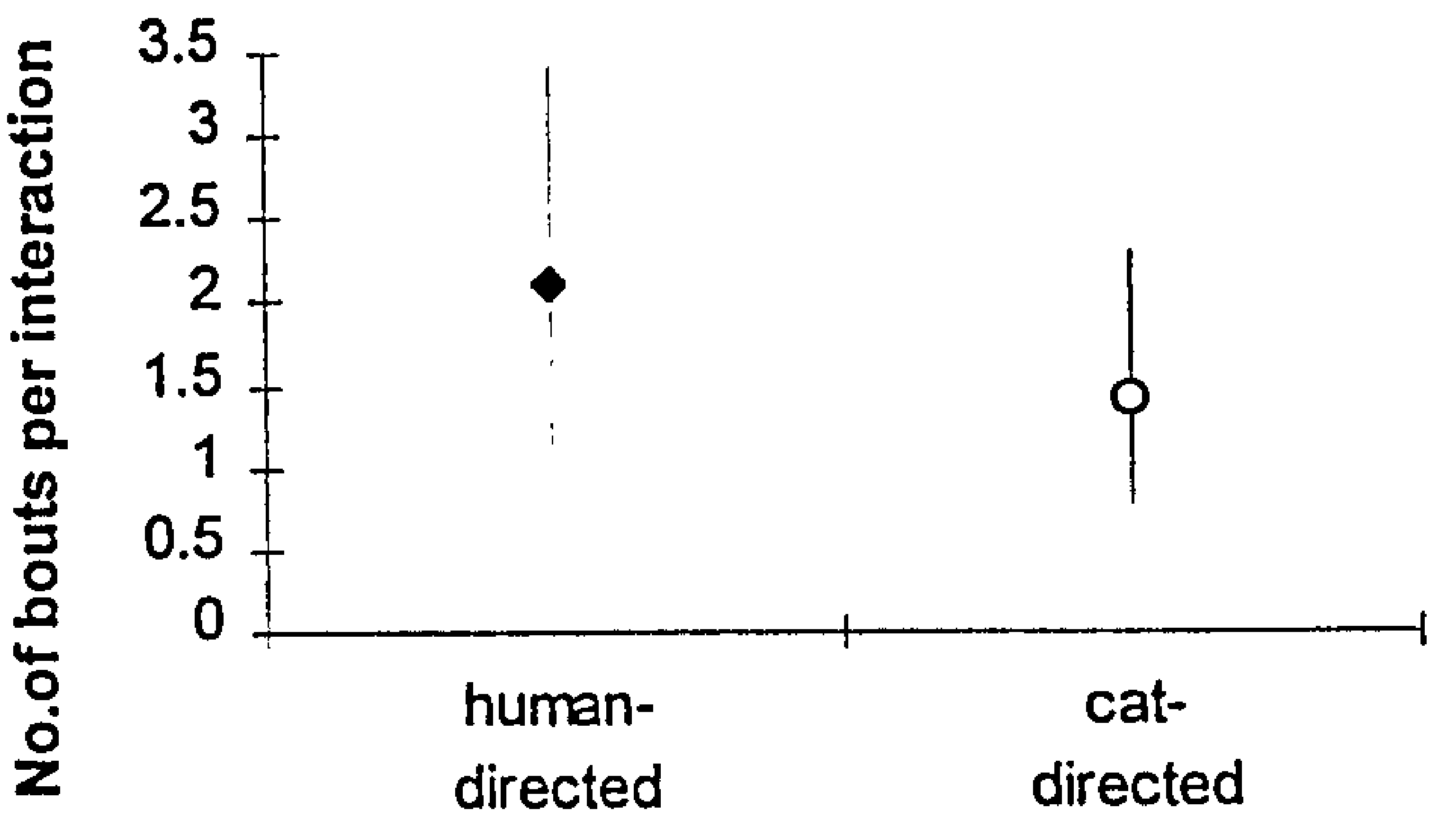


Figure 7.5. Mean (±SD) no. of single rubs per bout (back-transformed from a square root transformation).

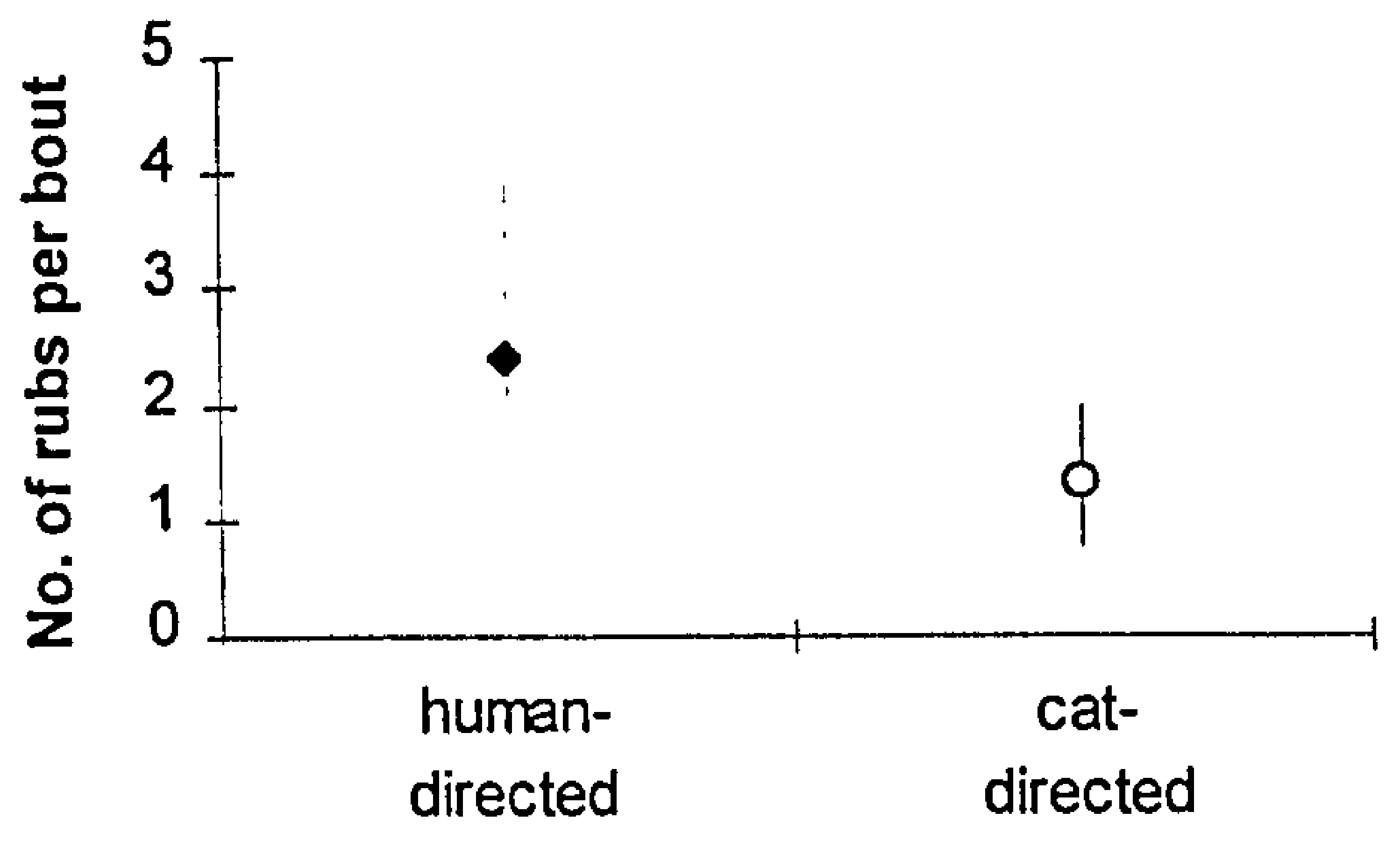
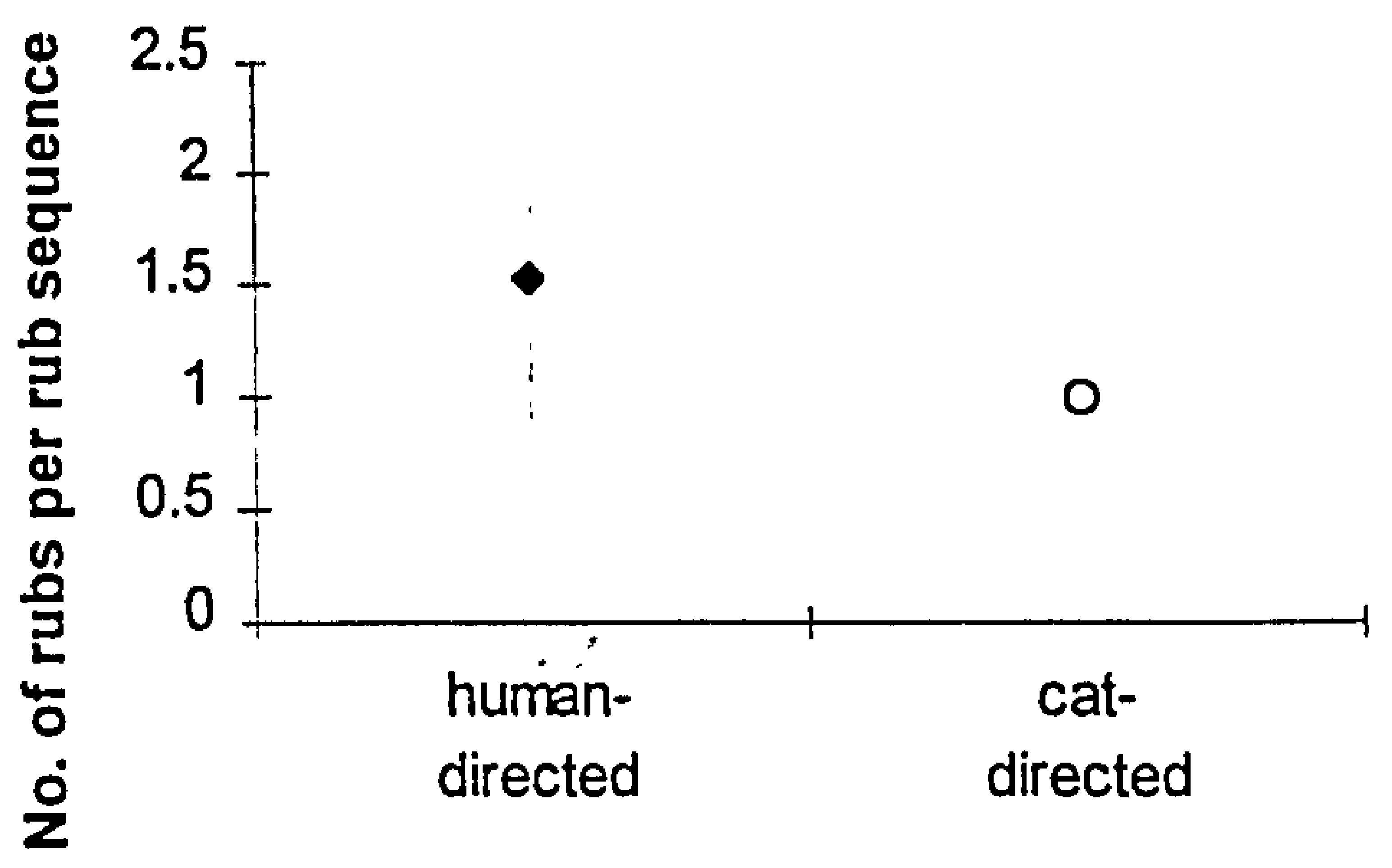


Figure 7.6 Mean (±SD) no. of single rubs per rub sequence, back-transformed from a square root transformation (p<0.0001). Standard deviation for the cat-directed bar was zero.



Human-directed rub interactions contained more bouts of rubbing than cat-directed rub interactions (See *Fig. 7.4*: $F_{1,59}$= 7.149, p<0.01). In addition, human-directed bouts of rubbing contained more rubs than cat-directed bouts (See *Fig. 7.5*: $F_{1,116}$= 32.304, p<0.0001). Human-directed rub sequences also contained more rubs than cat-directed rub-sequences (See *Fig. 7.6*: $F_{1,175}$=41.638, p<0.0001).

7.4 DISCUSSION

Firstly it should be noted that all the observed human-directed behaviours (see ethogram, *Fig. 7.1*) are based on behaviours of the cat which have other functions. Therefore, no human-directed behaviour has evolved from nothing. This is not surprising as signals nearly always evolve from other signals or from other behaviours that are already in the species' repertoire (Harper, 1991).

In fact, the majority, if not all, of the human-directed behaviours are based on the intraspecific social behaviours rather than solitary behaviours. This is not surprising as cat-human interactions are also social. Thus intraspecific social behaviours form the basis for all interspecific social behaviours.

The question remains as to whether these behaviours are used in the same context and manner in human-directed interactions as they are in cat-directed interactions, or whether they have actually evolved further to become distinct from intraspecific behaviour. This may have occurred either by a *change of context* in which the signal/behaviour is emitted, and/or by a *change in the physical nature of the signal.* These two aspects will be dealt with separately:

7.4.1 Context differences

The first obvious difference in context is the use of kitten/juvenile behaviours in the adult cat during human-directed behaviour. Two kitten behaviours (Knead Floor and Meiow; possibly also Purr[2] if this can be classed as a kitten behaviour[3]) are all noticeably obvious in many cat-human interactions. None of these behaviours play an important part in intraspecific adult communication: I never observed Knead Floor or Purr being used in an intraspecific adult interaction (although the apparent absence of Purr could have been due to its low amplitude). Adult cats occasionally used them solitarily without a human present, but never as part of a social interaction. Meiow was very occasionally used in intraspecific adult communication but only at a very low frequency (n= 8 out of a total of 2044 observed cat-cat interactions from 26 cats of the Southampton University colony). The fact that these three behaviours are considered to be part of the kitten and juvenile behavioural repertoire (Deag *et al*, 1988, Pg. 27, Bradshaw, 1992, Pg. 96), suggests that Knead, Meiow, and possibly also Purr, have come to be used in a different context (and presumably also have a different function) in human-directed behaviours (when they are used by the adult cat) as they do in cat-directed behaviours (when they are used by the juvenile cat).

The context of the other behaviours can be examined by comparing the categories represented in the human-directed linkage diagrams (*Fig. 7.2, Table 7.1*) with those in the cat-directed linkage diagram (*Fig 3.1, Table 7.2*). These temporal categories give an idea of the context in which each behaviour is exhibited.

Table 7.3 summarizes the contexts in which behaviours are found, in both the cat-directed and human-directed situation. The cat-directed contexts (neutered and entire) are taken from a variety of studies (Brown, 1993, van den Bos & de Vries, 1996, Deag *et al*, 1988, Feldman, 1994, and from the results from *Chapter 3*).

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[2] I did not record acoustic behaviours (*i.e.* Purr & Meiow) as part of this experiment. However, it is well known and documented that Meiow and Purr occur frequently in the cat-human relationship (*e.g.* Bradshaw & Cook, 1996).

[3] Purr is often thought to be a kitten behaviour, but Kiley-Worthington (1984) and Leyhausen, (1979) both recorded its use in intraspecific adult interactions.

Table 7.3 **Summary of contexts in which *Affiliative* behavioural signals occur.**
The *Non-Affiliative* behaviours have not been included in this table because their contexts are less well defined, and functions less well known in cat-cat interactions.† indicates that there are no studies on this behaviour in that type of cat interaction.

SIGNAL	CAT-CAT CATEGORY		CAT-HUMAN CATEGORY (Data from this study, *Chapter 7*)
	In neutered cats (Data taken from *Chapter* 3, & Brown, 1993)	***In entire cats*** (Data from various studies, details given below)	
Purr	†	Kitten/juvenile behaviour (Deag *et al*, 1988)	Affiliative
Meiow	†	Kitten/juvenile behaviour (Deag *et al*, 1988, Bradshaw (1992)	Affiliative
Knead floor	†	Kitten/juvenile behaviour	Affiliative
Roll	Play	Sexual (van den Bos & de Vries, 1996), submissive signal (Feldman, 1994)	Affiliative
Social Rub	Affiliative (Rub sub-category)	Sexual(van den Bos & de Vries, 1996)	Affiliative
Groom	Affiliative (Groom sub-category)	Inspection-affiliative (van den Bos & de Vries, 1996)	Affiliative
Sniff	Affiliative (Groom sub-category)	Inspection-affiliative (van den Bos & de Vries, 1996)	Affiliative
Tail Up	Affiliative (linked to both sub-categories)	†	Affiliative
Object Rub	Does not belong to any one category but more attached to Affiliative behaviours than any other (see *Chapter 3, Fig.3.1*)	†	Affiliative

This table demonstrates how the whole range of non-agonistic intraspecific behaviour types (Play, Sexual, Affiliative, Kitten behaviour), are all utilised by the domestic cat in the human-orientated situation as Affiliative behaviours. This is in contrast to the use of these behaviours in cat-directed interactions, where each set of behaviours has a quite distinct function.

Social interactions between cats must necessarily be complex as there are many different types of messages that need to be conveyed. Therefore a variety of signals have evolved for different functions. The maintenance of behaviours, particularly signals, in distinct contexts, is important for successful communication between individuals. Successful intraspecific communication will aid the fitness of an individual, whether solitary or gregarious.

Interactions between cats and humans are not so complex; they are either agonistic or non-agonistic. It is, firstly, **not necessary** for it to be as complex as cat-cat communication because there are fewer messages that need to be conveyed. Thus all the non-agonistic behaviours which may have a variety of different meanings when directed towards a cat, become grouped together as simply *Affiliative* behaviours when directed towards a human, and the differences between Play, Affiliative, Sexual and Kitten behaviours are not defined.

Secondly, it is **not possible** for cat-human communication to very complex. The human, being a different species, is unable to understand or reciprocate a cat's initiations of sociality in the same way as a conspecific. If the messages were any more complex, the human might not understand them. (There is not the same selective pressure on a human to understand as there is for a cat to successfully communicate.) In order to transfer information to the human, it is necessary for the cat to produce clearer and more understandable messages. This may have lead to, firstly, the grouping of many behaviours under one functional message (*i.e.* a change in context), as shown for the *Affiliative* behaviours in *Table 7.3*, and, secondly the physical change (ritualization) of signals so that they become more easily noticed by the human. This is dealt with in the next section.

7.4.2 Physical differences in signal structure

The basic physical structure of the human-directed signals are similar to those that are cat-directed (at least similar enough that we can call them by the same name). However, an ANOVA on the data in this chapter revealed that cat-human rubbing differs significantly from cat-cat rubbing. Rubbing signals were multiplied in both number (number of bouts per interaction, number of rubs per bout) and intensity (number of rubs per rub sequence) when human-directed; cat-directed rubbing on the other hand was found to be far more subtle and low in frequency.

Thus the rubbing signal, though appearing on the surface to be the same in both cat-cat and cat-human situations, is in fact physically different in the two situations. The signal is more prominent when human-directed as it is when cat-directed. This test was only carried out on rubbing but it may be that the same would be found of other important signals such as allogrooming (licking), object rubbing, and meiowing.

These results indicate that the rub signal has developed to be distinct in the two types of situations (cat-cat and cat-human). Rubs are multiplied and magnified in the human-directed situation, but not in the cat-directed situation. This difference has materialised via the process of ritualization, which can be described as the exaggeration of cues (Harper, 1991). Recent ritualization has occurred in the human-directed situation, but not in the cat-directed situation[4], thus resulting in the human-directed signal being more exaggerated and thus distinct from its corresponding cat-directed signal.

This process may have occurred through a genetic evolutionary process, or through a learning process. The latter could occur either within the lifespan of one individual through trial and

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[4] Note that ritualization must also have originally occurred in intraspecific interactions in order for the rub signal to have initially developed. Here, I am referring to the subsequent ritualization of this established intraspecific signal into a more exaggerated interspecific one.

error, or through cultural learning (Bradshaw 1992, Pgs. 78-79). It is most likely that the process involved a mixture of both these methods. Whether the process was genetic or cultural, the same factors apply for why the change occurred:

It is likely that ritualization has been caused due to the difference in 'receiver psychology' of the cat and human recipient. Guilford and Dawkins (1991) discuss factors affecting the evolutionary design of signals, and stress the importance of 'receiver psychology'; the ability of the receiver to detect signals, discriminate between signals, and to remember the signal. Humans have a different receiver psychology to cats; therefore human-directed cat signals have adapted in a different way to standard cat-directed cat signals. It is not necessary for a cat-directed signal to be repeated because cats are evolutionarily adapted to picking up such a message. Humans are not adapted to be receivers at all, so the cat must repeat and increase the size of the message in order to make it more prominent. In addition, it may be that humans do not reciprocate as cats do; this may also cause the prolonging of the signal.

There is also another possible reason for the occurrence of a split in the type of rubbing signal. It is likely that much of human-directed cat behaviour is exhibited as either a food- or attention-getting signal. This is in contrast to the message which is being given by the rub signal in the cat-cat situation (where it acts as a subtle *Affiliative* signal). A food-eliciting signal would favour a 'loud' prominent signal, whereas an *Affiliative* co-operative signal between members of a colony would favour a subtle cue (Kerby & Macdonald, 1988; see *Chapter 1, Section 1.6*). Thus the difference in the *type of message* that is being given by rubbing may cause a difference in the multitude (frequency) and magnitude (intensity) with which the signal is given. This mimics exactly what has occurred in the rubbing signal.

7.5 CONCLUSIONS

To conclude, cat-human behaviour is based on the intraspecific social signals of this species. However, there is evidence that the human-directed signals differ in two ways to those that are cat-directed: (i) signals are used in a narrower functional context in human-directed interactions than they are in cat-directed interactions, and (ii) some human-directed signals tend to be magnified in intensity and multiplied in number over those that are cat-directed. These changes may the result of three factors: (i) It is not *necessary* for cat-human signals to be as complex as cat-directed signals; this leads to the reduction in the number of contexts. (ii) It is not *possible* for cat-human interactions to be as complicated as cat-directed interactions, due to the fact that humans are not conspecific, and therefore have a different receiver psychology to a cat recipient, and (iii) A change in the signal's message may lead to a change in the signal's 'character'; for example, a change from a subtle signal to a 'loud' signal. All three of these factors will affect the type of selection pressure on the signal. This signal change may be brought about by genetic or cultural evolution.

Chapter 8:

HUMAN-DIRECTED SIGNALLING IN UNDOMESTICATED FELIDS: COMPARISONS WITH THE DOMESTIC CAT

8.1 INTRODUCTION

In the previous chapter, I established that interspecific signals performed by the domestic cat (towards humans) originate from intraspecific signals, but have now developed to be used in a wider context (*e.g.* kitten behaviours used by adults), and therefore possibly have different meanings (*e.g.* affiliative signal between cats used as attention-elicitor towards humans). I additionally established that the physical structure of certain signals (*i.e.* rubbing) has altered to be more repetitive and intensive when directed towards people. In the domestic cat, therefore, interspecific signals do differ from intraspecific signals, and are not simply redirected intraspecific signals.

Several published accounts suggest that undomesticated cats communicate with man in a similar way to domestic cats. Social rubbing appears to be the main affiliative signal used by undomesticated cats towards humans (*e.g. L.pardalis* (Leyhausen, 1979); *F.s.lybica* (Smithers, 1968); *L.wiedii* (Petersen, 1979), though Leyhausen (1979) also mentions that his ocelot used to hold its tail upright when greeting a human. These examples, though anecdotal, suggest that the ancestral species of the domestic cat may have had a similar behavioural repertoire of social communication to their descendants.

The initial aim of this chapter is to follow up the previous chapter with a different approach to a similar question; *i.e. what are the evolutionary origins of domestic cat interspecific signals?* Undomesticated felids have not had the opportunity to evolve specific human-directed signals, firstly because they have usually lived in captivity for only a few generations, and secondly because their breeding is normally controlled by humans. A study of the differences between human-directed behaviour in domestic and undomesticated cats can therefore be used to suggest which human-directed behaviours must have evolved in the domestic cat. The results from the previous chapter suggested that, in particular, domestic cats appear to *evolved* the ability to use kitten behaviours towards a human, even when adult (*i.e.* this is not just something that any species of cat will automatically do when interacting with a human). If this hypothesis is correct then we would not expect undomesticated cats to exhibit kitten behaviours towards humans.

In addition, it has been suggested that the ancestral domestic cat (thought to be similar to *F.s.lybica*, the African Wild Cat) must have had a genetic predisposition to domestication. It is not known whether the tractability of the ancestral domestic cat is a trait held only by this specific species, or by the whole lineage, or by the entire Felidae. There is very little published information on the behaviour of undomesticated cats to humans, and what little there is remains anecdotal. *Section 1.5.2* in *Chapter 1* discusses these accounts (summarized in *Table 1.3*). Interestingly, out of all the anecdotal accounts listed, the species that have been quoted as being the most **naturally** unfearful of man (*i.e.* without enforced taming) were all from the domestic cat lineage. However, as these accounts were anecdotal it is difficult to extract any definite evidence from these citations.

I therefore wanted to investigate whether there is an evolutionary basis to having a predisposition towards domestication, or whether all small cats could be domesticated if in the correct conditions. This 'predisposition for human-friendliness' is most probably based in the trait of behavioural plasticity which is present in many felids. This trait enables them to adapt to a wide range of social situations, which may include the human-orientated situation. The second aim of this study is therefore to address the following questions:

- Are some felid species/lineages more predisposed to human closeness and friendliness than others?
- Are some human-directed signals specific to certain felid species and/or lineages?

In an attempt to address these questions I took an approach which attempted to gain information from a wide source, in order to collect a large database, but without attempting to control for conditions at all. This was done by means of questionnaires to zoo keepers.

8.2 METHODS

A questionnaire was compiled and targeted at keepers of small felid species in zoos and wildlife parks in Britain and the USA. Questions were only asked about small felids. For the purposes of the questionnaire this was defined as 'cats of a lynx size or smaller'; *i.e.* the genera *Felis, Prionailurus, Herpailurus, Leptailurus, Leopardus, Oncifelis, Neofelis, Caracal, Catopuma, Oreailurus, Otocolobus, Profelis* and *Lynx* (See *Chapter 2, Section 2.1* for description of taxonomic system used). A follow-up questionnaire was sent out to those who replied, which asked more detailed questions about each cat. This was to avoid the original questionnaire being excessively long for every keeper (because it was not known how many cats each keeper looked after) when it was not necessary.

The questionnaires were designed in order that the following information could be gained for each individual cat which the keeper looked after.

(i) Does the cat ever

- Lie/Sit within 1m of human?
- Rub its head or body on a human?
- Lick a human?
- Roll within 1m of a human?
- Sniff a human?

and if so, how often?

(ii) Is the cat ever friendly in any other way not mentioned above?

(iii) Does this cat ever raise its tail in its interactions with humans?

(iii) Is the cat hand-reared?

(iv) Is the cat neutered or spayed?

(v) Do you know anything about the history of this cat which may have affected its relationship with humans?

The age and sex of the cat was also established.

The questionnaire was sent out to the keepers of every zoo/wildlife park in Britain and the USA which was known to keep small cats (established from the studbook records). See *Appendix II* for questionnaire in full.

A third, very brief questionnaire, consisting of 2 questions only, was sent out to keepers who had reported seeing a Tail Up position performed by a cat in an interaction with a human. This was sent out to establish exactly what position they had seen, and in what situation they had observed it. This will be discussed in detail in *Section 8.3.4*.

Standardizing questionnaire answers

There was variety in the ways that individual respondents answered the questions. For example, in response to the question 'How often did the cat....?', some clearly mentioned every time the behaviour occurred (*e.g.* '30 times a day'), whereas others answered this question less literally (*e.g.* 'daily'; an answer which could have meant once a day, or many times a day). To account for discrepancies of this kind (for example, the amount of time that a keeper spent in with the cat), a ranking system was used to standardize answers. This is outlined in *Table 8.0*.

Table 8.0 Ranking system used to standardize questionnaire answers.

7	More than 5 times a week
6	2-4 times a week
5	Once a week
4	2-3 times a month
3	Once a month
2	2-11 times a year
1	Once a year or less.
0	Never

All rates were converted to this system before being analysed.

Human-friendly behaviours

Some analyses required individuals to be given a 0/1 score for the presence or absence of human-friendly behaviours. Human-friendly behaviours were classified as any of the following:

- Rubbing their head or body on a human
- Grooming (licking) a human
- Rolling within 1m of a human
- Lying or sitting within 1m of a human
- Sniffing a human,

Respondents were asked how often they had observed each of these behaviours (closed question). The questionnaire also included an open question which asked keepers to describe any other friendly behaviour exhibited by the cat. Behaviours described by keepers in this section included:

- Ability to be hand fed.
- Giving keeper kittens to look after.
- Purring.
- Playing with the keeper's brush/mop/other tools whilst the keeper was using them.
- Letting the keepers stroke or scratch them.
- Climbing into the keeper's lap.

These behaviours were therefore also classed as 'friendly behaviours'. I have subsequently referred to cats that exhibited any form of human-friendly behaviour as ‘friendly’ cats.

Data analysis

The majority of cats did not exhibit any friendly behaviours towards humans, and therefore the entire data set was very skewed towards 0. As a result, categorical non-parametric methods were used for the analyses of this entire data set; in particular, the chi-squared test, the Kruskal-Wallis one way analysis of variance by ranks, and the Spearman's rank-order correlation co-efficient.

A subset of the data (which consisted only of cats which exhibited human-friendly behaviours) was subsequently analysed separately. This data was found to be normally distributed, and therefore parametric tests were used, which included a nested ANOVA and a MANOVA.

8.3 RESULTS

Questionnaires were returned from 68 zoos, from which data was extracted about 365 individual cats, comprising of 23 species in total. Five of these species could not be analysed due to the low sample size (n<5); these were *Profelis aurata* (n=2), *Catopuma temmincki* (n=2), *Felis silvestris lybica* (n=1), *Otocolobus manul* (n=2), and *Puma concolor* (n=4). Sample sizes varied for each of the remaining species, but ranged from 5 to 42, with a mean of 19.5±2.9 (Standard Error) for each species. *Table 8.1* lists the species about which questionnaires were returned with sample sizes of over 5. It also gives the sample sizes of various subsets of data, including handreared cats, and cats where the keepers did not enter the cage, since some analyses excluded these categories.

8.3.1 Human-friendly behaviours exhibited by undomesticated felids

The types of affiliative behaviours that undomesticated cats exhibit towards humans were investigated by asking keepers (a) closed questions about how many times they had observed each of six behaviours (rolling near a human, sniffing a human, lie/sit near a human, rub against a human, tail up towards a human, grooming a human), and (b) open questions about what other 'friendly' behaviours they had ever observed (answers from this included purring, playing, and being hand-fed; see *Section 8.2*). It is important to note that the type of question asked may affect the number of cats reported to carry out the behaviour.

Table 8.1. Species for which questionnaires were returned with total sample sizes of >5. Sub-totals are given for hand-reared and mother-reared cats, and for cases where keepers did not enter cages ("keepers out"), and where keepers did enter cages ("keepers in"). The number in parentheses gives the number of cats of that type which were reported to have shown some form of human-friendly behaviour (See *Section 6.3.3 (i)* for details). Divisions between sections of the table indicate lineages.

			Hand-reared		Mother-reared		
Species	Common name	Lineage	keepers in	keepers out	keepers in	keepers out	**Total** no. of cats about which questionnaires were returned.
Felis silvestris ornata	Indian desert cat	Domestic	0	0	12(3)	0	12
Felis silvestris silvestris	European wild cat	Domestic	0	0	14(2)	0	14
Felis margarita	sand cat	Domestic	1(1)	0	6(4)	2	9
Felis chaus	jungle/reed cat	Domestic	1(1)	0	17(7)	0	18
Felis nigripes	black-footed cat	Domestic	0	0	4(2)	1	5
Prionailurus bengalensis	leopard cat	*Panthera*	0	0	16(0)	0	16
Prionailurus rubiginosus	rusty-spotted cat	*Panthera*	0	0	5(1)	0	5
Prionailurus viverrinus	fishing cat	*Panthera*	1(1)	0	14(3)	7	22
Herpailurus yaguarondi	jaguarundi	*Panthera*	2(2)	0	3(3)	4	9
Leptailurus serval	serval	*Panthera*	4(3)	1	15(5)	8	28
Caracal caracal	caracal	*Panthera*	2(2)	1	21(6)	9	33
Lynx canadensis	Canadian lynx	*Panthera*	0	0	29(2)	0	29
Lynx lynx	Eurasian lynx	*Panthera*	1(1)	0	32(16)	6	39
Lynx rufus	bobcat	*Panthera*	9(8)	5	24(5)	4	42
Neofelis nebulosa	clouded leopard	*Panthera*	1(1)	4	2(2)	3	10
Leopardus pardalis	ocelot	Ocelot	2(2)	1	29(15)	7	39
Leopardus wiedii	margay	Ocelot	1(1)	0	11(10)	2	14
Oncifelis geoffroyi	Geoffroy's cat	Ocelot	2(0)	0	6(5)	0	8

Table 8.2 lists the affiliative behaviours which are commonly exhibited towards humans by the domestic cat, giving the number of undomesticated cats which were reported to exhibit each behaviour.

Table 8.2 No. of species in each lineage which were reported to exhibit each type of behaviour towards humans (hand-reared and mother-reared cats). All of the listed behaviours are known to occur in domestic cat-human interactions. The numbers in parentheses give the proportion of cats which exhibited that behaviour as a percentage of the total number of cats of that lineage which were human-friendly (as defined in *Section 8.2*), and which therefore had the opportunity to exhibit these behaviours. There were 114 human-friendly undomesticated cats (20 from the domestic cat lineage, 61 from the Panthera lineage, and 33 from the ocelot lineage).
† 51 cats were reported to use Tail Up but as some of these people did not return the third questionnaire (which checked that the sightings were genuine). It was therefore not possible to establish which of these were genuine sightings of Tail Up (see *Section 8.3.4*). Thus the values in the table are only those that could be established from the returned third questionnaires and percentage values are therefore not given.

Behaviour	domestic cat lineage	*Panthera* lineage	ocelot lineage	TOTAL
Rub against a human	2(10%)	14(23%)	6(18%)	22(19%)
Lie/sit within 1m of a human	18(90%)	50(82%)	26(79%)	94(83%)
Roll within 1m of a human	3(15%)	20(33%)	12(36%)	37(33%)
Groom human (lick)	1 (5%)	12(20%)	6(18%)	19(17%)
Sniff a human	14(70%)	54(89%)	26(79%)	94(83%)
Purr within 1m of a human	2(10%)	5 (8%)	0 (0%)	9 (8%)
Meiow within 1m of a human	0 (0%)	2 (3%)	0 (0%)	2 (2%)
Tail Up in presence of a human †	9	21	5	35-51
Tread with front paws within 1m of a human	0 (0%)	0 (0%)	0 (0%)	0 (0%)

This table highlights the fact that not all the social behaviours performed by the *domestic cat towards humans* are also performed by *undomesticated cats towards humans*. Notable differences between the use of the behaviours in domestic and undomesticated cats are as follows:(a) *Knead floor* was never performed by the adult undomesticated cats in human presence, (b) *Meiow* in the presence of a human was only reported in 2 cats (*L.serval* (1♂, 1♀) from the same zoo; no rearing details given), (c) *Purr* in the presence of a human was only reported in 7 cats (*P.concolor* (1♀), *Leopardus pardalis* (1♀), *Leopardus wiedii* (1♀), *Leptailurus serval* (1♀), and *Lynx rufus* (2♀, 1♂)), of which 4 were hand-reared.

However, the behaviours of *Rubbing* against a human, *Rolling* near a human, *Lie/Sit* near a human and *Grooming* a human occurred relatively frequently in undomesticated cats, as they do in the domestic cat. Lineage differences in these behaviours will be discussed in *Section 8.3.4*. *Tail Up* also occurred relatively frequently; this will be discussed in more detail in results *section 8.3.4*.

8.3.2 Keeper presence in cage

As keepers are presumably more likely to enter cages of 'friendly' cats than 'non-friendly' cats, it was thought that this variable might have shown up certain species to be less human-friendly than others. However, a Spearman's rank correlation of percentage of cats with keepers not going in against the ranked size of the cat species (taken from the head and body length, excluding the tail; Kitchener, 1991) was significant (rho=0.67, $p<0.01$), showing that the size, and therefore potential dangerousness of the cat is probably the factor which controls whether or not keepers go in with cats, rather than any behavioural factor. It may be that bigger cats are behaviourally less friendly to humans as well, but it was not possible to tease this apart from the size factor using the information available. This variable is therefore not helpful in helping us establish whether some species are more friendly than others.

Cases where keepers never entered the cats's cage were thus excluded from all future statistics, as the absence of the keeper in the cage naturally prohibits any friendly behaviour occuring.

8.3.3 Effect of hand rearing

Hand reared cats were found to:

(a) Be more likely to exhibit some form of human-friendly behaviour (presence/absence chi-squared 2 x 2 contingency table, $\chi^2=26.6$, df=1, $p<0.001$) than mother-reared cats, and

(b) If friendly, to exhibit friendly behaviours more frequently than mother-reared human-friendly cats (One way ANOVA, $F_{1,83}=35.3$, $p<0.0001$).

Behaviours that were classed as 'friendly' are defined in *Section 8.2* above.

Hand reared cats were therefore excluded from the majority of the following analysis. Cases where they have been included have been noted.

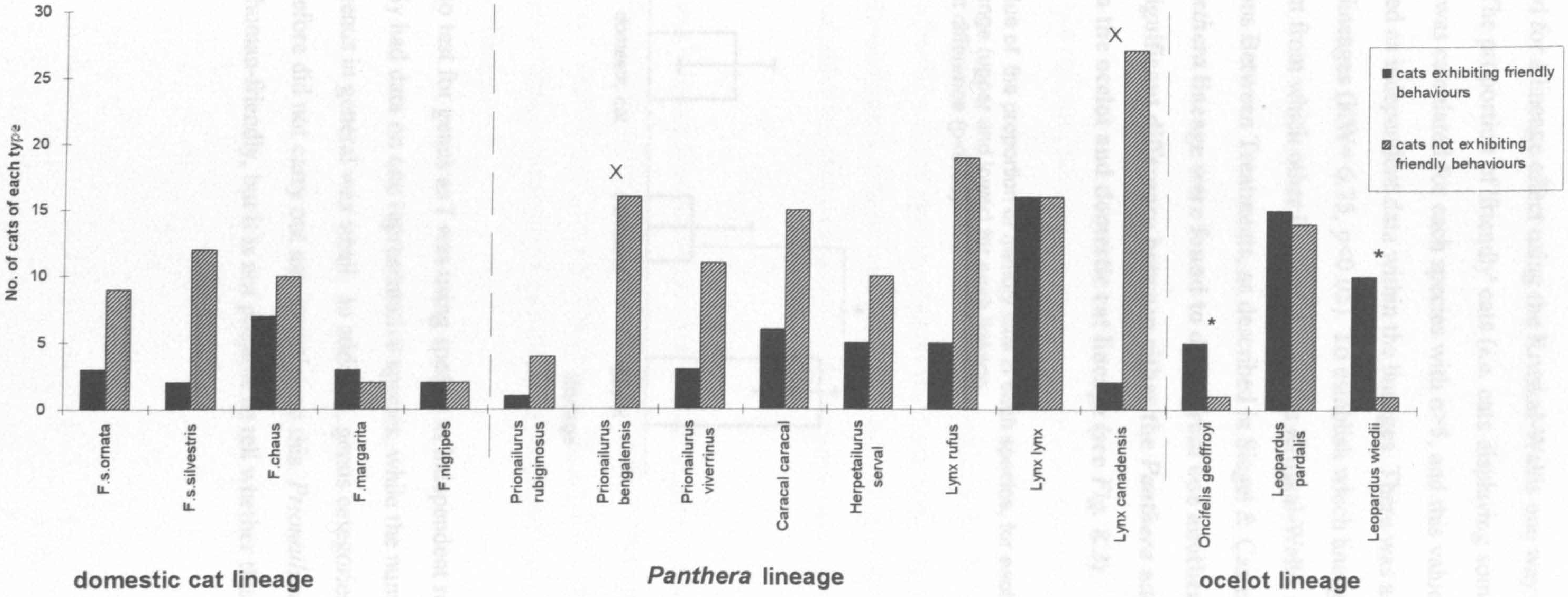
8.3.3 Effect of species and lineage

8.3.3.1 Effect of species and lineage on tendency to exhibit friendly behaviours

This analysis included the entire data set with the exception of hand-reared cats and cats whose keepers did not enter cages. This data set was very skewed towards the 0 end of the scale, and therefore categorical and non-parametric tests were used. Each cat was classified as either exhibiting human-friendly behaviours (presence) or not exhibiting human-friendly behaviours (absence), as defined in *Section 8.2.* 114 cats in total were found to exhibit some form of human-friendly behaviour, out of a total of 365 cats about which questionnaires were returned (31.2%). Every species contained some friendly individuals (See *Table 8.1* for summary).

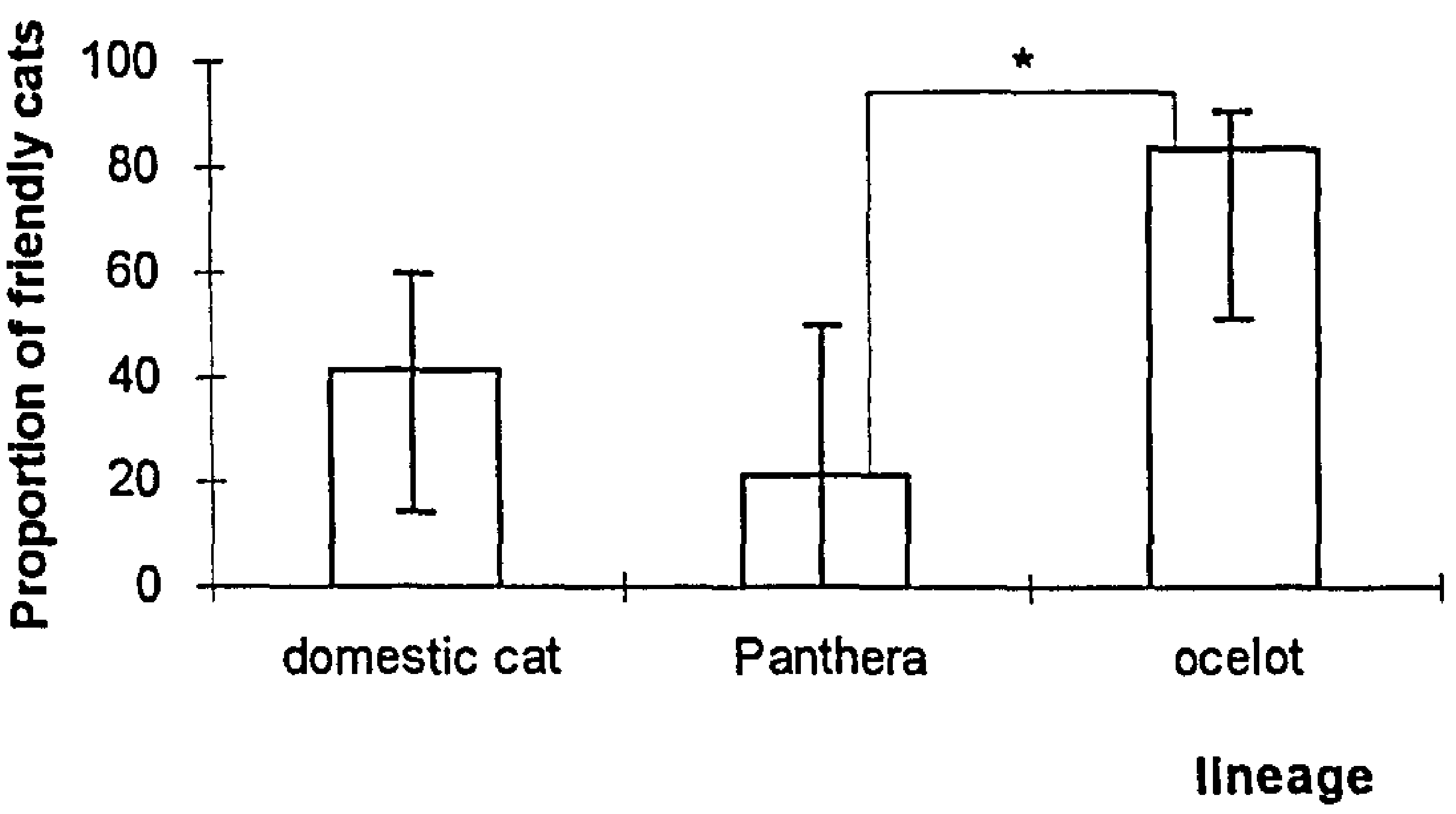
A chi-squared contingency table test (r x 2) was carried out in order to establish whether any species were significantly more or less likely to show friendly behaviours than expected (see *Fig. 8.1*). All species with sample sizes of over 5 (not including hand-reared cats or cats whose keepers did not enter cages) were included. It was necessary to combine some species together in two cases in order to increase the expected values so that there were no more than 20% of expected values <5 (Siegel & Castellan, 1988). *Felis margarita* was combined with *Felis nigripes*, and *Prionailurus rubiginosus* was combined with *Prionailurus viverrinus*. The chi-squared test was significant (χ^2=55.03, df=13, p<0.001). By examining the residuals and repeating the chi-squared test, excluding the species with high residuals from the contingency table, the species which were driving the significance were established: ***Leopardus wiedii* and *Oncifelis geoffroyi* (ocelot lineage), were both friendlier than expected, while *Prionailurus bengalensis* and *Lynx canadensis* (*Panthera* lineage) were both unfriendlier than expected.**

Figure 8.1 No. of cats of each species which (a) showed human-friendly behaviours (dark-shaded) and (b) did not show human-friendly behaviours (lightly shaded). Hand reared cats and cats whose keepers did not enter cages were not included. Only species with n>4 for the remaining cats were included (*Herpailurus yagourundi* and *Neofelis nebulosa were therefore excluded*) *= species which were more likely to show friendly behaviour than expected. X= species that were less likely to show friendly behaviour than expected.



I subsequently tested for a lineage effect using the Kruskal-Wallis one way analysis of variance by ranks. The proportion of 'friendly' cats (*i.e.* cats displaying some form of friendly behaviour) was calculated for each species with n>5, and this value for each species was then used as independent data within the lineages. There was a significant difference between lineages (KW= 6.75, $p<0.05$). To establish which lineages were significantly different from which other lineages, I used the Kruskal-Wallis method of Multiple Comparisons Between Treatments, as described in Siegel & Castellan (1988). **The ocelot and *Panthera* lineage were found to differ from one another significantly, but there was no significant difference between either the *Panthera* and domestic cat lineage, or between the ocelot and domestic cat lineage (see *Fig. 8.2*).**

Figure 8.2 Median value of the proportion of friendly cats in each species, for each lineage. The error bars show the range (upper and lower) for each lineage.
* denotes a significant difference ($p<0.05$).



It was not possible to test for genus as I was using species as independent replicates, and in some genera I only had data on one representative species, while the number of replicates for each genus in general was small. In addition, genus categories are constantly being revised. I therefore did not carry out any statistics on this. *Prionailurus* in general appeared to be less human-friendly, but it is not possible to tell whether this difference is significant.

8.3.3.2 Effect of species and lineage on the **rate** of human friendly behaviours emitted from cats classed as 'friendly'

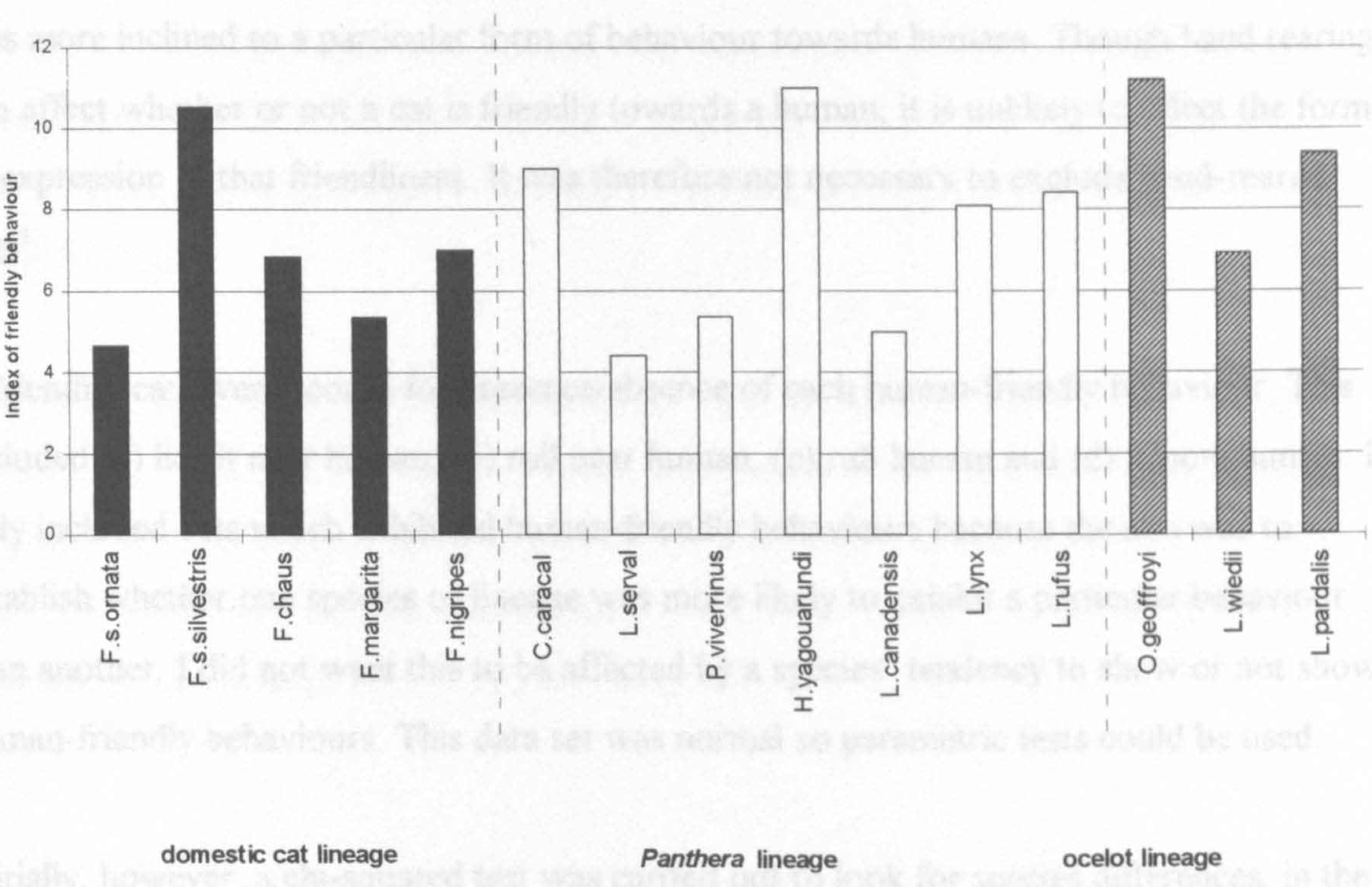
Only the cats which had exhibited some form of friendly behaviour (as defined in *Section 8.2*) were included in this analysis ('friendly' cats), because only friendly cats would have had the opportunity to exhibit these behaviours. Hand-reared cats were not included, nor were cats whose keepers did not enter their cages. A value for an index of friendly behaviour was calculated for each cat:

Index of friendly behaviour = **Rank (frequency lie down/sit near human)+ Rank (frequency rub on human) + Rank (frequency lick human) + Rank (frequency roll near human)**

where 'rank' implies the ranking system given in the methods (*Section 8.2, Table 8.0*). This system accounts for differences in the number of times that each keeper habitually visits each of the cats). As the maximum rank for each behaviour is 7, the maximum value for the index is 28. This subset of the data was normal and parametric tests were therefore used.

Fig. 8.3 shows the mean index of friendliness for each species. A nested ANOVA was carried out on this index to look at the effect of *species* and *lineage*. This was found to be non-significant for both lineage ($F_{2,12}$=1.19, ns), and species ($F_{12,14}$= 0.87, ns). This implies that there is no species or lineage effect on the **rate** that human-friendly behaviours are emitted from 'friendly' cats.

Figure 8.3 Mean index of friendly behaviour for each species which contained over 5 human-friendly cats. *P.rubiginosus* (n=1), *P.bengalensis* (n=0) , and *N. nebulosa* (n=2) were not included. Nested ANOVA was non-significant for both species effect ($F_{12,14}$=0.87, ns), and lineage effect ($F_{2,12}$=1.19, ns).



8.3.3.3 Are different types of human-directed signals specific to certain species and/or lineages?

Again, only cats that exhibited human-friendly behaviours ('friendly' cats) were included in this analysis. Cats whose keepers did not enter their cages were not included. Hand-reared cats were included, however, as the aim of this section was to find out whether one species was more inclined to a particular form of behaviour towards humans. Though hand rearing can affect whether or not a cat is friendly towards a human, it is unlikely to affect the form of expression of that friendliness. It was therefore not necessary to exclude hand-reared .cats[1].

'Friendly' cats were scored for presence/absence of each human-friendly behaviour. This included (a) lie/sit near human, (b) roll near human, (c) rub human and (d) groom human. I only included cats which exhibited human-friendly behaviours because the aim was to establish whether one species or lineage was more likely to exhibit a particular behaviour than another. I did not want this to be affected by a species' tendency to show or not show human-friendly behaviours. This data set was normal so parametric tests could be used.

Initially, however, a chi-squared test was carried out to look for species differences, in the presence and absence of (a) rubbing human, (b) lie/sit near human, (c) grooming human, and (d) rolling near human. A limitation of the chi-squared test is that it should not be used in cases where over 20% of the expected values are less than 5 (Siegel & Castellan, 1988). As the number of friendly cats in each species was low, the data did not meet this requirement. This causes the chi-squared value to be more significant than it should be. However, the majority of behaviours were non-significant, (*Rub*, χ^2=7.61, df=10, ns; *Lie /Sit*, χ^2=13.52, df=13, ns; *Roll*, χ^2=16.14, df=13, ns), so this is not a problem for these behaviours. Lick was found to be significant (χ^2=21.97, df=11, $p<0.05$), but as this was only just significant, it is probably most likely that this is an artefact of the low numbers

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[1] However, I did repeat the MANOVA on a data set including only mother-reared cats to check this assumption. There was no difference between the results achieved from this, and the results from the data set which included all cats (all variables were non-significant, as was the multivariate test of all the variables together).It was not possible to repeat the chi-squared, as the expected values were too low.

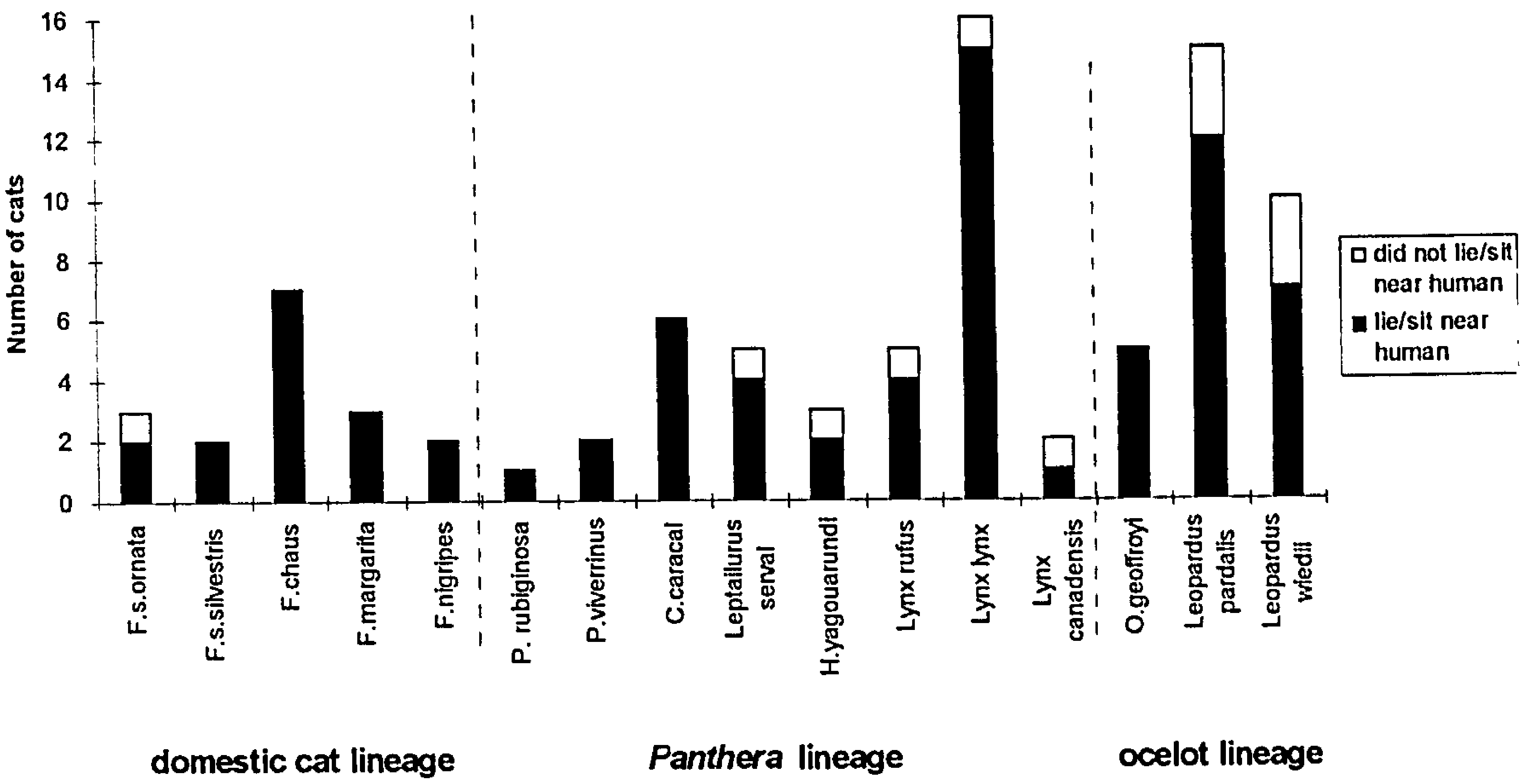
involved.

A MANOVA was then carried out to look at the effect of lineage on each behaviour separately, and on all the four behaviours together. The proportion of cats in each species which had been seen to carry out a behaviour was calculated for each behaviour, and a MANOVA used to look for differences between lineages, using each species as an independent measure within each lineage. There was found to be no difference between lineage for any of the four behaviours (*Rub*, $F_{2,9}$=1.63, ns; *Lick*, $F_{2,9}$=1.25, ns; *Lie/Sit*, $F_{2,9}$=0.25, ns; *Roll*, $F_{2,9}$= 2.42, ns), nor for the multivariate test of the four together ($F_{8,12}$=0.89, ns).

Despite the fact that neither species nor lineage was significant, I have included graphs showing the number of cats exhibiting each behaviour as a reference for presence/absence data for each species (see *Figs. 8.4- 8.7*). The exact number of cats in each category has been used rather than a percentage because of the low numbers involved. Hand-reared cats have been graphed separately to mother-reared cats.

Figure 8.4 No. of **friendly cats in each species, showing presence /absence of *lie/sit near human*** for (i) mother-reared cats and (ii) hand-reared cats. All species included regardless of number of friendly cats in each species. *P.bengalensis* not included as there were no friendly cats in this species.

(i) Mother-reared cats



(ii) Hand-reared cats

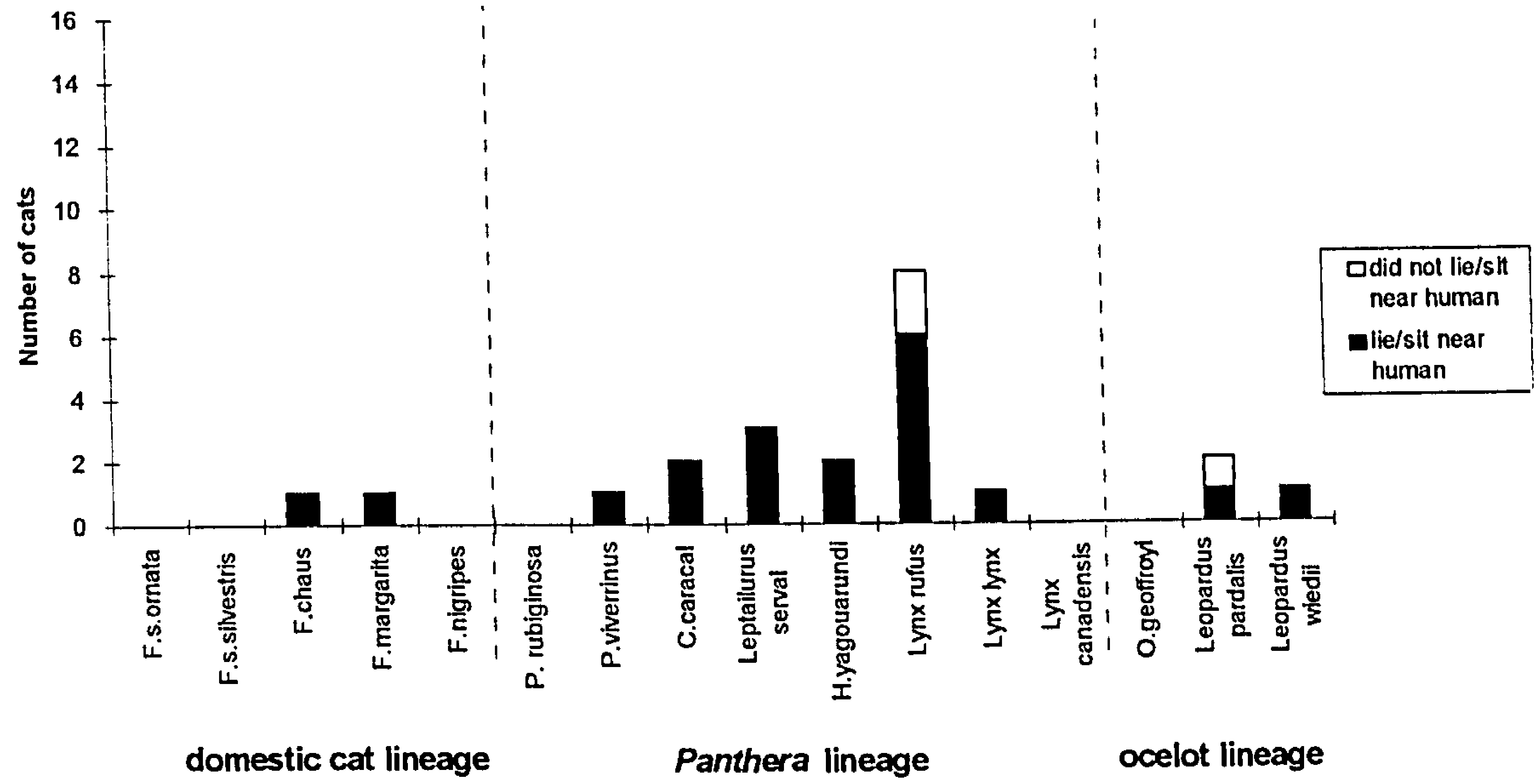
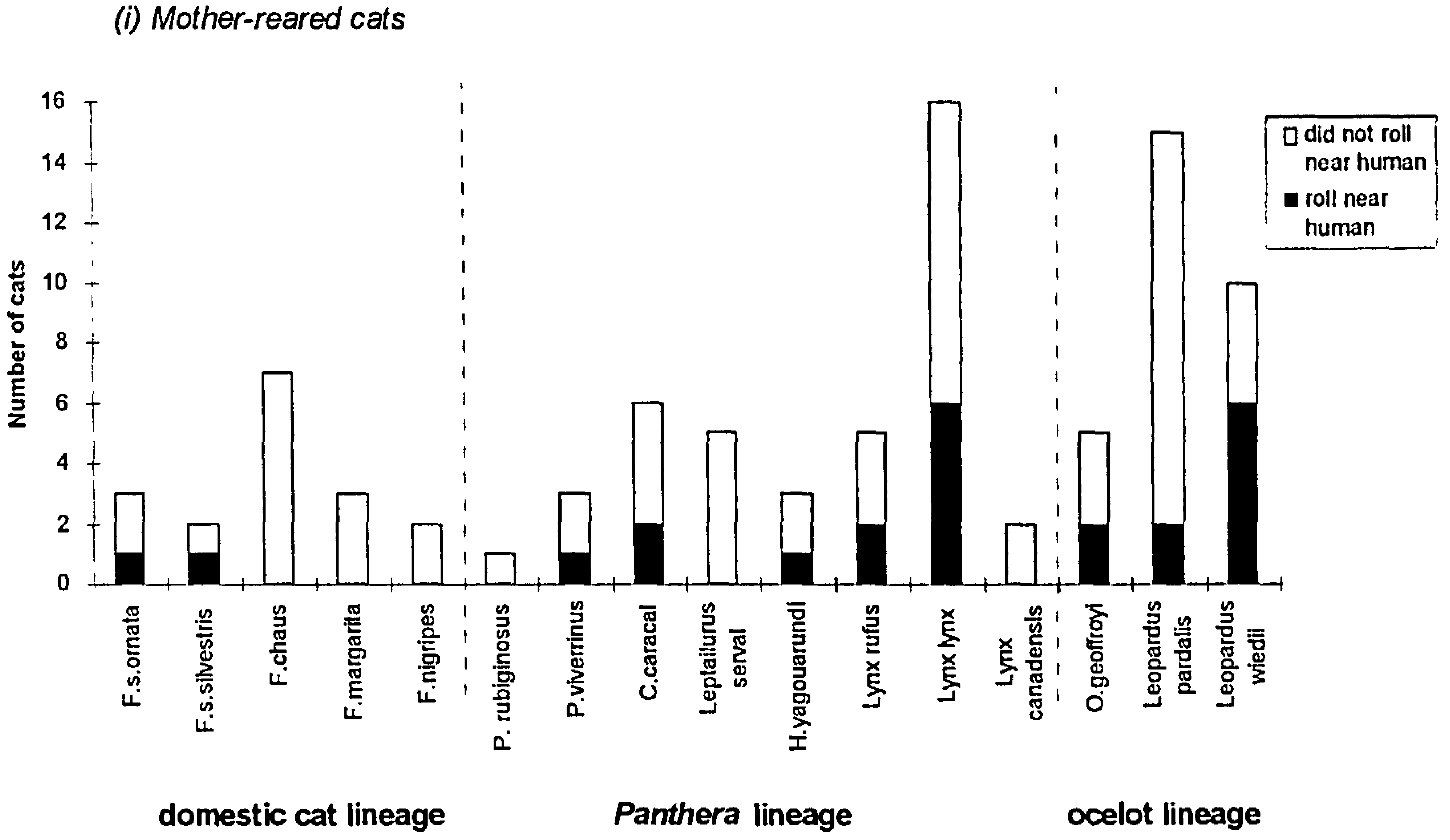


Figure 8.5 No. of friendly cats in each species, showing presence /absence of ***roll near human*** for (i) mother-reared cats and (ii) hand-reared cats. All species included regardless of number of friendly cats in each species. *P.bengalensis* not included as there were no friendly cats in this species.



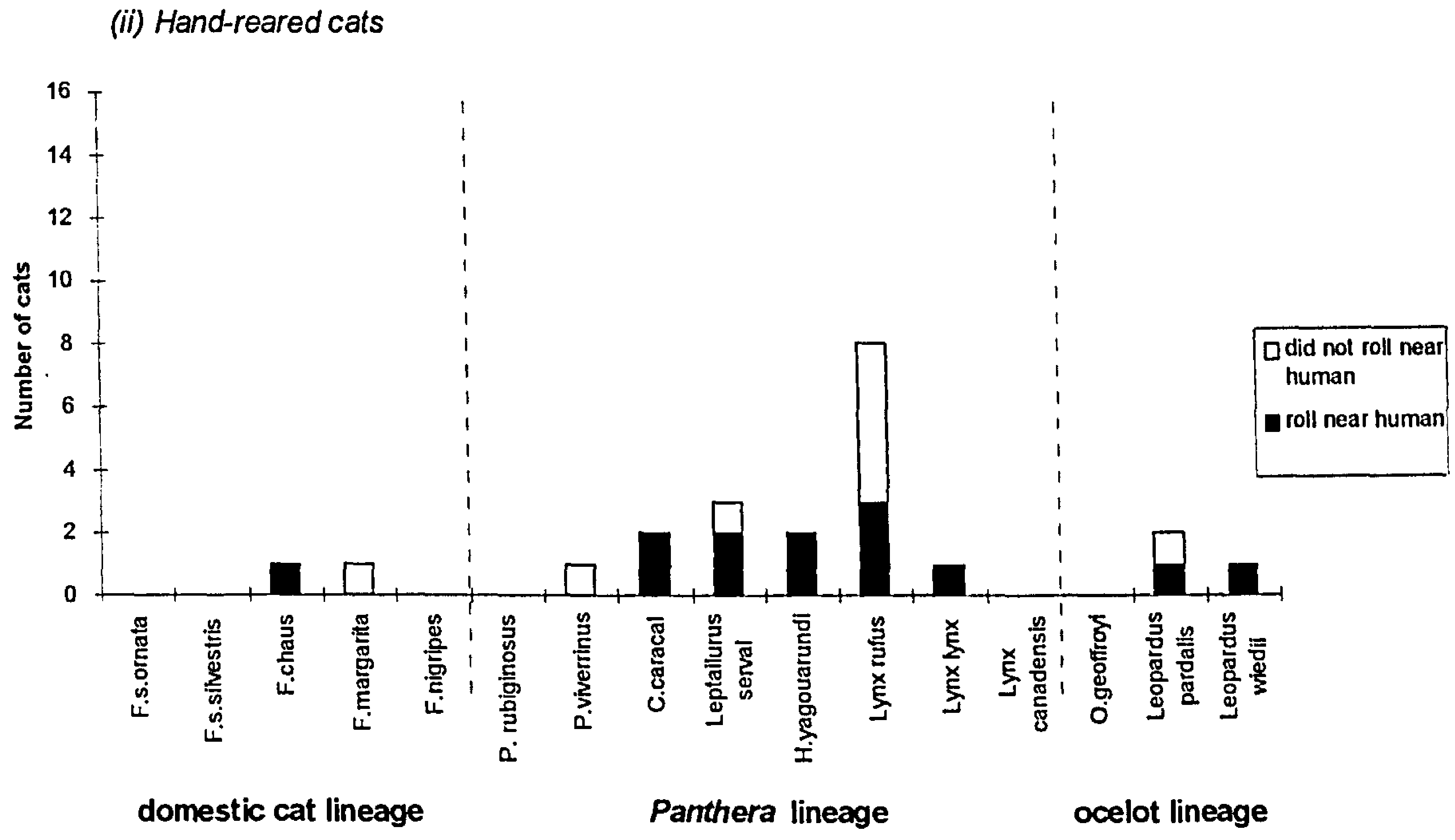
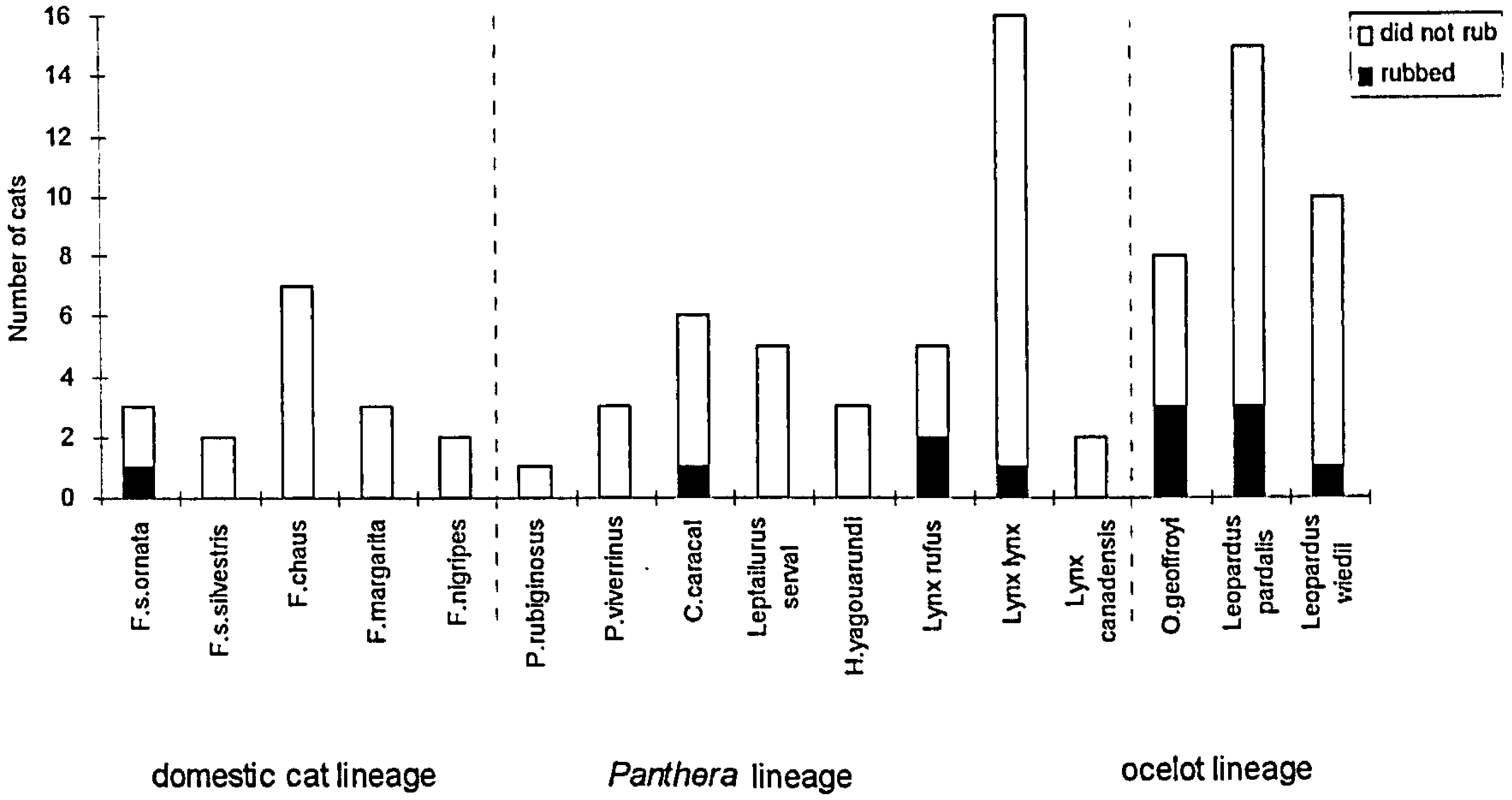


Figure 8.6 No. of friendly cats in each species, showing presence /absence of ***rubbing humans*** for (i) mother-reared cats and (ii) hand-reared cats. All species included regardless of number of friendly cats in each species. *P.bengalensis* not included as there were no friendly cats in this species.

(i) Mother-reared cats



(ii) Hand-reared cats

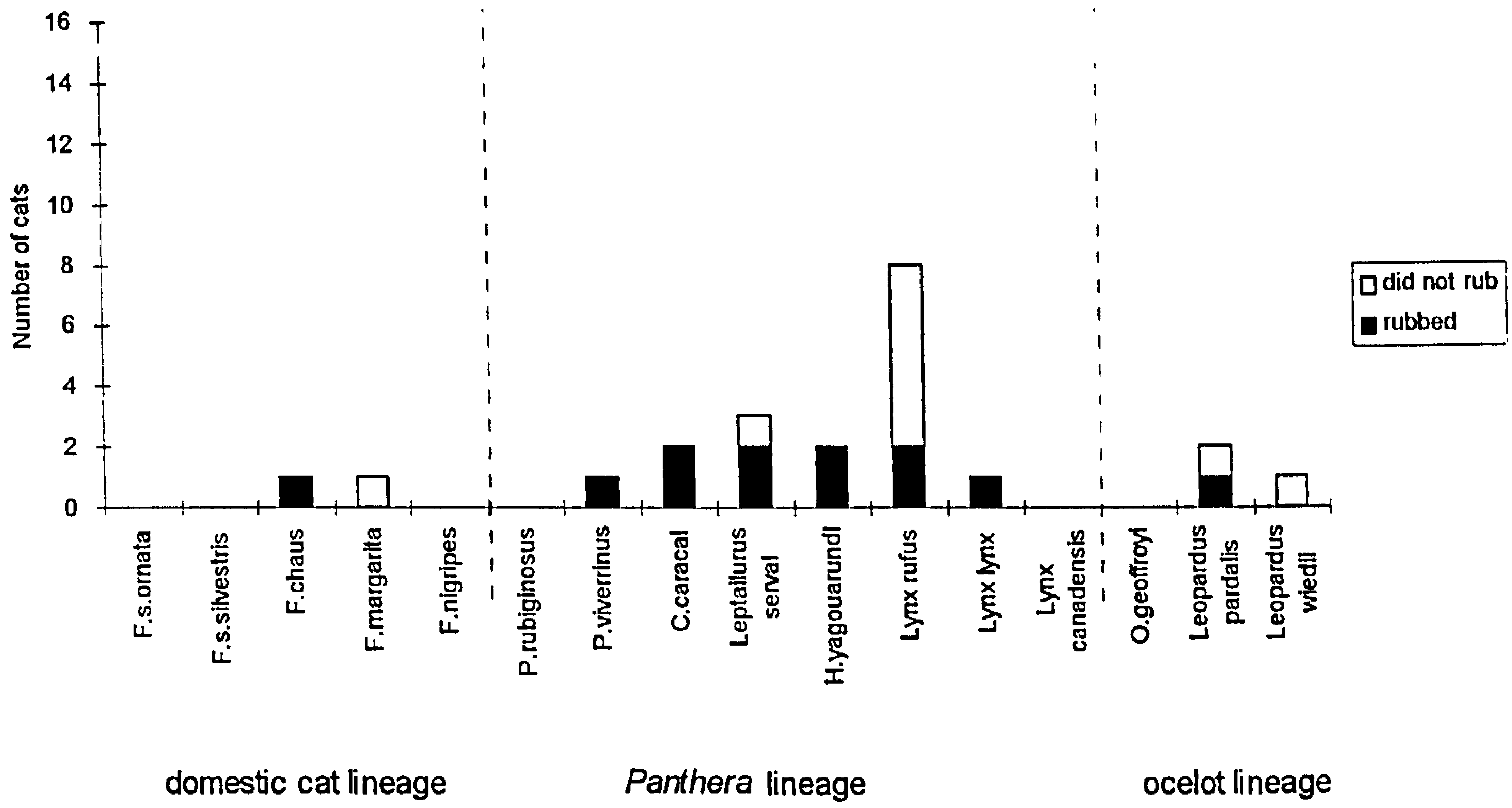
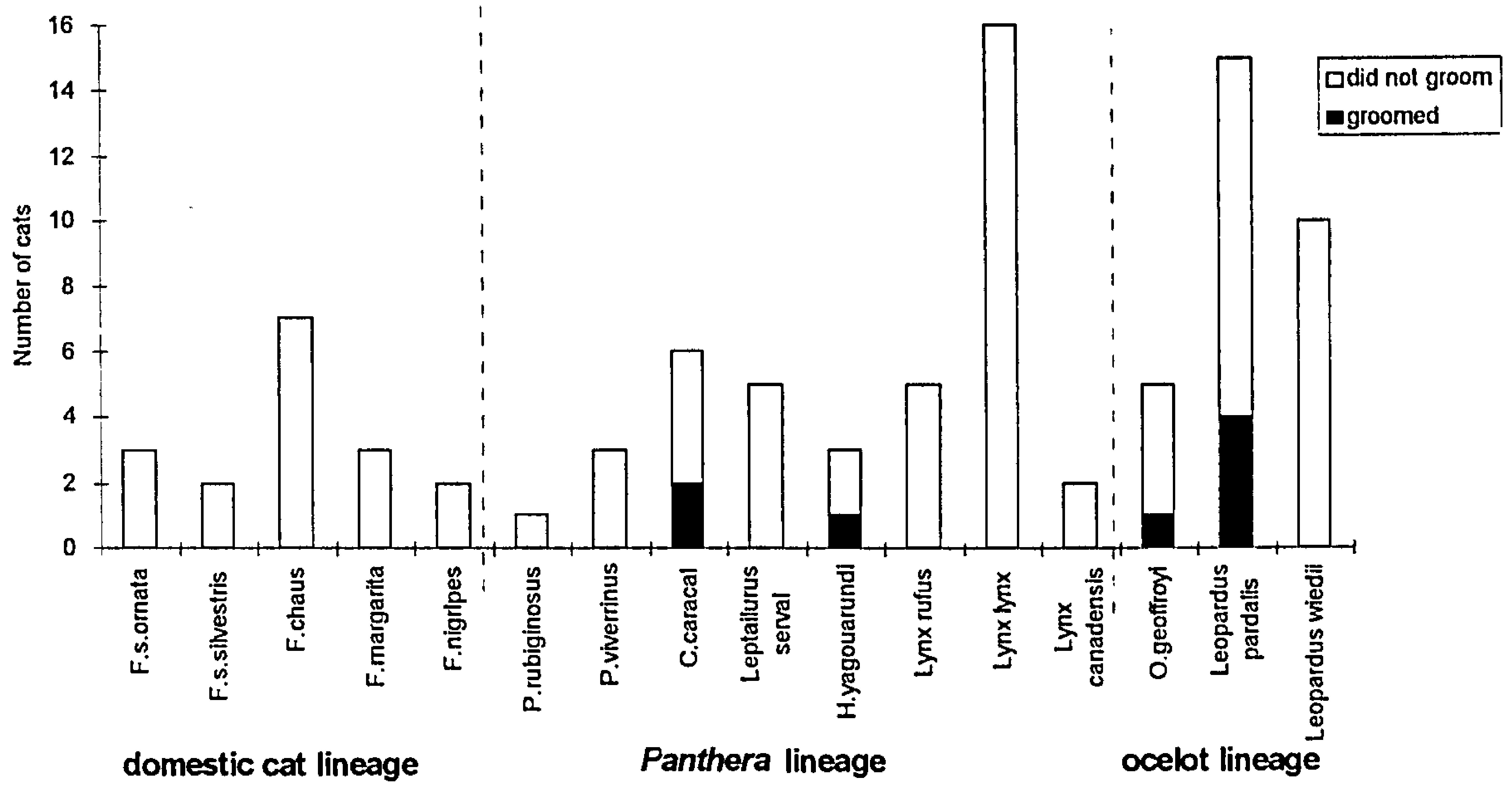
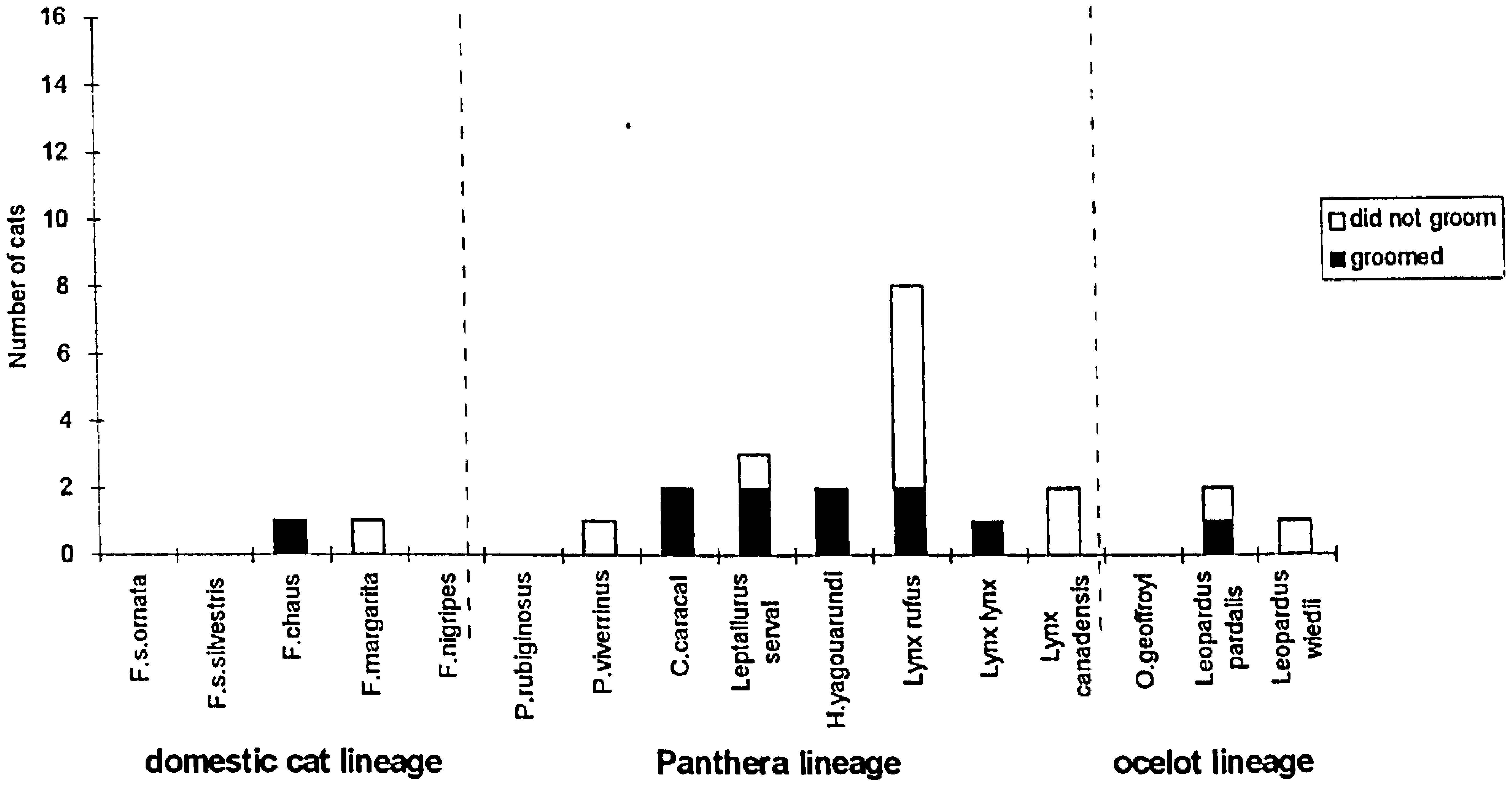


Figure 8.7 **No. of friendly cats in each species, showing presence /absence of *grooming humans (licking)* for (i) mother-reared cats and (ii) hand-reared cats. All species included regardless of number of friendly cats in each species. *P.bengalensis* not included as there were no friendly cats in this species.**

(i) Mother-reared cats



(ii) Hand-reared cats



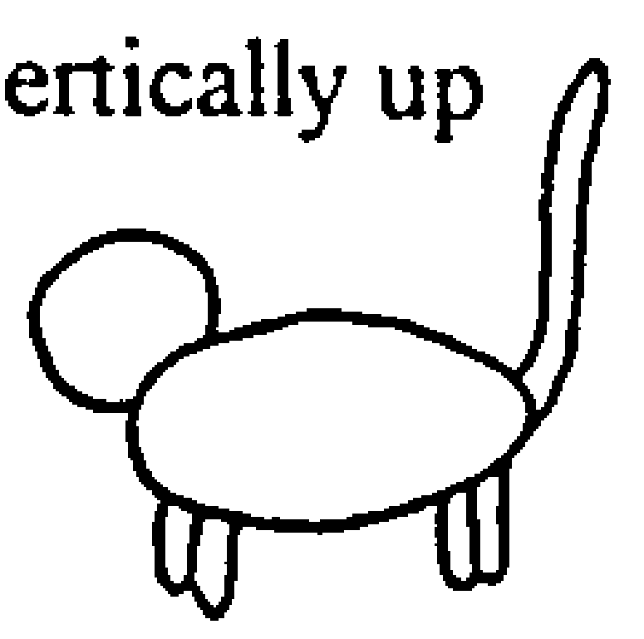
8.3.4 Occurrence of Tail Up in human-friendly encounters.

A third, very brief, questionnaire was sent out keepers who reported the Tail Up position being used by cats towards humans. The aim of this questionnaire was to establish in what situations the Tail Up position was being performed, and to confirm exactly what kind of Tail Up position they had observed. The original question asked was "Have you ever seen this cat **raise its tail like a domestic cat** in its interactions with you?". The subsequent brief questionnaire asked keepers to circle the diagram which most resembled the tail position they had seen, out of four possibilities, which included Tail Up, Tail Half-Up, Tail Bent-Up, and a fourth position which was described by Leyhausen (1979), which I called Tail Aggressively Raised (*Fig. 8.8*).

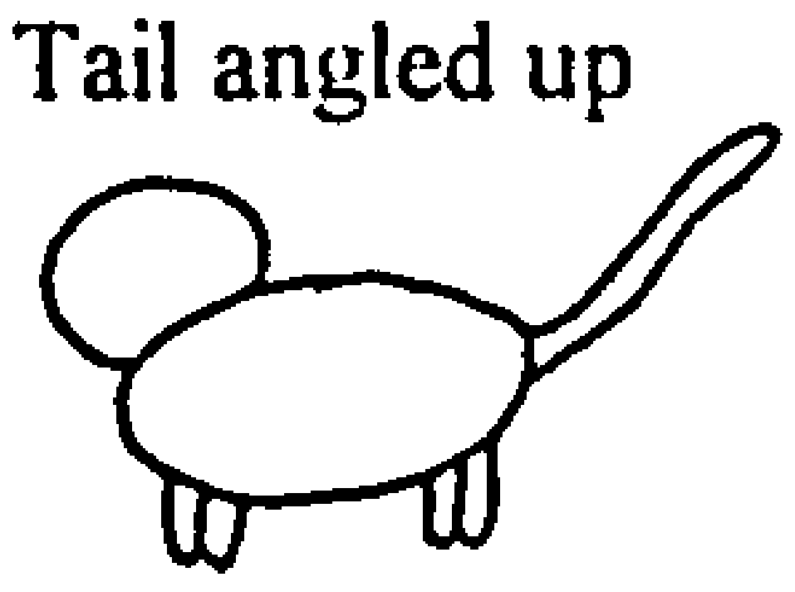
Figure 8.8 **The first question of the third questionnaire, which aimed to establish exactly what type of Tail Up position the keepers had seen (See *Appendix III C* for whole questionnaire).**

Please ring the diagram below which corresponds to the tail up position that you had in your mind when describing the above situation, or draw your own diagram if none of these apply.

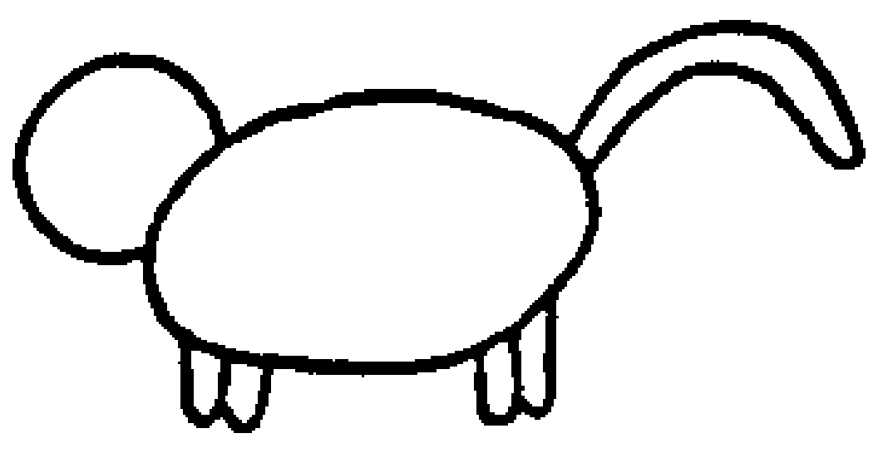
A. Tail vertically up



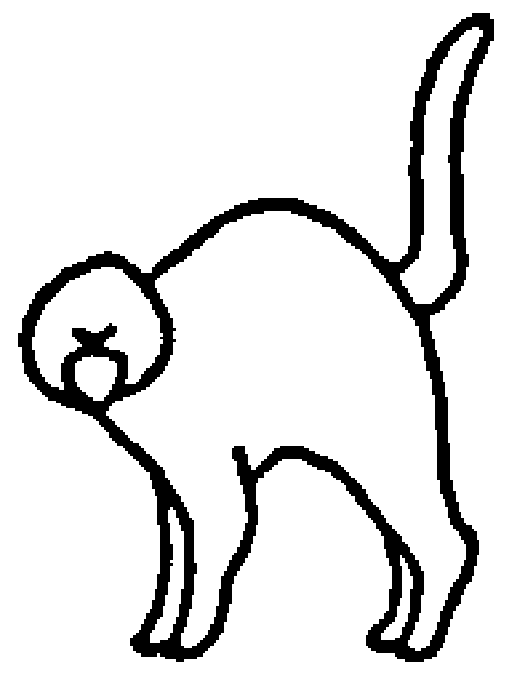
B. Tail angled up



C. Tail bent-up



D. Tail aggressively raised



E. Other (either explain or draw yourself)

From the original questionnaire, 51 cats were reported to **"raise their tail like domestic cats"**. Subsequent brief questionnaires were sent out about all of these cats and were returned about 38 cats. Three of these cats were reported to only use position D (see *Fig. 8.8* for description of position). I was interested only in positions A&B (position D was not the friendly tail position that I was referring to in the original question), so these three cats were excluded from the analysis. Some cats were reported to use both position D (in aggression) and positions A&B (in non-aggressive situations) but only the situations concerning A&B are discussed in following section. No cats were reported to use position C (Tail Bent-Up). The results described below therefore refer only to the use of Tail Up (A) and Tail Half-Up (B). As Tail Up and Tail Half-Up were shown in *Chapter 5* to be used in similar situations to one another, and as many of the keepers reported that they had seen both these tail positions in the same cat, in the same situations, the results of these two tail positions were combined. The following results will discuss the situations and species in which Tail Up and Tail Half-Up were used.

It was not possible to carry out any meaningful statistics on this data as there were too few individuals involved (n=35). This was confounded by the effect of species (9 different species) and of hand-rearing (8 individuals were hand-reared). I have therefore simply described the data using actual frequencies and percentages, with the intention of giving some suggestion as to the situations in which Tail Up appears to be used in undomesticated cats cats, and also possibly some explanation as to why Tail Up occurred in these 35 cats when it did not in any of the other 354 cats about which questionnaires were returned.

8.3.4.1 Species reported to perform Tail Up

Table 8.3 gives a summary of the numbers of cats of each species which were observed to exhibit Tail Up in interactions with humans. It is important to note that 23 of the 35 cats which were reported to perform Tail Up were from one zoo, and reported by one keeper. It may be therefore that this data is not reliable. However, I would be surprised if this was the case as this keeper's behavioural observations are normally very accurate (I worked at this zoo collecting the data for *Chapter 3*), and I additionally telephoned him to confirm his answers.

Table 8.3 shows that Tail Up position appears to be particularly performed by *F.s.ornata* (7 individuals) and *Lynx lynx* (8 individuals), though percentage-wise, *P.rubiginosa* shows the highest value, with 80% of cats exhibiting Tail Up (but n=4). However, it is impossible to make any definite species conclusions as the numbers are so small.

Table 8.3 **Numbers of cats of each species which were reported to perform Tail Up or Tail Half-Up, (see *Fig. 8.8*). The figures in bold type in the second column indicate that these cats all came from the same zoo (as mentioned in the above paragraph). The percentage of cats performing Tail Up as a proportion of the total number of cats in that species (about which questionaires were returned) is given in parentheses.**

Species	Number of cats in different zoos	Number of cats of each species which were reported to put their Tail Up		
		Hand-reared	**Mother-reared**	**Total**
F.s.ornata	***7*** (*i.e.* all in one zoo)	0	7	7 (58%)
F.chaus	***2*** (*i.e.* all in one zoo)	0	2	2 (11%)
domestic cat lineage				9 (45%)
C.caracal	***1*** (*i.e.* all in one zoo)	1	0	1 (3%)
P.rubiginosa	***4*** (*i.e.* all in one zoo)	0	4	4 (80%)
L.serval	1;1;1	2	1	3 (11%)
L.lynx	**6**;1;1	1	7	8 (20%)
L.rufus	2;2;1	4	1	5 (12%)
***Panthera* lineage**				21 (34%)
L.pardalis	1;***4***	0	5	5 (13%)
ocelot LINEAGE				5 (15%)
TOTAL		8 (25.8%)	27(8.9%)	35 (9.6%)

A larger proportion of hand-reared cats performed Tail Up/Tail Half-Up (25.8%) than did mother-reared cats (8.9%).

8.3.4.2 Situations in which Tail Up occurred

Only 48% of cats which exhibited Tail Up when a human was present had been previously classed as 'human-friendly' (as defined in *Section 8.2*). This appears to indicate that the Tail Up position towards humans may not always be acting as an affiliative behaviour.
Figs. 8.9 & 8.10 show the percentage of cats (as a percentage of the total number of cats which were observed to perform Tail Up), showing Tail Up in each of various different situations. In **mother-reared cats** which were reported to perform Tail Up (or Tail Half-Up), this position was most commonly used when the keeper approached, either with or without food (92% of mother-reared cats which had been reported to perform Tail Up,

Figure 8.9 **Mother-reared cats only:** Breakdown of the number of cats showing Tail Up in different situations (black bar), as a proportion of the number of cats which had been reported to show Tail Up at all, and which had been reported to carry out each of the charted behaviours. The percentage for each variable is given above the bar. Actual frequencies were charted because the values were so low in some variables.
+ indicates that this behaviour did not occur in these cats at all.

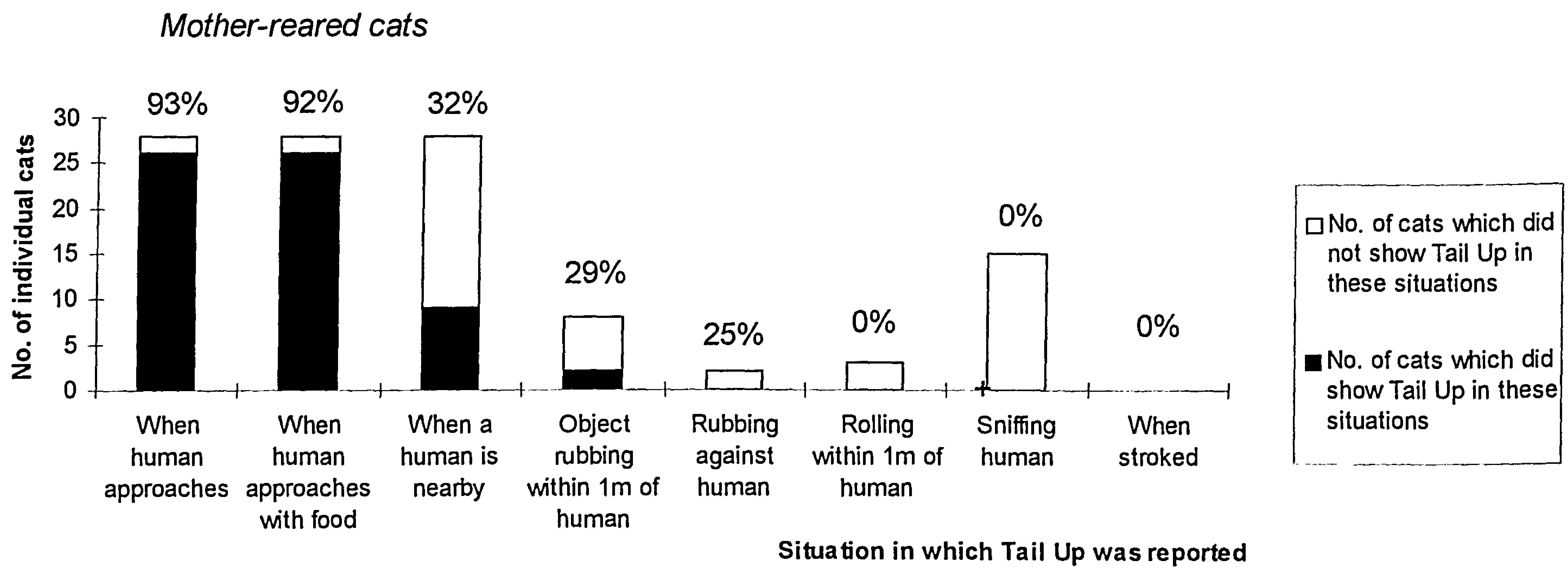
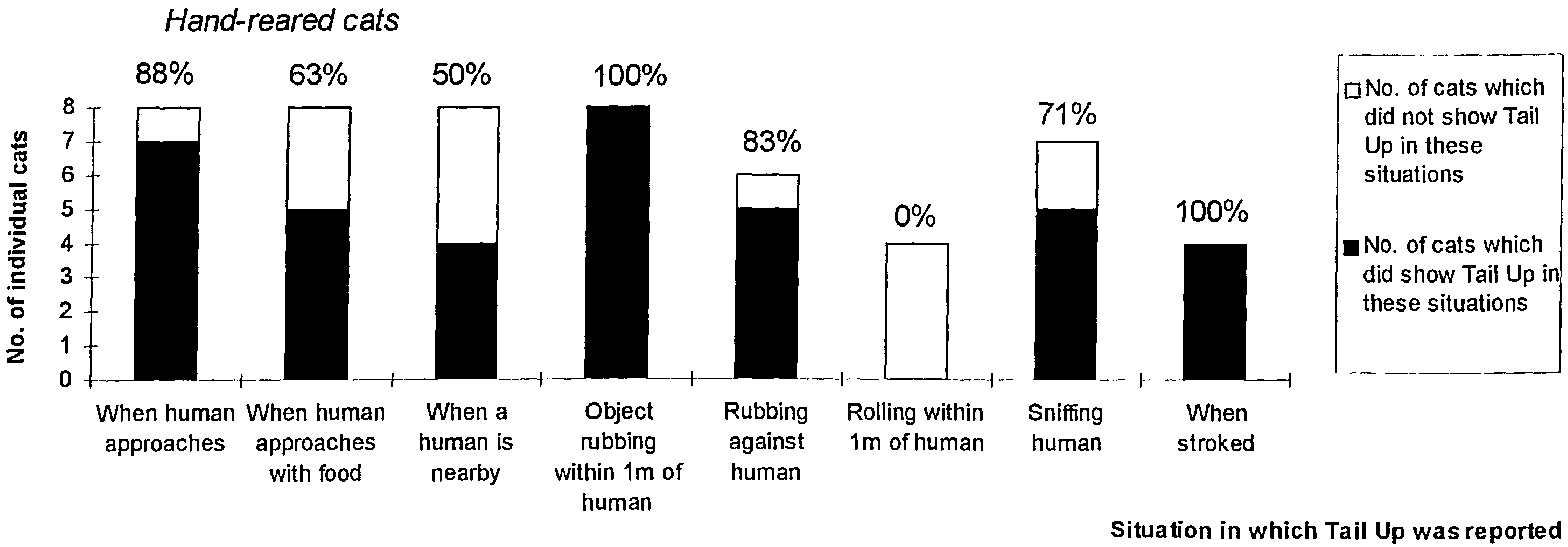


Figure 8.10 **Hand-reared cats only:** Breakdown of the number of cats showing Tail Up in different situations (black bar), as a proportion of the number of cats which had been reported to show Tail Up at all, and which had been reported to carry out each of the charted behaviours. The percentage for each variable is given above the bar. Actual frequencies were charted because the values were so low in some variables.



performed it when a human approached with food; without food, 93%; see *Fig. 8.9*). In **hand-reared cats,** Tail Up was also used commonly in these two situations (88% without food, 63% with food), but it was used more commonly in other situations such as when object rubbing (100% of cats which were reported to perform the Tail Up, performed it whilst object rubbing; 83% whilst rubbing against a human; 71% whilst sniffing a human, and 100% when stroked). In mother-reared cats these latter behaviours are not so common, and Tail Up is performed less in these situations (object rubbing near human 25%, rubbing against human 0%, sniffing human 0%; see *Fig. 8.9*).

8.4 DISCUSSION

8.4.1 The use of Tail Up in human-directed interactions by undomesticated cats

The finding that undomesticated cats do use Tail Up in situations other than the *Spray* situation was surprising given the results of *Chapter 3 (Section 3.3.1.3.3)*, which had suggested that Tail Up was **never** used by undomesticated cats out of the *Spray* situation. In addition, it is at odds with the theory that rubbing is motivationally attached to Tail Up as a result of the link through scent marking (See *Section 6.5*). In this section I will therefore discuss the possible implications of the results from this chapter only; the different threads from different chapters will then be discussed as a whole in the general discussion (*Chapter 9*).

I spoke on the telephone to several (though not all) of the keepers who had reported the performance of Tail Up, and established that the use of Tail Up when humans approached (either with or without food), appeared to be as a result of, in their words, "excitement" (caused by the fact that the cats associated the presence of humans with food).Kiley-Worthington (1976) describes excitement as occurring when "the animal shows an increase in activity and performs more different activities more often", although this definition is subjective and unfortunately not based on the findings of any scientific procedure. Kiley-Worthington stated that an increase in "excitement" leads to an increase in postural tonus, which she describes as a head or tail elevation. She reports that "excitement" may include situations of frustration or internal conflict. An automatic raising of the tail when excited may explain the high percentage use of Tail Up in situations when the keeper is approaching. It may be the conflict between wanting the food and being fearful of the keeper which causes this.

This explanation, if correct, may also be used to explain the other results. Hand-reared cats were highly likely to exhibit Tail Up in the following situations; Object Rubbing near a human, Rubbing against a human, Sniffing a human, and when stroked. It may be that these situations cause motivational excitement in hand-reared cats, thus explaining the performance of Tail Up. Mother-reared cats were less likely to exhibit Tail Up in these situations. This is perhaps caused by the fact that these situations are less exciting for mother-reared cats which are not as socialised to humans as hand-reared cats, although, on the other hand, I would expect that internal conflict would be higher for mother-reared cats in these situations.

If this theory is correct, it indicates that the Tail Up behaviour is *not acting as a social behaviour in these human-directed situations*, but instead is an autonomic reaction, occurring as a result of excitement. This hypothesis is backed up by the finding that only 48% of cats which exhibited Tail Up had been classed as human-friendly; if Tail Up was acting as a social behaviour towards humans, I would expect that all cats which were found to exhibit Tail Up would be human-friendly. This theory that motivational excitement causes a high postural tonus (Kiley-Worthington, 1976) and therefore causes the tail to raise, links with the finding that Tail Up is commonly used in play (a source of excitement) during the initial Run Approach (See *Section 6.2.2.3*), and that Tail Wave and Tail Jerk, which may also be caused by an increase in postural tonus, occur at times of frustration (see *Section 3.4.6*).

This interpretation questions the use of Tail Up in human-directed situations in the *domestic cat.* We have established that Tail Up acts as a social affiliative behaviour in domestic cat-cat interactions (*Chapter 6*), but that, in the undomesticated felids, it does *not occur socially* (only occurs as an autonomic response with excitement, and also as a facilitating action with spraying). *Chapter 7* has established that in *human-directed* domestic cat interactions, Tail Up does occur in the social affiliative context. However, whether Tail Up has a specific function in the human-directed context, or whether it just occurs as a result of being motivationally connected to the other social affiliative behaviours (as a result of its affiliative function in intraspecific interactions) is not known. What we can say in summary, however, is that Tail Up in the *domestic cat* occurs in a social affiliative situation; towards both members of its own species and the human species (though it may not have a specific function in the human-directed situation). *Undomesticated felids*, in contrast, do not specifically use Tail Up in a social affiliative situation in the domestic cat, although Tail Up may occasionally be seen in this context towards humans, as a result of motivational excitement.

8.4.2 Comparison of human-directed behaviour in the domestic cat and undomesticated felids: Ethogram differences.

The undomesticated felids have not had the opportunity to evolve any specific human-directed behaviours, because they have not had the time. A study of the differences between human-directed behaviour in domestic and undomesticated cats can therefore be used to suggest which behaviours must have evolved in the domestic cat.

Undomesticated cats were found to exhibit many similar human-directed behaviours as the domestic cat (see *Table 8.2, Section 8.3.1)*, including *Rubbing* against a human, *Rolling* near a human, *Sniffing* a human, *Lie/Sit* near a human (obviously), *Grooming* a human, and *Tail Up* (although evidence suggests that Tail Up in the undomesticated felids may be occurring as an autonomic response (see *Section 8.4.1*), rather than as a social behaviour).

There were also some differences between the cat-human ethograms of the domestic cat and the undomesticated:

- *Knead front paws* was never performed by the adult undomesticated cats in human presence.

- *Meiow* in the presence of a human was only reported in 2 cats.
- *Purr* in the presence of a human was only reported in 7 cats, out of the 114 possible undomesticated cats which were human-friendly[2].

The fact that domestic cats have more opportunity to exhibit social behaviours must be taken into account when interpreting these differences. In particular this may affect behaviours such as Purr (and possibly also Groom), which generally occur in the domestic cat during a long interaction (*e.g.* sitting on human's lap). Thus the low number of undomesticated individuals exhibiting Purr (7 out of 114 individuals which were human-friendly) may be due to circumstance, rather than to any behavioural factor. This may also be the reason for the relatively low number of human-friendly undomesticated cats which exhibited the behaviours of rubbing against a human (22), rolling near a human (37), and grooming a human (19).

However, the fact that Meiow only occurred twice cannot be attributed to this as it is a behaviour which could occur from a distance. The infrequent use of this behaviour therefore must be due to behavioural factors, as must the total absence of Kneading. These findings indicate that the domestic cat must have evolved the ability to use these kitten behaviours as an adult, during domestication.

These results therefore appear to back up the findings of the previous chapter. Firstly we can conclude that certain adult behaviours (social rubbing, rolling, grooming, sniffing, and lying/sitting near human, and possibly also purring[3]) can be directly transferred from the intraspecific context to the interspecific context. All of these behaviours (except

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[2] I have quoted the number of human-friendly cats as a comparison rather than the total number of cats, because, if a cat is not human-friendly, this restricts its capacity to exhibit behaviours towards humans.

[3] Purring is most frequently cited as a kitten behaviour (Bradshaw, 1992, Deag *et al*, 1988). However, Kiley-Worthington (1984), and Leyhausen (1979) both report that it occurs in adult cat-cat interactions as well. This suggests that this behaviour should fall into the adult behaviour category, although the fact that it only occurred 7 times suggests that it may belong to the kitten behaviour category. However, this could be explained by the fact that purring only occurs in long interactions (*e.g.* sitting on human's lap) and therefore does not occur much in zoo felids.It is therefore impossible to know which category this belongs to.

purring) were shown to be performed in intraspecific affiliative interactions in undomesticated felids (*Chapter 3*), and in this chapter they have been shown to be performed in interspecific affiliative interactions. The ability to perform these behaviours in a human-directed situation is as a result of their innate behavioural plasticity rather than a result of any evolutionary process. No evolution can have been necessary for these behaviours to be carried out in the human-directed situation[4]. It is likely that all species of felid would be able to carry out these behaviours towards a human if given the correct conditions.

However, it appears that undomesticated felids cannot naturally revert to using kitten behaviours (*i.e.* Meiow & Knead Floor and possibly Purr[3]; Deag *et al*, 1988) as an adult, in contrast to the domestic cat, which does use kitten behaviours when adult (towards humans). This difference suggests that the domestic cat has evolved (either genetically or culturally) to be able to perform kitten behaviours as an adult, in a human-directed situation. This persistence of juvenile characteristics into the adult population is known as neoteny, and has been frequently cited as being one of the behavioural adaptations which occurs during domestication (Ratner & Boice, 1975, Fox, 1967). Neoteny may have been encouraged by artificial selection of paedomorphic individuals (Fox, 1978). It has been suggested that neoteny may actually help to increase the behavioural plasticity of a species, thereby encouraging domestication (Boice, 1973, Ratner & Boice, 1975). If this is the case then it would suggest that the domestic cat is the most behaviourally flexible of all the felids.

Thus we can conclude that domestic cat-human behaviours originate from at least two types of intraspecific behaviour; *(a) from intraspecific adult social and sexual behaviours* (due to the natural behavioural plasticity of the cat), and *(b) from intraspecific kitten behaviours* (due to the persistence of juvenile characteristics which is likely to have

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[4] This does not rule out the possibility that these cat-cat behaviours have been enhanced and modified (ritualised) in the domestic cat specifically for interspecific use (*e.g.* incessant rubbing where undomesticated species would only rub occasionally). *Chapter 7* investigated this, and found that certain behaviours were modified slightly, despite being basically the same behaviours as those that are used intraspecifically.

occurred as a result of evolution through domestication). There may also be a third origin, *from non-social behaviour* (*i.e.* Tail Up). This is discussed in more detail in the *general discussion.*

8.4.3 Species and lineage differences in the tendency to show human-friendly behaviours

The above section has discussed the fact that the *form of expression* of human-friendliness is similar in all human-friendly felids, and that it is unaffected by either species or lineage. However, the results also indicate that a cat's *initial tendency* to become tame/show friendliness is affected by both species and lineage, although, once friendly, the frequency of the human-friendly behaviour, and the type of friendly behaviour that is exhibited is not.

Cats of the *Panthera* lineage are less likely to become friendly towards humans than those in the ocelot lineage, which show the highest proportion of friendly cats. The domestic cat lineage appears to lie approximately between the other two in its tendency to be friendly, but it is not significantly different from either so we cannot definitely ascertain which population it belongs to, nor whether it might form one of its own if more data was collected. Correspondingly, certain species within these lineages are more/less likely to show human-friendly behaviours; *P. bengalensis* and *L. canadensis* (*Panthera* lineage) are less human-friendly than expected while *L.wiedii* and *O.geoffroyi* (ocelot lineage) are both more friendly than expected. Guggisberg (1975) mentioned that captive individuals of *O. geoffroyi* are known to become tame in captivity; a statement which supports the findings of this chapter.

Considering that the domestic cat has evolved from the domestic cat lineage we would have predicted that the cats from this lineage would have emerged as being the most likely to exhibit human-friendly behaviours. It therefore comes as a surprise that the three species representing the ocelot lineage are as friendly, if not more so, than the domestic cat lineage. Looking at the evolutionary tree (See *Fig. 1.1; Introduction*) it seems likely, therefore, that the ancestral felid which subsequently diverged into all three of the Felidae lineages must have had a predisposition for human-friendliness[5]. The results from this chapter indicate that the *Panthera* lineage may have lost some of this predisposition, it being less likely to be friendly than the cats of the ocelot lineage. However, the tendency has not disappeared altogether (just over a quarter of the mother-reared cats in the Panthera lineage did exhibit human-friendly behaviours; 43 out of 161 cats in total). In comparison, about two-thirds of the ocelot lineaged cats (30 out of 46), and a third of the domestic lineaged cats(18 out of 53) exhibited human-friendly behaviours.

This low tendency to be friendly amongst *Panthera* lineaged cats cannot be due to the size of the cats (it could be that keepers discourage friendliness from large and dangerous cats), because the tendency is maintained amongst the smaller members of this lineage (for example, *P.bengalensis & P. rubiginosa*), and in fact, *Lynx lynx*, one of the largest members of this lineage to be included in the questionnaire, was one of the friendliest species of the *Panthera* lineage.

The domestic cat is thought to have practically 'domesticated itself' (Zeuner, 1963), a phenomenon presumed to be caused by *Felis silvestris'* predisposition for human-tolerance. This predisposition caused the species to take advantage of the high density of food which results from human settlements. Individuals that are the most tolerant to humans are at an advantage because they can take advantage of, not only the rubbish scraps, but also of direct human hand-outs. Thus this 'friendly' tendency is selected for because being 'friendly' is a good strategy, leading to increased food supply and possibly better shelter. The initial stages of domestication, at least, are therefore thought to have occurred without any attempt on the human's part to forcibly restrain or artificially select for human-tolerant individuals (Zeuner, 1963), although subsequent artificial selection by humans (caused by humans giving more food and shelter to the friendlier cats, rather than by forced captivity) may have contributed to this process (Serpell, 1988).

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[5] This 'predisposition for human-friendliness' is most probably based in the trait of behavioural plasticity which is present in many felids. This trait enables them to adapt to a wide range of social situations, which may include the human-orientated situation. Thus the more behaviourally flexible a species is, the more we would expect cats to be able to adapt to being human-tolerant.

Considering this, it seems surprising that members of the ocelot lineage, which I have found in this chapter to have a similar predisposition for human-tolerance, (possibly even more so than the domestic cat lineage), have not followed the same pattern. It may be that the reason for this is due to habitat segregation of humans and felids. The majority of cats in the ocelot lineage are thought to live primarily in forest areas, for example, *Oncifelis guigna* (kodkod), *Leopardus pardalis* (ocelot), *Leopardus wiedii* (margay), and *Leopardus tigrina* (tiger cat or oncilla) (Kitchener, 1991, Guggisberg, 1975), where humans rarely inhabit. However, some species do live in more open areas; *Oncifelis geoffroyi* is sometimes found in open bush on the plains or in shrubby woodland, while the Pampas cat (*Oncifelis colocolo*) often inhabits open grasslands (Guggisberg, 1975, Kitchener, 1991). These types of habitats would be more likely to contain human settlements. It therefore seems surprising that the plains-living cats have not taken advantage of the human-orientated niche, particularly *Oncifelis geoffroyi*, which was shown to have a strong tendency to exhibit human-friendly behaviours in this chapter.

On the other hand it may be that these species do take advantage of human food sources, but that they just have not become domesticated to the same extent as the domestic cat, in which case any association of a species with humans may not be widely known. There is little literature on the relationship of the cats of the ocelot lineage with humans. Ocelots are generally thought avoid human habitations, with exception of raidings of chicken houses, either occasionally (*Leopardus pardalis & Oncifelis colocolo*, Guggisberg, 1975), or frequently (*Oncifelis guigna*, Philippi, cited in Guggisberg, 1975).

Human settlements cause clumping of the food distribution. This is thought to be the reason why domestic cats often live in groups; living in a social group under these conditions is more advantageous than living a solitary territorial life (See *Chapter 1, Section 1.3.1* for more information). If South American cats of the ocelot lineage are tolerant of humans and do sometimes live in close vicinity to them (a possibility which is suggested by the results of this chapter but which would need to be backed up by observational evidence), then it follows that they also may live in closer proximity to their conspecifics, collecting around human settlements like the domestic cat.

This speculation is interesting because the results from *Chapter 3* showed that *Oncifelis geoffroyi* (from the ocelot lineage) was more social to other members of its species than any of the other three species (from domestic cat and *Panthera* lineages) that I observed (See *Section 3.3.3*). Perhaps there are areas in South America where some members of the ocelot lineage (in particular *O.geoffroyi*) do live in groups near human settlements? Unfortunately there is little published information on the behaviour of undomesticated cats around human settlements. However H.L.Blonk (cited in Guggisberg, 1975) postulated a high degree of social behaviour for the kodkod, which has been reported to raid chicken houses (Guggisberg, 1975). Unfortunately the reference for this is not given, so it is not possible to find out any more information about what observational evidence Blonk had for postulating this hypothesis. Rengger (cited in Guggisberg, 1975) stated that ocelots live in male/female pairs with exclusive territories. More recent research has pointed towards their solitariness (Emmons, 1987), although Emmons (1988) reported that social meetings were common, with cats remaining together for long periods of time.

8.4.4 Criticisms of the study

The use of questionnaires as a tool for collecting data produces a number of problems. Firstly, the use of questionnaires produces the problem of respondent reliability. However, Carlstead (1997) studied the reliability and validity of zookeeper ratings of animal behaviour and found behavioural observations of keepers to be extremely reliable.

Secondly, by using questionnaires, one accepts that conditions are not controlled. Each data point is affected by a number of conditions that cannot be controlled for (*e.g.* size of cage, personality of keeper, type of food, whether cat lives alone or with others *etc.*). However, on a positive point, the use of questionnaires allows access to a vast amount of data that would otherwise be unavailable. The alternative method available to me in studying this subject was to experimentally test the behaviour of a few undomesticated cats to humans. I decided against this because zoo conditions are in general logistically uncontrollable anyway, and therefore this method would have resulted in little amounts of uncontrolled for data in comparison to the large amounts of uncontrolled for data which were collected using the questionnaire.

In hindsight, the construction of the questionnaire could have been slightly improved. The split between the initial and follow-up questionnaire worked very well. However, having to send out a third questionnaire about the Tail Up position was not ideal, though could not be avoided due to the fact that I was not expecting so many cats to have exhibited the Tail Up behaviour. Another problem was caused by the fact that the type of question asked differed according to the behaviour; closed questions were asked about some behaviours (*e.g.* rubbing, rolling), but not about others (*e.g.* Purr, Meiow), for which the answers to open questions were relied upon (*e.g.* "What other human-friendly behaviours have you ever seen?"). This could result in some occurrences of Purr and Meiow being missed.

8.5 CONCLUSIONS

We can conclude that undomesticated felids have a natural ability to redirect adult sexual and social affiliative behaviours towards other species (not necessarily just humans). This ability probably stems from their innate behavioural plasticity, which allows them to modify their behaviour to the current social situation. However, the results also conclude that undomesticated cats cannot naturally revert to performing kitten behaviours (*i.e.*Knead and Meiow) when adult (at least in a human-directed context, and probably in others also). The domestic cat, in contrast, is known to commonly use these two behaviours towards humans. This discrepancy between the two suggests that the domestic cat has evolved (culturally or genetically) in order to be able to use kitten behaviours towards humans as an adult (neoteny).

Tail Up appears not to be being used as an affiliative social behaviour by undomesticated felids towards humans, in contrast to its use in the domestic cat, where it usually occurs in an affiliative social context. This difference may be as a result of the fact that, in domestic cat-cat interactions, Tail Up has a social affiliative function in intraspecific signalling. It seems likely that its use in this context in human-directed situations is as a result of its motivational connection with affilaitive behaviours in the domestic cat, rather than because it has any particular function as such (see *Section 8.4.1*).

The ease with which a species can become human-friendly is affected by lineage. The ocelot lineage was found to have a particular predisposition for human tolerance. As the ability to become human-tolerant is likely to be based in the trait of behavioural plasticity, this finding may indicate that the ocelot lineage is more behaviourally flexible than the other two. The finding that the domestic cat lineage is not the lineage with the highest predisposition to human tolerance brings up the question as to why members of the ocelot lineage have not also been domesticated.

Chapter 9: GENERAL DISCUSSION

It is thought that the domestication of *Felis silvestris* caused this species to increase its rate of social interactions, both within its own species, as a result of the groups which formed around human settlements where there was a high density of resources, and towards humans, as a result of the resources that humans could provide. Such a change in sociality is likely to have been associated with a change in the social signalling of the species. The aim of this thesis was to investigate the origins of the signals displayed by the domestic cat today, and to explore the changes that may have been caused by domestication.

In this discussion, I shall attempt to summarize the findings of this thesis by bringing together the different threads covered by different chapters, looking firstly at the evolution of *intraspecific* signalling, and secondly at the evolution of *interspecific* signalling in the domestic cat. I shall then discuss the function and evolution of the Tail Up posture, attempting to bring together evidence from different parts of the thesis. Some applied aspects of this study will then be discussed, followed by suggestions for future work.

9.1 THE EVOLUTION OF INTRASPECIFIC SIGNALLING IN THE DOMESTIC CAT

Undomesticated felids have the ability to exhibit all the major social behaviours that are exhibited in the domestic cat (*Chapter 3*). In the wild, each social behaviour is likely to have a role in a specific social context. This may include sexual behaviour (*e.g.* social & object rubbing, rolling, and grooming), mother-young interactions (*e.g.* grooming), kitten social play (*e.g.* rolling and pawing), and territorial defence (*e.g.* aggressive or defensive behaviours such as Tail Under, Hiss, Growl, Ears back, Mouth threat *etc.)*. However, in captivity, felids performed social behaviours out of these contexts, and adult cats of all types of sex combinations were found to frequently exhibit affiliative behaviours to one another out of the sexual context. This is an unexpected finding, considering that all the species studied are thought to be exclusively solitary in the wild. The cats did not simply attempt to avoid one another in the cage, as one might predict[1].

The ability of these cats to *(a) use behaviours in a broader social context than they would in the wild,* and *(b) be more affiliative to one another and interact socially more often than they would in the wild* is likely to be a result of the trait of behavioural plasticity. This allows individuals to adapt behaviourally to a given social situation, and is generally considered to be a trait of the Felidae, and of the Carnivora as a whole (Macdonald, 1983, Macdonald *et al*, 1987, Kruuk, 1975, Leyhausen, 1988). It is a learning ability, and would be expected to be present, at least to some extent, in the majority of higher animals.

We can conclude that the ability of the domestic cat to form close-knit affiliative groups and exhibit high frequencies of affiliative behaviour has not evolved recently. It seems likely that a felid species from any lineage would be at least partially able to adapt their behaviour in this way (within a lifetime) if conditions allowed (*i.e.* if food was of high density and clumped; see *Section 1.3.1*).

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[1] However, one pair of captive sand cats (*Felis margarita*) have been reported to simply avoid one another, living a solitary life within a captive paired environment, by altering their active times so that when one was active, the other was asleep (Bennett & Mellen, 1983).

However, the results from *Chapter 4* do suggest that domestic cats may have evolved in other ways. Various authors have found that free-living domestic cat groups have social ranking systems, although these are not manifested as strict linear hierarchies (Liberg, 1983, Natoli & de Vito, 1991, Kerby & Macdonald, 1988; see *Section 1.3.1.2*). Macdonald *et al* (1987) hypothesizes that these social structures are maintained by subtle behaviours such as social rubbing, which tend to be asymmetrically directed within a dyad. I tested for the presence of a similar system in groups of undomesticated felids and found no evidence for the existence of a systematic signalling system acting to maintain hierarchy (though a hierarchy itself may have existed through aggressive and defensive interactions). This absence of a subtle signalling system in undomesticated felids suggests that domestic cats must have evolved their social rubbing system through domestication[2].

In addition, the domestic cat was found to have evolved one new social behaviour; the Tail Up signal. Behavioural evidence from undomesticated felids (*Chapter 3*) suggested that Tail Up was only ever exhibited as an integral part of spraying (scent-marking)[3], and never used in a social context. *Chapter 5* found that the Tail Up posture in domestic cats is utilised as a visual signal of intention to be affiliative, with the ultimate function of reducing aggression between cats. Its absence as a social behaviour in undomesticated felids suggests that this social function must have evolved during domestication, although a general increase in the use of Tail Up may have occurred earlier, possibly in *F.s.ornata* (see *Section 9.3* for details).

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[2] This conclusion depends on Macdonald *et al*'s (1987) hypothesis being correct; his data did support his hypothesis, but did not provide conclusive evidence for it.

[3] Although subsequent questionnaire data found that a few undomesticated felids did use this tail position in a different situation towards humans (probably when motivationally excited). This is discussed in more detail in *Section 9.3*.

9.2 THE EVOLUTION OF DOMESTIC CAT-HUMAN (INTERSPECIFIC) SIGNALLING

The results from *Chapters 7 & 8* indicate that cat-human signals have originated from three different sources:

(1) From adult social and sexual behaviours

These include Social Rub, Groom (lick), Roll near human, Sniff human, Lie/Sit near human, and possibly also Purr[4]. These behaviours were found to be present in:
(a) Both undomesticated cat and domestic cat intraspecific adult social and sexual interactions (*Chapter 3*).
(b) Undomesticated felid interactions towards humans (*Chapter 8*), and
(c) Domestic cat interactions towards humans (*Chapter 7*).
It can therefore be concluded that felids have the ability to redirect these behaviours towards a different receiver species without any evolution having occurred to make this possible. This is probably due to the behavioural plasticity of the Felidae (Macdonald *et al*, 1987, Kruuk, 1975, Leyhausen, 1988).

However, *Chapter 7* showed that although inter- and intraspecific behaviours are superficially similar in form, they do differ slightly. Firstly, these behaviours occur in broader (and different) contexts towards humans than they would if utilised in the intraspecific situation. Again, this is likely to have occurred naturally as a result of the innate behavioural flexibility of the felids. Secondly it was shown that social rubbing behaviour occurs at a higher intensity and more repetitively when human-directed than it does when cat-directed. However, it is not possible to tell from the data available whether this change has occurred as a result of genetic evolution, cultural evolution, or whether it

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[4] Purr is most commonly cited as a kitten behaviour (*e.g.* Deag *et al*, 1988, Bradshaw, 1992). However, there are references to its use in interactions between *adult* domestic cats (Kiley-Worthington, 1984, Leyhausen, 1979, Pg. 293). It is therefore impossible to establish whether this use in adulthood is as a result of neoteny, or whether adult undomesticated felids also perform this behaviour. I was unable to record this behaviour in undomesticated felids due to recording methods. It is therefore impossible to tell whether Purr belongs to category 1 or category 2.

is just as a result of behavioural plasticity causing an individual to alter its behaviour within one lifetime[5].

(2) From intraspecific kitten and juvenile behaviours

These include Meiow, Knead front paws, and possibly Purr[4]. The pattern found for these behaviours was as follows:

(a) In *cat-cat interactions in the domestic and undomesticated felids* these behaviours were either extremely uncommon (Meiow) or absent (Knead)(*Chapter 3*). Purr was never heard in undomesticated felids, but it is impossible to tell whether his is as a result of the low amplitude at which it was emitted, or whether undomesticated felids do not purr as adults.

(b) In *human-directed* interactions by the *undomesticated felids*, these behaviours occurred only at a very low level (Meiow; 2 out of the 114 human-friendly cats exhibited this behaviour), or not at all (Knead). (*Chapter 8*). Purr occurred in 7 out of 114 cats.

(c) In *human-directed* interactions by the *domestic cat*, all three of these behaviours (Knead, Meiow and Purr) occur a great deal (*Chapter 7*).

It can therefore be concluded that felids do not have a natural ability to exhibit kitten behaviours when adult. This indicates that some behavioural evolution has occurred during domestication in order for this ability to develop. It is likely that this evolution has been encouraged by artificial selection by humans for paedomorphic individuals (Fox, 1978), though the repetitive use of these kitten behaviours (particularly of Meiow) may have occurred as a result of either natural selection (*e.g.* humans give more food to cats which meiow more) or even just as a result of individuals learning that more food is given if they meiow more.

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[5] It would have been possible to establish the process involved if we had asked questions about the bout length and intensity of social rubbing in the questionnaire to keepers of undomesticated felids. However, this question was not included. I spoke to some keepers about this, who seemed to think that rubbing only ever occurred briefly. If this is so, it would indicate that rubbing behaviour has evolved rather than being individually learnt (unless the length of rubbing is affected by the tameness of cats). However, as this evidence is anecdotal it is impossible to state conclusively one way or another.

Whether Purr should be included in this category or not will depend on whether *undomesticated* felids are found to exhibit Purr in cat-cat interactions.

(3) From non-social behaviours

This includes the behaviour of Tail Up. The inclusion of this behaviour (and therefore this category) depends on whether the Tail Up in human-directed situations can be classed as a social behaviour (it occurs in a social affiliative context) or not (it probably does not have a social function in the human-directed situation). Assuming that it is a social behaviour, it is most likely to have originated from the Tail Up posture which was originally a *non-social* behaviour (occurring with spraying or as an autonomic reaction with excitement (see *Section 9.3*). However, it is likely that the use of the social Tail Up in human-directed interactions occurred as a result of its social use in cat-cat interactions; therefore although it ultimately originated from a non-social behaviour, it use in human-directed interactions may have originated from the intraspecific social behaviour.

9.3 THE EVOLUTION OF THE TAIL UP SIGNAL

9.3.1 Summary of results

The context and causation of the Tail Up posture were found to differ according to the species of the initiator (*i.e.* undomesticated or domestic cat) and the species of the recipient (*i.e.* human or cat recipient). The findings can be summarized below:

In *undomesticated felids*, Tail Up does not generally appear in a social situation. It was found to be exhibited either as (a) a part of spraying (*i.e.* scent-marking)(*Chapter 3*), and (b) as an autonomic reaction caused by motivational "excitement" caused by the appearance of food or a human stimulus (in which case it *may* occur as part of a social interaction between humans and cats, but in this case the sociality does not appear to be the cause of the behaviour) (*Chapter 8*).

In *the domestic cat*, Tail Up almost always occurs in a social affiliative context. In cat-cat interactions it occurs as a signal of intention to be affiliative (*Chapter 6*), while in cat-human interactions it occurs temporally with the affiliative behaviours (*Chapter 7*).

9.3.2 Conjectures on the evolution of the Tail Up signal

Ewer (1974), used current knowledge of the behaviour of the viverrids to give clues about the possible evolution of wild felid behaviour. The viverrids are the family that have diverged least from the ancestral animal from which the Feloidae emerged; thus their behaviour is expected to be similar to that of the ancestral felid. There is a similar relationship between the domestic cat and the four related wild species that I observed in this study, in particular *F.s.ornata*, which is thought to be very closely related to the domestic cat (Kratochvil & Kratochvil, 1976; see *Section 1.1.1*). We can therefore use *F.s.ornata* as a model of the solitary ancestral cat from which the domestic cat is thought to have evolved, under the assumption that it will have evolved at a far slower rate than the domestic cat, which has necessarily evolved quickly in order to take advantage of its changing niche. Other species of felid, whose common ancestors with the domestic cat are more evolutionarily distant, can be used to investigate at what point in the evolutionary chain certain behaviours evolved. In this section I have therefore used the behavioural data collected on the undomesticated cats in *Chapter 3 & 8* to give clues about the evolution of this signal.

The *Tail Up signal* of domestic cats is most likely to have evolved from the *Tail Up non-social behaviour* that can be seen in undomesticated felids. Logically, there must have been a middle stage whereby the Tail Up posture was motivationally attached to the affiliative signals (rubbing in particular), but not acting as a signal (*Chapter 6*). This motivational attachment will have been the basis for the start of the evolution of the Tail Up posture as an affiliative signal. The steps leading from a *Tail Up posture that is motivationally connected to rubbing* to a *Tail Up signal* (of intention to be affiliative) have already been discussed in *Chapter 6 (Section 6.4)*, so I do not intend to reiterate them. However, the initial steps that led the Tail Up non-social behaviour to become motivationally attached to rubbing has not been discussed.

The results from *Chapter 3* indicate that Tail Up in undomesticated felids is only ever used as part of Spray. However, the results from *Chapter 8*, which looked at interactions between undomesticated felids and humans, indicated that it could also be used towards humans, and that it appeared to be exhibited as an autonomic reaction during motivational excitement[6]. The fact that undomesticated felids appear to perform Tail Up in these two different ways means that there are two possible hypotheses which can be generated about the evolution of a Tail Up-Rub motivational connection. These are discussed below:

***Hypothesis 1:** Motivational "excitement".*

Chapter 8 found that cats tended to raise their tails when "excited"; this may include times of frustration and/or internal conflict. The inclusion of humans into the lives of captive undomesticated felids may increase the frequency of "excitement" of the cats, due to the fact that human presence causes an internal conflict between wanting food/human stimulus (*e.g.* through stroking), and wanting to flee.

The inclusion of humans into the niche of the undomesticated cat which was to evolve into the domestic cat may have caused an increase both in rubbing (against humans) and therefore also in Tail Up due to the motivational excitement occurring at the same time. The two behaviours may have become motivationally attached through this. However, it is difficult to see how a strong motivational attachment between Tail Up and rubbing could have evolved because it seems unlikely that there would be any advantage to this. More data would be need on the exact use of Tail Up in undomesticated felids for this hypothesis to be substantiated.

***Hypothesis 2:** Scent-marking connection.*

Tail Up has to be performed during spraying in cats and is therefore strongly temporally connected to Spray in all felids (see *Chapter 3, Section 3.3.1.3,* for a discussion of

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As defined by Kiley-Worthington (1976) as occurring when "the animal shows an increase in activity and performs more different activities more often".

spraying in felids). In addition, *Chapter 3* demonstrated the temporal connection between spraying and object rubbing, in all four undomesticated species studied *(F.chaus, O.geoffroyi, F.s.ornata, C.caracal)*. This connection has also been observed in other species (*Panthera leo*, Schaller, 1972; *Neofelis nebulosa*, Wemmer & Scow, 1977; *Panthera tigris*, Smith *et al*, 1989), and asserted in a review of scent rubbing (Reiger, 1979). The link between spraying and object rubbing is not surprising as they are both methods of scent marking (Reiger, 1979, Feldman, 1994, Natoli, 1985b; see *Chapter 1, 1.3.2.1.*). Ewer (1973) reports that in the dwarf mongoose, anal sac marking (similar to spraying) is never exhibited without also cheek rubbing, the two methods apparently indicating different messages. It is possible that this is also the case in the cat.

As a result of the Spray-Object Rub temporal connection, Tail Up and object rubbing often occur close in time to one another by mutual association with spraying (though Tail Up and Object Rub never occur **simultaneously** in *F.chaus, O.geoffroyi,* or *C.caracal*; see *Table 9.1*). This three-way connection was shown for all four undomesticated species in *Chapter 3* (See *Figs.3.2-3.5*), and has also been documented in domestic cats (Macdonald, 1987). As object rubbing is the same behavioural action as social rubbing it seems possible that this may have been the initial starting point for the strong motivational connection that exists in domestic cats between Tail Up and rubbing (both social and object). However, more research on the spray patterns of different species would have to be carried out for this hypothesis to be strengthened.

The problem with both of these hypotheses is that it is difficult to see how a motivational attachment with rubbing could have evolved because it seems unlikely that there would be any advantage to this.

Felis silvestris ornata: Halfway stage?

Table 9.1 summarizes the different tail positions found to occur with each of the two types of rubbing behaviours (Object Rub and Social Rub), in each felid species that was closely studied in *Chapter 3*.

Table 9.1 Tail positions found to accompany each type of rubbing behaviour (Object Rubs & Social Rubs in the five species observed in *Chapter 3*. **Tail Neutral** implies Tail Curved or Tail Down; **Tail Up** implies Tail Up or Tail Half-Up. † = Rubs not observed in this species by author, but a keeper of eleven of these cats has reported that he has seen them rubbing socially with Tail Up. However, it is not known whether they rub with Tail Up all of the time or only some of the time.

Increasing relatedness to the domestic cat ➔

	O.geoffroyi	***C.caracal***	***F.chaus***	***F.s.ornata***	***F.s.catus***
Object Rub	Tail Neutral	Tail Neutral	Tail Neutral	Tail Neutral and Tail Up	Tail Up
Social Rub	Tail Neutral	Tail Neutral	Tail Neutral	†	Tail Up

F.s.ornata was observed object rubbing with both Tail Up and Tail Neutral on different occasions. Furthermore, the keeper of eleven individuals of this species has reported that he has seen them socially rubbing with Tail Up. However, it is not known whether they exhibit Social Rubs with Tail Up all of the time or only some of the time. These two findings suggest that *F.s.ornata* may represent a halfway stage between rubbing **without** Tail Up (as in *O.geoffroyi*, *C.caracal*, and *F.chaus*) and rubbing **with** Tail Up (*F.s.catus*). However, why this motivational connection between rubbing and Tail Up developed in the domestic cat and not in any of the undomesticated species is unknown, as there does not appear to be any particular advantage to having this motivational link. (Although the presence of this association allowed the evolution of the Tail Up signal as a signal of intention to be affiliative, as described in *Section 6.4*).

9.4 APPLIED IMPLICATIONS OF THE STUDY: Social interactions as a form of environmental enrichment.

Chapter 3 showed that captive undomesticated felids will exhibit a large amount of social affiliative behaviour to one another, and will usually preferentially rest together in the same spot rather than resting alone, despite the fact that they are thought to be solitary in the wild. Studies of captive animal welfare generally assume that welfare is compromised if animals cannot perform the natural behavioural repertoire of wild conspecifics (Bayne *et al*, 1992), and that behaviours that are more common in the wild are more important for the welfare of the captive animal (Thorpe, 1967). Thus the importance attached to social interactions in solitary animals is low, because social interactions occur little in the wild. However, Veasey *et al* (1996) suggests that it is perhaps not the 'missing behaviours' which cause welfare problems, but in fact the void which the missing behaviours create; this void is often filled with stereotypies. I would suggest that social interactions could be used to fill the void; they have an advantage over more mechanical forms of environmental enrichment, because social partners are constantly stimulating and constantly changing, unlike a food ball or food pole which may decreases in stimulation value with time.

Although some zoos already have a practise of keeping felids in pairs or small groups, felids are often kept singly. My data in *Chapter 3* indicates that felids adapt very well to a social life. This finding suggests that the presence of a social partner might enhance welfare by filling the behavioural void (caused by the change in food provisioning). However, it must be noted that there is also potential for the presence of a social partner to cause an *increase* in stress, if the enclosure is too small or the pair of cats too aggressive (this might be solved by a change in partner). However, my data indicates that the chance of this is relatively low, as only two of the 20 felid groups/pairs that I observed had a high rate of aggression, one of which was kept in an extremely small enclosure. However, it must be taken into account that pairs of cats that are extremely overtly aggressive to one another will have been separated by the keepers, so this quoted data refers only to tolerant groups/pairs.

It would therefore be interesting to carry out a study to investigate the introduction of a social partner on the welfare of singly kept felids, as measured by the rate of stereotypies or level of urinary cortisol, which can be collected with a syringe from the floor of an indoor enclosure (Carlstead *et al*, 1992).

It would also be interesting to investigate whether the frequency of certain affiliative behaviours such as social rubbing/allogrooming/resting together (as indicators of a dyad's overall social compatability) could be correlated with welfare. If this was found to be so, the assessment of these behaviours in felids could be used as a quick and easy indicator of welfare, which could be used by zookeepers or zoobreeders wanting to assess welfare.

Mellen (1991) investigated whether certain behaviours are indicative of a cats' likelihood of reproducing; however, she did not consider the possibility that these behaviours may also be indicative of welfare (good welfare often leads to increased reproduction).

9.5 OTHER FUTURE WORK

Firstly the applied welfare aspect of this study would be interesting to follow up. This has been elaborated upon in the previous section.

On a less applied note, it would be useful to carry out some observations in order to accept or reject Macdonald's hypothesis that social rank in domestic cat colonies is maintained by social rubbing behaviour. This could be done by measuring rank within dyads in a variety of objective ways (*e.g.* using a food order or measures of aggression or defence), and then correlating to the asymmetry and direction of rubbing within the dyad.

Additional experiments and observations about the Tail Up posture would be valuable in that they would help support or invalidate the hypothesis about the function of the Tail Up signal. Firstly, observations similar to those carried out in *Section 6.2* (on a different group of feral cats) would be helpful in establishing whether the function of the Tail Up signal (as a signal of intention to be affiliative) definitely occurs in all free-ranging cats. Secondly, experimental methods could be also be attempted by using a 3D cat-shaped model with a moveable tail instead of a silhouette. It would also be interesting to further investigate the use of Tail Up during motivational excitement in undomesticated felids, as this may help to distinguish between the two hypotheses outlined in *Section 9.3.*

A study of kitten behaviour in undomesticated felids would also be very valuable, in order to establish to what extent the behaviours of Purr, Meiow, and Knead are used. It would be useful to know this in order to definitely establish the origins of these behaviours in intraspecific signalling. In addition, a study of purring in undomesticated felids would be invaluable, for the similar purpose. However, this would probably be logistically difficult to organise, as it could only be achieved by using throat microphones and radiotransmitters, as used by Kiley-Worthington (1984).

9.6 IN CONCLUSION

The trait which initially allowed *Felis silvestris* to shift its ecological niche towards the human-orientated situation was that of behavioural plasticity. This allowed individuals to alter their behaviour according to the current social situation, causing individuals to become more tolerant of both their own species and the human species. My results indicate that subsequent behavioural evolution is likely to have occurred, either culturally or genetically, or probably the two in combination. Evolution of signalling appears to have occurred in three areas. Firstly, a systematic signalling system has evolved to maintain a social ranking system in colonies of domestic cats. Secondly, neoteny has occurred, causing adult cats to exhibit juvenile behaviours towards humans. This is likely to have been a result of artificial selection as well as natural selection. Thirdly, a new social signal has evolved, the Tail Up signal, which has the function of signalling an intention to be affiliative in colonies of domestic cats. This probably evolved in group-living domestic cats because it was adaptive to reduce aggression, although it may now be present in all free-ranging domestic cats (solitary house cats and group-living feral cats).

ETHOGRAM OF BEHAVIOURS RECORDED IN THIS STUDY

This includes behaviours exhibited by all five study species, domestic and undomesticated: See Appendix V for details of behaviours exhibited by each species.

Some of these descriptions are based on 'An ethogram for behavioural studies of the domestic cat, *Felis silvestris catus*', by the U.K. Cat Behaviour Working Group, (1995). However, it was necessary to make additions in the cases that the behaviour may involve a human, and in the cases where the behaviour was exclusive to the undomesticated cat species.

TAIL POSITIONS See *Fig. 5.1, Pg. 114* for ethogram.

TAIL MOVEMENTS

Tail Jerk:	A rapid flick of the tail in either side to side or up to down motion, more frequently from up to down. These are subdivided into starting from different tail positions, and can start from the following: tail up position (tail up jerk), tail curved position (tail curved jerk), tail down position (tail down jerk), or from a sitting position (sit jerk). This is equivalent to the tail twitch described in the U.K. Cat Behaviour Working Group Ethogram (1995).
Tail Wave:	A slow and gentle wave of the tail from side to side. This occurs in the following different tail positions: tail up position (tail up wave), tail curved position (tail curved wave), tail down position (tail down wave), and from a sitting position (sit wave). This is equivalent to the tail swish described in the U.K. Cat Behaviour Working Group Ethogram (1995).
Tail Quiver:	Tail is usually held in either the Tail Up or the Tail Half-Up positions and is quivered rapidly.
Tail Swish	A violent swish of the tail; more rapid than a tail wave but smoother than a Tail Jerk.

LOCOMOTORY BEHAVIOURS

Approach:	One cat moves towards another while looking at it.
Follow:	One cat travels closely behind another.
Move Away:	One cat walks away from another cat.
Run Away	One cat runs away from another.
Run Approach	One cat approaches another at a running pace.
Walk Past	One cat walks past another at a close distance of about 2m or less, and may look at the other cat as they go past.

SOLITARY BEHAVIOURS

Flehmen	Cat opens its mouth slightly with upper lip elevated and head tilted upwards, generally investigating an object, another cat, or the air (see Leyhausen, 1979, and Hart & Leedy, 1987).
Object rub:	Cat rubs its body or head and neck along the ground or against an object. (See Leyhausen, 1979, and Turner, 1988.)
Roll (asocial)	Cat rolls on the ground when there is no other cat or human nearby.
Spray	Cat directs a jet of urine backwards against some object. The tail is raised vertically and, in some species quivered as the urine is discharged. The U.K. Cat Behaviour Working Group (1995) distinguish between this and *Pseudospray*, which they categorize as being exactly the same as *Spray* but with no urine being emitted. However, I was not normally close enough to make this distinction reliably and so I classified both *Spray* and *Pseudospray* into one group. Spray should be distinguished from urination, which more normally occurs in a squatting position, and not against an object (Wemmer & Scow, 1977). These so-called 'squat urinations' are usually buried and it appears likely that the two types contain different information (Bradshaw, 1992).

DISTANT SOCIAL BEHAVIOURS

Watch	One cat idly observes another cat or human. This can be distinguished by the way in which the cat's eye and head movements track what it is watching. This is not necessarily directed at another cats eyes (which distinguishes it from *Stare*)
Stare:	This is similar to *Watch*, but involves a more fixed stare, with the cat not being easily distracted by any other activity around it. It is often directed at the other cats eyes, and may frequently be followed by the recipient cat looking away.
Chase:	One cat chases another at a fast running pace.
Pounce:	Cat leaps at or onto another cat, usually preceeded by *Run Approach.*
Crouch:	This was defined as when the cat crouches in a defensive manner. Cats also often sit in a crouching position. This was not included as being crouching.
Ears Back	Ears are held at the rear of the head.

Ears Flat	A cat flattens its ears to its head, such that they tend to lie flush with the top of the head.
Pause	Cat suddenly pauses in what it is doing and remains alert to any activity.

CONTACT SOCIAL BEHAVIOURS (including sexual behaviours)

Non-Agonistic:

Allogroom	One cat licks another cat. This may also be applied to humans, in which case it implies a cat licking a human.
Copulate	A male cat mounts a female cat and achieves intromission. This behaviour is characterized by the female uttering a sharp howl at the moment of ejaculation and sometimes twisting out of the male's grasp. It is usually preceeded by several *Mount* attempts, and by treading, and the neck grasp. The female also treads with her back feet and assumes the lordosis position (crouched down with hindquarters raised and tail turned aside).
Jostle Play	One cat struggles with another cat, raking with its hind legs and pulling the opponent towards its body with its forepaws. It is mainly a play behaviour, and is distinct from *Fight*, which is much more intense. Jostle Play lacks some of the features of *Fight.*
Jump Up:	One cat jumps up with its fore legs resting on a human, its hind legs on the ground.
Knead (also known as Treading):	Cat pummels paws into object, floor, or human, in a kneading motion. Claws may be in or out.
Lordosis	A female cat crouches down and raises her hindquarters to present her genitals to a male when in a receptive oestrous state. Her tail is turned aside and her belly pressed close to the ground. This is sometimes characterized by treading with the hind legs (see *Chapter 1, Section 1.3.3 & 1.4.3*).
Mount:	One cat attempts, but fails to achieve, intromission.The mounting cat normally holds the recipient firmly at the nape of the neck whilst mounting. This is also sometimes accompanied by treading movements of the hind legs (see *Chapter 1, Section 1.3.3 & 1.4.3*).
Nuzzle	One cat pushes its head against the head or, more uncommonly, the body of another cat. This resembles the form of a brief *Rub* but there is no rubbing action, only a gentle push.

Paw	One cat pats another individual with its forepaw, keeping claws retracted.
Rub cat or human (Social Rub):	Cat rubs another cat or human (see Macdonald *et al*, 1987). Subdivisions include*:* *Rub Head* (one cat rubs its head on another), *Rub Flank* (one cat rubs its flank on another), and *Rub Tail:* (one cat rubs its tail on another). A *rub sequence* implies one rub movement, which may include rub head followed by rub flank or rub tail, or may imply the whole sequence of rub head, rub flank, rub tail, or any sequence which involves one rubbing movement. *Rub both* implies that both cats rubbed on each other at the same time.
Roll (Social):	A cat rolls on the ground in the presence of another cat or human.
Sniff cat or human:	One cat smells the body of another cat or human. In cat-cat interactions, it may be subdivided into: *Sniff Nose* (two cats touch/sniff each other with the nose), *Sniff Rear* (one cat smells the peri-anal area of another cat), and *Sniff Body* (ne cat smells the flanks or tail of another cat).
Touch nose	Two cats touch/sniff each other with the nose.

Agonistic:

Arch Back	A cat curves its back upwards and stands rigidly. The tail is usually tensely curved and the fur may be piloerected.
Back Off	One cat suddenly stops and moves backwards rapidly.
Bite	One cat snaps its teeth at or succeeds in nipping another animal.
Cuff	One cat strikes another cat with its forepaw, usually with claws extended.
Fight	Two cats engage in physical contact, often grappling with one another , scratching and biting as they turn over, sometimes including vocalisations.
Mouth Threat	Cat gapes its mouth and puts its ears back in the expression that would normally be attributed to a hiss, but no sound is made.
Present Neck	One cat holds its neck by the mouth of another cat which is often vocalising at the time (either *Growl* or *Worra*).
Snapbite	One cat opens its mouth and snaps it shut, as if biting the air. This is normally directed towards another cat.

ACOUSTIC BEHAVIOURS

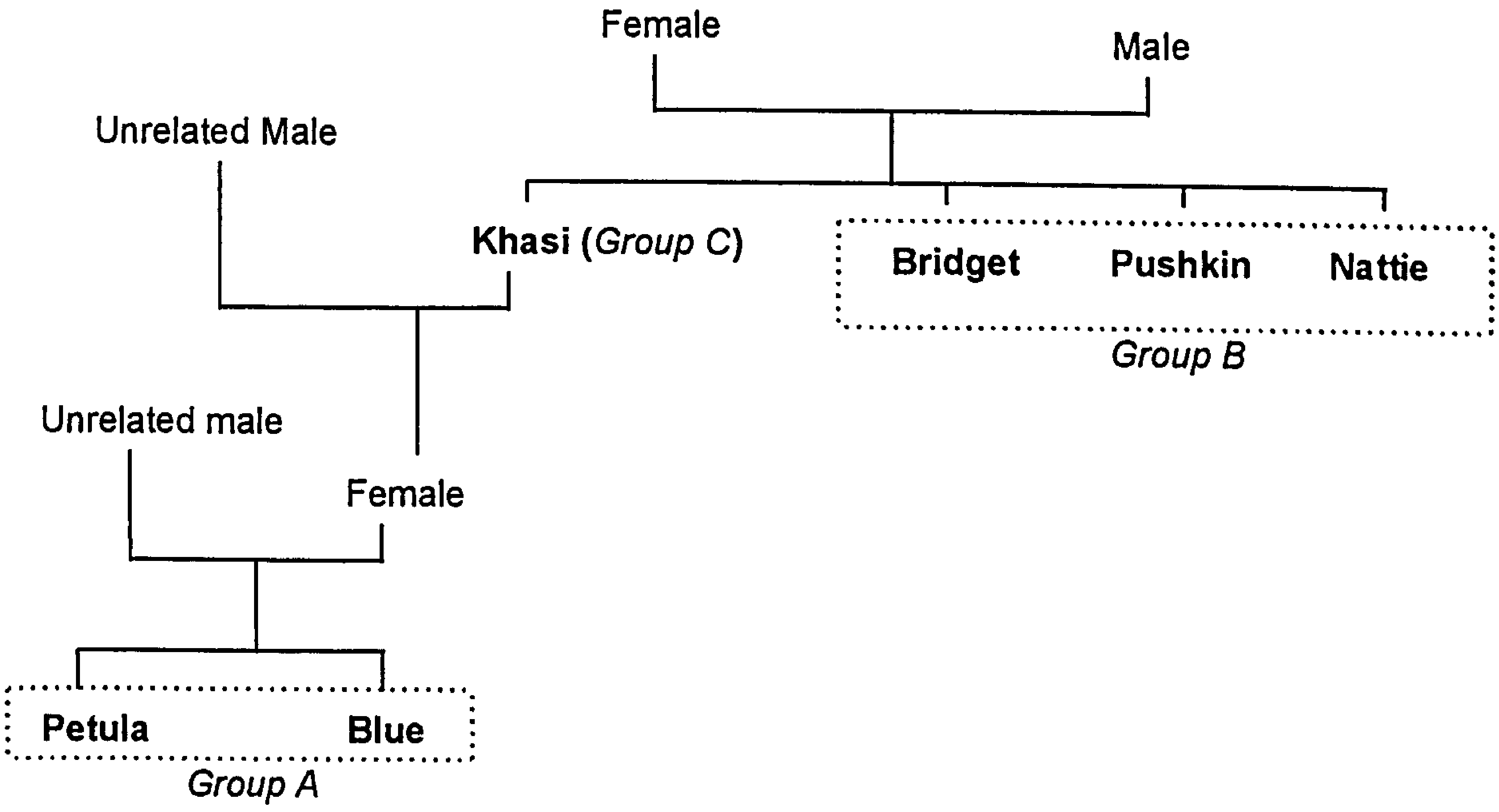
This list may not exhaustive, as I was not concentrating on acoustic behaviours. However, I did record the common sounds, which were as follows. (See *Chapter 1, Sections 1.3.2.3 & 1.4.2.2):*

Growl	A low growling sound.
Gurgle	A noise similar to a person gargling in their throat. This is described in detail by Peters (1984)
Hiss	A long drawn out SSSS noise, which is unvoiced.
'Ow' / 'Keiow'	A sharp explosive high pitched noise. The sound was a brief loud cry.
Krrrr	A long drawn out noise similar to a person rolling their tongue, but with a 'K' sound at the beginning of the noise.
Meiow	A distinct sound made usually when the cat is trying to obtain something (usually food) from another cat (usually its mother), or human.
Worra	A long drawn out low sound, rather like a repetitive growling sound: Worrrrr-Worrrrr-Worrrrr *etc.*, and can occur over and over for long periods of time. I observed it particularly in *Felis chaus*, but the noise is similar to that emitted by domestic cats preceeding an aggressive attack.
Yowl	A cat makes a long drawn out vocalisation.

Appendix II:
RELATEDNESS OF THE UNDOMESTICATED CAT GROUPS

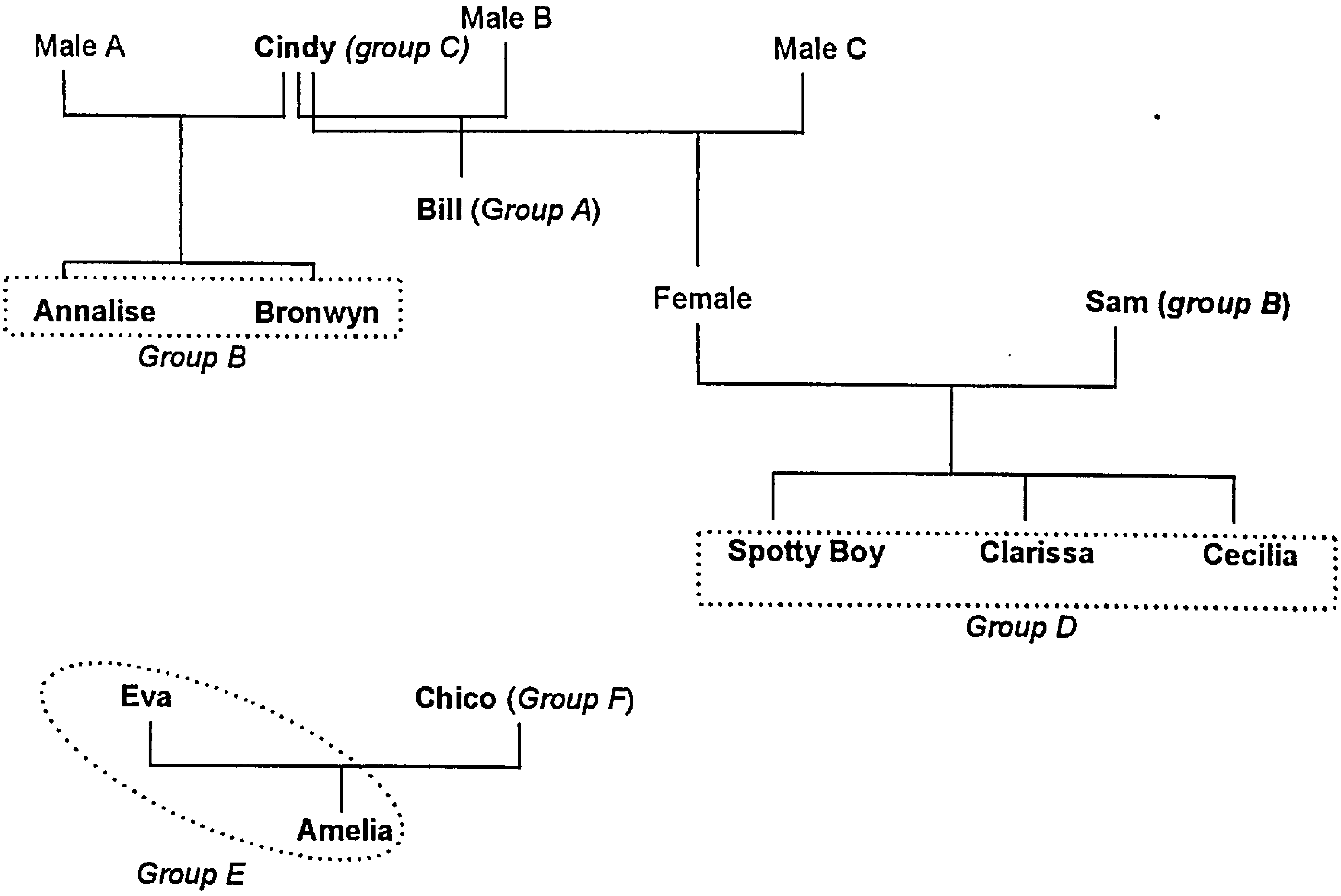
(Names are only given to the cats that were used in the study. Other cats are just labelled male or female.)

(A) Felis silvestris ornata



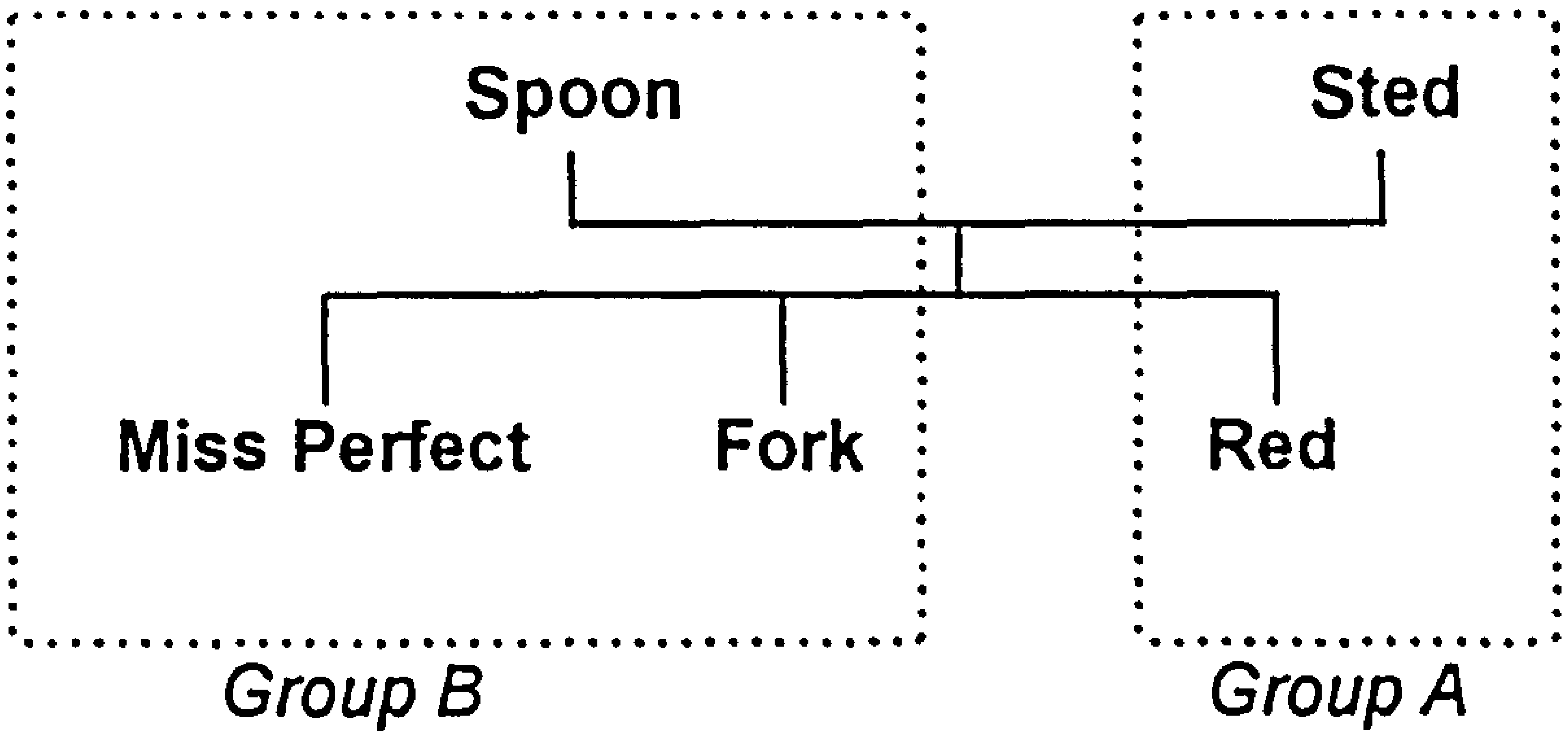
Unrelated cats:
Jhalor (*Group C*)

(B) Oncifelis geoffroyi



Non-related individuals included:
Tilly (*Group A*)
Arthur (*Group C*)
Stella (*Group F*)

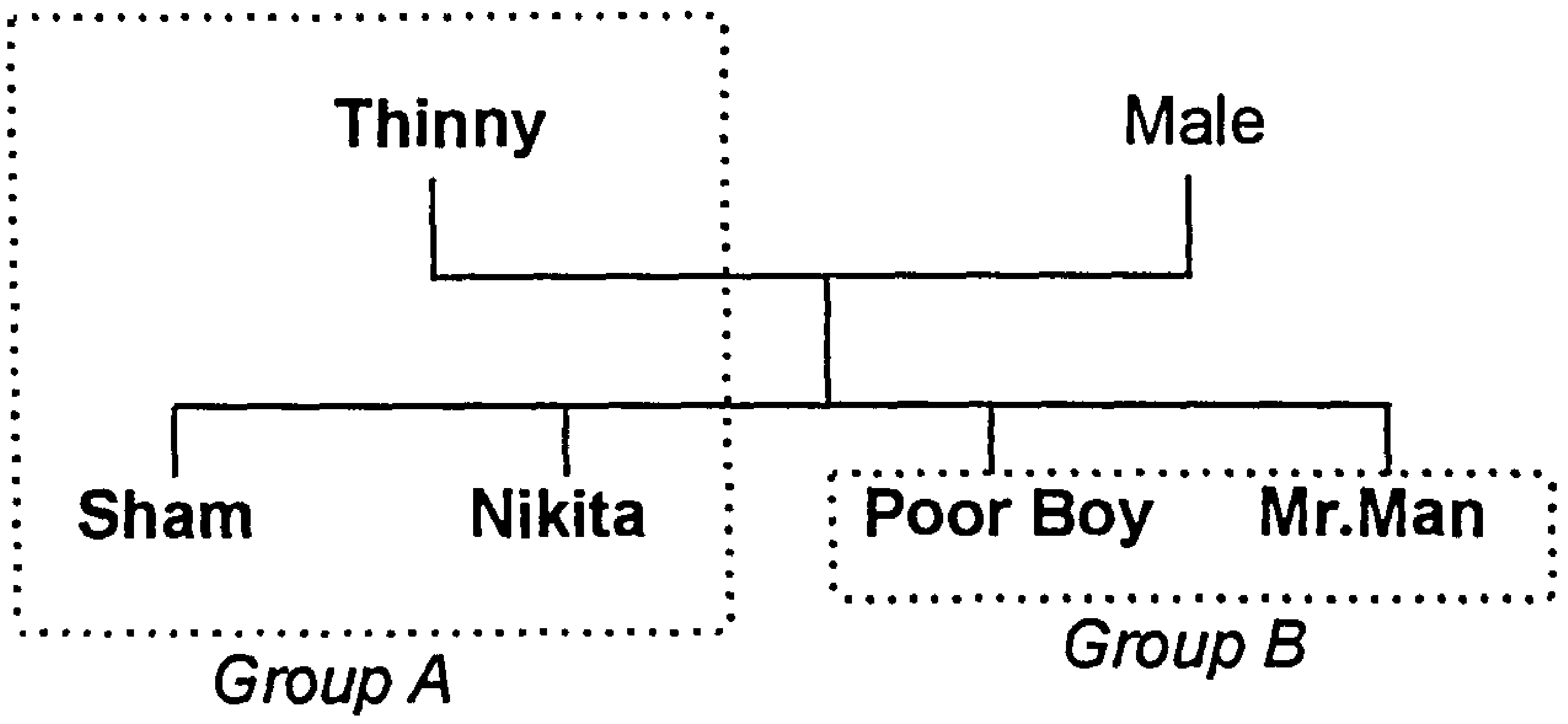
(C) Caracal caracal

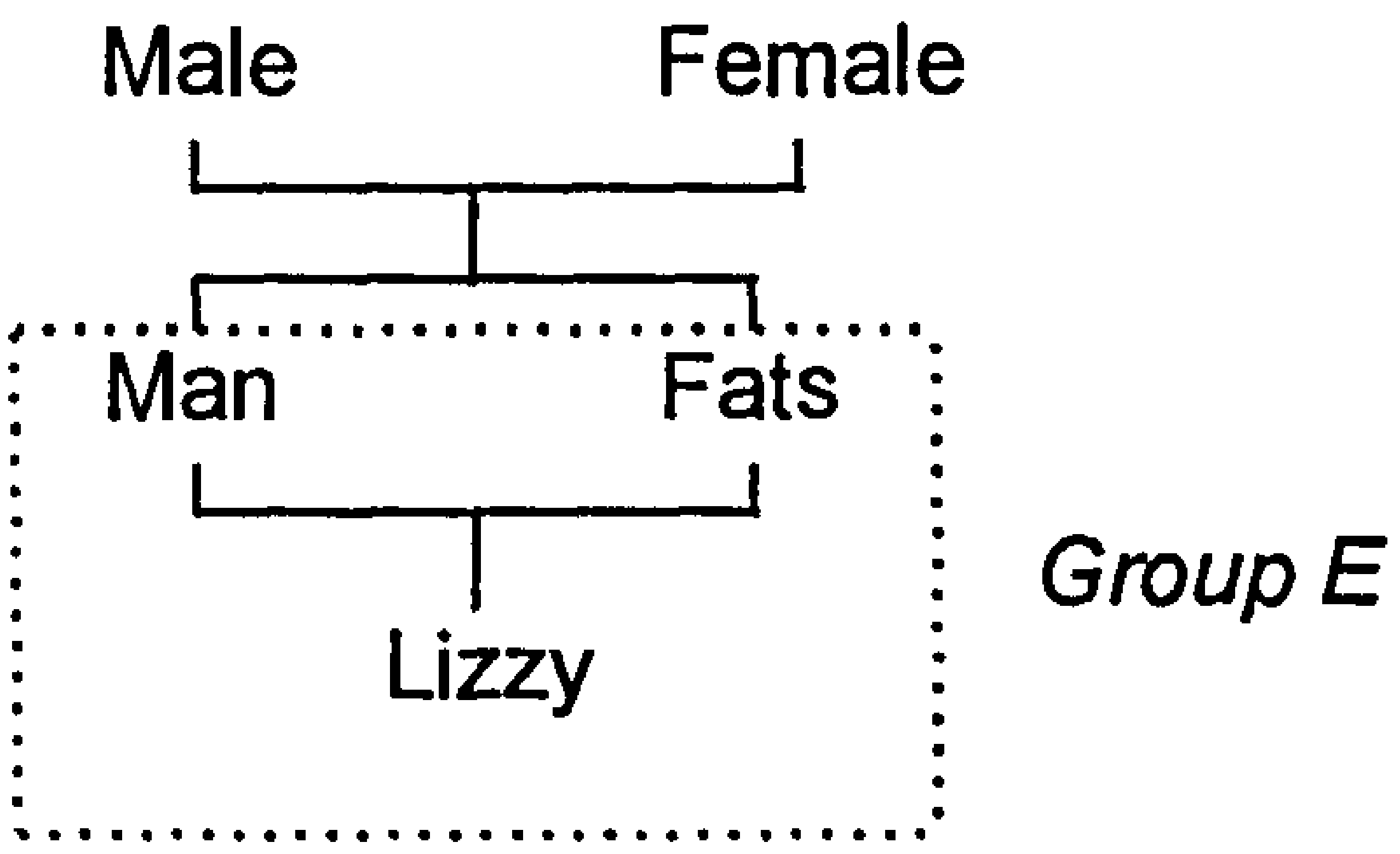


Big and **Small** *(Group E)* are siblings and littermates.

Unrelated individuals:
Eater (*group C*)
Nafisa (*Group F*)
Mustapha (*Group F*)
Bod (*Group D*)
Runner (*Group D*)

(D) Felis chaus



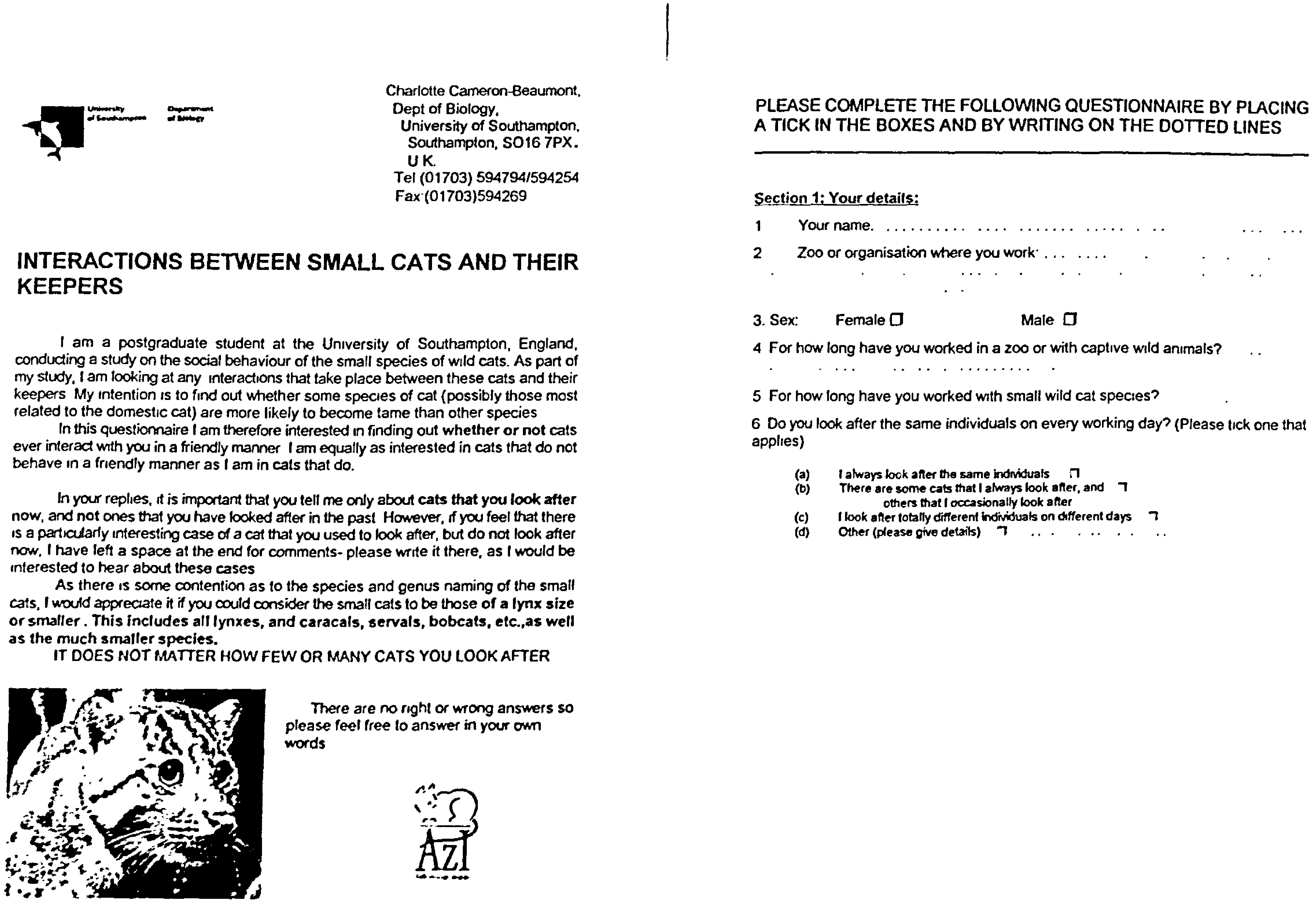


Thick and **Thin** (*group D*) were siblings and littermates

Unrelated individuals:
Bianca (*Group C*)
Stripey (*Group C*)

QUESTIONNAIRES

(A) First questionnaire sent out to most cat keepers in Britain, Canada, USA and Australia.



Charlotte Cameron-Beaumont,
Dept of Biology,
University of Southampton,
Southampton, SO16 7PX.
U K.
Tel (01703) 594794/594254
Fax (01703)594269

INTERACTIONS BETWEEN SMALL CATS AND THEIR KEEPERS

I am a postgraduate student at the University of Southampton, England, conducting a study on the social behaviour of the small species of wild cats. As part of my study, I am looking at any interactions that take place between these cats and their keepers My intention is to find out whether some species of cat (possibly those most related to the domestic cat) are more likely to become tame than other species

In this questionnaire I am therefore interested in finding out **whether or not** cats ever interact with you in a friendly manner I am equally as interested in cats that do not behave in a friendly manner as I am in cats that do.

In your replies, it is important that you tell me only about **cats that you look after** now, and not ones that you have looked after in the past However, if you feel that there is a particularly interesting case of a cat that you used to look after, but do not look after now, I have left a space at the end for comments- please write it there, as I would be interested to hear about these cases

As there is some contention as to the species and genus naming of the small cats, I would appreciate it if you could consider the small cats to be those **of a lynx size or smaller . This includes all lynxes, and caracals, servals, bobcats, etc.,as well as the much smaller species.**

IT DOES NOT MATTER HOW FEW OR MANY CATS YOU LOOK AFTER

There are no right or wrong answers so please feel free to answer in your own words

PLEASE COMPLETE THE FOLLOWING QUESTIONNAIRE BY PLACING A TICK IN THE BOXES AND BY WRITING ON THE DOTTED LINES

Section 1: Your details:

1 Your name. ....

2 Zoo or organisation where you work ....

3. Sex: Female ☐ Male ☐

4 For how long have you worked in a zoo or with captive wild animals? ....

5 For how long have you worked with small wild cat species?

6 Do you look after the same individuals on every working day? (Please tick one that applies)

- (a) I always look after the same individuals ☐
- (b) There are some cats that I always look after, and others that I occasionally look after ☐
- (c) I look after totally different individuals on different days ☐
- (d) Other (please give details) ☐ ....

(A) First questionnaire, Page 2.

Section 2: Questions on the cats

THE FOLLOWING QUESTIONS WILL REFER TO ALL THE SMALL CATS THAT YOU LOOK AFTER. THIS INCLUDES ALL CATS OF A LYNX SIZE OR SMALLER. **It does not matter how few or many cats you look after.**

Please write only about small cats that you look after at the moment.

1. List in the table opposite any individual cats that have been friendly to you, or which have exibited any of the behaviours described in the table
Then for each cat which you have listed
How often on average have you
(a) Had these behaviours carried out towards you, if at all?
(b) Seen these cats carry out these behaviours towards other people, if at all?

Please think about all the species that you look after, even if you only look after them occasionally.

IF NONE OF THE CATS WHICH YOU LOOK AFTER HAVE BEEN FRIENDLY IN ANY OF THESE WAYS, JUST TURN TO QUESTION 2.

Write your answers in the following table, using as many or as few columns as necessary. (Continue on the inserted sheet over the page if necessary)

		Please use a different column for each cat					
CAT SPECIES Use either Latin or common nameor both.		**EXAMPLE** Felis caracal Karacal lynx					
PET NAME/NUMBER		Cindy					
AGE (Estimate)		4 yrs					
SEX		F					
LIE/SIT NEAR HUMAN (within 1m)	*near you*	2x per week ..					
	near others	No					
ROLL NEAR HUMAN (within 1m)	*near you*	No					
	near others	No					
RUB THEIR HEAD	*against you*	Only once ever (last yr)					
	against others	No					
RUB THEIR BODY/ TAIL	*against you*	About 10x in 3 years					
	against others	Once only					
LICK HUMAN	*with you*	No					
	with others	No					
RUB AGAINST AN OBJECT (eg wall/post) **NEAR HUMAN** (within 2m)	*with you*	2x per week					
	with others	Have seen it only twice ever					
OTHER FRIENDLY BEHAVIOUR (Please give details)	*with you*	She had kittens and let me hold them (once last year)					
	with others	She let others hold them too.					

(A) First questionnaire, Page 3.

Please continue on this page if necessary:
(if you need still more pages, either photocopy this one or write/phone me for another)

		Please use a different column for each cat					
CAT SPECIES Use either Latin or common name or both.							
PET NAME/NUMBER							
AGE (Estimate)							
SEX							
LIE/SIT NEAR HUMAN (within 1m)	*near you*						
	near others						
ROLL NEAR HUMAN (within 1m)	*near you*						
	near others						
RUB THEIR HEAD	*against you*						
	against others						
RUB THEIR BODY/ TAIL	*against you*						
	against others						
LICK HUMAN	*you*						
	others						
RUB AGAINST AN OBJECT (eg. wall/post) **NEAR HUMAN** (within 2m)	*near you*						
	near others						
OTHER FRIENDLY BEHAVIOUR (Please give details)	*with you*						
	with others						

2. **Now please list all the cats which you look after but which you have <u>not</u> seen** carry out any of the above behaviours. Give the number of cats of each species which are not friendly, and then the **sex and age** (estimate) of each.

Species of cat (use either common or Latin name or both)	*No of individual cats of that species which have not been friendly*	*Sex & corresponding age (estimate) of each cat.*
EXAMPLE: *Siberian lynx*	....2......	(F, 6yrs) (Unsexed, 4mths)
EXAMPLE: *Geoffroy's cat/ Felis geoffroyi*	....4......	(F, 4yr) (F,1yr)(M, 7yr) (M,1yr,

(Please continue below if you need more room)

(A) First questionnaire, Page 4.

THANKYOU FOR YOUR CO-OPERATION

I am very grateful to you for filling in the questionnaire I hope it will prove an interesting study If you would like to know about the results of it, then please include a note at the top of the questionnaire saying this, and I can let you have a summary of what I have found.

I would appreciate it if you could leave me your telephone no or fax no. in case I have a query about the questionnaire However, this is not essential, and I understand if you do not wish to

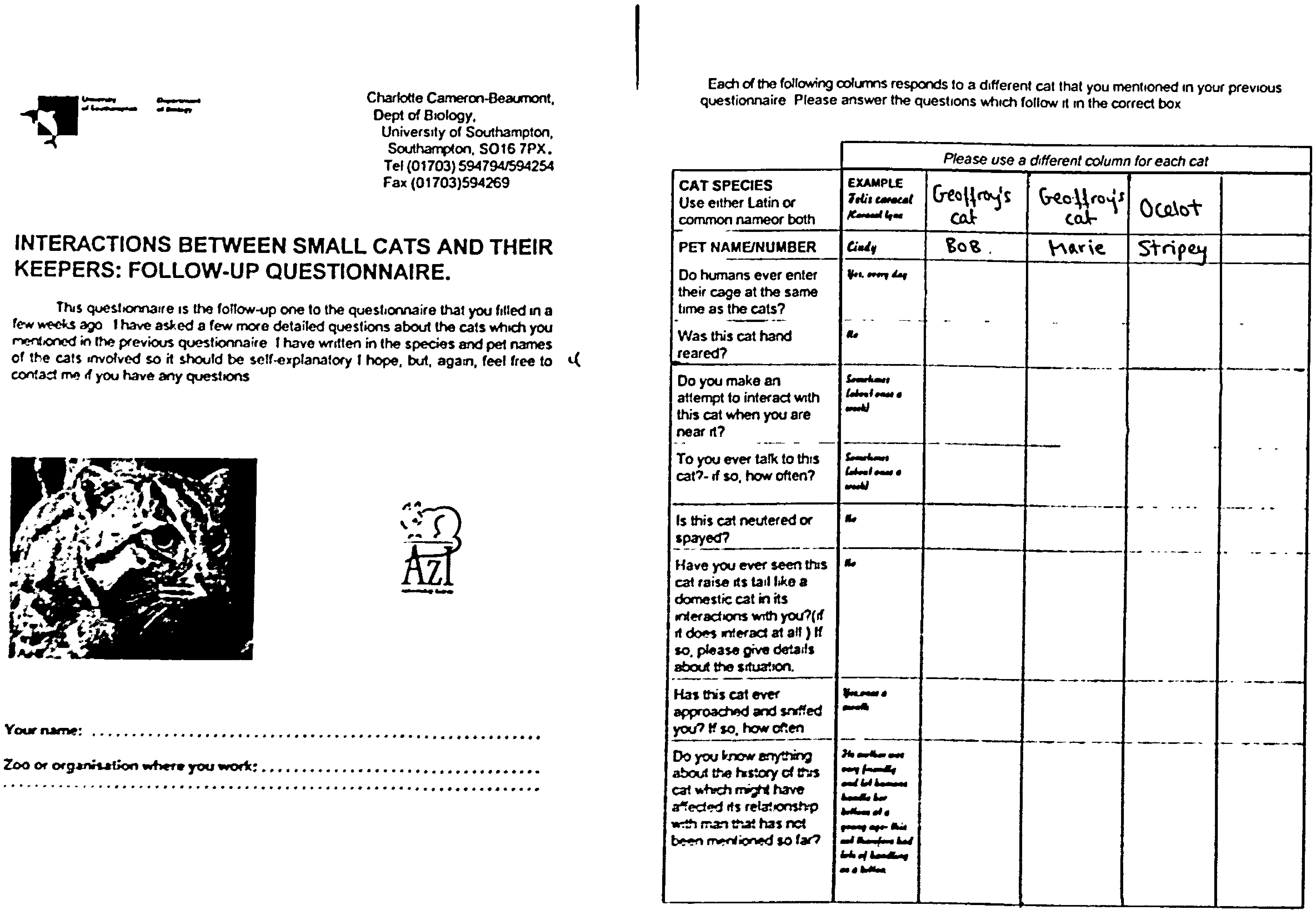
Tel /Fax No ....

If you do not mind, I would be interested in contacting you again, specifically about the friendly cats Please tick here if you do not mind filling in a further questionnaire of about the same length as this one. ☐

If you have any additional remarks about the questionnaire, or would like to tell me anything else that is not covered in the questionnaire (eg about cats that you used to look after but do not now), please write it here:

PLEASE RETURN IN THE STAMPED ADDRESSED ENVELOPE PROVIDED

(B) Second follow-up questionnaire sent to keepers who answered the first.



Charlotte Cameron-Beaumont,
Dept of Biology,
University of Southampton,
Southampton, SO16 7PX.
Tel (01703) 594794/594254
Fax (01703)594269

INTERACTIONS BETWEEN SMALL CATS AND THEIR KEEPERS: FOLLOW-UP QUESTIONNAIRE.

This questionnaire is the follow-up one to the questionnaire that you filled in a few weeks ago I have asked a few more detailed questions about the cats which you mentioned in the previous questionnaire I have written in the species and pet names of the cats involved so it should be self-explanatory I hope, but, again, feel free to contact me if you have any questions

Your name: ....

Zoo or organisation where you work: ....

Each of the following columns responds to a different cat that you mentioned in your previous questionnaire Please answer the questions which follow it in the correct box

	Please use a different column for each cat				
CAT SPECIES Use either Latin or common nameor both	**EXAMPLE** *Felis caracal* *Caracal lynx*	Geoffroy's cat	Geoffroy's cat	Ocelot	
PET NAME/NUMBER	*Cindy*	BOB.	Marie	Stripey	
Do humans ever enter their cage at the same time as the cats?	*Yes, every day*				
Was this cat hand reared?	*No*				
Do you make an attempt to interact with this cat when you are near it?	*Sometimes (about once a week)*				
To you ever talk to this cat?- if so, how often?	*Sometimes (about once a week)*				
Is this cat neutered or spayed?	*No*				
Have you ever seen this cat raise its tail like a domestic cat in its interactions with you?(if it does interact at all) If so, please give details about the situation.	*No*				
Has this cat ever approached and sniffed you? If so, how often	*Yes, once a month*				
Do you know anything about the history of this cat which might have affected its relationship with man that has not been mentioned so far?	*Its mother was very friendly and let humans handle her kittens at a young age- this cat therefore had lots of handling as a kitten.*				

(B) Second follow-up questionnaire, Page 2.

Please continue on this page.

	Please use a different column for each cat				
CAT SPECIES Use either Latin or common name or both					
PET NAME/NUMBER					
Do humans ever enter their cage at the same time as the cat?					
Was this cat hand reared?					
Do you make an attempt to interact with this cat when you are near it?					
To you ever talk to this cat?- if so, how often?					
Is this cat neutered or spayed?					
Have you ever seen this cat raise its tail like a domestic cat in its interactions with you?(if it does interact at all) If so, please give details about the situation.					
Has this cat ever approached and sniffed you? If so, how often.					
Do you know anything about the history of this cat which might have affected its relationship with man that has not been mentioned so far?					

THANKYOU FOR YOUR CO-OPERATION

Thankyou very much for filling in this second questionnaire

If you have any additional remarks about the questionnaire, or would like to tell me anything else that is not covered in the questionnaire, please write it here

PLEASE RETURN IN THE STAMPED ADDRESSED ENVELOPE PROVIDED

(C) Third questionnaire, sent only to keepers who had reported seeing the Tail Up position.

University of Southampton | Department of Biology

Charlotte Cameron-Beaumont,
Department of Biology,
University of Southampton,
Southampton, SO16 7PX.
Tel:(01703) 594794
Fax:(01703)594269

Dear

In the questionnaire that you filled in several months ago, you mentioned that the following cat(s) **raised their tail like a domestic cat** in their interactions with you:

Cat species *Name of cat* *Situation in which you reported a tail up position occurring:*

Many keepers have reported this, and it is an interesting finding, so I wanted to be sure of the exact tail position which you have seen. Please ring the diagram below which corresponds to the tail up position which you had in your mind when describing the above situation, or draw your own diagram if none of these apply:

A. Tail vertically up

B. Tail angled up

C. Tail bent-up

D. Tail aggressively raised

E. Other (either explain or draw yourself)

Finally, in which of the following situations have you seen the cat raise its tail as you have shown above?

	Definitely seen	*Possibly seen*	*Don't know*	*Never seen*
When rubbing against an object when you are nearby	☐	☐	☐	☐
When rubbing against you or another human	☐	☐	☐	☐
When rubbing against other cats	☐	☐	☐	☐
When rolling on the ground when you are nearby	☐	☐	☐	☐
When you approach	☐	☐	☐	☐
When you approach with food	☐	☐	☐	☐
When being touched by a human	☐	☐	☐	☐
When sniffing you	☐	☐	☐	☐
When you are nearby	☐	☐	☐	☐
In aggression	☐	☐	☐	☐
Other (please state)	☐	☐	☐	☐
When being stroked by a human	☐	☐	☐	☐

THANKYOU VERY MUCH FOR YOUR HELP.
I HAVE ENCLOSED AN ADDRESSED AIRMAIL ENVELOPE FOR RETURN.

Appendix IV:
MATRICES OF RAW DATA

(Each matrix contains data in the upper diagonal only. If a behaviour is absent from the matrix, this indicates that it did not occur.)

Matrices (i), (ii), (iii), (iv) &(v) give the raw data which were used in *Chapter 3* to calculate *Figs. 3.1-3.5* (significant behavioural links). These are sequence-linked matrices (see *Chapter 2*) calculated from cat-cat interactions. The entire matrices are given; however, in practice, for calculating the adjusted residuals, the behaviours which occurred in less than 10 interactions were deleted from the matrix before carrying out the statistical test.

The key for the behaviours is listed below (descriptions are to be found in *Appendix I*):

tu	Tail Up	ch	Chase
tt	Tail half-Up	po	Pounce
tc	Tail Curved	mt	Mount
td	Tail Down	sr	Sniff Rear
tf	Tail Under	tn	Touch Nose
si	Sit/Lie Down	bi	Bite
sw	Sit With	fo	Follow
rh	Rub Head	pw	Paw
rf	Rub Flank	gu	Gurgle
rt	Rub Tail	ow	Keiow/Ow noise
or	Object Rub	gr	Growl
sn	Sniff	wo	Worra
ap	Approach	pn	Present Neck
ma	Move Away	mh	Mouth Threat
wp	Walk Past	fb	Fight
ra	Run Away	hs	Hiss
jb	Jostle Play	cb	Copulate
ar	Arch Back	nz	Nuzzle
ro	Roll	yo	Yowl
rp	Run Approach	lo	Lordosis
cu	Cuff	sp	Spray
mw	Meiow	rb	Rub Both
bo	Back Off	co	Crouch
tj	Tail Jerk	sb	Snapbite
tw	Tail Wave	kr	Krrrr noise
pa	Pause	ag	Allogroom
kn	Knead	sg	Self-groom
tq	Tail Quiver	ts	Tail Swish
wa	Watch	sq	Squeal
sa	Stare		

(i) *Felis silvestris catus:* **Sequence-linked matrix (the number of times each behaviour was observed in an interaction with each other behaviour).**
A smaller version of this matrix (without the behaviours that occurred in less than 10 interactions) was used to calculate chi-squared residuals for *Fig. 3.1, Chapter 3.*

	rp	bi	ch	co	cu	eb	ra	fo	pa	ag	hs	mw	or	pw	po	rf	rh	rol	rt	sn	sq	sr	sa	sw	tj	tn	ts	tu	wa	fb	wp
rp	0	20	41	45	44	26	28	20	7	10	0	2	6	12	39	0	9	11	0	19	0	4	47	4	2	6	25	63	82	34	5
bi	0	0	16	3	27	43	8	17	1	30	0	0	0	9	104	0	4	12	0	19	1	7	41	12	4	2	25	8	47	78	0
ch	0	0	0	14	42	20	4	5	5	10	1	1	2	4	26	0	0	1	0	8	0	2	23	3	2	3	18	9	28	29	1
co	0	0	0	0	10	4	15	6	3	2	2	1	0	3	12	0	1	4	0	4	0	1	7	1	0	1	6	16	55	7	0
cu	0	0	0	0	0	66	33	17	6	14	8	5	2	3	28	2	16	39	0	22	16	4	80	9	4	5	49	32	38	54	5
eb	0	0	0	0	0	0	63	12	7	24	5	0	6	17	60	0	16	56	0	32	27	9	161	10	10	7	109	31	33	114	0
ra	0	0	0	0	0	0	0	1	13	11	5	1	0	7	6	0	1	40	0	7	22	2	61	2	1	3	53	54	40	72	8
fo	0	0	0	0	0	0	0	0	1	6	0	6	2	10	26	9	30	8	0	23	2	16	21	9	4	5	11	18	21	13	10
pa	0	0	0	0	0	0	0	0	0	0	1	0	0	1	5	0	0	1	0	0	1	0	18	0	1	0	11	6	4	4	1
ag	0	0	0	0	0	0	0	0	0	0	0	0	0	10	19	0	8	14	0	49	1	12	23	42	6	15	26	5	14	45	1
hs	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	3	0	0	0	1	1	0	0	3
mw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	0	0	0	0	3	1	1	3
or	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	10	8	0	10	0	3	6	11	0	2	8	6	2	6	2
pw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	12	39	0	14	0	0	21	14	2	2	18	11	9	34	2
po	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	11	0	18	3	8	72	7	7	3	49	20	61	96	0
rf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	68	3	14	7	0	4	0	12	1	1	0	11	1	0	11
rh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42	13	33	0	12	16	49	3	15	15	60	7	15	25
ro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	21	4	53	36	4	10	56	31	18	90	6
rt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
sn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	26	25	110	5	44	23	51	27	32	23
sq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	19	0	1	1	19	5	5	23	0
sr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	9	4	6	11	19	11	8	10
sa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	9	1	135	46	52	136	18
sw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	12	7	38	15	21	9
tj	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	8	11	10	5	8
tn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	27	8	9	7
ts	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	44	131	1
tu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48	22	54
wa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44	19
fb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
wp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(ii) *Felis chaus:* **Sequence-linked matrix (the number of times each behaviour was observed in an interaction with each other behaviour).**

A smaller version of this matrix (without the behaviours that occurred in less than 10 interactions) was used to calculate chi-squared residuals for *Fig. 3.2, Chapter 3.*

	tu	tt	tc	td	tf	sl	sw	rh	rf	or	sn	ap	ma	wp	ra	ro	rp	cu	bo	tj	tw	pa	wa	sa	ch	po	mt	sr	tn	bl	fo	pw	gu	ow	gr	wo	pn	mh	fb	hs	nz	yo	sp	eb	rb	co	ag	sg
tu	0	1	0	5	0	1	0	2	0	2	2	3	3	0	0	0	0	0	0	0	1	1	3	1	0	2	1	3	0	1	2	1	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0
tt	0	0	2	4	0	0	0	4	0	0	0	0	6	0	1	0	0	0	0	0	4	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
tc	0	0	0	9	0	3	0	5	0	0	3	5	14	1	0	0	0	0	3	1	10	5	5	0	0	1	0	1	1	1	6	0	0	1	2	1	3	2	2	0	3	4	0	2	2	0	0	0
td	0	0	0	0	10	56	109	37	1	3	109	487	517	168	26	8	34	13	24	1	62	249	370	80	3	5	3	23	5	9	34	3	52	6	125	6	9	68	5	84	14	15	2	48	14	15	7	39
tf	0	0	0	0	0	10	2	1	0	1	3	7	7	2	1	1	1	1	1	0	2	4	6	6	0	1	0	0	1	0	0	0	0	0	2	1	0	2	2	4	0	0	0	2	0	4	0	3
sl	0	0	0	0	0	0	6	14	0	1	24	28	48	4	3	6	1	5	8	0	63	14	134	16	0	3	0	3	4	3	4	4	2	1	9	2	4	7	4	8	2	2	1	7	5	6	2	23
sw	0	0	0	0	0	0	0	11	0	0	65	101	34	14	0	0	0	2	19	0	12	22	47	8	0	0	1	1	3	4	0	1	1	0	0	0	2	1	0	3	13	0	0	5	2	0	13	40
rh	0	0	0	0	0	0	0	0	1	2	20	29	25	5	1	0	0	1	5	1	16	9	19	2	0	3	1	7	2	2	7	0	0	0	1	3	4	1	3	1	6	2	0	4	8	2	3	9
rf	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
or	0	0	0	0	0	0	0	0	0	0	1	3	3	1	0	0	0	0	0	0	1	1	2	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	1
sn	0	0	0	0	0	0	0	0	0	0	0	93	68	16	1	2	0	5	12	0	16	25	36	6	0	4	1	10	4	6	14	2	0	2	0	1	1	1	4	2	13	0	1	4	4	1	4	37
ap	0	0	0	0	0	0	0	0	0	0	0	0	282	59	6	8	7	6	16	0	33	164	195	34	1	3	2	19	5	5	23	2	38	3	49	3	3	34	4	30	10	8	1	19	12	7	4	32
ma	0	0	0	0	0	0	0	0	0	0	0	0	0	98	4	7	17	7	17	1	48	154	223	38	2	4	1	14	6	10	24	4	43	5	65	5	8	34	4	39	9	9	2	26	12	10	3	19
wp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	3	0	1	0	10	38	67	11	0	1	0	3	0	1	5	1	14	0	6	1	1	8	2	6	1	0	0	4	0	3	0	9
ra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	1	0	0	1	9	9	5	0	0	0	1	0	0	0	0	0	0	2	0	0	1	1	4	0	1	0	4	0	2	0	2
ro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	19	10	10	1	1	0	0	0	0	1	0	0	1	16	0	0	5	0	15	0	0	0	9	0	3	0	1
cu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	5	4	3	1	1	0	0	1	1	1	0	0	0	2	0	1	1	1	5	1	0	0	3	0	1	1	5
bo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	7	22	9	0	1	0	1	0	3	3	1	0	0	1	0	3	1	1	3	3	1	0	5	4	1	0	10
tj	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0
tw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	66	19	1	4	1	4	5	6	19	3	0	1	6	5	9	8	5	2	6	7	1	9	2	3	0	9
pa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	150	59	0	3	0	2	2	4	11	1	18	4	55	4	5	26	6	41	5	6	1	28	2	7	3	7
wa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	3	0	5	3	7	9	5	22	3	46	4	3	40	5	37	8	6	3	14	9	9	3	27
sa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	6	1	0	0	20	4	1	7	3	28	0	2	1	19	0	3	0	4
ch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
po	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	2	2	1	0	0	2	1	1	0	2	1	0	0	1	2	0	0	0	1
mt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
sr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	1	0	0	0	0	0	0	2	0	0	0	1	0	3	0	1	1
tn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	0	0	2	0	0	1	0
bl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	1	0	0	1	2	1	0	1	0	1	0	0	0	1	3
fo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	2	3	5	3	3	1	3	6	1	3	2	1	1	3
pw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
gu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	1
ow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0
gr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	13	2	19	2	9	0	20	0	7	0	0
wo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	1	2	0	2	0	1	0	1
pn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	3	0	5	0	2	0	2
mh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9	1	4	0	9	0	3	1	1
fb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	0	1	0	3
hs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	26	0	7	0	3
nz	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	2	6
yo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0	0
sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
eb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	3
rb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
co	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
ag	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
sg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(iii) Felis silvestris ornata: **Sequence-linked matrix (the number of times each behaviour was observed in an interaction with each other behaviour).**

A smaller version of this matrix (without the behaviours that occurred in less than 10 interactions) was used to calculate chi-squared residuals for *Fig. 3.3, Chapter 3.*

	tu	tt	tc	td	sl	sw	or	sn	ap	ma	wp	ra	rp	cu	mw	bo	tj	pa	tq	wa	sa	ch	po	sr	tn	fo	pw	ow	mh	hs	sp	eb	co	kr	ag	sg
tu	0	0	0	3	0	0	3	0	2	2	2	4	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0
tt	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
tc	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
td	0	0	0	0	23	20	3	9	83	64	33	20	3	1	0	2	0	48	0	69	0	2	1	0	4	4	0	0	1	2	2	0	4	2	0	8
sl	0	0	0	0	0	1	1	4	17	11	5	8	3	4	0	5	1	6	1	57	0	0	0	0	2	3	1	1	1	5	0	4	4	0	0	11
sw	0	0	0	0	0	0	0	9	19	2	1	0	0	0	0	0	0	4	0	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	5
or	0	0	0	0	0	0	0	0	2	2	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
sn	0	0	0	0	0	0	0	0	11	6	5	3	2	0	0	0	0	3	0	7	0	0	0	1	4	0	0	0	0	0	0	0	0	0	1	2
ap	0	0	0	0	0	0	0	0	0	51	13	7	0	3	0	3	1	38	0	54	0	3	2	0	4	1	0	0	1	2	0	1	2	1	0	8
ma	0	0	0	0	0	0	0	0	0	0	19	0	2	1	0	2	0	38	0	51	1	3	0	0	3	1	1	0	0	2	2	2	3	1	0	4
wp	0	0	0	0	0	0	0	0	0	0	0	13	0	1	0	0	0	18	0	25	0	1	0	0	2	0	0	0	0	1	2	0	3	0	0	2
ra	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	2	1	9	0	17	0	0	0	0	0	1	0	0	0	2	1	2	6	0	0	0
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
cu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	5	0	0	2	0	0	0	0	0	0	2	0	1	1	0	0	1
mw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	8	0	0	0	0	0	0	0	0	0	2	0	6	3	0	0	1
tj	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
pa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	1	3	2	0	0	1	0	0	0	2	1	3	4	1	1	4
tq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
wa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2	1	1	4	1	1	2	4	1	7	8	2	0	7
sa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
ch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0
po	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
tn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
fo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
pw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
hs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0
sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
eb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1
co	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
kr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ag	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
sg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(iv) Caracal caracal: **Sequence-linked matrix (the number of times each behaviour was observed in an interaction with each other behaviour).**

A smaller version of this matrix (without the behaviours that occurred in less than 10 interactions) was used to calculate chi-squared residuals for *Fig. 3.4, Chapter 3.*

	tu	tl	tc	td	tf	sl	sw	rh	rf	or	sn	ap	ma	wp	ra	jb	ro	rp	cu	mw	bo	tj	lw	pa	lq	wa	sa	ch	po	mt	sr	tn	bl	fo	pw	gu	ow	gr	mh	fb	hs	nz	sp	eb	co	sb	kr	ag	sg
tu	0	1	7	20	1	2	0	1	1	2	0	12	17	14	0	0	0	3	2	0	2	12	13	5	3	14	5	1	0	0	0	0	0	1	0	1	1	1	0	2	7	0	7	2	3	0	0	0	0
tl	0	0	5	3	0	0	0	0	0	0	0	2	4	3	0	0	0	1	0	0	0	5	3	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
tc	0	0	0	18	1	1	0	0	0	0	0	7	22	14	1	0	0	1	0	0	1	20	16	7	0	12	4	0	0	0	0	0	0	0	0	2	1	0	1	0	5	0	1	3	1	1	0	0	0
td	0	0	0	0	13	72	61	12	2	1	56	342	396	176	41	2	4	37	27	1	26	56	108	206	3	282	123	3	7	1	25	4	6	33	11	13	22	56	15	7	219	7	8	55	35	14	1	25	45
tf	0	0	0	0	0	6	0	0	0	0	0	3	7	4	2	0	1	1	3	0	2	3	5	4	0	7	4	1	1	0	0	0	0	3	2	1	3	4	2	2	9	0	0	7	4	2	0	0	2
sl	0	0	0	0	0	0	6	2	0	1	14	27	36	14	8	1	13	5	12	0	10	6	17	25	0	137	30	4	0	0	5	2	3	7	7	5	9	15	10	4	49	2	1	24	18	6	0	9	26
sw	0	0	0	0	0	0	0	4	0	0	33	43	16	2	0	0	2	0	5	0	8	3	0	12	0	26	6	0	0	0	2	3	1	0	4	0	0	1	5	0	7	5	0	4	0	0	0	44	33
rh	0	0	0	0	0	0	0	0	2	0	6	12	7	2	0	0	0	0	0	0	1	1	1	4	0	3	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2
rf	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
or	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
sn	0	0	0	0	0	0	0	0	0	0	0	44	34	5	0	0	0	1	2	0	2	3	3	13	0	13	0	0	0	0	6	1	1	2	0	0	0	0	1	0	0	4	0	0	0	0	0	21	8
ap	0	0	0	0	0	0	0	0	0	0	0	0	210	53	9	1	1	7	11	0	10	21	43	129	1	123	58	1	2	1	18	2	4	15	6	3	8	25	4	4	95	3	5	18	14	5	1	18	36
ma	0	0	0	0	0	0	0	0	0	0	0	0	0	122	4	1	4	13	12	0	9	45	72	129	3	167	66	2	3	0	13	3	0	7	6	6	2	27	10	2	117	1	7	27	16	1	1	13	21
wp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	7	3	0	3	21	41	46	2	85	21	2	0	0	2	0	0	1	1	3	0	6	6	2	46	2	4	9	8	1	0	1	7
ra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	5	1	3	0	8	8	0	17	7	1	1	0	0	0	0	4	0	4	6	3	0	5	11	0	0	8	5	2	0	0	1
jb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	3	0	0	8	4	1	0	0	0	0	0	0	5	0	0	2	3	1	7	0	0	4	4	0	0	0	1
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	6	4	9	14	0	11	13	3	1	0	0	0	1	4	0	0	6	6	0	2	19	0	0	11	8	3	0	0	1
cu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	6	6	0	15	9	2	1	0	0	0	0	3	2	2	2	7	1	6	21	0	0	15	4	1	0	0	2
mw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
bo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	8	0	11	8	0	0	0	0	0	1	5	0	1	8	3	1	1	8	1	0	10	1	5	0	2	2
tj	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	16	1	24	17	0	0	0	1	0	0	2	3	2	0	6	4	1	24	0	1	7	8	0	0	1	1
lw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	2	45	38	3	0	0	1	1	0	7	3	4	3	14	4	5	56	2	3	17	13	2	0	2	5
pa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	128	54	1	1	1	1	1	6	12	1	4	13	16	9	2	73	1	1	16	14	7	0	4	14
lq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
wa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	4	4	0	5	1	4	18	5	7	16	21	16	6	74	1	4	28	24	9	1	7	24
sa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	1	8	2	2	32	4	2	102	0	0	30	15	2	0	0	9
ch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	3	0	0	4	2	0	0	0	0
po	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	3	0	0	2	3	0	0	0	0
mt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	8	0	0	0	1	0	0	0	1	0	0	0	1	0	3	1
tn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
bl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	4	0	0	0	0	0	0	1	0	1	0	1	1
fo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	12	2	3	2	3	2	0	3	2	8	0	1	2
pw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	9	0	0	3	0	0	0	0	3
gu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	2	1	0	0	2	1	2	0	0	0
ow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	5	1	12	0	0	1
gr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	39	0	0	10	9	0	0	0	2
mh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	4	5	0	0	1	2
fb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	6	3	1	0	0	0
hs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52	34	0	0	1	16
nz	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2
sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
eb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	5	0	0	2
co	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
sb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
kr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ag	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23
sg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ng	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(v) *Oncifelis geoffroyi:* Sequence-linked matrix (the number of times each behaviour was observed in an interaction with each other behaviour).

A smaller version of this matrix (without the behaviours that occurred in less than 10 interactions) was used to calculate chi-squared residuals for *Fig. 3.5a, Chapter 3.*

	tu	tt	tc	td	tf	sl	sw	rh	rf	rt	or	sn	ap	ma	wp	ra	jb	ar	ro	rp	cu	mw	bo	tj	tw	pa	tq	wa	sa	ch	po	mt	sr	tn	bi	fo	pw	gu	ow	gr	mh	fb	hs	cb	nz	yo	lo	sp	eb	rb	co	sb	ag	sg
tu	0	3	3	7	0	3	2	1	0	0	1	7	5	10	2	3	0	0	0	1	1	0	0	0	0	2	0	4	0	1	1	0	1	2	2	1	0	0	1	1	0	0	0	0	0	0	0	6	1	0	1	0	1	1
tt	0	0	17	13	0	11	5	7	1	0	0	13	17	46	7	5	0	0	0	1	0	0	1	8	1	10	0	7	0	0	1	1	2	7	3	3	1	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	2	2
tc	0	0	0	13	0	14	13	7	2	0	0	30	48	63	14	7	0	0	0	3	1	2	1	9	2	21	0	12	0	1	1	1	7	7	2	4	2	0	0	5	0	0	0	0	3	0	0	1	0	1	0	0	6	7
td	0	0	0	0	0	118	120	40	17	0	3	212	339	348	53	46	1	1	5	15	8	5	10	21	3	99	0	121	5	7	9	9	61	103	21	33	21	0	3	12	2	6	6	9	2	1	2	5	6	10	9	1	39	41
tf	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
sl	0	0	0	0	0	0	43	25	9	0	3	146	70	138	20	12	1	0	15	2	8	2	7	6	14	24	0	183	6	2	2	4	27	143	15	16	24	0	1	17	0	4	5	5	11	1	3	1	5	7	2	3	46	75
sw	0	0	0	0	0	0	0	51	12	1	0	129	211	99	15	2	2	0	10	5	4	0	2	7	7	32	0	44	3	0	2	4	8	67	16	11	19	0	7	3	2	3	2	5	10	1	0	0	4	4	0	0	90	77
rh	0	0	0	0	0	0	0	0	36	2	1	38	91	76	10	5	0	0	2	6	1	3	2	6	4	11	1	11	0	1	0	4	6	20	6	5	5	1	0	1	1	2	0	4	2	1	1	0	1	4	1	0	8	12
rf	0	0	0	0	0	0	0	0	0	2	0	7	32	28	4	4	0	0	0	1	1	1	0	2	2	2	0	3	0	0	0	1	3	4	1	2	0	1	0	1	0	0	0	2	0	1	1	0	0	1	0	0	0	3
rt	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
or	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	2
sn	0	0	0	0	0	0	0	0	0	0	0	0	373	298	57	18	0	0	4	12	3	5	9	15	10	89	1	74	0	5	3	9	49	89	22	42	18	2	4	10	0	2	3	7	12	1	1	4	4	10	1	0	59	52
ap	0	0	0	0	0	0	0	0	0	0	0	0	0	494	81	27	1	1	6	3	8	4	9	30	11	161	2	122	2	6	5	10	104	152	21	52	18	2	4	16	3	4	5	4	18	1	1	5	7	16	4	2	48	44
ma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	92	25	2	1	10	18	8	6	10	28	9	164	3	153	5	5	3	4	66	144	18	30	20	2	2	18	3	4	2	6	17	1	3	6	5	14	5	2	31	32
wp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	1	0	0	2	3	2	5	3	2	48	1	54	0	1	0	1	11	22	0	7	4	1	0	1	0	0	0	0	2	0	0	0	2	4	1	0	1	4
ra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	9	5	1	4	5	0	10	0	24	7	4	5	0	3	7	6	3	2	0	0	6	1	1	3	2	1	1	1	2	2	1	7	0	1	3
jb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	2	3	0	14	3	0	0	0	1	7	4	0	18	0	1	5	2	1	1	1	0	0	1	0	4	0	1	1	1	8
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	4	0	9	0	15	3	3	4	0	4	6	4	3	2	1	0	3	0	0	0	0	1	0	0	0	1	0	7	0	2	1
cu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	2	0	7	5	2	1	0	1	1	2	1	1	0	1	8	1	1	3	1	0	1	1	0	3	1	1	0	0	2
mw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	2	0	1	0	2	1	1	2	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1
bo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	6	0	10	2	0	1	1	0	5	2	2	4	0	0	1	0	1	2	1	0	0	0	0	1	0	0	0	1	1
tj	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	1	20	0	1	3	0	6	5	2	3	0	0	0	7	0	0	1	0	1	0	0	0	0	2	3	0	0	4
tw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	12	0	0	1	0	2	4	3	0	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3
pa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	84	4	0	2	0	16	32	8	12	5	0	1	5	2	1	0	0	8	0	0	1	2	7	0	0	12	9
tq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
wa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	5	6	1	20	62	13	13	23	0	2	15	1	2	3	0	2	0	0	1	9	9	9	3	18	31
sa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	2	0	0	5	1	0	4	0	0	0	0	0	3	0	0	0	0	2
ch	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	3	3	0	0	0	1	0	0	0	1	0	0	0	0	1	0	2	0	0	0
po	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	8	2	1	0	0	2	0	0	1	2	0	0	0	0	1	0	4	0	2	0
mt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	12	6	1	0	1	2	0	1	0	7	0	0	0	0	0	0	0	0	7	4
sr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	5	41	2	0	2	3	0	1	0	1	3	0	0	2	2	2	0	0	10	5
tn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	11	15	0	1	0	0	2	1	2	12	1	0	1	2	2	1	0	18	29
bi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	0	4	10	1	4	4	8	2	0	0	0	3	1	3	0	15	8
fo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	5	0	2	1	5	1	0	0	1	2	1	0	0	8	7
pw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	1	3	1	3	1	0	1	0	3	0	1	1	5	11
gu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	7	4
gr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	3	0	1	1	0	4	0	1	1	2	3
mh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1
fb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	4	3
hs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
cb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	1	0	5	7
nz	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3
yo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
lo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
eb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
rb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	4
co	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
sb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ag	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	62
sg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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