

8 Social Behaviour

Introduction

For many years it was thought that the domestic cat was an essentially solitary creature, which only tolerated the close proximity of its conspecifics for mating and while rearing offspring. It has often been said that the lion is the only fully social felid. However, while it is true that the social system of the lion is complex, involving communal hunting and cooperation within both male and female groups, social interaction between members of otherwise solitary felid species has been observed (Caro, 1989). Studies of the social structure of groups of domestic cats have shown that they are not just artefacts of the conditions under which house cats are kept; in fact, social structure is most clearly present in groups that are barely tolerant of human company. Looking objectively at the vast range of population densities recorded for domestic cats ([Fig. 8.1](#)), it seems very unlikely that a uniform system for intraspecific interactions could be effective, when individual cats can find themselves spaced at anything from an average of ten to several thousand metres apart. In common with other members of the Carnivora that can adapt to a wide range of population densities, the social structure that pertains to each population of domestic cats varies according to the ecological circumstances in which they find themselves (Macdonald, 1983). Essentially, groups may be formed when the availability and dispersion of food allows two or more individuals to live in close proximity, and on all the occasions that this has been documented much of this food has stemmed from man's activities. This inevitably raises two questions: whether such coalitions can ever occur without man's tacit collaboration and, if not, how the necessary behaviour patterns evolved, unless they are a by-product of domestication.

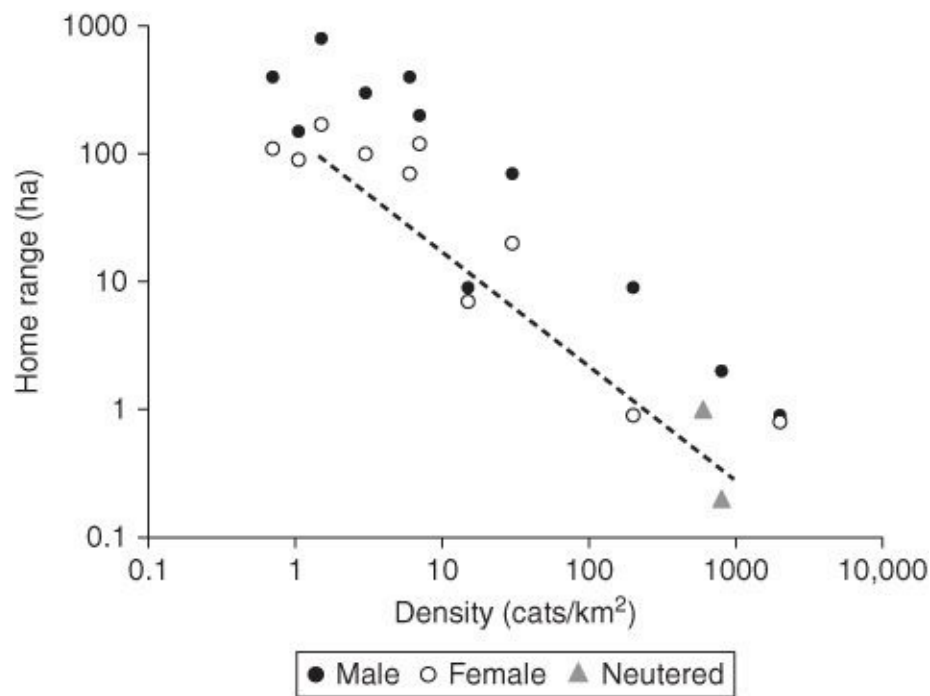


Fig. 8.1. The relationship between home range size and cat density, for entire males, females and neuters. The broken line indicates the size of home range expected if each part of the available space was allocated to the home range of one male and one female; points well above this line indicate overlap between the ranges of members of the same sex, while points well below indicate that not all the available space is used (data from Liberg and Sandell, 1988, with additions from Chipman, 1990, and J.W.S. Bradshaw, unpublished).

Solitary Cats

The question of whether cats kept singly in households are truly solitary will be left to the following chapter, but it can be argued that, like the dog that appears to perceive its human owners as part of its ‘family’, most cats direct species-typical behaviour towards their human keepers. Truly solitary cats that have little conspecific or human contact for much of the year have not been studied in much detail, not least because they are difficult to locate and harder to approach. The European wildcat (*Felis s. silvestris*), although not the closest wild ancestor to the domestic cat, is thought to be almost entirely solitary and may be genetically predisposed to be so, since even its kittens are very difficult to domesticate. Largely solitary populations of *Felis s. catus* are also known, for example those in the bush of south-east Australia and on some uninhabited

islands. Generally, these populations support themselves by hunting and, because it is rare for prey suitable for domestic cats to be highly abundant in any one location for any length of time, social groups are rare. Under such circumstances cats are rarely seen in the company of other cats, except for male/female pairs at oestrus, and females with juveniles. The adults are usually territorial to some extent, although the mechanism whereby such territories are maintained, given that individuals so rarely encounter one another, is not clear. When food is more patchily distributed, but each patch or group of patches is still insufficient to support more than one cat, home ranges can overlap quite extensively, but some system of temporal separation may then operate, so that two cats rarely hunt the same area at the same time. Scent marking has been implicated in maintaining this ‘time-sharing’ arrangement (see [Chapter 5](#), this volume). As discussed in [Chapter 7](#), the home ranges of females encompass sufficient food and shelter for their needs and those of their offspring while they are dependent. Even when cats are well dispersed, the home ranges of males are larger than those of females ([Fig. 8.1](#)) – 3.5 times larger on average. Male ranges of up to 10 km² have been recorded, and it is likely that some males, labelled as ‘transient’ in most studies, either have even larger home ranges than this or are more or less nomadic (Liberg and Sandell, 1988). Male ranges appear to be dictated by the availability of breeding females, whether these are solitary or social, and the degree of competition for them; the factors determining the size of individual male ranges will be discussed further below.

Group-living Cats

Both wide-ranging surveys and more detailed studies of small areas have documented the existence of colonies of domestic cats. The conditions for the establishment of these colonies almost always involve a localized concentration of food, arising deliberately or accidentally from human activities (Kerby and Macdonald, 1988). Some occur around rubbish dumps, studied in locations as diverse as Portsmouth naval dockyard in the UK and a Japanese fishing village. Others are more direct products of provisioning, such as the semi-wild populations often found on industrial and hospital sites or in various public areas in Rome. Farm cats are provisioned both directly and indirectly, by direct handouts of food, by the concentration of rodents in grain stores and sometimes by the theft of food intended for livestock. The size of the colonies seems to be very variable; in one survey of 300 colonies on industrial sites in the UK, most comprised between one and ten individuals but 7% contained over 50 cats. The

critical factors determining the size of the colonies are the availability of food, infant mortality due to feline panleucopenia and other viruses, and direct killing of adults by man.

Small colonies may consist of a single social unit, while larger colonies usually contain several such groups. Most of the groups that have been studied have turned out to consist of females, usually related, together with their offspring, including immature males, and unrelated mature males. Spontaneous movement of females between groups seems to be rare, probably because while females within a group are generally tolerant of one another, they usually attack outsiders on sight, both males and females, and these attacks generally become more intense when there are young kittens in the group. Mature males are only loosely attached to any one group and, as with solitary cats, their home ranges tend to be larger than those of females.

Sexual Behaviour of Females

Apart from the contact between mother and offspring, described in [Chapter 4](#), this volume, the only essential component of social behaviour required of a solitary female is that leading up to mating. In solitary individuals, there will be a strong territorially based tendency to attack any cat, and one of the main functions of courtship behaviour may simply be to bring the sexes together without fighting for long enough for copulation to take place. Even within a colony of cats, where all individuals are familiar to one another, if a male shows more than a fleeting sexual interest in an anoestrous female, the female will move away and if necessary spit and strike out with her claws. In pro-oestrus the behaviour of the female changes, first subtly as a tendency to move about more than usual, and then as an increase in object-rubbing (see [Chapter 5](#), this volume). Males that approach at this stage are greeted with less hostility than before, but prolonged contact is still not tolerated. Over the next 24 h the rubbing increases in intensity and persistent bouts of rolling occur, accompanied by purring, stretching and rhythmic opening and closing of the claws. Males are now permitted close to the female, and may be allowed to lick her, but at this stage any attempts at mounting result in a considerable display of aggression.

Complete sexual receptivity does not ensue until the beginning of oestrus, which is often indicated by an abrupt change in behaviour. The rolling of pro-oestrus is interrupted by the female adopting the lordosis position, suddenly crouching with her head close to the ground and her hind legs treading and partly

extended. Her tail is laterally displaced, uncovering the perineum, and it is at the moment that this display first appears that an experienced male will first attempt to mount. Grasping her neck in his jaws, he begins his copulatory thrusts, while the female treads backwards with her hind legs so that the perineum is rotated further backwards and upwards, until the male achieves intromission. At this point the female usually emits a loud, piercing cry, and within a few seconds jumps away from the male and turns on him, spitting and scratching. The female then grooms her genital region and begins to roll vigorously. Several minutes later she will adopt the lordosis position again, and this cycle of events can be repeated, with the interval between copulations lengthening, over the next 1 or 2 days (Michael, 1961). Multiple copulations are normally needed to trigger ovulation, and without copulation ovulation does not occur. On the one hand, it has been suggested that this induced ovulation is an adaptation to solitary living, preventing the female from ovulating wastefully, before she has been able to attract a male. On the other hand, the whole process of pro-oestrus, when the female is attractive to males but not receptive, and also the need for multiple matings, could also be devices to enhance competition between several males courting one female, and may therefore not only be an adaptation that enhances the female's fitness, but also to living at high density.

Social aspects of maternal behaviour

Females tend to stay within a single social group for much of their lives; a solitary cat may occasionally join an established group, and formerly group-living females can become solitary, but migration between groups by females seems to be rather rare (Liberg and Sandell, 1988). Devillard *et al.* (2003) found that some females dispersed at 1–2 years of age from their study colony of intact, high-density cats and suggest that cats may show intraspecific variability of dispersal patterns related to changes in environment, density, mating system and social organization. Their general tendency to remain in their natal group, combined with the amicable treatment of fellow members of the group, contrasting with aggression towards outsiders, implies that group-living females defend a communal core territory, which is likely to include their denning sites and their major source of food. Large colonies usually consist of one or more 'central' groups of related females that defend areas that contain the best resources for feeding and denning, together with other 'peripheral' females that are either solitary or form smaller groups that occupy inferior territories (Macdonald *et al.*, 2000). Central females generally produce more surviving offspring than peripheral females, suggesting that combining their efforts to

defend their resources gives them a genuine reproductive advantage.

The other obvious benefit from cooperation between the female members of a group is the communal denning and nursing of kittens. While in large groups such collaborations tend to be within mother–daughter pairs, in small groups all the adult females may nurse each other's offspring and the litters are often pooled in communal dens. Females will aid in the birth, then groom, nurse and guard each other's kittens. Pooling of litters may also facilitate the learning of a family identity among the kittens, enabling them to form kin-based alliances once adult. Other advantages may also exist for such pooled litters. In one study, communal litters occupied twice as many nests as solitary litters over the first 6 weeks after birth. The reasons for such frequent nest moves are uncertain, but may help to maintain concealment of kittens from predators and avoid possible infanticide (Feldman, 1993). Kittens are gradually moved to nests nearer to the food source as they develop towards independence in both solitary and communal litters, so facilitation of weaning may be a reason for repeated moves. Whatever the reason, kittens from communal nests spend less time alone and are therefore at less risk from predators during such movements than kittens from a female raising her kittens alone. Kittens from pooled litters also leave the nest earlier than those in solitary litters, suggesting that communal denning may confer some developmental advantages on the kittens.

However, there are also disadvantages to communal living. Several contagious diseases are ideally suited to transmission within a communal den and between cats sharing concentrated food sources. On the oceanic Marion Island, the feline panleucopenia virus was introduced deliberately as a measure to control the feral cat population, and not only was there a fourfold decrease in the population, but the proportion of cats living in groups declined also. Once a virus infects a farm cat colony, it may spread rapidly to all members, and not just within core groups that share nests and resting places (Macdonald *et al.*, 2000): transmission between colonies may simply be low because migration of cats from one farm colony to another is rare, as is close contact between cats in different colonies.

Male Behaviour

There is very little evidence for cooperative behaviour between intact male cats; for example, Dards (1983) never observed any amicable behaviour between any of the mature males in a Portsmouth dockyard. When two unfamiliar males meet

for the first time they may initially sniff each other, but this quickly gives way to aggression, including the arched-back posture (Fig. 5.1), growling and yowling. If one male goes on to the defensive, indicating the other's superiority, it will tend to crouch, hiss and strike out with its fore-claws. After repeated encounters, overt aggression is reduced but the original winner will tend to spray urine and rub objects more frequently than the loser (de Boer, 1977b). Affiliative behaviour between intact males appears to be restricted to juveniles from the same family group, which may associate together until they become sexually mature and disperse (Macdonald *et al.*, 2000).

Territoriality and the mating system

The size and organization of home ranges and the mating system of male domestic cats tend to vary according to the environmental conditions and density of the particular cat population. The home ranges of males are, on average, about 3.5 times larger than those of females living under the same ecological conditions, but this apparently simple relationship conceals a great deal of variability. In rural areas where cats are living at low density (100–300 cats/km²; Liberg *et al.*, 2000), males maintain exclusive home ranges which may overlap those of several females. They may defend access to females in oestrus during the mating season thereby securing most, if not all, of the matings. This system is classified as polygynous (Pontier and Natoli, 1996; Say *et al.*, 1999), whereby each male copulates with several females at each oestrous period. The females may interact at a high rate with such a male when he is present, and may appear to be trying to prolong the male's presence in that part of his home range that encompasses their core area (Macdonald *et al.*, 1987). Outside the breeding season, male ranges in such low-density populations tend not to overlap a great deal, but in the breeding season their ranges expand and overlap considerably, as they try to gain access to as many receptive females as possible. This may be exaggerated when the intervention of man reduces the number of mating opportunities through the neutering of females within a male's normal home range. Yearling males in this environment often stay close to their mother or maternal group, but as they grow they come under increasing attack from older males. In their second or third years, they usually disperse away from their mother's home range. Individual males that do not emigrate appear not to become sexually mature. At this stage they may become strongly solitary, avoiding contact with all other cats, but most eventually come to challenge the successful breeding males for access to females. Males in rural populations may not start reproducing until around the age of 3 years (Say *et al.*, 1999).

Where cat densities are high (up to 3000 cats/km²; Liberg, 2000), such as in urban populations, territories are indistinct and overlapping, encompassing large multi-male–multi-female groups of cats (Natoli *et al.*, 2000). Here, even those males holding territories may be unable to monopolize all of the receptive females, leading to a promiscuous mating system in which both males and females mate with several partners at each oestrous period (Natoli and De Vito, 1991; Say *et al.*, 2002). Aggregations of males around receptive females are commonplace where cat population densities are high, and their most surprising feature is that under these circumstances the males are often less aggressive towards each other than when there is no available female in the vicinity. Natoli *et al.* (2007) point out that the cost associated with the exclusion of all other males would be too high for the resident male – while he was fighting with one competitor, others might exploit the situation and mate successfully with the female. So he opts instead for sharing the mating opportunities and therefore the paternity of litters with other males (Say *et al.*, 1999, 2001). Males in dense populations begin reproducing as soon as they reach sexual maturity (Say *et al.*, 1999) and may be less likely to disperse. Devillard *et al.* (2003) observed no evidence of male dispersal at any age over 8 years in the colony they studied. Possibly the reduced inter-male aggression seen in high-density populations enables juvenile males to remain.

Genetic analysis of paternity in Devillard *et al.*'s (2003) study showed that highly inbred mating occurred in that colony, presumably due in some part to the non-dispersal of males. There did not appear to be any decrease in litter size, survival probabilities or body weight of offspring as a consequence, suggesting that perhaps there are only low costs associated with inbreeding in domestic cats (Devillard *et al.*, 2003). Where colonies are not isolated, there may be more outbreeding than inbreeding (Yamane, 1998).

Reproductive success in males

Studies of the mating system have advanced considerably since Menotti-Raymond and O'Brien (1995) developed a technique using DNA to determine the paternity of kittens. Researchers are now able to accurately measure male reproductive success under different social and environmental circumstances.

Say *et al.* (1999) analysed the paternity of kittens born in two contrasting habitats (rural versus urban) with different densities of cats (234/km² versus 2091/km²). They found a high rate of multiple paternity in the urban population, with 70–83% of litters having more than one father, whereas this was much

lower in the rural population, with only 0–22% of litters having more than one father (Fig. 8.2). One might expect the rural males to obtain exclusive siring of kittens; however ‘satellite’ males are sometimes able to copulate with females in the absence of the resident male (Say *et al.*, 2002).

Males having a territory overlapping that of females, therefore, have varied reproductive success depending on the local population density. In urban areas, such males do not have complete control of receptive females or full paternity of single litters. However, they do achieve the highest reproductive success: Natoli *et al.* (2007) found that the resident male sired the highest percentage of kittens but monopolized only one whole litter out of nine, and co-sired the highest number of other litters.

Males with the largest home ranges include the most female home ranges and have the highest reproductive success (Say and Pontier, 2004). They may also successfully reproduce with females whose home ranges do not overlap theirs – in Say and Pontier’s (2004) study, 28% of kittens were sired by males whose recorded home ranges did not overlap with the kittens’ mothers’ home ranges. This indicates that males may make quick excursions outside their ranges to find new mating opportunities. Thus, although ranging more widely decreases the probability of siring all the kittens in any single litter (Say *et al.*, 2001), apparently using a large area increases fertilization success by allowing a male more mating opportunities (Sandell, 1989). In group-living situations, therefore, a male’s ability to maintain a large home range may be one of the main keys to improved mating success and, interestingly, has been found to be independent of his agonistic behaviour, which is conventionally interpreted as an indicator of ‘social rank’ (Say and Pontier, 2004).

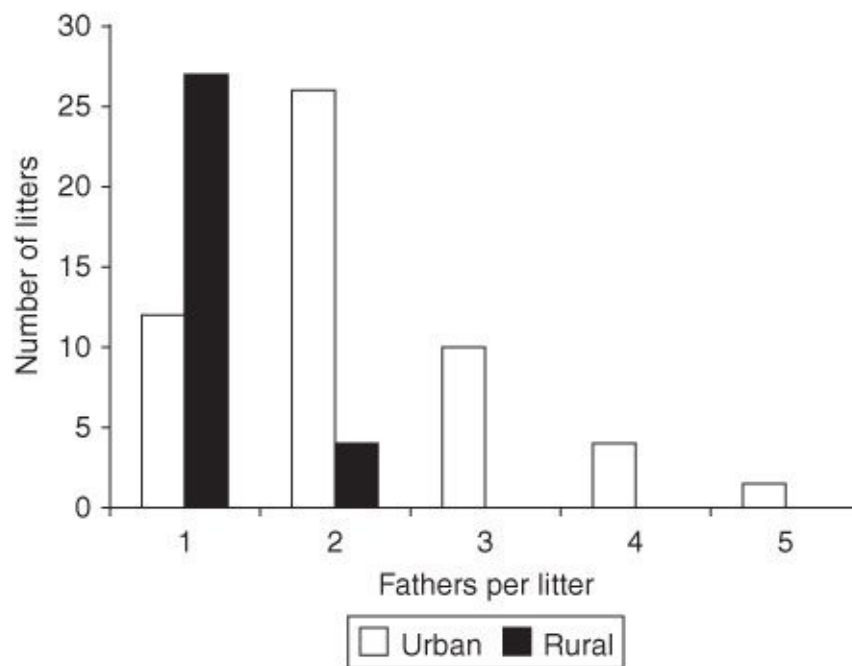


Fig. 8.2. Distribution of the number of fathers per litter in a rural and an urban population (redrawn from Say *et al.*, 1999).

Body weight has also been shown to affect reproductive success. Yamane (1998), studying a group-living population on a small island, identified two different reproductive tactics according to body weight of the male. Heavier males courted females both of their own group and of other groups. Lighter-weight males courted females only of their own group. Observations of the extra-group courting attempts suggested this may be a fairly unsuccessful tactic by the heavy males as their courtship rank was reduced in such groups. DNA evidence, however, revealed that over half the kittens from groups of females were fathered by ‘extra-group’ males. Yamane suggests that the discrepancy between observed copulation and actual paternity may indicate that some female choice may be operating on the mating system in that particular group of cats.

The question of whether females exert choice over which males sire their kittens has produced equivocal results. Natoli *et al.* (2000) found that, although females copulated with several males during a single oestrous period, there was no evidence of mate choice to be found. Ishida *et al.* (2001), however, found that their females did not accept all mounting or copulation attempts and in particular appeared to avoid inbreeding with close kin (1/4 or higher degrees of relatedness). More distant relatives were not refused.

One other important variable affecting the reproductive success of males is the degree of oestrus synchronization amongst females. When oestrus is asynchronous a more competitive male can attain higher reproductive success than lower-ranking males through priority of access to females. This allows him to copulate with more females or to copulate with the same female several times to ensure paternity (Say *et al.*, 2001; Say and Pontier, 2004). When oestrus is synchronized, as is often the case in dense urban populations, a single male will not be able to monopolize all the females and other males will be able to mate with them too. Say *et al.* (2001) found that variance in male reproductive success was four times greater in those years when females bred asynchronously, with dominant males siring the highest proportion of offspring.

Infanticide

When one coalition of male lions succeeds in ousting another group of males from a group of females, they usually kill all the cubs in the pride, thereby bringing the lionesses into oestrus more quickly than if they had completed lactation through natural weaning. Examples of infanticide by male domestic cats have been reported (e.g. Macdonald *et al.*, 1987; Pontier and Natoli, 1999). In the latter study, six cases of infanticide were directly observed in rural populations of cats. It is unclear just how common this phenomenon is, although it may be one factor causing the aggression shown by nursing females towards strange males. It has not been described for high-density populations, and Say *et al.* (2001) suggest that synchronicity of oestrus in females in densely populated breeding groups may help reduce the risk of infanticide through the mixing of paternity that ensues (see section on reproductive success in males). Since the birth interval in the domestic cat is only 4 months, compared with 19 months in the lion, the advantage to be gained from infanticide in bringing a female into breeding condition may not be great (Natoli, 1990). In temperate climates the second (autumn) litter rarely produces surviving offspring, but it is possible that its chances of success are increased by bringing the time of conception forward by even a few weeks. Infanticide might also be a successful strategy when cat density is low and adult females, food or suitable nest sites are at a premium. A non-breeding male could enhance the chances of his own future offspring surviving by attempting to kill all the offspring of the current resident male, so that when that male lost his position, and he took over, his own kittens might be born in the best nest sites (as selected by the surviving females) and be fed sufficiently well to reach adulthood. However, it is still unclear whether infanticide is a common strategy among feral cats, or an aberration only.

practised by a very few. This is discussed in more detail by Pontier and Natoli (1999).

Social Communication

We have seen that, where there is a sufficient concentration of food, cats form more or less stable groups, the basis of which is usually the cooperative rearing of kittens by related females. The role of males in these groups is still poorly understood, and may vary with population density. The membership of these groups is generally stable outside as well as during the breeding season, and as for other social Carnivora, the social structure is maintained by a 'glue' of interactive behaviour patterns. In other species these patterns have been interpreted as indicating some kind of hierarchical organization, and an individual's position in the hierarchy is usually estimated by the behaviour patterns it exhibits towards other members of its group. Some of the most revealing of these patterns are those indicating submission, where one individual signals that it wishes to 'back down' from an encounter. However, no such pattern has been identified in the cat, which tends to ward off aggressive approaches with defensive, rather than submissive, behaviour. Whereas consistent patterns of aggressive interaction have sometimes been identified between males, and interpreted as a 'dominance hierarchy', the collaboration between females is more cooperative than hierarchical, because it is common for all the females in a group to breed simultaneously. Certain behaviour patterns appear to strengthen the bonds between individuals, and to build up a group identity. These social behaviours include scent marking, mutual grooming (alogrooming) and mutual rubbing (allorubbing), and these will be discussed in turn. To put these into a social context, the flow of interactions within social groups will be described first.

In a number of published studies, not only has the behaviour of particular individuals been recorded, but also the partners they chose to interact with, whether those individuals were considered separately, as close relatives or as representatives of a particular age/sex class. In colonies that obtain some of their food by hunting, the cats tend to visit their core area independently, neither avoiding one another nor tending to always be present with a particular partner. However, when they are present they tend to single out particular partners for interaction. For example, Wolfe (see Curtis *et al.*, 2003) studying two colonies found that some adult cat dyads were within 1 m of each other more often than

would be expected by chance – these he referred to as preferred associates. Proximity was not dependent on location, so cats were not simply aggregating at preferred resources at the same time. Some cats appeared actively to avoid one another too – in a colony of intact cats these were mainly male–male pairs, while in a neutered colony there was no effect of gender (Wolfe, 2001; see also Crowell-Davis *et al.*, 2004). Macdonald *et al.* (2000) discuss in more detail the preferences cats had for proximity to both kin and particular age/sex classes for the cats in three study colonies. More detailed examination of the quality of social behaviour in such colonies confirms that the interactions are highly structured, and the colonies are far more than simple aggregations around food sources.

Tail up

Cats usually precede amicable interactions by raising their tail to the vertical. In feral cats, tail-up precedes both sitting down with another cat and rubbing on another cat (see [Fig. 8.3](#)). Pet cats approach a tail-raised silhouette of a cat faster than one with its tail down, confirming that the vertical tail signals an intention to interact amicably (Bradshaw and Cameron-Beaumont, 2000).

Allogrooming

Cats spend a great deal of time grooming, and there is no evidence to suggest that a solitary cat is any less clean than a cat that is groomed by others. The function of allogrooming, which is most often directed to the head and neck area of the recipient (Van den Bos, 1998), is therefore likely to be primarily a social one, except in the case of young kittens that are groomed by their mother before they become competent at grooming themselves. In one study of allogrooming in an indoor colony of neutered adults (Van den Bos, 1998) the flow of allogrooming bouts within pairs of cats was asymmetric, with cats showing more aggression grooming rather than the other way round. Grooming was also associated with aggressive behaviour in 35% of interactions (with groomers showing aggressive behaviour more often than groomees). Other colony studies also indicate that the higher the density of cats the less aggression and the more allogrooming occurs, suggesting that allogrooming may be a way of redirecting potential aggression and reducing tension between cats living together. Although Van den Bos could not detect any effect of degree of relatedness on frequency or duration of grooming, Curtis *et al.* (2003) studying a different neutered colony of

cats found kin preference in both allogrooming and proximity.

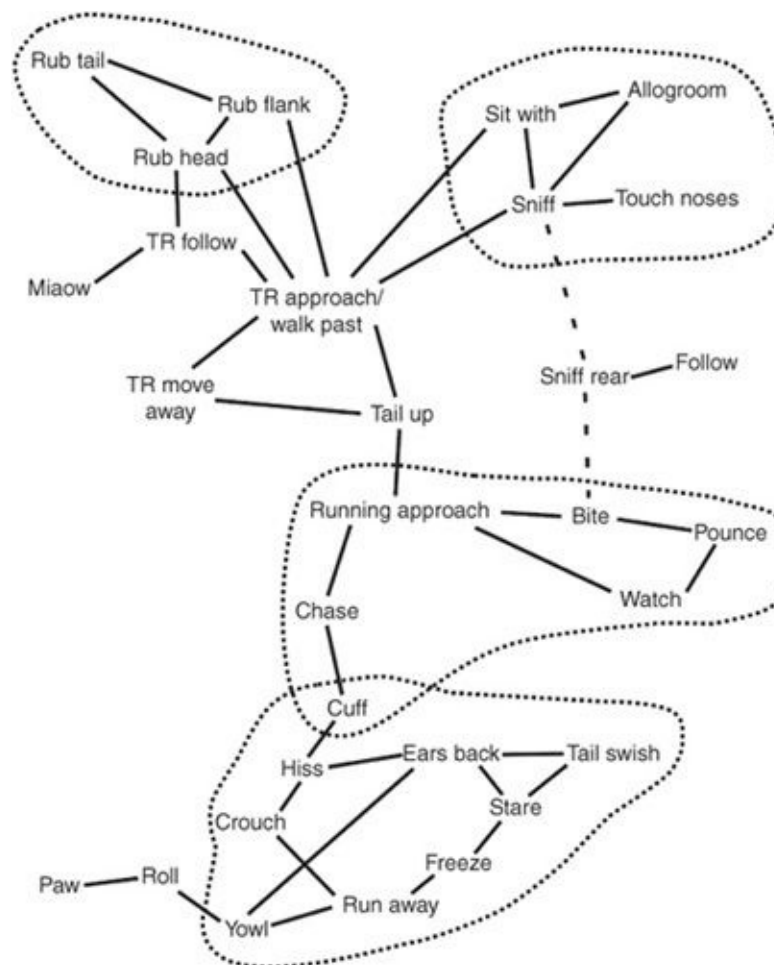


Fig. 8.3. A classification of social behaviour patterns performed by neutered cats (i.e. excluding sexual behaviour). Patterns that are very likely to be performed by the same cat during a single interaction with another cat in its own social group are joined by solid lines. The patterns fall into clusters, most of which have self-evident functions. Amicable interactions (top) often begin with the tail-up signal (centre) either when the cat is stationary (tail up) or moving (TR): these fall into two types, one consisting of allorubbing (top left) and the other mutual sniffing and grooming (top right). At the bottom is a defensive cluster, and above it a cluster of aggressive patterns, linked together by chase/cuff. Of the patterns not strongly linked to any of these groups, miaow may be an attempt by one cat to alert another that it is following with the intention of initiating a bout of rubbing; paw may be an attempt at initiating an interaction which triggers aggression in the other cat and is followed by roll and then defensive behaviour; follow/sniff rear (only weakly linked to other patterns, shown by broken lines) may be followed by amicable sitting together or by aggressive behaviour, presumably depending upon the reaction of the cat being sniffed. (Data collected by Sarah

Brown and analysed by Charlotte Cameron-Beaumont, derived from 2044 interactive sequences between 42 neutered cats in three permanent groups. Solid lines represent positive 2 × 2 associations; $P < 0.001$ by chi-square.)

Allorubbing

There is increasing evidence that one of the key behaviour patterns that cements an existing cat group together is mutual rubbing, in which pairs of cats rub their foreheads, cheeks, flanks and sometimes tails together. There may be two communicative aspects to this behaviour, one being the tactile signals exchanged and the other the potential mixing of the two cats' individual scents. So far neither aspect has been investigated separately, so that for the present the function of this display has to be deduced from the behaviour of the animals that initiate it, and the behaviour patterns that precede and follow it in the course of a social interaction.

Several studies have shown that rubbing flows markedly asymmetrically between members of a colony of cats, with females initiating rubbing more than males, and young animals initiating more rubs than older ones ([Fig. 8.4](#)). For kittens, rubbing may indicate the strength of their relationship towards the lactating females that suckle them, because a close relationship has been found between the number of times that each kitten rubs on a particular female and the number of nursing bouts it receives from that female. It is unclear which participant initiates interaction – does each female permit a kitten to suckle in proportion to the number of rubs she has received, or does each kitten rub in direct response to being nursed? Whichever way round this is, rubbing does seem to have special significance as far as nursing is concerned; for example, the levels of grooming and nursing that females give to individual kittens in a pooled litter are not closely related.

The significance of allorubbing between adults can be explored further by examining the behavioural context in which it occurs. Two studies of neutered feral colonies showed that an individual that is about to rub almost always raises its tail as it approaches the other cat (Brown, 1993; Fig. 8.5). The form of the rubbing itself depended upon whether the receiving cat also raised its tail. If it did, both cats usually rubbed simultaneously; if not, the recipient cat sometimes only rubbed after the initiator had, or not at all. Females and males may use rubbing differently: in a neutered colony of (presumably) related cats, Cafazzo and Natoli (2009) found that while tail up and rubbing were generally displayed by females towards males, sniffing nose was more often displayed by males towards females. However, Barry and Crowell-Davis (1999) did not observe any allorubbing in 20 neutered pairs of female indoor cats, possibly because the

majority of these pairs consisted of unrelated individuals.

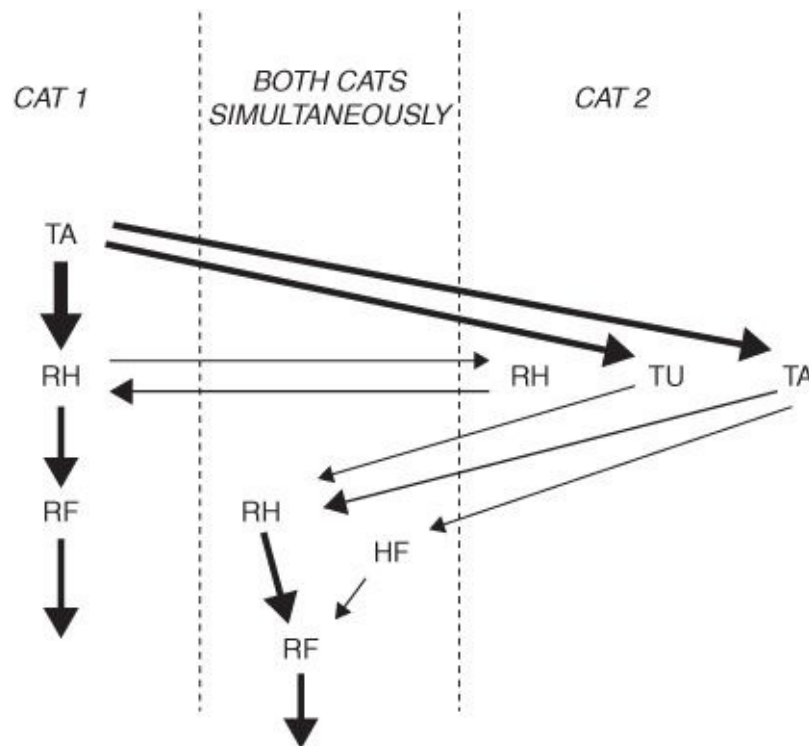


Fig. 8.5. Typical sequences of behaviour that contain head or forehead rubbing between cats. Cat 1 approaches Cat 2 with its tail raised (TA). If Cat 2 does not raise its own tail, Cat 1 rubs its head (RH) on Cat 2, which may reciprocate before Cat 1 rubs its flank (RF) on Cat 2. If Cat 2 does raise its tail (TU) or approaches Cat 1 with its tail raised, they simultaneously rub heads or foreheads (HF) together, before rubbing flanks together. Widths of arrows are proportional to frequencies (except for those emanating from RF). All transitions derived by first-order Markov chain analysis, excluding those with probabilities worse than 0.001 by chi-square (Brown, 1993).

Anthropomorphically, rubbing seems to be highly affectionate but it appears to be used predominantly when the relationship is somewhat one-sided, and may be the nearest the cat has to a behaviour pattern that is used between individuals to reduce conflict through reinforcement of affiliative bonds. However, it is unlike the appeasement behaviours shown by other social carnivores to avoid escalating aggression during interactions, since rubbing is rarely seen in interactions involving any kind of overt aggression. Exceptions to this have been recorded, as when a particular tomcat was occasionally mildly aggressive towards a female that persistently attempted to rub against him (Macdonald *et al.*, 1987), but even in this case there was no evidence to suggest that the female

rubbed to appease the tom.

Scent marking

Social odours feature prominently in the lives of many mammalian species. Scents can be specific to a particular individual, are fairly stable with time and offer the considerable advantage that they can be deposited in the environment and later detected and decoded by a conspecific in the absence of the emitter. The scents known to be used as marks by cats include those carried in and by the urine and faeces, and those originating in skin glands on the head. Urine scent marks are known to convey individual- and group-specific information (described in more detail in [Chapter 5](#), this volume), although the way this information is used in social interactions is uncertain. Male cats frequently spray urine when consorting with an oestrous female, and it is possible that the rate of spraying is an indicator of mating success. Any possible role of this scent marking in the selection of sexual partners either by the male or the female remains unclear.

Social Structure

The communicative repertoire of the domestic cat, although not as complex as that of the most social carnivores – the wolf, for example – nevertheless suggests the existence of a social system into which all social interactions should fit. There is significant disagreement as to how that system should be conceptualized. The earliest studies of cat sociality, performed on laboratory colonies, used the dominance or ‘peck order’ concept to derive hierarchies, based on priority of access to resources such as food (e.g. Winslow, 1938). However, when behavioural ecologists began to study free-living cat colonies, they could find little evidence for dominance hierarchies, apart from older males preventing younger males from breeding: cat society appeared to revolve around coalitions between females, which were usually egalitarian (Macdonald *et al.*, 1987). Both of these approaches have been used in the interpretation of social interactions within multi-cat households: some authors (e.g. Crowell-Davis *et al.*, 2004; Cafazzo and Natoli, 2009; [Fig 8.6a](#)) have espoused the hierarchy, while others (e.g. Rochlitz, 2005b) have expressed doubts as to whether it is useful to apply this approach to pet cats. The usual alternative approach involves focusing on the way that each cat uses the space available (Bernstein and Strack,

1996; Bradshaw and Lovett, 2003; Fig. 8.6b), based on the idea that cats are fundamentally territorial animals.

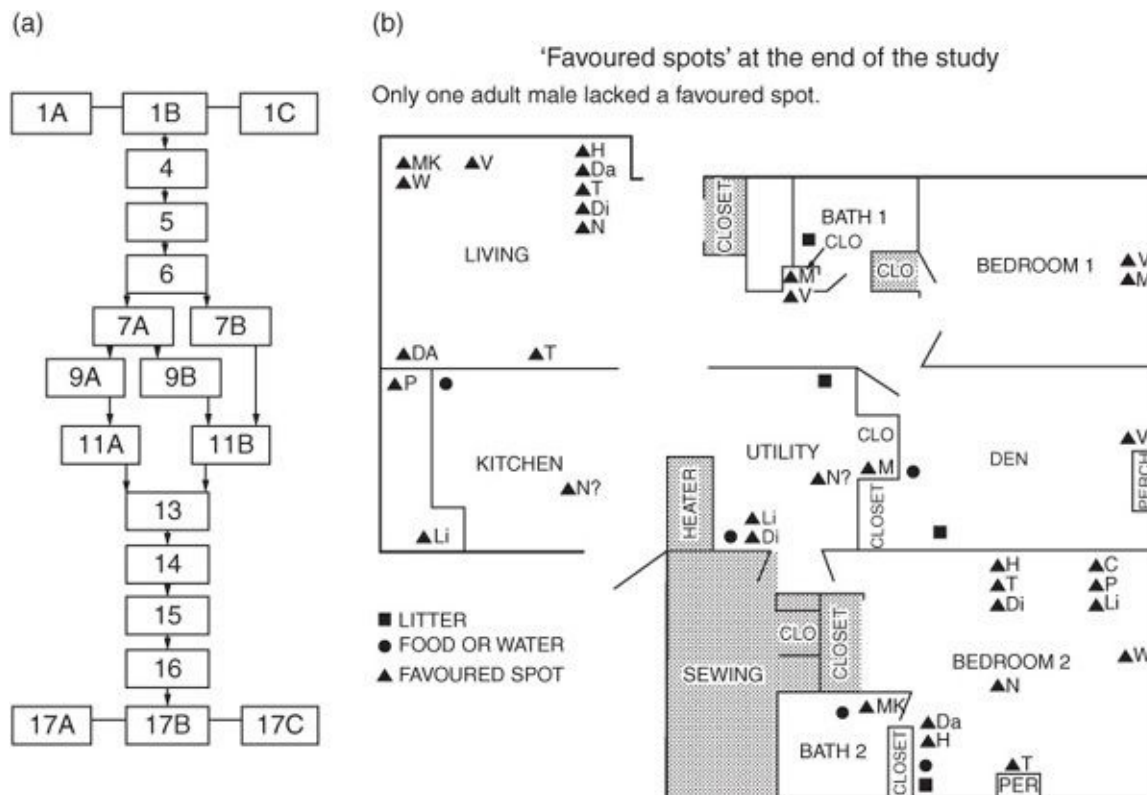


Fig. 8.6. Contrasting approaches to the characterization of social structure in multi-cat households. (a) A dominance hierarchy based on agonistic interactions (from Knowles *et al.*, 2004); each box represents a different cat ($N = 19$ out of 27 cats present) and the numbers indicate dominance rank, suffixed by letters indicating cats of equivalent rank. (b) Favoured resting locations for 13 cats (from Bernstein and Strack, 1996); most cats had several of these and many were shared between two or more individuals.

Dominance can be a loosely defined concept (Drews, 1993) and also one that may mean more to the human observer than to the animals themselves (Appleby, 1993). In any group of animals, it is usually possible to measure consistent asymmetries in the exchange of competitive behaviour between pairs of animals. Combining these dyadic interactions into an overall structure can reveal apparent hierarchies – for example, a more or less linear hierarchy in which one individual is dominant over all others in the group and, at the lower end, one or more are subordinate to all others. Robust mathematical techniques now exist for the construction of such hierarchies (e.g. Bang *et al.*, 2010), but it is often

unclear whether these constructs reflect everything that is of importance to the animals themselves, or whether they are an artificial construct created by the human observer. First of all, the 'hierarchy' can change markedly depending on which behaviour pattern(s) are used to construct the dominance relationships (e.g. Natoli *et al.*, 2001), and the context in which interactions are observed. Secondly, the fact that a hierarchy may be apparent to the human observer does not mean that it is also apparent to the cats themselves, or that position in the hierarchy is something to which each cat aspires. In other words, some groups of cats may behave *as if* they inhabit a hierarchy, but are in fact simply reacting to the cats around them in their own individual way, or as a consequence of learning from previous encounters the optimal manner in which to interact with others. However, the cats themselves are unlikely to be aiming to achieve a species-specific structure, adopting any particular 'role' within that structure, or determining behaviours based on changing their role within the structure. Indeed, because today's domestic cats are only a few thousand generations removed from their solitary territorial ancestor, and hunting remains a solitary activity, it is difficult to see how a species-specific social structure could have evolved, nor its value in determining social behaviour.

The apparent hierarchies that can be recorded from cats kept in high-density colonies may simply reflect stress brought on by overcrowding: it has been suggested that the 'lowest-ranking' cats in these groups would normally disperse (Durr and Smith, 1997). In feral breeding colonies, cooperation between females has been described as 'centripetal' and not 'hierarchical' (Macdonald *et al.*, 1987), but functional hierarchies can often be derived among males, in which older males harass younger males, especially juveniles, thereby preventing them from mating. Adult male cats rarely, if ever, cooperate, and this hierarchy appears to be a simple 'pecking order' in which younger males learn to avoid older, more experienced males with which they cannot (yet) effectively compete. Although 'dominant' resident males achieve more matings than 'subordinate' resident males, doubt has been cast on whether older males actually have more reproductive success (Say and Pontier, 2004): females show strong preferences for non-kin males (Ishida *et al.*, 2001), resulting in many – even a majority of – kittens being fathered by males from outside the colony (Yamane, 1998). Thus the most successful strategy for a male cat would appear to be to visit any neighbouring colonies as often as possible. On such visits, even males that appear dominant in their own colony behave like subordinates, suggesting that 'dominance' is not an individual characteristic but a consequence of the learnt interactions within familiar groups. In multi-cat households, even neutered cats

can behave in a ‘bullying’ way, thus affecting the movement or activity of the other cats (see [Chapter 11](#), this volume). However, the behaviour of the majority of cats in such agglomerations appears to be regulated by mutual avoidance, time-sharing and, for some pairs of (especially related) individuals, active affiliation (Bernstein and Strack, 1996), possibly derived from normal female–female behaviour.

Most of the behaviour patterns that have been put forward as indicators of dominance and submission are part of normal offensive and defensive behaviour, as occurs in other contexts, for example between unfamiliar individuals. In some but by no means all colonies, older males mount younger males, but it is not clear whether this is dominance-assertion or merely an outlet for sexual tension in the proximity of unreceptive females (Yamane, 1999). Feldman (1994b) has reported juvenile males in one colony performing the rolling behaviour normally characteristic of oestrous females, apparently as a submissive behaviour towards older males, but this does not seem to occur universally. Macdonald *et al.* (1987) speculated that rubbing behaviour might be an indicator of subordinate status in large colonies, but this has yet to be confirmed by subsequent observations. Overall, it appears that the ritualized (i.e. evolved, species-typical) signals described in other species as determining dominance relationships are missing from the domestic cat’s repertoire. This is consistent with the idea that they have no species-typical social structure other than whatever emerges as a consequence of each cat learning about the likely responses of others under different circumstances. In this conception, Macdonald *et al.*’s ‘centripetal’ system can be thought of as arising from the persistence into adulthood of normal affiliative relationships between mothers and their female offspring.

The Functions of Domestic Cat Sociality

There has been a good deal of speculation over the advantages that cats might gain from living in groups, but to date not a great deal of evidence has been found for any of the alternatives. Given the wide range of group sizes and the highly artificial surroundings in which some of the largest groups find themselves, it is probably not surprising that a functional explanation that appears to apply to a group in one type of situation does not apply in another. Certainly a great deal of care is needed when extrapolating from the sociality of domestic cats to that of wild felids. Social structures in wild species of Carnivora

have been refined by millions of years of natural selection; not only is *Felis catus* only a few thousand generations old, but the circumstances under which it has evolved have not been consistent, as the niches supplied by man's activities have continually changed.

To recap, cooperation appears to revolve around the activities of females attempting to pool their ability to defend resources, and thereby obtain maximum benefit for their offspring from the concentrated food source that has allowed the colony to become established. When all the females within a group are closely related, and they usually are, this can be extended to include their relatives' offspring. The best evidence for this comes from the much poorer breeding success of peripheral females compared with central females at Horspath Farm (Kerby and Macdonald, 1988). At that farm this crucial spatial status was determined by kinship. The two central lineages had much higher breeding success than the peripheral lineages (even though some central individuals would occasionally breed in peripheral sites), which consisted of four side-branches of the original central lineages and two lineages based on immigrants. After several generations, these peripheral lineages would probably die out, or emigrate; meanwhile, if the central lineage bred successfully, it would tend to fragment and push some of its females to peripheral positions. In practice, this process is likely to be disturbed by man's activities (culling, the taking of kittens for pets, changes in the amount of food and shelter available), and so is unlikely to be readily apparent in all colonies.

The Origins of Sociality in the Domestic Cat

Since there are no published accounts of the behaviour of group-living *F. silvestris* apart from the domestic cat, we can only speculate as to how the sociality of which this species is evidently capable arose in the first place. Virtually all the social groups that have been studied have relied on concentrations of food supplied by man. This raises the possibility that sociality in the domestic cat has arisen secondarily, as a by-product of domestication; *F. s. lybica* is essentially solitary and territorial. If we assume that *F. s. lybica* originally exploited anthropogenic environments as a commensal, and that those niches contained reliable sources of prey that could feed more than one queen and litter, then individual animals capable of forming coalitions with kin might out-compete individuals that could not. This would pave the way for the rapid evolution of cooperative behaviour. Subsequently, as the cat was domesticated,

man might have deliberately chosen individuals that tolerated the close proximity of other cats, because one highly territorial cat would not have achieved the desired effect. Later on, those cats that also displayed affiliative behaviour towards people might have been selected from the original, conspecific-tolerant, population. The affiliative behaviours that adult cats direct towards each other and towards people may have been derived from those shown by kittens towards their mothers, carried into the adult state by a process of progressive artificial neotenization.