



6 Group-living in the domestic cat: its sociobiology and epidemiology

DAVID W. MACDONALD, NOBUYUKI YAMAGUCHI AND
GILLIAN KERBY

Introduction

From its sacred origin in ancient Egypt, the domestic cat, *Felis silvestris catus*, has spread worldwide as a household pet. When cats revert to the wild they are similarly ubiquitous, but whereas the pet cat has brought joyous companionship to people, its feral counterpart ranks highly amongst alien carnivores as a blight on native wildlife (Macdonald & Thom, 2000). Without fretting about a precise definition of 'feral', it is clear that such cats, living in varying degrees of dependence upon man, occur from subantarctic islands (Van Aarde, 1978) to industrial cities (Rees, 1981), at densities varying from less than one to more than 2,000 per square kilometre (reviewed in Macdonald *et al.*, 1987; Liberg & Sandell, 1988). The consensus is that cat populations can be divided into those in which females form groups, at least loosely resembling those of lions, *Panthera leo*, and those in which they live solitarily, generally in a territorial pattern typical of most wild felids (Corbett, 1979; Liberg, 1981; Konecny, 1983; Macdonald *et al.*, 1987; Liberg & Sandell, 1988; Caro, 1989; Macdonald, 1994). Kerby & Macdonald (1988) suggested, in the first edition of this book, that differences in predictability and patchiness of resources result in a continuum of social organisation, with large colonies and solitary cats at opposite ends (Macdonald, 1983; see also Chapter 7).

Their capacity to live under contrasting environmental circumstances, added to their accessibility and distinct coat-colour genetics, make free-ranging cats a useful 'model' for studies of how ecological factors affect felid sociality, most of which are difficult to study and many of which are endangered. Their advantages as a model is enhanced by huge advances in the mapping not only of the cat genome (Menotti-Raymond *et al.*, 1999), but also that of their crucially important virus, Feline Immune Deficiency virus (Carpenter & O'Brien, 1995). Domestic cat sociobiology is also a rich vein of enquiry for those interested in the processes and consequences of domestication. In particular, the question arises as to whether domestication has extended the behavioural flexibility of the domestic cat beyond the adaptability of wild felids confronted by the same ecological circumstances.

Recent craniometric and genetic studies on cats throughout Italy strongly suggest that domestic cat, the European wildcat and African wildcat belong to the same polytypic species, *Felis silvestris* [Schreber 1777] (Randi & Ragni, 1986, 1991). The European,

Felis s. silvestris, and African, *Felis s. libyca*, wildcats probably diverged from a common ancestor approximately 20,000 years ago (Randi & Ragni, 1986, 1991). The domestication of the African wildcat probably began approximately 4,000 years ago in Egypt (Serpell, 1988; see also Chapter 9). Although little is known of African wildcats, our team undertook a preliminary radio-tracking study, of which the preliminary results suggested a social organisation similar to that of Scottish wildcats (which have been studied in depth: e.g. Corbett, 1979; Daniels, 1997; Daniels *et al.* unpublished). Intriguingly, African wildcats in Saudi Arabia had access to human refuse and middens around which feral domestic cats congregated in colonies, yet the wildcats appeared not to form colonies (Macdonald, 1996b). Fragmentary evidence such as this adds to the logical possibility that a capacity to form large aggregations may have been fostered by domestication. However, no behaviour pattern has ever been recorded amongst free-ranging domestic cats which has not also been documented in other felids (see also Chapter 3), although association with people has made commonplace resources such as shelter and clumped, predictable and abundant food.

Besides the sociobiological questions fruitfully provoked by the domestic cat, they have long been favoured subjects for medical, veterinary and behavioural research. Our proposal here is that these topics link, through epidemiology, to the widely accepted and great risks posed by feral cats to conservation. Most commonly, people think of feral cats as predators, with the capacity to decimate local faunas (e.g. Jones, 1977; Karl & Best, 1982; Apps, 1983; Kirkpatrick & Rauzon, 1986; Churcher & Lawton, 1987; Kay Clapperton *et al.*, 1994; Boitani, 1999; Macdonald & Thom, 2000). More insidiously, they are susceptible to micro- and macro-parasites of which some are deleterious to humans, livestock and other wild animals (Dubey, 1973; Parsons, 1987; Gaskell, 1994; Gaskell & Bennett, 1994a, b, Pastoret, Brochier & Gaskell, 1994; Wright, 1994). This includes a potentially catastrophic risk to isolated populations of endangered wild felids (Mochizuki, Akuzawa & Nagatomo, 1990; McOrist *et al.*, 1991; Roelke *et al.*, 1993). Much of what is known of the physiology, pathology and epidemiology of domestic cats is based on laboratory studies. The epidemiology of cat diseases under more natural environments, and in the context of their sociobiology, is a new

field (Yamaguchi *et al.*, 1996; Courchamp *et al.*, 1998; Macdonald, Yamaguchi & Passanisi, 1998).

In this chapter, we will discuss first the factors determining whether adult female felids, including the domestic cat, form groups. Secondly, we explore the dynamics of cat groups before, thirdly examining how the details of their social behaviour relate to epidemiology in free-ranging cat colonies. These topics are interesting in their own right, but our ultimate motive in addressing them is their relevance to conservation, especially in terms of the threats posed by domestic cats as disease reservoirs (Macdonald, 1996a; Yamaguchi *et al.*, 1996) and agents of hybridisation (Reig, Daniels & Macdonald, 2000; Daniels & Macdonald, unpublished; Daniels *et al.*, unpublished), as well as their more generally acknowledged threats through predation and competition (Macdonald & Thom, 2000).

Forming groups and resource availability

Females of all feline species are, in effect, incipiently group-living, in that for over 80 per cent of their adult lives they are likely to be accompanied by dependent offspring (Caro, 1989). Nevertheless, it is conventional to refer to both males and females of most of the 37 or 38 species of felids as asocial because independent adults do not form permanent groups (reviewed in Creel & Macdonald, 1995). Only among cheetahs, *Acinonyx jubatus*, and lions do adult males live in groups, and females live communally only in the lions and domestic cats (Kerby & Macdonald, 1988; Caro, 1989). Macdonald (1983, 1994) interpreted these groups in terms of the Resource Dispersion Hypothesis, which proposes that the dispersion of resources may be such that the smallest territory that will provide adequate security for the primary social unit may also support additional group members (see also Macdonald & Carr, 1989). In mammalian societies, food and shelter are likely to be the limiting resources for females, whilst females are generally the limiting resource for males. Therefore we consider the factors affecting group-living as partly separate, and in this review we focus largely on females. Theories relevant to the evolution of sociality in felids have been reviewed by Packer (1986) and Caro (1989), and they identify prey size, density and encounterability as important factors.

Prey size and density

For carnivores, Wrangham *et al.* (1993) could detect no correlation between a predator's foraging group size and its population density (an index of food density), a finding in accord with the generalisation that group size and territory area may be determined, independently, by the abundance and dispersion, respectively, of available food (Macdonald, 1983). Thus, foraging group size might be affected by the body mass of prey (analogous to the richness of a food patch) as distinct from their abundance.

One female lion, weighing approximately 141 kg (this, and subsequent weights refer to the average body weight of an adult female), can generally monopolise carcasses of less than 100 kg, but is unlikely to keep other females at bay from larger carcasses (Packer, 1986). Similarly, Aldama & Delibes (1991) observed that a young independent female Spanish lynx, *Lynx pardina* (c. 13 kg) joined its mother and a six-month-old sibling to eat yearling fallow deer, *Dama dama*, weighing about 20–25 kg. These field observations clearly suggest the importance of prey size to potential group formation. However, while large prey may facilitate group-living, it does not demand this. Cougars, *Puma concolor* (46.4 kg) in the north of their geographical range hunt solitarily for mule deer, *Odocoileus hemionus* (48.8 kg), or even elk calves, *Cervus canadensis* (109.3 kg) (Caro, 1989). Not surprisingly, temporary associations of cougars occur at their large kills (Seidensticker *et al.*, 1973). However, as Caro (1989) suggested, prey density may be insufficient for these cougars to sustain groups throughout the year. We therefore interpret the cougars' behaviour as one step on a continuum. This continuum leads to Schaller's (1972) report that when seven lionesses in a pride fed mainly on wildebeest, *Connochaetes taurinus* (122.3 kg) an average of 6.4 of them ate together, whereas when they killed Thomson's gazelle, *Gazella thomsoni* (13.3 kg) only 3.6 fed together. When zebra, *Equus burchelli* (226.7 kg) moved into one pride's range, Schaller saw feeding groups of seven lionesses eating together. These observations suggest that another key factor in group formation is the abundance of accessible large prey.

Predator density and habitat type

Van Der Meer & Ens (1997) suggest that it is helpful to think of predatory lives as falling into three

determining activities: searching for prey, handling prey, and encountering conspecifics. Clearly the latter is a prerequisite to group formation, which may thus be more likely in populations where the likelihood of such encounters is high, all else being equal. Packer (1986) argues that because lions live at higher densities than other big cats, there is greater scope for females to come into close proximity. Indeed, the continuous availability of conspecifics may be a distinction between the lions and cougars studied by Schaller (1972) and Seidensticker *et al.* (1973), respectively. Ultimately, these differences are determined by the density of available prey (Schaller, 1972; Macdonald, 1983; Sandell, 1989).

Furthermore, habitat type is likely to affect conspecific relationships: a carcass is much more conspicuous to scavengers in open habitat. Lions watch for vultures and may travel several kilometres to where these birds have landed (Packer, 1986). In contrast, tiger, *Panthera tigris*, kills are extremely difficult to locate in dense vegetation (Sunquist, 1981). Therefore, felids in open habitats are much more likely to encounter conspecific (and other) competitors, and perhaps therefore more likely to form

defensive coalitions. In this context, the behaviour of woodland-dwelling lions raises such interesting questions as whether their tendency to live in groups is a neutral or even maladaptive ghost of their evolutionary past, or fully adaptive.

Probability of group formation

In this section, our aim is to identify the factors that favour group formation, and to assemble these in a general model that can be applied to the variation in female felid sociality overall, and domestic cat groups in particular. The nub of the argument is that the probability that adult female felids will meet and stay together is strongly related to the probability of sharing food resources, commonly a kill. The detailed procedure to estimate the probability of sharing a kill is described in the Appendix 6.1.

Table 6.1 summarises the available data which we use to parameterise rates of intake from carcasses which are or are not shared (equations 8 & 9 in Appendix 6.1). Adult female population density is shown as animals per 100 km². For cheetah in the Serengeti, we use the actual population density of

Table 6.1. Relative prey size (w_i/x_i), population density (n_i adult female/100 km²), day-range (r_i km), prey capture rate per day (h_i), maximum prey consuming rate per day (y_i/x_i) and habitat type with possible survey distance (z_i km) of feline species. See Appendix 6.1 for details.

Species	w_i/x_i	n_i	r_i	h_i	y_i/x_i	Habitat (z_i)
(1) Lion	1.51	7.9	4.8	0.09*	0.20	Savannah (3.0)
(2) Tiger	0.49	2.5	6.5	0.12	0.20	Forest (0.5)
(3) Jaguar	0.63	1.2	6.3	0.10	0.20	Forest (0.5)
(4) Leopard	0.83	8.1	7.2	0.14	0.20	Open woodland (1.0)
(5) Cheetah	0.30	18.8	6.6	0.50	0.20	Grassland (3.0)
(6) Cougar	1.70	1.93	7.2	0.08	0.20	Woodland (0.5)
(7) Lynx	0.11	4.16	9.4	1.00	0.08	Woodland (0.25)
(8) Bobcat	0.42	2.86	4.2	0.25	0.08	Dry scrub (1.5)
(9) Solitary cat	0.03	20.8	2.6	2.00	0.08	Grass-wood (0.5)
(10) Group cat	1.82	2000	0.6	1**	0.08	Farm (0.5)

*Not the prey capture rate of a pride.

**Fed once a day.

(1) Serengeti: Schaller 1972; (2) Chitawan: Sunquist 1981, (3) Pantanal (Brazil): Crawshaw & Quigley 1991, Jorgenson & Redford 1993; (4) Kruger: Bailey 1993; (5) Serengeti: Schaller 1972, Caro 1994, Laurenson 1994; (6) Idaho: Hornocker 1970, Seidensticker *et al.* 1973; (7) Cape Breton (Nova Scotia): Parker *et al.* 1983; (8) Idaho: Bailey 1974; (9) Orongorongo Valley (New Zealand): Fitzgerald & Karl 1979 & 1986; (10) Oxford: Kerby 1987. The following references were also used to estimate the missing values: Packer 1986, Rabinowitz & Nottingham 1986, Caro 1989, Powers *et al.* 1989, Wrangham *et al.* (1993).

adult females in female-rich areas. They follow rich patches of migratory prey (mainly Thomson's gazelle) and are observed at higher density than would be expected from their total population (Caro, 1994). We also use observed daily travel distances (r_p , not the linear bee-line distance between daily fixes). The minimum amount of meat which a latecomer can expect to share when it arrives at a carcass is zero, and because we are considering only a mother and her independent daughter, the maximum number of individuals to encounter per unit time is one. The results of the calculations are shown in Figure 6.1.

Probability of group-living

When there is no food loss to other animals the intake rate per body weight from an unshared kill per unit time is greater than that from a shared kill ($Q_i' > Q_i$, see Appendix 6.1 for details). Therefore, even considering the costs of hunting for herself, it may be advantageous for an individual animal to hunt alone and, more importantly, eat alone rather than try to find

another female's kill. The arrows in Figure 6.1 indicate the daily requirement of meat (edible parts of prey) per kilogram of body weight for an adult female of these species (y_i'/x_i). It is obvious from Figure 6.1 that, in so far as our assumptions are valid, most of these species cannot rely heavily on another individual for their food. Indeed, the graph suggests that only lions have the potential to fulfil their daily food requirement by feeding entirely on another female's prey. Similarly, when a rich food source is available, it is more than enough to feed several domestic cats.

For lions, in this exercise we have used data for females which already live in groups. Clearly, this might be inappropriate for the hypothetical conditions under which female lions live solitarily. However, as Packer (1986) suggested, high lion density may be a prerequisite for sociality, rather than its consequence. Furthermore, single females can kill an adult wildebeest (150–200 kg) or an adult zebra (c. 300 kg) (Schaller, 1972). It therefore seemed sensible to use data from pride females in our analysis of prey-sharing between two hypothetical solitary females.

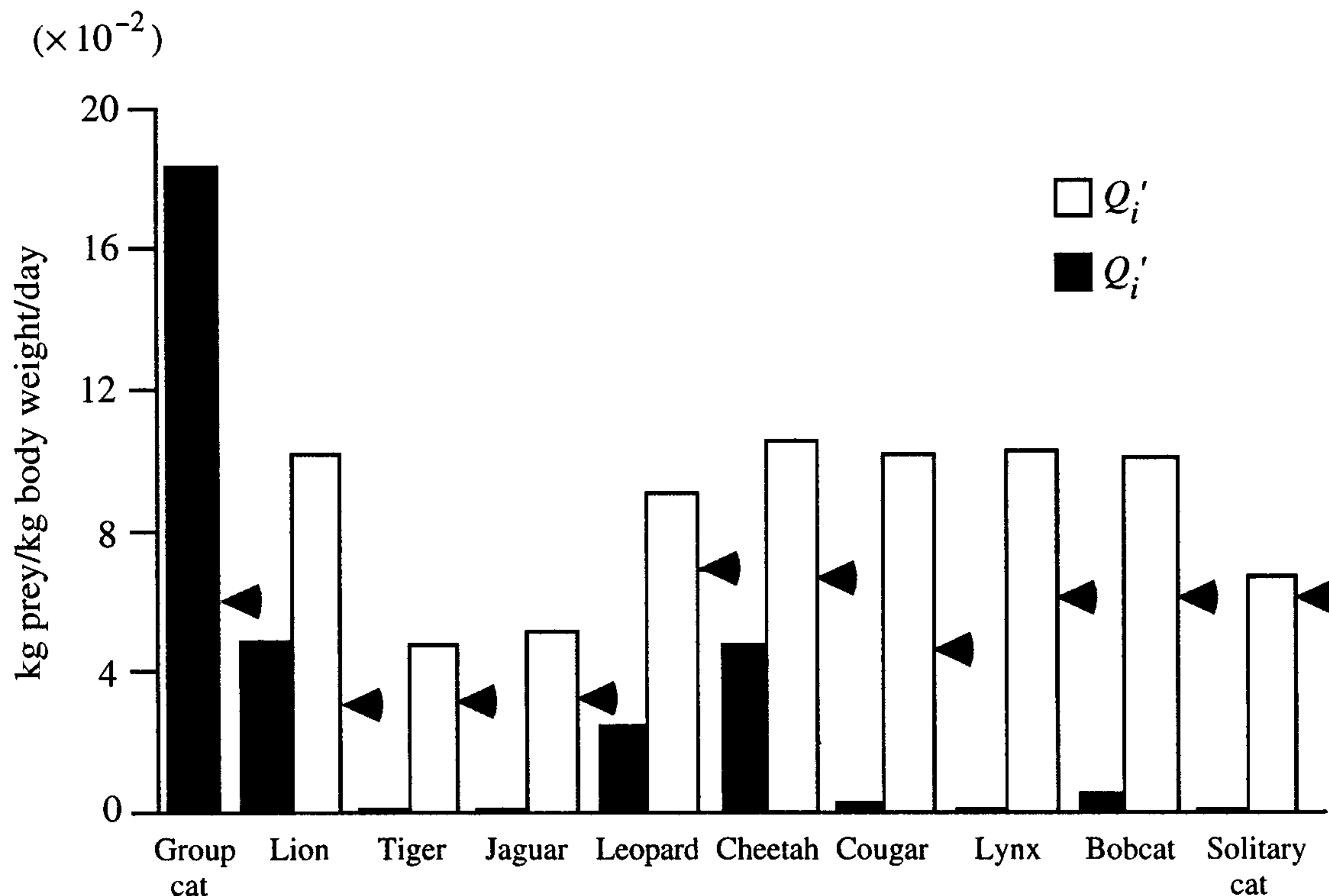


Figure 6.1. Expected daily intake of food (edible parts of prey) per kg of body weight. The Q_i is by sharing the kill made by another female and the Q_i' is by hunt-and-eat-alone tactics. The arrows indicate the daily food requirement of each species.

For simplicity, we have assumed that the loss to competitors or scavengers was nil. However, Cooper (1991) estimated that almost 20 per cent of the edible components of lions' prey was lost to spotted hyaenas, *Crocuta crocuta*, if no adult male was present. Caro (1994) estimated that approximately 9 per cent of the edible parts of male cheetahs' prey was lost to spotted hyaenas. These figures may push the hypothetical solitary felids towards communal feeding if the sociality increased their capacity to resist scavengers at the kill.

When would solitary felids live in groups?

Domestic cats living on wild prey such as rabbits, *Oryctolagus cuniculus*, and rodents, tend to be solitary and do not form groups despite substantial home range overlap (Corbett, 1979; Jones & Coman, 1982; Apps, 1983; Konecny, 1983; Fitzgerald & Karl, 1986). In contrast, domestic cats with access to clumped food resources live in groups (Kerby & Macdonald, 1988; Liberg & Sandell, 1988). This prompts the question of whether other feline species would also form groups if their food intake rate per body weight from a shared kill per unit time (Q_i) fulfilled the conditions that allow lion and domestic cat to do so. Field studies, ideally manipulative ones, could answer this question.

Social organisation of group-living domestic cats

Early studies of free-ranging domestic cats tended to consider concentrations of cats around resource centres as aggregations rather than social structures (Laundré, 1977). Subsequently, it became clear that the behaviour of individuals in these colonies is far from socially random (Macdonald *et al.*, 1987; Kerby & Macdonald, 1988). Cats choose to sit together, and each individual favours the company of some over others. These associations are largely governed by the age, sex, social status and blood ties of the individuals involved (Macdonald *et al.*, 1987; Kerby & Macdonald, 1988; Liberg & Sandell, 1988).

A detailed description of our study colonies and methods is found in Kerby (1987), Macdonald *et al.* (1987), Kerby & Macdonald (1988) and Yamaguchi *et al.* (1996). From these, we present a comparison of three different sized colonies of free-ranging cats: small, medium and large. The small colony had

between four and nine adult cats. In the medium colony between seven and 11 adults were observed and in the large colony between 16 and 25 adults were observed. In total, approximately 3,000 hours of observation with data on over 63,000 interactions and 59,000 measurements of proximity were recorded within these colonies (Macdonald & Apps, 1978; Kerby, 1987).

The detailed dynamics of social interactions between individual adults were most usefully elucidated in the small colony (see Macdonald *et al.*, 1987; Kerby & Macdonald, 1988). On the other hand, quantitative analysis of the social interactions on the basis of sex, age, social status and kinship was more feasible on the basis of the data collected in our larger colonies. These results are abstracted from the publications cited above and additional analyses which we will report fully elsewhere. When we refer to a result as statistically significant this indicates a probability of <0.05 that it occurred by chance; unless specified otherwise, the statistical test was Wilcoxon Signed Rank test.

Social organisation of cats living in groups

Where once the salient image of the domestic cat was as one who walks alone, our studies of farm cats reveal complex social relationships. For example, early in our cat studies, our thinking was influenced by the following observation. A piebald female lay down in her nest of straw bales to give birth to three kittens. Some 18 days later, with the kittens flourishing, a second cat squeezed through the entrance to the nest. The newcomer greeted her piebald sister, and she too went into labour. Tightly cramped on a squirming bed of kittens, the newcomer rolled over to expose her underside and her sister licked at her vulva, even as the first kitten emerged. It was the piebald sister, not the mother, who licked the newborn kittens clean, and it was she who chewed the membranes and bit through the umbilicus. The second female bore five kittens that day, and each was largely 'delivered' by her sister. Thereafter, the two females groomed and nursed each other's kittens indiscriminately, and continued to do so over the following days. Since that first observation by Macdonald & Apps (1978), we have found communal breeding to be unexceptional amongst farm cats.

Adult females associate in lineages which are the building blocks of cat society. Large colonies embrace

several such lineages, each of which usually consists of related adult females and successive generations of their offspring. Females frequently interact within their lineage, and to a much lesser extent outside it. The overall pattern within a lineage of cats is of a well-integrated, amicable group. This is in marked contrast to the hostility with which members of such lineages generally treat outsiders. Bigger lineages tend to occupy the best 'Central' area around the resource centre. Smaller lineages tend to be spatially 'Peripheral', but nonetheless have access to the 'Central' area to feed. We refer to these categories as Central and Peripheral females (Kerby 1987).

Adult males do not seem to be socially tied to any particular lineage, but can again be distinguished as those which are observed around the 'Central' resource centre frequently, and those which are not. The latter roam widely. Therefore, we distinguish 'Central males' and 'Peripheral males', although this distinction does not have the same genealogical implications of these adjectives as when applied to females. Juveniles and kittens automatically belong socially to their mother's lineages. Offspring of Central lineages can access the resource centre easily and suffer lower mortality than do those of Peripheral lineages (Kerby & Macdonald, 1988).

Is it possible to make generalisations about social relationships within a group?

Because people are familiar with pet cats, it is widely recognised that each individual exhibits a particular behavioural character. These character traits permeate each cat's social relationships. Such individual variation may or may not be adaptive, and it strikes us as plausible that it exists also in wild carnivore societies (although rarely documented). The social dynamics of the group differed between our colonies, and some of these differences may reveal characteristics typical of large, medium and small colonies. Here, however, we present some generalisations that may describe some aspects of farm cat society. Of course generalisations, by definition, miss important detail and exception; in this case, our data on the proximity maintained between cats were gathered *ad libitum* and therefore do not represent a sample stratified by, for example, activity or location. They therefore do not distinguish differences that may exist between, for example, instances when the cats were or were not feeding: such distinctions might be very revealing: it is

quite plausible that cats prefer their own lineage members while eating, but other lineages for mating – a possibility illustrated by Ethiopian wolves, *Canis simensis* (Sillero-Zubiri, Cottelli & Macdonald, 1996). However, our account of cat proximities is based on a coarser resolution, and similar caveats apply to other categories of data, such as behavioural interactions.

Social dynamics

In our small colony there were only two lineages and one adult male. Adult females from different lineages were seldom observed within 10 metres of each other, whereas Central lineage members were within this distance of other Central lineage members for an average of $24.5 \pm 1.91\%$ (mean \pm standard error) of the occasions when they were at the resource centre, compared to only $0.51 \pm 0.20\%$ within 10 m of Peripheral lineage members. However, the larger colonies embraced many lineages and the resource centres were crowded, and we could detect no effect of lineage on nearest neighbour until cats were closer together, at around 5 m, within which they again preferred their own lineage members to others.

The nature of interactions between two cats can be summarised by their type, rate and prevailing direction from initiator to recipient (asymmetry). Figure 6.2 summarises these three measurements for the Central lineage members (SM, DO and PI) and the adult male (TM) present in our small colony. As the figure shows, the rates of different types of interaction varied between pairs of cats. For example, neither female was ever seen to be aggressive to TM although he was quite often so to them. Furthermore, the magnitude of asymmetry in the direction of interactions differed not only between cats, but also between behavioural categories for given pairs of cats. In general, in the small colony where there were only two lineages and one adult male, the relationships between individuals were rather simple and clear cut. On the other hand, it was not easy to find such clear cut relationships in larger colonies, perhaps because relationships among individuals became more complicated as colony size increased as well as because of the different demographic and environmental circumstances.

Table 6.2 indicates that in both colonies, adult males were not particularly interactive with kittens regardless of the colony sizes. However, there is an interesting difference in adult male behaviour

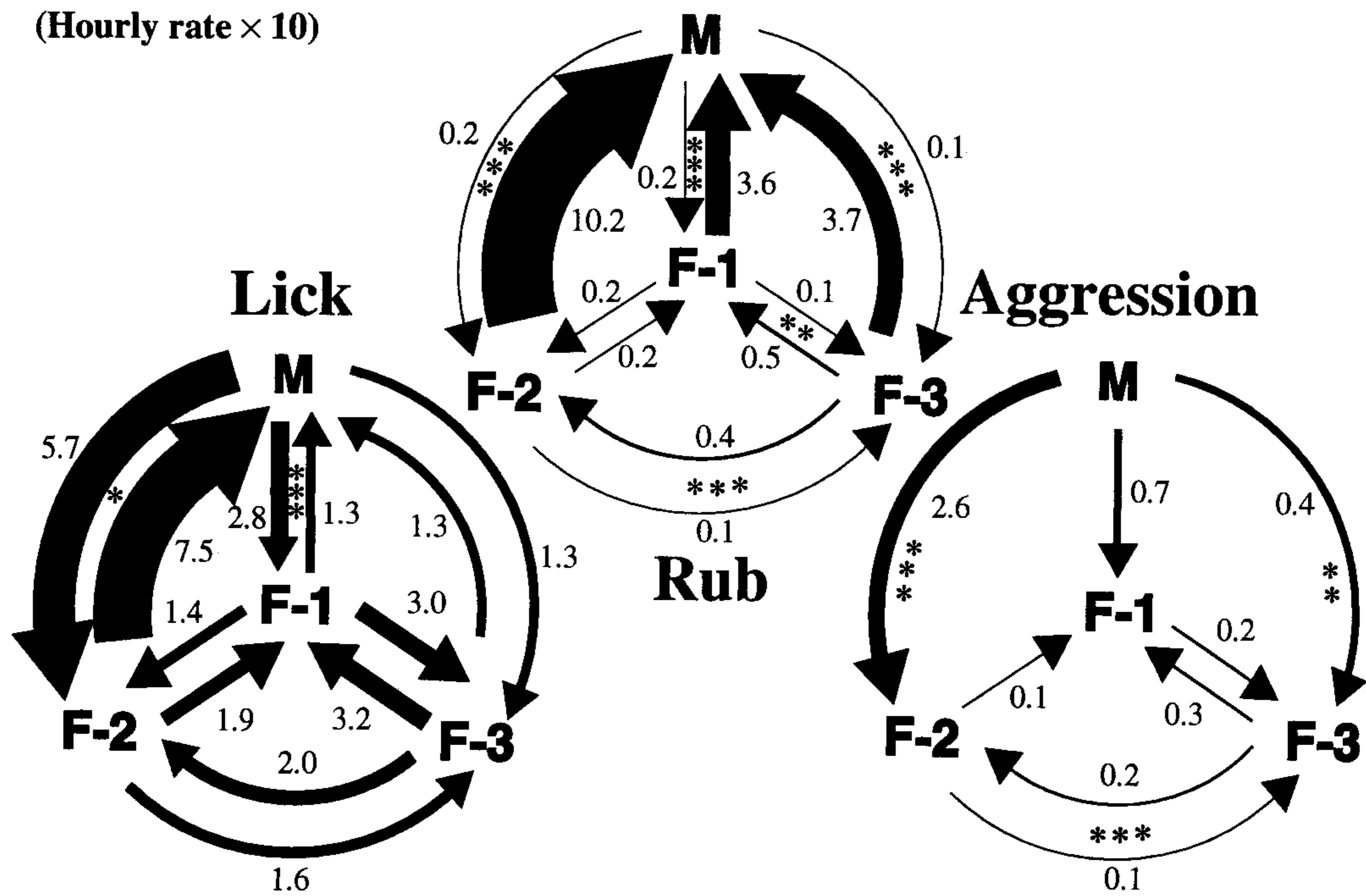


Figure 6.2. Sociograms of the relationships between adult cats at the small colony when the colony members were an adult male, TM, an adult female, SM, and her two adult daughters, PI and DO. Numbers are hourly rates (× 10) of initiation of the behaviours from one cat to another whilst the pair was observed around the resource centre together. The asterisks indicate the statistical significance of the asymmetry of flow between each pair detected by chi-squared tests (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Table 6.2. Interaction partner preferences for adult males at the medium and the large colonies

Behaviour	Colony	Age-sex classes					
		AM	AF	JM	JF	KM	KF
All combined	Large	a	a	a	ab	b	b
	Medium	b	b	a	ab	c	c
Aggressive	Large	a	b	b	c	c	c
	Medium	ab	abc	a	abc	bc	c

Within each behaviour category, age-sex classes with the different letter differ significantly in their frequency as interaction partners (Mann-Whitney U -test with significant level $p < 0.05$). Categories denoted 'a' are most preferred, whilst those denoted 'c' are least preferred interaction partners to which adult males initiated the behaviour. AM, adult male; AF, adult female; JM, juvenile male; JF, juvenile female; KM, kitten male; KF, kitten female.

between the two colonies. In the large colony they initiated aggressive behaviour towards other adult males more than towards any other age-sex classes. On the other hand, in the medium colony, they did so to juvenile males. Possible explanations for this can-

not be offered unless the difference of colony demography is understood. In the large colony the ratio of adult males:adult females was 1:1.58 and the adult male:juvenile male ratio was 1:0.44. However, in the medium colony adult male:female ratio was 1:0.78

and adult male:juvenile male ratio was 1:0.59. Under circumstances where females are fewer and numerous juvenile males may be potential challengers to adult males, adult males may prolong the juveniles' subordination by heightened aggression towards them.

The main lesson from these comparisons is that the social dynamics of cat groups may differ with circumstances. Further aspects of this were detailed by Kerby & Macdonald (1987). Here, however, we offer some tentative generalisations.

Adult females: core of the society

In our three study colonies, Central lineages comprised more adult females (1–5, mode 3), than did Peripheral lineages (1–2, mode 1). Central females spent more time (*c.* 70 per cent of all scans) around resource centres than did the Peripheral lineages (*c.* 30 per cent). Closer kin were tolerated at closer proximity (Figure 6.3). Van Den Bos & De Cock Buning (1994) propose the reasonable (although clearly not inviolable) generalisation that the closer two cats were, the more affiliated they were. A methodological caveat in the case of our study is that recording one individual as the nearest neighbour of the target cat does not exclude the possibility that several other cats

were also within the vicinity. Nonetheless, explicitly adopting the foregoing assumption, one might use a tendency to close proximity between a pair of cats as an indicator, by proxy, of a strong social tie between them. If so, then this evidence may suggest stronger social ties among closely related adult females compared with those among less closely related adult females. Central females shared the central nest zone (close to the resource centre) and achieved higher reproductive success than did the Peripheral females (Kerby 1987). In the large colony, the overall reproductive success of the Central lineage was 1.55 ± 0.55 (weaned kittens per female per year) which was significantly greater than that (0.42 ± 0.10) of the Peripherals (one-tailed Mann–Whitney *U*-test). Communal kitten care was recorded in 25 to 70 per cent of observed occasions of rearing kittens, and generally involved lineage members.

Lineages may split. In the large colony, after the death of female '62', the matriarch of the most successful Central lineage, her eldest adult daughter '68' became significantly more aggressive to some of her kin. Disentangling the effects of age on changing relationships is difficult; for example, in this case three of female 68's female kin were adult (80, 81, 91) at the time of her mother's death whereas two (94, 96) became adult later. Nonetheless, during the ensuing two years, and considering only those periods for which the recipient females were adult, female 68 appeared to be more aggressive to her two younger adult half-sisters '81' and '91' than to her other half-sister '80' and to her own two daughters '94' and '96' (Figure 6.4). This is only one lineage and hence not a basis for generalisation in detail, but the point we wish to make is that female '68' had different qualities of relationship within her female kin, with the possible consequence of influencing which ones were more likely eventually to move away from the lineage socially and spatially. Since resource centres are likely to be occupied, such females are likely to be peripheralised and, ultimately, to suffer poor reproductive success. In analysing data such as those summarised in Figure 6.4 an obvious caveat is that one must beware of relationships changing within the study period (for example, perhaps following the death of female 62). In this particular case, the data stem from interactions logged over two years during which female 68 remained the most aggressive female and the distribution of her aggressive interactions was similar in both years.

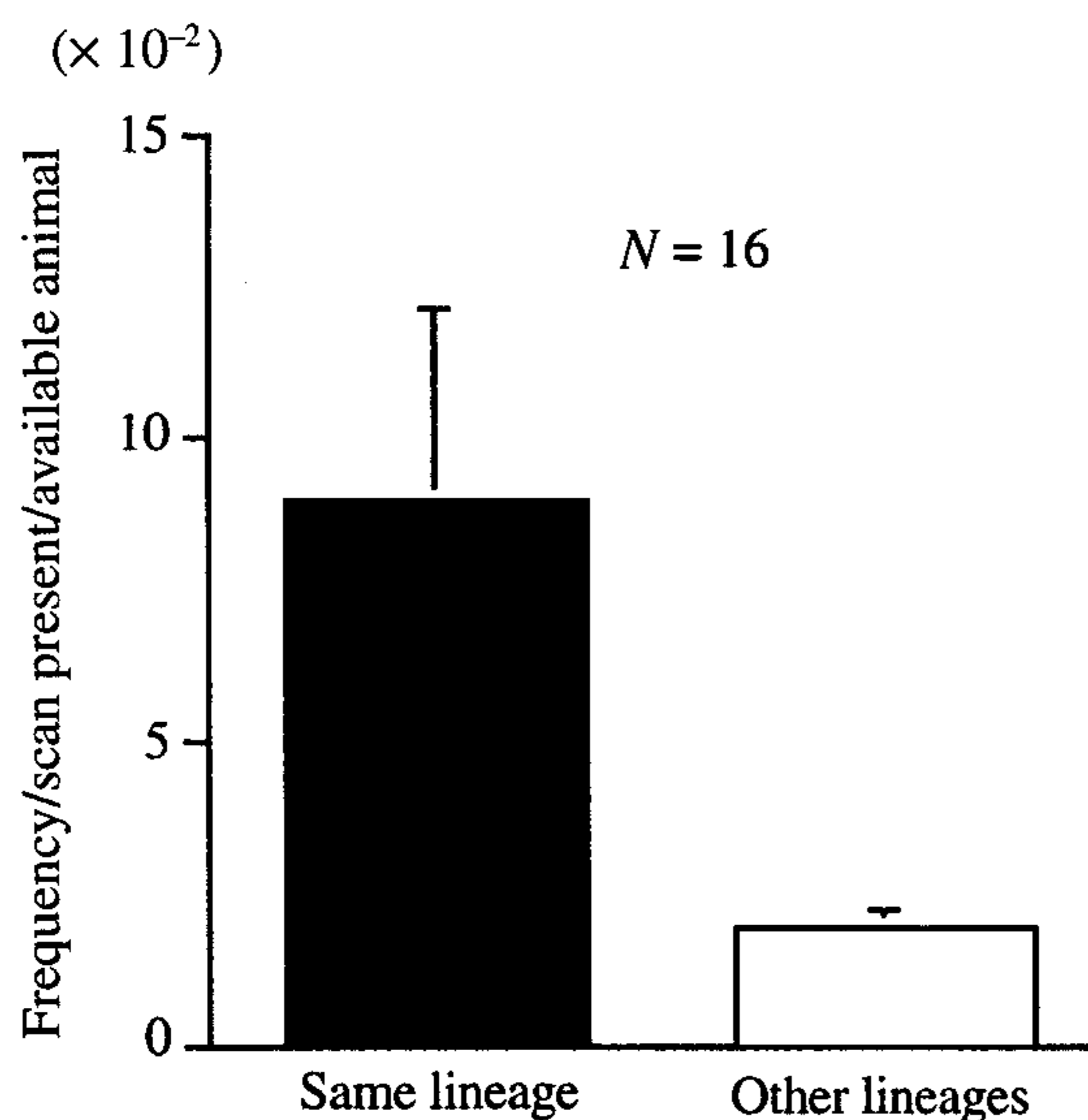


Figure 6.3. The frequency that an average adult female was within 5 m of another adult female. Values were corrected for availability and are derived from regular scans of all animals present. A nearest neighbour was allocated for each animal and the distance between them was recorded. Each column represents the mean and each bar represents the standard error.

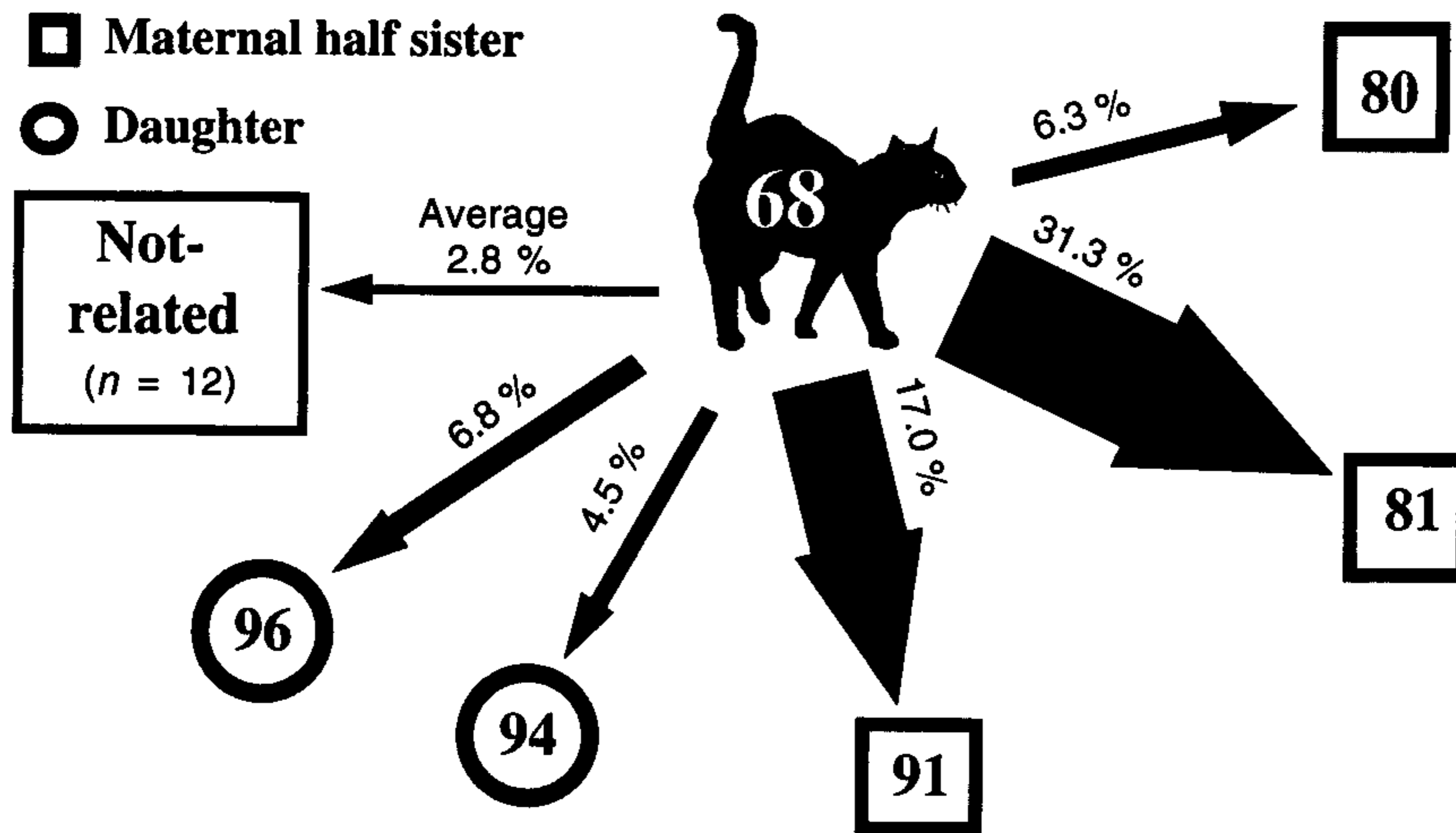


Figure 6.4. Aggressive behaviour of female 68 ($n = 158$) towards other adult females in her lineage. Data were collected during two year period following female 62's death.

Adult males: to stay or not to stay

Like adult male lions, adult male cats also seem to be attached to female lineages only temporarily. Nonetheless, while they are present, males may be a focus of attention. In the small colony, the only adult male often had one of the three Central lineage females within 10 m (c. 40 per cent of occasions when he was at the resource centre, in contrast, each female had another female within 10 m on only c. 25 per cent of such occasions). The alluring effect of the male was obvious.

By definition, Peripheral males spent less time around the resource centre (c. 15 per cent of all scans), than did Central males (c. 60 per cent). However, in the large colony, Peripheral males were nonetheless highly interactive when they were around the resource centre. They scent-marked and mate-called frequently, and were highly sexually active and overtly aggressive. Central males were less interactive, showed closer proximity to other cats, rarely scent-marked or mate-called and only occasionally attempted to mate. Central males tended to persecute younger males, but, were defensive rather than offensive when threatened by Peripheral males (Kerby, 1987). Therefore, it may be that Peripheral males are reproductively more successful. However, in the medium colony, comprised of proportionally fewer females and more juvenile males, the Central males' behavioural patterns were rather similar to those of the Peripheral males in the large colony. Half the young males recruited into the medium and the large colonies became Central and the other half became Peripheral. The consequences of these generalisations for farm cat society await a detailed paternity study.

Juveniles and kittens

Both juveniles and kittens seemed to become socially integrated to their natal lineage automatically. Male juveniles' social ties (where these are indicated by patterns of proximity, see above) are significantly stronger with their male littermates than with their (at least) maternal half-brothers of different ages (Figure 6.5). They also significantly preferred (i.e. maintained proximity to) related male juveniles in comparison to related male kittens. Similarly, male kittens significantly preferred their male littermates to their older brothers (Figure 6.6). They also significantly preferred related male kittens to related male juveniles. Similarly, female kittens significantly preferred their female littermates to their older sisters (Figure 6.7). Kittens maintained stronger ties with related kittens than with related juveniles and vice versa. In this context, Bradshaw & Hall (1999) also suggest that ties established during the socialisation period are likely to endure throughout life if the cats remain in company.

Although farm cats and lions are unusual amongst the Felidae in sharing the trait of forming multi-female, multi-male groups united by close proximity and frequent interaction, there are differences in character between the societies of the two species. In lion society, females usually stay in their natal pride but young males disperse at two to four years of age, often with their cohort mates of similar age (Pusey & Packer, 1987). Subsequently, these males form a coalition to take over a different pride and thereby obtain exclusive access to the females. No such male coalition has been reported in domestic cat society.

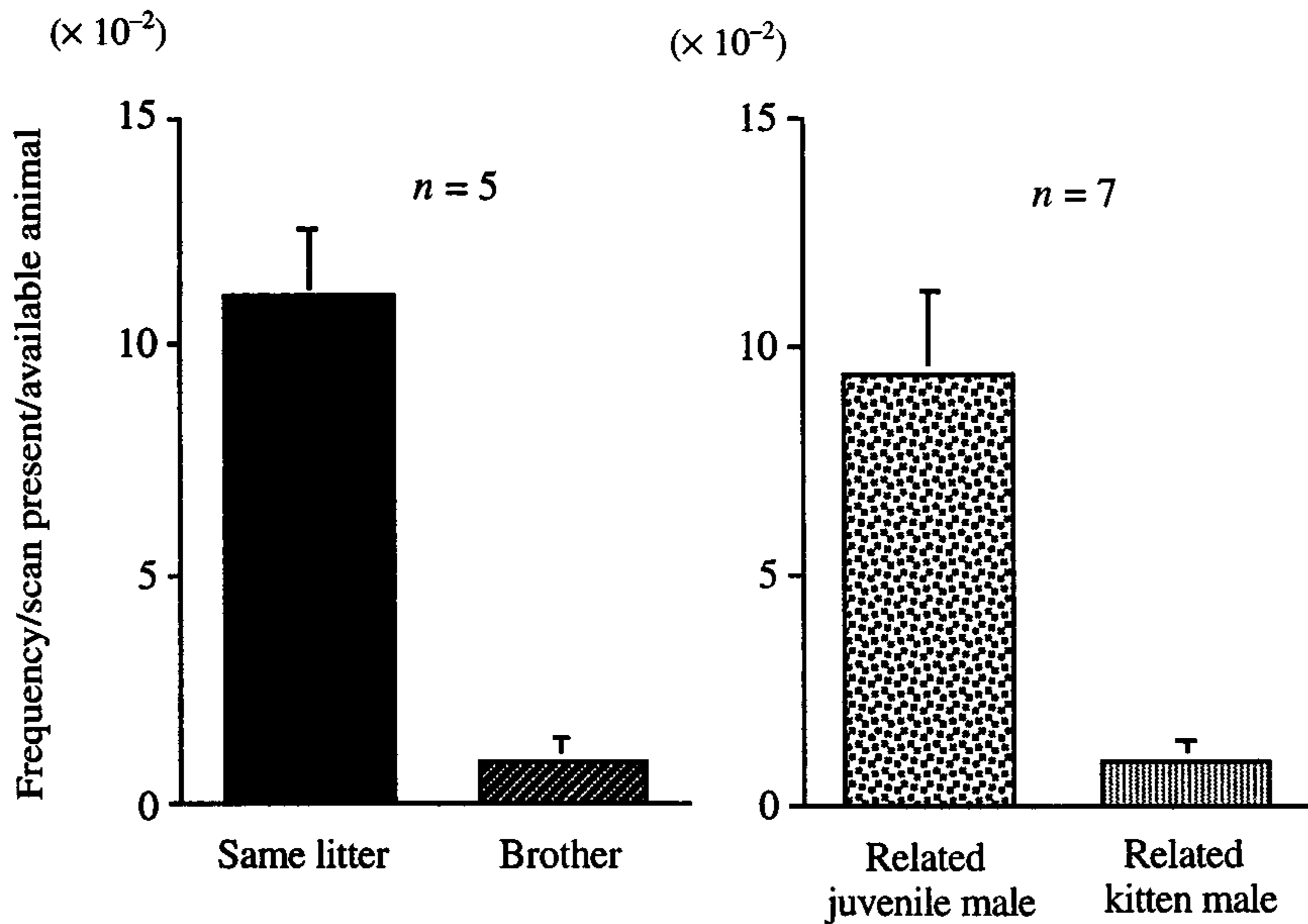


Figure 6.5. The frequency that an average juvenile male was within 5 m of a same-litter male sibling, different-litter sibling (at least maternal half-brother), related juvenile male and related kitten male. Values were corrected for availability and are derived from regular scans of all animals present. A nearest neighbour was allocated for each animal and the distance between them was recorded. Each column represents the mean and each bar represents the standard error.

However, our results may indicate strong ties between young male contemporaries of similar age, which then disperse separately. This prompts the interesting question of whether such affiliations would apply for same-sex littermates throughout the Felidae; our results reveal that despite ample opportunity for potential same-sex liaisons between immature males of different ages, the observed spatial ties were amongst those of similar ages (i.e. between kittens, or between juveniles but not between kittens and juveniles). If this result from farm cats does apply across the felids it would strengthen our suspicion that solitary felids are 'pre-adapted' to develop male coalitions. In this sense, the rudiments of lion society may be apparent in groups of domestic cats and, perhaps, also in the social behaviour of other small felids. The fact that male coalitions have apparently not arisen amongst farm cats is presumably attributable to differences between the ecology of cats and lions in such factors as the size, dispersion and defendability of females and of prey.

Mother-kitten relationship

The spatial ties of adult females to their own sons/daughters are significantly stronger than those to their nephews/nieces (Figure 6.8). Indeed, there was no evidence that they discriminated the latter from unrelated kittens. Female lions can distinguish their own offspring from other related cubs in a crèche, and the cubs can distinguish their own mother from other

related lionesses (Pusey & Packer, 1994). It is unsurprising that amongst our cat colonies there were strong spatial ties between females and their own offspring, and in the laboratory kittens of up to ten weeks of age approach their mother more than she approaches them (Deag, Manning & Lawrence, 1988; see also Chapter 3).

The domestic cat descended from the solitary African wildcat approximately 4,000 years ago (Serpell, 1988; see also Chapter 9). This is an exceedingly short time in terms of their molecular evolution, and represents a time scale on which substantial differentiation might not normally be expected. In contrast, lion and leopard diverged from a presumably solitary ancestor approximately one million years ago (Janczewski *et al.*, 1995). It may be helpful to draw a loose parallel with species of closely related bird that are either colonial or non-colonial: Beecher (1991) reported that parent-offspring recognition was well developed in the colonial birds, but absent or weak in the non-colonial ones. For non-colonial animals, a good operational assumption may be that all young in a female's den are her own, a rule which would not hold in colonial species. Perhaps the more long-standing sociality of lions might have involved selection for more finely tuned kin recognition (Pusey & Packer, 1994). The parallel with non-colonial birds, although perhaps flawed in that most mammals have acute olfactory abilities, nonetheless raises the interesting observation that despite millions of years of presumed solitary parenthood, female domestic cats

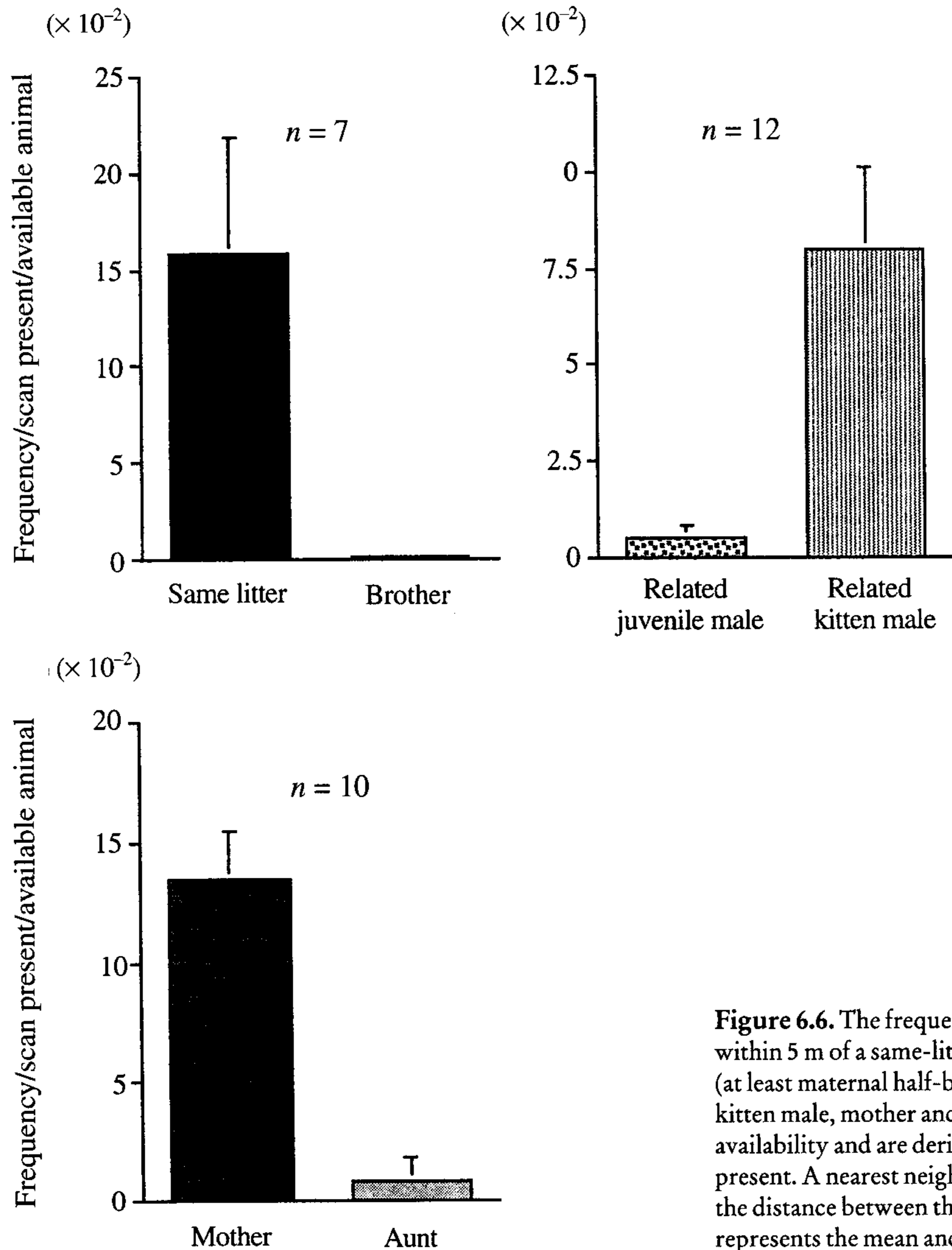


Figure 6.6. The frequency that an average kitten male was within 5 m of a same-litter male sibling, different-litter sibling (at least maternal half-brother), related juvenile male, related kitten male, mother and aunt. Values were corrected for availability and are derived from regular scans of all animals present. A nearest neighbour was allocated for each animal and the distance between them was recorded. Each column represents the mean and each bar represents the standard error.

are demonstrably able to recognise their own kittens. One might also speculate that the considerable extent to which lion prides, like domestic cat groups, are comprised of relatives, might have diminished any such selection compared with affected species which breed in a colony consisting of many unrelated individuals.

Health status and epidemiology in group-living cat society

Domestic cats are susceptible to a number of micro- and macro-parasites, many of which are pathogenic (Dubey, 1973; Nichol, Ball & Snow, 1981; Parsons, 1987; Hosie, Robertson & Jarrett, 1989; August, 1994;

Chandler, Gaskell & Gaskell, 1994). Numerous parasites of domestic cats also affect humans, livestock and wild carnivores (Chandler *et al.*, 1994), and have implications for both medical research and wildlife management as well as the welfare of their host. As the cat has become one of the most popular companion animals, feline medicine has been studied extensively in the laboratory (August, 1994; Chandler *et al.*, 1994). In the last ten years or so, there have been two important events concerning feline epidemiology. One was the isolation of feline immunodeficiency virus (FIV) which causes feline acquired immunodeficiency syndrome (FAIDS), similar to AIDS in humans caused by human immunodeficiency virus (HIV) (Pedersen *et al.*, 1987). The second was an

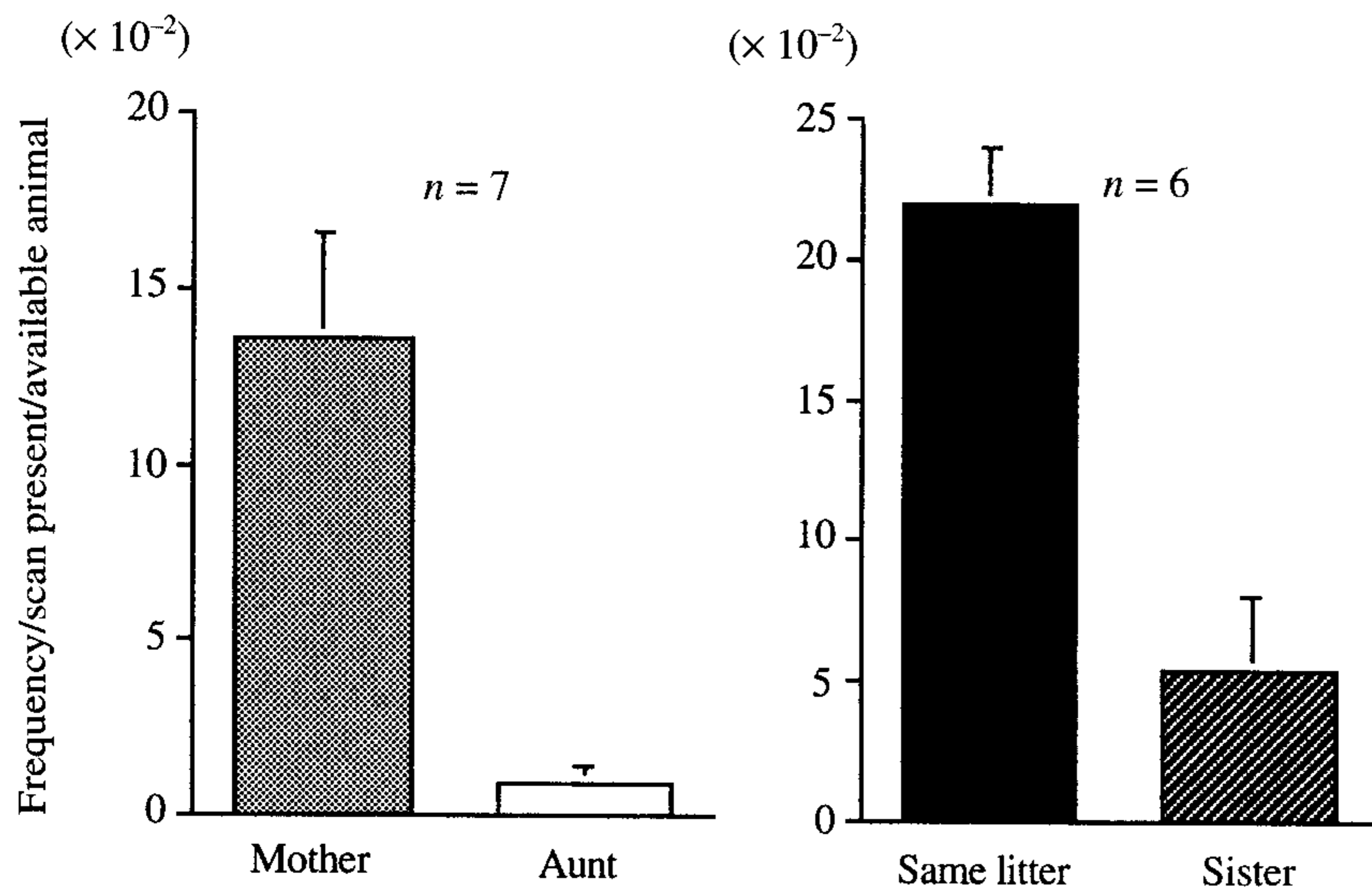


Figure 6.7. The frequency that an average kitten female was within 5 m of a same-litter female sibling (same litter), different-litter sibling (at least maternal half-sister), mother and aunt. Values were corrected for availability and are derived from regular scans of all animals present. A nearest neighbour was allocated for each animal and the distance between them was recorded. Each column represents the mean and each bar represents the standard error.

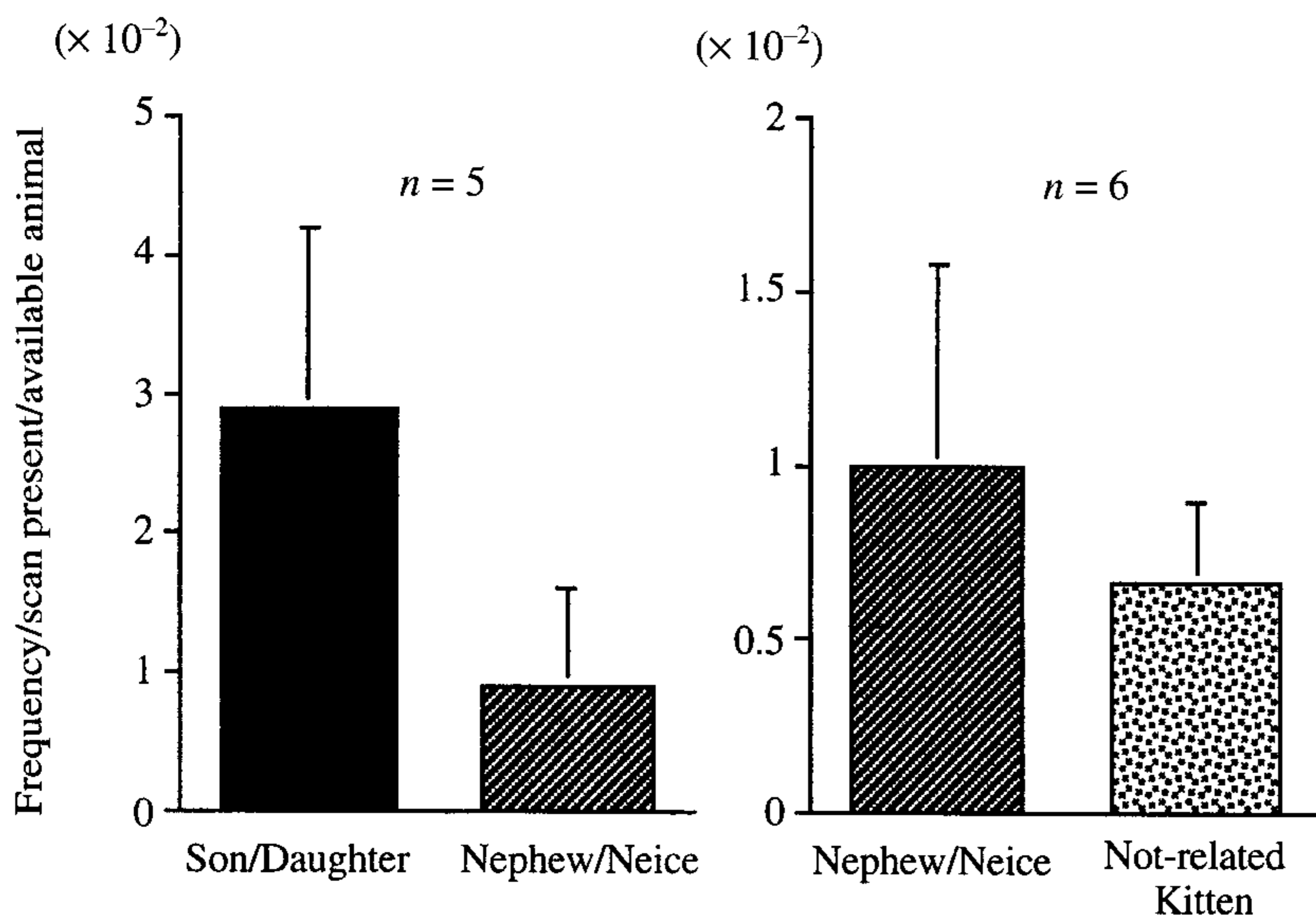


Figure 6.8. The frequency that an average adult female was within 5 m of a son/daughter, nephew/niece and unrelated kitten. Values were corrected for availability and are derived from regular scans of all animals present. A nearest neighbour was allocated for each animal and the distance between them was recorded. Each column represents the mean and each bar represents the standard error.

outbreak of canine distemper virus in Serengeti lions which killed an estimated 30 per cent of the population (Harder *et al.*, 1995). Following these, cat epidemiology has been highlighted as a major issue not only in medical research, but also in the conservation of wild felids (Mochizuki *et al.*, 1990; McOrist *et al.*, 1991; Roelke *et al.*, 1993; Carpenter & O'Brien, 1995; Roelke-Parker *et al.*, 1996; Daniels, 1997; Van de Woude, O'Brien & Hoover, 1997; Daniels *et al.*, 1999). The contention of this chapter is that domestic cat populations exhibit wide variability in their spatial and social organisation, on a spectrum from solitary, low population density to social, high population density. We argue, therefore, that domestic cats in

populations of contrasting organisation offer useful, and contrasting, models of socio-epidemiology for the whole spectrum of wild felid populations. Nevertheless, little is known about epidemiology in free-ranging cats (Yamaguchi *et al.*, 1996; Macdonald *et al.*, 1998).

To investigate the relationships among social factors, individual health and epidemiology in free-ranging cats, we studied a fourth very large colony of 50 to 80 individuals. The details of our methodology are described in Yamaguchi *et al.* (1996) and Macdonald *et al.* (1998). We assessed the health of each individual on the basis of veterinary examination and 14 haematological parameters, and a further 14

measures of blood biochemistry. For epidemiology, blood, mucus and faecal samples were tested for the following pathogens: feline rotavirus (FRoV), feline immunodeficiency virus (FIV), feline leukaemia virus (FeLV), feline herpesvirus 1 (FHV), feline calicivirus (FCV), feline coronavirus (FCoV), feline parvovirus (FPV), cowpox virus (CPoV), *Haemobartonella felis*, *Chlamydia psittaci*, *Toxocara cati*, *Toxascaris leonina*, *Toxoplasma gondii*.

Difference of health condition in relation to sex, age and social status

In our study colony a significantly greater proportion of adult females (81%) than adult males (47%) was clinically normal (chi-squared test: $p < 0.05$), in parallel with findings for the Serengeti cheetah (Caro *et al.*, 1987). While there were few links between sex-age class and individual health, there were strong relations between health and social status. For example, Central females had significantly less gingivitis (Mann-Whitney U -test: $p < 0.01$) and ulceration of the mouth (Mann-Whitney U -test: $p < 0.05$) than did Peripheral females. Peripheral females had significantly higher numbers of eosinophils (unpaired t -test: $p < 0.05$) than did Central females. This eosinophilia might be related to a greater incidence of intestinal nematode infestation (Hawkey & Hart, 1986) in the Peripheral females. Unlike females, there were no significant differences in health condition between Central and Peripheral males.

As we discussed above in the context of lineages, no link between adult female age and Central versus Peripheral status was found (the important determinant of a female's social status was her mother's lineage); therefore the explanation for differences in these findings between Central and Peripheral females may lie in their sociobiology. Although we do not have the longitudinal data to distinguish cause and effect in any relationship between status and health, we can at least conclude that the significant differences in health between Central and Peripheral females are corollaries of social status.

In general in mammalian society a female's most important resources are food and shelter. In large outdoor enclosures, most females relocated their nests closer to food sources as litters approached weaning (Feldman, 1993). The importance of easy access to resources for a female's reproductive success and survival is clear. Where resources are concentrated in

a central area, Central status close to the resource centre is likely to be more advantageous than Peripheral status, and, therefore is probably associated with better health.

On the other hand, to males, females are generally the limiting resources. Hence, Peripheral status has different implications for males and females. Amongst females, Peripheral individuals are essentially subordinate outcasts, whereas, as discussed above, Peripheral males are arguably the most reproductively active and dominant individuals, although any differential in reproductive success between Central and Peripheral males is unknown. This summary is in sharp contrast to the discovery made by Caro, Fitzgibbon & Holt (1989) in the Serengeti, where nomadic male cheetahs were in poor health compared with resident males. Resident male cheetahs are thought to be dominant and reproductively more successful than the nomadic ones (Caro *et al.*, 1989), perhaps analogous to the Peripheral males in our cat colonies. A nomadic life, roaming widely, might seem physically more demanding than a resident life. Two counteracting forces may therefore be at work amongst male domestic cats: the most dominant, healthiest individuals may be most likely to adopt nomadism, and thereby face the most debilitating lifestyle.

Pathogen prevalence in the colony

Overall, pathogens appeared to be highly prevalent in our study colony (Figure 6.9), including 100 per cent antibody prevalence for FCV, FHV and FRoV. Worldwide, feral cats have an FIV infection rate of 16% ($n = 6,818$), compared to only 5% ($n = 12,166$) for cats kept indoors, and 12% ($n = 27,166$) for household cats with outdoor access (Courchamp & Pontier, 1994). In England and Wales, 14% of 59 pet cats and 27% of 90 feral cats were positive for FIV antibody (Bennett *et al.*, 1989). In comparison with the overall rates for feral cats, our study population had a high prevalence of FIV (53%). On Marion Island, South Antarctic, FPV was artificially introduced to control feral cats, and in 1982, 83% ($n = 115$) had antibodies to the virus (Van Rensburg, Skinner & Van Aarde, 1987). Our study population had an even higher prevalence (96%) of antibodies to FPV. A great proportion of colony cats (up to 95% in some colonies) kept in catteries that had suffered mortality due to feline infectious peritonitis had antibodies to FCoV

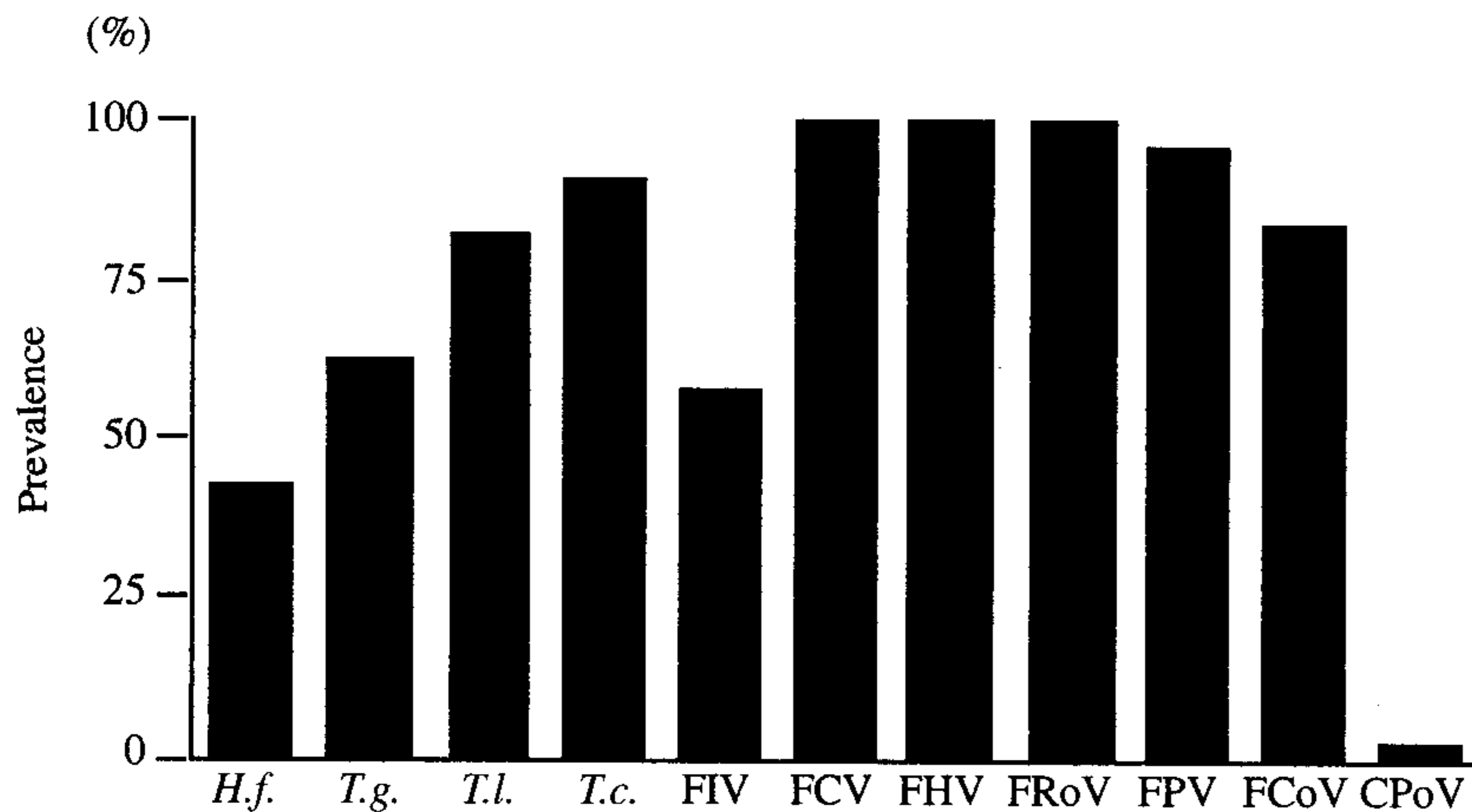


Figure 6.9. The prevalence of various parasites in a colony. *H.f.*, *H. felis*; *T.g.*, *T. gondii*; *T.l.*, *T. leonina*; *T.c.*, *T. cati*; FIV, feline immunodeficiency virus; FCV, feline calicivirus; FHV, feline herpesvirus 1; FRoV, feline rotavirus; FPV, feline parvovirus; FCoV, feline coronavirus; CPoV, cowpox virus.

(Pedersen, 1976; Stoddart & Bennett, 1994), as did up to 20% of household cats (Pedersen, 1976). Levels of FCoV in the free-ranging farm cats in our study population were almost as high as those of catteries. Levels of *T. gondii* in our study population were higher than recorded previously in the UK (45% antibody prevalence: Bennett *et al.*, 1990). The ascarid worm *T. cati* is generally the most prevalent endoparasite of cats, found in about 10% of the adult population, while *T. leonina* is found in about 5% (Nichol *et al.*, 1981). Considerably higher prevalence was found in our feral farm cat colony, with nearly all faecal samples providing evidence of infection (91% for *T. cati* and 82% for *T. leonina*).

The lack of evidence for *C. psittaci* in our study population contrasts with previous work, which recorded a high prevalence of antibodies in feral cats (69% of 36 samples) and farm cats (45% of 51 samples) in Britain (Wills & Gaskell, 1994). FeLV was also absent from our study population, whereas antibodies were previously found in 18% of 1,204 sick cats and 5% of 1,007 healthy cats in Britain (Hosie *et al.*, 1989).

Socio-epidemiology of free-ranging domestic cats

The high prevalence of pathogens among farm cats in our study colony might be associated with their use of 18 communal latrines. Pathogens that can be transmitted via excreta, such as FPV, FRoV, FCoV, *T. cati*, *T. leonina* and *T. gondii* could readily be transmitted within and between groups (Gaskell, 1994; Gaskell & Bennett, 1994b; Wright, 1994). Rats, *Rattus norvegicus*, were present, and might maintain a per-

manent reservoir of *T. gondii* for cats which preyed upon them (Webster, 1994). High rates of social interaction and close proximity between individuals around resource centres would increase transmission and prevalence of pathogens spread by direct contact or short distance aerosolisation, such as FCV, FHV, FCoV, FIV, FPV and *T. gondii* (Gaskell, 1994; Gaskell & Dawson, 1994b; Jarrett, 1994; Shelton, 1994; Wright, 1994). When feral farm cats rear young cooperatively, kittens are licked or suckled by more than one female. This may facilitate transmission through contaminated saliva or direct contact.

During the mating period high energy expenditure and social tension could make males less resistant to pathogens and more susceptible to infection (Khansari, Murgu & Faith, 1990). Peripheral males roam between groups in search of oestrous females. This tactic is likely to be energetically more costly than that of Central males which remain with a single female in a feeding group throughout most of her oestrous period. A complicating factor is that Central males tended to be younger than Peripheral males at our very large colony, but whether this is a generally true is uncertain. Wild young adult male lions (3.3–4.5 years) had significantly lower levels of serum testosterone than did old adult males (6.1–9.8 years) (Brown *et al.*, 1991) even though lions can become sexually mature at two years old (Schaller, 1972). In feral cat colonies, younger Central males may similarly differ from older Peripheral males in testosterone titres and therefore in aggression (Sapolsky, 1987). However, in contrast to females or Central males, all Peripheral males tested were positive for FIV, which is thought to be transmitted by biting (Hopper, Sparkes & Harbour, 1994). Peripheral males are likely to play an

important epidemiological role both within and between colonies.

Interestingly, age, sex and social status had no significant effects on the prevalence of any infectious pathogens tested in the colony. This may suggest that once such a pathogen is introduced into a group-living feral cat colony at high population density and with a high interaction rate, every cat, regardless of age, sex or status, is vulnerable to infection through within-group transmission. The absence of *C. psittaci* and FeLV was probably because they had simply not yet reached the colony, although we cannot exclude the possibility that they had failed to establish themselves in the colony. In this context, epidemiologically as well as genetically, dispersal may emerge as a key parameter: farm cat colonies may be large, but they may also be widely dispersed. The possibilities for transmission between colonies may therefore be restricted, whereas contact within colonies is intense. By illustrating these consequences of spatial fragmentation, farm cat colonies may offer an interesting model for epidemiological studies and for the related phenomenon of metapopulation dynamics and associated fundamental issues in conservation biology.

Group-living and the emergence of a new pathogen: the case of FIV

FIV-related lentivirus infection has been detected not only in domestic cats, but also in other wild felids (Carpenter & O'Brien, 1995). To date, however, there is little direct evidence that FIV has pathological effects in wild felids, despite the fact that it is recognised as one of the leading causes of death in domestic cats. Brown *et al.* (1994) raised the possibility of an historical genetic accommodation between FIV and its host, leading to co-evolved host-parasite symbiosis. If some wild felids have co-evolved with FIV so that it no longer causes disease, this is clearly not the case for domestic cats. Recent molecular biological work suggests that the domestic cat became infected with the current pathogenic FIV rather recently (Carpenter & O'Brien, 1995). Domestication began only an estimated 4,000 years ago, but nonetheless might have affected the relationship between FIV and its host. So far, all tested African wildcats ($n = 3$) and European wildcats ($n = 87$) have been negative for antibodies to FIV (McOrist *et al.*, 1991; Artois & Remond, 1994; Carpenter & O'Brien, 1995; Daniels *et al.*, 1999). This may suggest that at relatively low

population density with low interaction rate (e.g. European wildcat: Daniels *et al.*, 1999), prevalence and pathogenicity of FIV has been low. As domestication altered cat social behaviour, favouring high population density and group-living, rates of transmission doubtless increased, and perhaps FIV became more pathogenic. Furthermore, in farm cats we found a significant positive correlation between clinical abnormality and FIV in females, but not in males. Perhaps stronger selection for genetic resistance to FIV has occurred in males, compared with females, possibly because males are frequently involved in fights, and biting is the primary means of FIV transmission (Hopper *et al.*, 1994).

Controlling disease transmission

Little is known of the pathogenicity of domestic cat diseases to other felids. Infection of a pathogen-free domestic cat with cougar FIV resulted in the establishment of a persistent infection, but no pathogenicity was observed, and inoculation of domestic cats with lion FIV failed to produce detectable infection (Carpenter & O'Brien, 1995). It is not yet clear whether differences in disease outcome are determined primarily by characteristics of the strain of parasite or of its feline host. However, where an endangered felid's range overlaps that of feral cats it is prudent to assume the possibility of transmission of infectious diseases. In particular, reproductively successful Peripheral feral males should be targeted for disease monitoring and control. Resource centres that allow large populations of feral cats to build up, and which might attract wild felids, should be discouraged. Because of close similarities in their societies, disease in group-living domestic cat society may serve as a model for disease in lions. Indeed, some recent evidence supporting this expectation came, sadly, in the form of the decimating effect of CDV (canine distemper virus) on lions in the Serengeti (Roelke-Parker *et al.*, 1996). However, one cannot distinguish whether either or both of group-living or high population density was the characteristic that precipitated this CDV epizootic and, indeed, there are no comparative data on its prevalence among the solitary leopards of the area. Lions live at higher population density than other big cats, and there is evidence of several density-dependent effects, most viral outbreaks occurring when either the absolute population size or the number of susceptibles is

highest (Packer *et al.*, 1999). However, once this disease had entered the lion population, very rapid within-group transmission was likely to be favoured by group-living, and this situation might usefully be modelled by infectious disease in farm cat colonies.

Unfortunately, many wild felids live in small, isolated populations (Nowell & Jackson, 1996). The potential for disease to damage endangered felid populations is particularly great where the population has become inbred (O'Brien & Evermann, 1988), or there is a low or non-existent antibody response to viruses and other pathogens. The Iriomote wildcat, *Prionailurus iriomotensis*, for example, numbers only 80–100 individuals in total, and lives on a small Japanese island. The Iriomote cat has no antibodies against FPV or FIV, and may be very vulnerable (Mochizuki *et al.*, 1990). The main point, however, is that the socio-epidemiology of wild mammals in general, and felids in particular, is poorly understood yet extremely important.

Concluding remarks

In group-living domestic cat society, adult females with their offspring form core groups; several core groups can occupy a resource-rich site, forming a colony with which adult males are associated. This raises the question of how similar farm cat and lion societies may be. Where food resources are concentrated, two types of females, Central and Peripheral, are observed. In our colonies the former were healthier and reproductively more successful individuals which formed larger lineages. The latter suffered poor health, had lower reproductive success and fewer close kin. Some Peripheral females were probably outcasts from Central lineages.

Within a lineage, social ties between mothers and their own offspring appear to be very strong, though it is still unclear if mothers discriminate in favour of their own offspring even when they nurse them communally. Kittens have strong ties with their littermates and such ties seem to be maintained after they become juveniles. This social arrangement could, under selective pressure, provide the basis for the evolution of coalitions between male littermates and/or similar-aged relatives. We suggest that this may be how male coalitions were formed in the first place among similar-aged relatives in lions. Whether this reflects any functional equivalence or not, hints of convergence between the societies of lions and group-

living domestic cats not only highlight the flexibility of the feline social system, but raise intriguing evolutionary questions. If conditions were to allow, perhaps other solitary-living felids would form groups too. Our analysis, using a simple algebraic exploratory model and field data, suggests that early forces favouring group-living may be food availability, mediated by both intra- and interspecific competition. As the social system of domestic cats changed, so too did the strategies of their pathogens. These pathogens may add a cost to group-living domestic cats, in so far as their physiology may not be as flexible as their society. Indeed, the society of these farm cats – and especially roaming males – and their potential to interact with wild felids, combine with their epidemiological status to raise concerns about conservation.

Acknowledgements

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Appendix 6.1

Calculation procedure to assess the probability of sharing a kill by two independent females

The intake from the shared kill per unit time in habitat i : P_i (dimension: kg s^{-1}), is a function of prey size: w_i (kg), and encounter rate at the kill: e_i (s^{-1}).

$$P_i = f(w_i, e_i) \quad (1)$$

The encounter rate, e_i , could be expressed as a function g that relates predator population density, n_i (m^{-2}), prey capture rate per female, h_i (s^{-1}) and searching rate, a_i ($\text{m}^2 \text{s}^{-1}$) in the habitat i .

$$e_i = g(n_i, h_i, a_i) \quad (2)$$

The foregoing review suggests that, in equation (1), P_i increases when either or both of w_i or e_i increase, whereas in equation (2), e_i increases with either or all of n_i , h_i or a_i . As they are, in general, territorial, wild felids will not behave as 'ideal and free' predators in the sense that 'ideal' means that each animal can choose the habitat that maximises its fitness, and 'free' means that there are no costs involved with entering that habitat (Weber, 1998). However, a mother and her independent daughter which shares her territory/ home range prior to dispersal, may indeed behave as 'ideal and free' predators inside their shared territory. Indeed, the first feline groups may have been formed between mothers and independent daughters (Packer, 1986; Macdonald, 1994). We will explore, therefore, the application of equations (1) and (2) to a mother and her independent daughter sharing her territory, where both of them use each part of the territory randomly. Under these circumstances, what is the probability that they form a group on the basis of sharing a kill?

All else being equal, e_i would increase linearly with h_i , n_i and a_i . Then, e_i can be simplified to

$$e_i = bh_i n_i a_i \quad (3)$$

where the b is time (s). Similarly, P_i would increase linearly with e_i , such that

$$P_i = (c(c'w_i - v_i - v_i') - v_i'')e_i \quad (4)$$

where v_i (kg) is the amount of the carcass which has already been eaten by the female which made the kill by the time her daughter arrives. The v_i' (kg) is the amount of the kill which has already been lost (e.g. to scavengers) by the time the latecomer arrives. The v_i'' (kg) is the amount of the kill which will be lost subsequent to the arrival of the second female. The c' is a dimensionless coefficient to adjust the prey body weight for edible weight, and c is a dimensionless coefficient to make the unit $c(c'w_i - v_i - v_i')$ to the expected share of each female after the second female joins the first, when there is no loss to other animals. Equations (3) and (4) can be rewritten as

$$P_i = (c(c'w_i - v_i - v_i') - v_i'')bh_i n_i a_i \quad (5)$$

If there are no sympatric scavengers or competitors (including conspecifics) strong enough to challenge even one female, the value of v_i' will be 0. If scavengers or competitors take some share of the kill when only one female is present, but not when two females are there, then the value of v_i' is not 0, but, v_i'' is 0. If the scavengers and competitors can take a/some share even when the two females are at the kill, both v_i' and v_i'' are > 0 .

The intake from a kill that is not shared in habitat i will be: P_i' (kg s^{-1}) and would be a function of prey size, w_i (kg), and the prey capture rate per female, h_i (s^{-1}).

$$P_i' = (c'w_i - v_i''')b_i \quad (6)$$

where v_i''' (kg) is the amount of the kill that will be lost to scavengers when the female eats alone. If there are few scavengers and competitors strong enough to challenge the female, the value of v_i''' is 0. But, if not, v_i''' is > 0 .

We assume that a female will eat at the maximum rate during the first unit time following the capture, and thereafter will eat at much reduced rate. On the basis of these assumptions, because the two females meet on $bn_i a_i$ occasions per unit time, the maximum value of v_i can be written as follows:

When $n_i a_i$ is smaller than 1:

$$v_i = by_i + y_i' \frac{(1-b)}{n_i a_i} \quad (7)$$

When $n_i a_i$ is greater than 1:

$$v_i = \frac{y_i}{n_i a_i} \quad (7')$$

where y_i is the maximum amount of food which a female can eat per unit time (kg s^{-1}), and y_i' is the average amount of food which a female must eat per unit time to survive (kg s^{-1}).

Because the intake rate cannot readily be compared among felids of different body weight (a lion would eat more than 100 times as much as a domestic cat), we divide it by adult female body weight x_i (kg). Then the intake rate per body weight from the shared kill per unit time in habitat i , Q_i (s^{-1}), and that from the kill that is not shared per body weight per unit time in habitat i , Q_i' (s^{-1}) are respectively as follows:

$$Q_i = \frac{(c(c'w_i - v_i - v_i') - v_i''')bh_i n_i a_i}{x_i} \quad (8)$$

$$Q_i' = \frac{(c'w_i - v_i''')b_i}{x_i} \quad (9)$$

Parameter values

These simple algebraic formulae give us the opportunity to use the available field data on a variety of felids within a single framework to seek generalisations linking their food supply to their social lives. We select one day as the unit time. We use average female predator's body weight for x_i , and average weight of the main prey species (three-quarters of an adult female's body weight: Schaller, 1972) for w_i . We define the main prey as that on which the predator relies for more than 75% of its kills. For example, when lions in the Serengeti capture prey as the following percentage: wildebeest (122.3 kg) 37%; zebra (226.7 kg) 24%, buffalo, *Syncerus caffer* (562.5 kg) 15%; Thomson's gazelle (13.3 kg) 12%; topi, *Damaliscus lunatus* (82 kg) 3%; hartebeest, *Alcelaphus buselaphus* (94.5 kg) 2%; warthog, *Phacochoerus africanus* (40 kg) 2%; eland, *Taurotragus oryx*, (225 kg) 1% and others 4%, we calculate the w_i as follows:

$$w_i = \frac{(122.3 \times 0.37 + 226.7 \times 0.24 + 562.5 \times 0.15 + 13.3 \times 0.12)}{(37 + 24 + 15 + 12)} \times 100 = 210.9 \text{ (kg)}$$

It is difficult to assess v_i , v_i' , v_i'' and v_i''' in the field, and few data are available; however, v_i''' may be bigger in lions and cheetahs than in other felids (Schaller, 1972; Packer, 1986; Caro, 1994). However, v_i' is expected to be small relative to v_i''' because it depends on how effectively competitors can find the female which first captured prey before the second female

finds her. For simplicity, say v_i' , v_i'' and v_i''' equal 0 and use the maximum amount (PMA) that a female can eat in one feeding period to calculate y_i . We use 20% of the body weight as the PMA for larger felids, as a lion and a tiger can eat this amount within a day (Schaller, 1972. Sunquist, 1981), and 8% for smaller felids as a feral cat can eat this amount daily (Jones 1977). We also calculated y_i' as percentage of body weight: lion 3.5, tiger 3.8, jaguar, *Panthera onca*, 3.9, leopard, *Panthera pardus*, 8.1, cheetah, 7.6, cougar, 4.9, lynx, *Lynx canadensis* 6.0, bobcat, *Lynx rufus* 6.0 and feral cat 6.0 (following sources given in Table 6.1). We use $\frac{3}{4}$ for c' to adjust the prey body weight for edible weight (Schaller, 1972), and $\frac{1}{2}$ for c because we assumed the two females are equal. The a_i is not available, but could be given as follows:

$$a_i = z_i r_i \quad (10)$$

Where r_i (m s^{-1}) is the distance which the species can travel per unit time in habitat i , and z_i is the range (m) which the species can survey for another female from a random point in habitat i . The r_i for bigger species in open grassland or open savannah may be a radius of 3 km (Durant, 1998). There are no data to assess such survey distance in other habitats. As estimates, we use 1 km for bigger species living in scrub-woodland habitat and 0.5 km for the species in forest or woodland. For smaller species we use estimates half those for larger species.