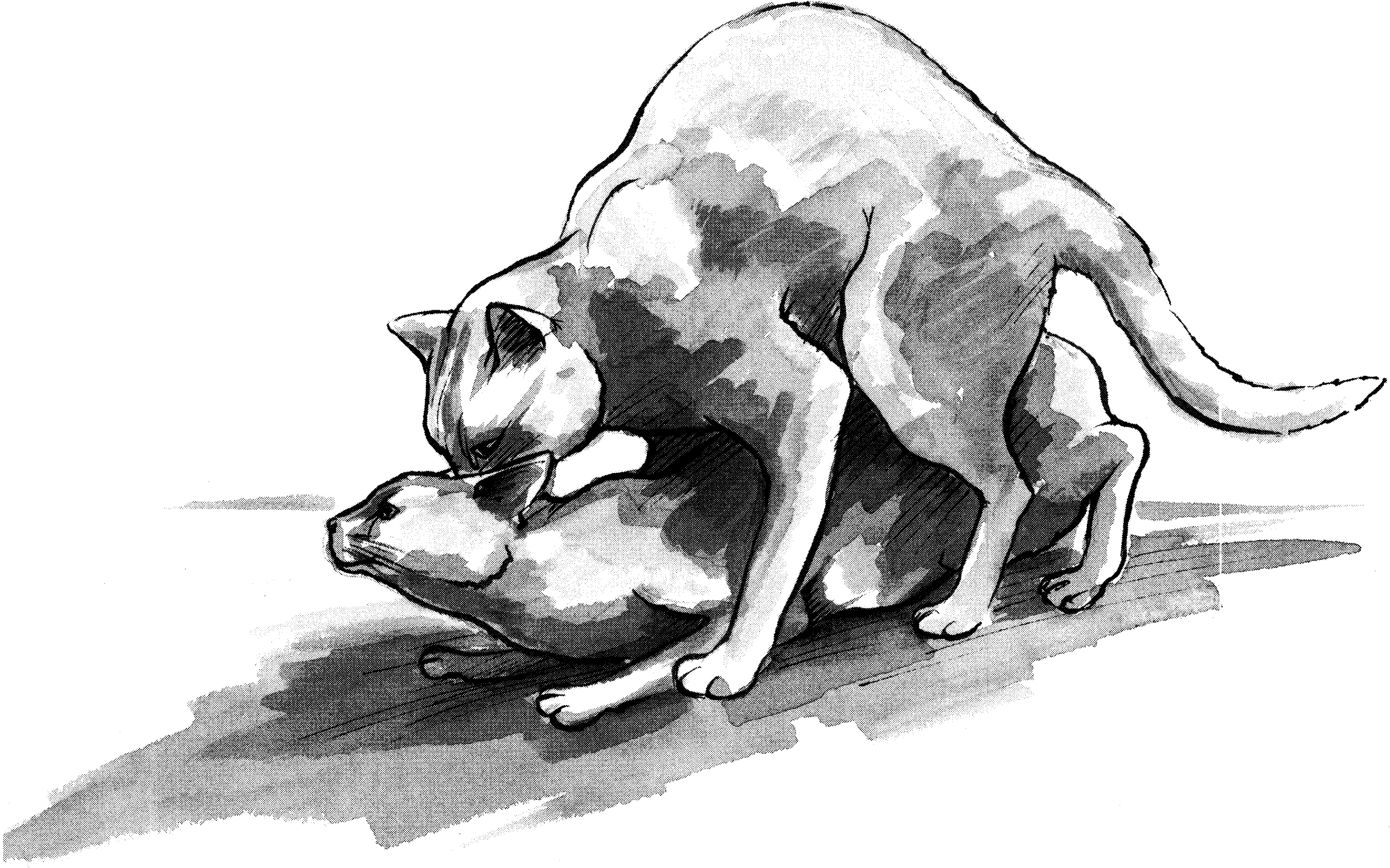

7 Density, spatial organisation and reproductive tactics in the domestic cat and other felids

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Introduction

As its vernacular name implies, the domestic cat has a long history of coexistence with man, but it is still capable of reverting back to the feral state. The cat enjoys a very special status as a domestic animal. There has been little artificial human selection in cats, and many cats are allowed complete freedom of movement. In many respects the cat's way of life more closely resembles that of certain 'wild' human symbionts, like the rat or the house sparrow, than that of a true domestic, such as the dog. It is therefore probable that many, if not most, factors influencing the social behaviour of wild felids are also operative in the domestic cat.

Wild felids are difficult to study. They are shy and rare, and they often live in remote or inaccessible areas. Domestic cats are, at least in the non-feral state, tame; they occur at high densities all over the world and are available for study just outside the gates of universities (and sometimes even inside). Besides being interesting study objects in themselves, domestic cats also are excellent model animals for studies on how different ecological factors shape social organisation, including spacing, more generally in the Felidae. The intermediate position of the domestic cat between a solitary way of life, which is typical for most wild felids, and more well-developed group-living, resembling that of the lion, *Panthera leo*, might also shed light on factors favouring social life.

Domestic cats live under an extreme diversity of ecological situations, resulting in an enormous variation in densities. Our main purpose in this review is to assess whether, in spite of this variation, a general pattern exists in the spatial organisation of cats. According to classical mating system theory (Trives, 1972; Emlen & Oring, 1977; Clutton-Brock & Harvey, 1978), reinforced by more recent developments regarding the relations between spacing, resources and breeding tactics (Clutton-Brock, 1989; Sandell, 1989; Davies, 1991; Reynolds, 1996), dispersion of females in species where males provide no parental care depends on resource abundance and dispersion, while male dispersion primarily is expected to depend on female dispersion. Since the cat is a polygynous or promiscuous species with no male parental care (Leyhausen, 1979; Liberg, 1983; Natoli & De Vito, 1991), we thus expect that females compete over food and other environmental resources to improve their production and rearing of offspring, while males compete primarily for access to receptive females. These hypotheses will be tested here with the data available on domestic cats. We will also review mating system and sexual selection in cats. Finally we have included a brief comparison with wild felids to assess the generality of the patterns, and to reveal possible effects of domestication.

Scientific literature on the behaviour and ecology of free-roaming domestic cats has increased rapidly in the last decades, from fewer than a dozen articles in 1975, to more than one hundred in 1986, and twice as many in 1998. Since these studies also cover cat populations at the extreme ends of such ecological gradients as food abundance and distribution, we are in a position to test hypotheses on the influence of these factors on spacing and other social behaviour.

This review is based primarily on published studies, but results from a few unpublished disssertations are also included. Methods and results have been critically examined, and problems connected with the evaluation and synthesis of results are discussed.

Definition of terms

Cat terminology is a little bewildering, which is why we begin by giving our defintions of terms. With the term 'domestic cat', we mean all categories of *Felis silvestris catus* L. With 'house cat', or 'house-based cat', we are referring to domestic cats that live in close connection with people who assume some responsibility for feeding the cats and have access to buildings for rest and shelter. A house cat can be said to have an 'owner'.

With 'feral cat' we mean a domestic cat that is not attached to a particular household, and thus has no specific 'owner'. This does not mean that it cannot live close to humans on a more anonymous basis. Feral cats might be found in densely populated areas such as large cities as well as in the wilderness. A feral cat can subsist either entirely on its own, hunting and scavenging like any wild carnivore, or by being fed unintentionally by humans at a refuse depot, or by direct hand-outs from 'cat lovers'. The latter source seems to be especially common in larger cities (Tabor, 1983; Natoli *et al.*, 1999).

The two main categories of domestic cats are thus 'house cats' and 'feral cats'. Most cats belong to one or other of these two categories. There might also be an intermediate state, that we could call 'semi-feral'. With a semi-feral cat we mean a cat that has enough connection to one or several households that it is known by these 'semi-owners', but lives most of its life away from these 'semi-owners'. Of course there is no clear-cut line between 'feral', 'semi-feral' and 'house' cat, but in most specific cases the distinction is not diffucult to make.

Among house cats we recognise some subcategories. A 'farm cat' is a house cat that lives on an agricultural farm. Sometimes it is relevant to categorise house cats according to how close they are to their owners. Cats that live in intimate connection with a particular owner (or owners), are allowed inside the home and treated as members of the family, are referred to as 'house pets'. House cats that are not allowed inside the living quarters of people, but are restricted to other buildings are referred to as 'barn cats' or 'shed cats'. Both house pets and barn/shed cats can have complete freedom of movement and take part in the social life of the local cat population. One category of cats that we do not treat in this review is that of 'indoor cats', i.e. cats that are not allowed to roam freely and are under constant control of their owners, mainly staying indoors or in a kennel, or only walked on a leash outdoors.

Density

We begin with a section on cat population density. This is important for our later discussion of spatial organisation for two reasons: density is both a potential causative factor and a dependent variable in relation to spacing behaviour.

Population densities reported in the various cat studies show tremendous variation, from about one cat per square kilometre to more than 2000 cats per km^2 (Table 7.1). This certainly calls for an explanation. Our basic hypothesis is that density of both free-ranging house and feral cats is determined ultimately by food abundance.

One problem when testing this hypothesis is that many different methods are used to determine densities (see Table 7.1). Thus, one should keep in mind that there is a large variation in accuracy between studies. Also, especially when dealing with urban cat colonies, there might be a problem of defining over which area to measure density. For example, by including only the regular feeding area for a specific cat colony in Rome when estimating density, a figure of more than 14,000 cats per km^2 was calculated, a figure that might be misleading considering that the measurement only concerned a group of fewer than 80 cats (Natoli *et al.*, 1999). In confined areas, even higher densities might be reached. Tabor (1989) reported a group of 50 cats living their entire life in a yard enclosed by a block of apartment houses in suburban Amsterdam. The yard area was 0.14 hectares, which yields a density of more than 21,000 cats per km^2, even when counting only the 30 cats that were feral and not allowed inside the houses. Therefore in this review we only consider density figures for cat colonies that are not confined and where we know the total home ranges of the cats.

Another problem is the almost universal lack of quantitative data on food abundance. All authors report the type of food available to their cats and, in most cases, some estimate of relative abundance. But this is insufficient for a normal regression analysis of density over food abundance. Instead we have grouped the studies into three broad density classes, and relate these to a rough estimate of the food situation (Table 7.2).

Densities above 100 cats per square km^2 were found only in urban areas where cats fed on rich supplies of refuse or were fed daily by large numbers of 'cat lovers', i.e. people not owning the cats, but who frequently placed cat food at traditional places. Intermediate densities (5–100 cats per km^2) were found in farm cat populations where the cats were supplied with most of their food requirements by owners, and in rural feral populations subsisting on very rich, often clumped natural prey such as colonies of ground-nesting seabirds. Densities below five cats per km^2 were found only in rural feral populations subsisting on widely dispersed prey, mainly rabbits and rodents.

This is certainly not a satisfactory test of our food hypothesis, but it does indicate that absolute food abundance is at least roughly related to density. However, once the general level of density is set by the food resources, other factors might also operate on a finer scale. In a residential area in central Brooklyn, New York, a difference in density between two neighbouring sectors could not be explained by a difference in food resources, but possibly by access to shelter in the form of abandoned buildings and the like. However, both areas had very high densities (2 and 5 cats per ha, respectively) and the authors judged there was a surplus of food in both sectors (Calhoon & Haspel, 1989).

A factor that might seriously affect densities is

Table 7.1. *Characteristics of cat studies referred to frequently in this chapter*

Study No.	Location	Duration of study (years)	Study area size km^2	Method[a]	Habitat	Food			Cat status	Group/ Solitary[b]	Pop.dens. N/km^2	References
						Type	Rel. abund.	Distrib.				
1	Jerusalem Israel	1	0.03	V	Residential urban area	Garbage bins	High	Clumped	Feral	G	2300–2800	Mirmovitch 1995
2	Ainoshima Japan	1.5	0.1	R, V	Fisher village	Fish dumps	High	Clumped	Feral	G	2350	Izawa 1984, Izawa *et al.* 1982
3a	Rome Italy	1.5	0.02	V	City park	Cat lover handouts	High	Clumped	Feral	G	1000–2000	Natoli 1985
3b	Rome Italy	0.5	0.06	V	Market square	Cat lovers, market refuse	High	Clumped	Feral	G	1200	Natoli & de Vito 1988, 1991
4	New York USA	1.5	0.33	R	Residential urban area	Garbage containers	High	Mod. clumped	Feral (some pets)	S?	300–500	Calhoon & Haspel 1989, Haspel & Calhoon 1989
5	Canberra Australia	0.8	One farm 0.1	R	Farm land	Farm feeding rodents	High	Clumped	Farm cats	G	High	Barrat 1997
6	Portsmouth England	4	1	V	Dockyard	Anon. handouts	High	Mod. clumped	Feral	G	300	Dards 1978, 1983
7	Canberra Australia	0.8	1	R	Edge suburb/rural	House food	High	Clumped	House pets	G/S	200	Barrat 1997
8	Oxford England	3	1	V, R	Pig farm	Regular feeding	High	Clumped	Farm cats	G	High	Kerby 1987, Kerby & Macdonald 1988
9	Cornwall England	0.5	One farm 0.16	V	Dairy farm	Milk, some prey	Medium	Clumped	Farm cats	G	30	Panaman 1981
10	Lorraine France	0.2	0.75	R	Farm land	Milk wastes	Medium	Clumped	Farm cats	G	?	Pericard 1986
11	Wisconsin USA	0.5	One farm	V	Dairy farm	Milk, some prey	Medium	Clumped	Farm cats	G	?	Laundré 1977
12	Dassen I. South Africa	1.3	2.2	R, V	Subtrop. scrub	Rabbits, birds, carcasses	Medium	Dispersed	Feral	S	20–50	Apps 1983, 1986
13	Hebrides Scotland	2	1	V	Sand dunes	Rabbits, food scrapes	Medium	Mixed	Semi-feral	G/S	19	Corbett 1979
14	Zürich Switzerland	1	1.3	R, V, I	Farm land	Farm feeding rodents	Medium	Clumped	Farm cats	G	14	Turner & Mertens 1986

15	Kerguelen I. Ind. Ocean	2	600	V	Subantarct. heath	Rabbits, seabirds	Medium	Mixed	Feral	S	10–15	Derenne 1976, Pascal 1981
16	Avonmouth England	1.5	1.8	R, V	Dockyard	Food wastes, handouts, birds, rodents	Medium	Mixed	Feral	S	10–15	Page *et al.* 1992
17	Marion I. South Africa	1.5	33	V	Subantarctic heath	Seabirds	Medium	Clumped	Feral	S	5–14	van Aarde 1978, 1979
18	Illinois USA	5	52	R, I	Farm land	Farm feeding rodents	Medium	Clumped	House cats	G	6.3	Warner 1985
19	Devon England	0.5	0.6	R, V	Dairy farm	Milk, some prey	Medium	Clumped	Farm cats	G	6	Macdonald & Apps 1978
20	Revinge Sweden	8	20	R, V, I	Ranch land	House food, rabbits, rodents	Medium	Mixed	Mixed	G/S	3–7	Liberg 1980, 1981, 1984
21	Macquarie I. New Zealand	?	120	T, V	Subantarctic heath	Rabbits, seabirds	Medium	Mixed	Feral	S	2–7	Jones 1977
22	Monach I. Scotland	2	2.4	R	Dunes, heath	Rabbits, birds	Low	Dispersed	Feral	S	3,7	Corbett 1979
23	Hastings New Zealand	3	5.2	R	Farm land	Rodents, birds	Low	Dispersed	Feral	G/S	3.5	Langham & Porter 1991, Langham 1992
24	Galapagos Pac. Ocean	1	10 +15	R, V	Tropical scrub	Rodents, lizards, birds	Low	Dispersed	Feral	S	2–3	Konecny 1983, 1987
25	Victoria Australia	4	190	R	Subtrop. grassland	Rabbits	Low	Dispersed	Feral	S	1–2	Jones & Coman 1982
26	Po Delta Italy	2	42	R, V	Reclaimed, cropland	Farm food, nat. prey	Medium/low	Mixed	Mixed	S	1,4	Genovesi *et al.* 1995
27	Orongorongo New Zealand	2	15	R	Grassland, bush	Rats, rabbits	Low	Dispersed	Feral	S	1	Fitzgerald & Karl 1986
28	Schiermonnikoog Netherlands	1	40	R	Rural open land	Rabbits, rodents, birds	Low	Dispersed	Feral	S	0,9	Langeveld & Niewold 1985

[a] R, radio tracking; V, visual sightings; I, interviews with owners; T, trapping and shooting.

[b] G, group-living; S, solitary.

Table 7.2. *General food situation in three density categories of cat populations. For study number., refer to Table 7.1.*

Density category (no. cats/km^2)	General characteristics of food situation	Study no. (see Table 7.1)
More than 100	Rich clumps (garbage bins, fish dumps, cat lover handouts)	1, 2, 3, 4, 6, 7
5–50	Thinner clumps (farms and other households, bird colonies on islands, or rich dispersed prey	9, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Fewer than 5	Scarce dispersed prey, might occur in patches, but no rich concentrations of food.	23, 24, 25, 26, 27, 28

human control. It is interesting to note that two rural populations where the cats were based mainly, or to a large extent, at non-farming households (Liberg, 1980; Warner, 1985) and where one might expect a lower tolerance of large cat groups, also had lower densities than two populations where the cats lived on dairy farms (Panaman, 1981; Turner & Mertens, 1986). Warner (1985) also reported that within his study area farms with domestic livestock (cattle, pigs, etc.) had three times as many cats per residence as households without livestock (13.5 and 4.3, respectively). Direct control operations are also common, both in urban feral populations (Natoli, 1985, Natoli *et al.*, 1999) and in rural populations (e.g. Hubbs, 1951; Pascal, 1980, Genovesi, Besa & Toso, 1995).

The only comparable density figures for wild small felids are for populations of European wildcat, *Felis s. silvestris*, which exhibit densities from less than one (Stahl, 1986; cited in Genovesi *et al.*, 1995) and up to three animals per km^2 (Corbett, 1979). This agrees rather well with figures for feral cats in Australia, New Zealand and Italy of one to two cats per km^2 (Jones & Coman, 1982; Fitzgerald & Karl, 1986; Genovesi *et al.*, 1995) and is an indication that the same factors may determine the densities of wild felids and feral cats living in similar habitats.

Home range size

Two basic methods have been used to determine home range size: radio-tracking and sightings of identified individuals. Radio-tracking naturally gives a less biased result, since locating the subjects is not dependent on habitat visibility. Also the risk of missing less frequented parts of the home range is higher when range size is based only on sightings. We therefore expect that the sighting method will yield smaller home range estimates than radio-tracking, which is supported by data from Izawa, Doi & Ono (1982). With very large samples, as in the study by Dards (1978), the sighting method will also yield reliable results, especially if the study is conducted in a confined area and all parts are evenly searched by the observer. In the course of our review we noted that home range sizes based on only sightings were from either urban studies, or studies of single farm cat groups. All others (multiple farm cat groups, rural feral populations) have used radio-tracking.

Due to differences in sampling methods, length of tracking periods, sample size and, especially, the methods used to calculate range size, there is great variation in the data on home range size. As far as possible we have used values resulting from the 'convex polygon method' (Mohr & Stumpf, 1966).

Some authors have split up their tracking data into subperiods. We find monthly ranges rather meaningless, since there is no biological reason to expect monthly differences. But seasonal ranges based on various biological criteria can be useful for answering certain questions. For cats the most relevant division would probably be into mating and non-mating seasons. For female cats, it might also be meaningful to consider litter rearing periods separately (e.g. Corbett, 1979; Fitzgerald & Karl, 1986).

A few studies have differentiated between diurnal and nocturnal tracking (Langham, 1991; Barrat, 1997). Most cats moved over larger areas during night, but there were exceptions. In this review we have used the larger range from whichever part of the day that might cover.

Female home range size

As with density, there is a 1000-fold variation in mean home range size given in the different studies. Female ranges span from 0.27–0.29 ha in the city of Jerusalem

(Mirmovitch, 1995) to 170 ha in the Australian bush (Jones & Coman, 1982). Our primary hypothesis is that female range size is determined by food abundance and distribution. If these are the only factors influencing range size, females are expected to include just enough space to give them access to the food needed to get them through the year. Unfortunately the lack of data on food abundance again prevents a direct test of this prediction. It is obvious, however, that food has just as strong an influence on female home range size as on cat density. In fact we found a significant negative correlation between female home range size and density (Figure 7.1). We believe the reason for this correlation is that density and female home range size each are correlated to a third factor, namely food abundance and distribution. The smallest female ranges were found in those urban feral populations that subsist on rich, clumped food resources; intermediate ranges were found in farm cats; and the largest ranges were shown by feral cats living on dispersed natural prey (Table 7.3). The wide scatter of points around the regression line in Figure 7.1 is caused by the farm and house cats, which get food from their owners, independently of their range size. If only feral cats are considered the correlation is even higher ($r = -0.97$, $n = 7$, $t = 8.63$, $p < 0.001$).

Unfortunately dispersion and abundance of food in these studies are correlated, so that the most abundant food is also the most clumped, e.g. the fish dumps in the Japanese study (Izawa *et al.*, 1982), the refuse bins in Jerusalem (Mirmovitch, 1995) and the cat lover feeding stations in Rome (Natoli 1985), while the least abundant food also is the most dispersed, i.e. the natural prey available to feral cats in unsettled areas (e.g. Derenne, 1976; Jones, 1977; Fitzgerald & Karl, 1986). The only simultaneous study of these two aspects of food resources was provided by Konecny (1983) who found that when food occurred in patches, the feral cats in his study moved over larger areas than when it was evenly distributed, in spite of a higher overall food abundance in the former case. However, more studies of that kind are needed before we can quantify the relative influence of abundance and dispersion of food on cat home range sizes. Until then we have to conclude that both factors might (probably) influence the home range size of female domestic cats.

However, factors other than food abundance and distribution can also affect the spacing and range sizes of cats. Many female house cats on farms or from

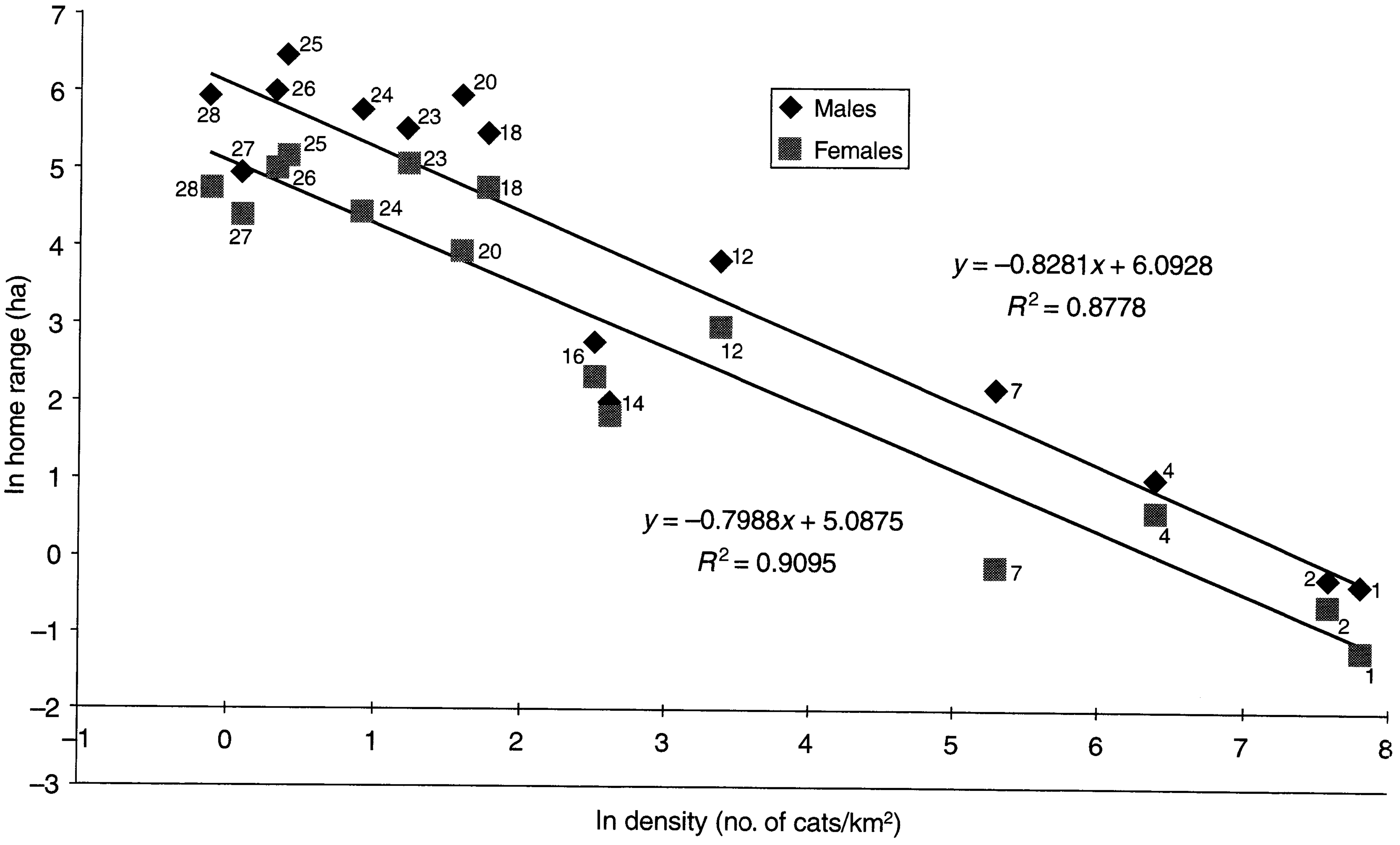

Figure 7.1. Relationship between density and home range size in male and female cats. Numbers refer to study number in Table 7.1. Regression lines are shown. Scales are transformed to natural logarithms.

other households, which could stay near their homestead for their entire lives as far as food acquisition is concerned, still move considerable distances away, usually to hunt natural prey in the surrounding fields (see e.g. Laundré, 1977; Liberg, 1980; Warner, 1985; Barrat, 1997). Possibly hunting in itself is an innate need which the cats strive to satisfy, independent of the need for food (see Chapter 8).

Distribution of shelter can also influence cat spacing. For example, some of the female cats living on fish dumps in Japan with relatively small home ranges, still moved far away from the food source itself, obviously in search of appropriate resting places (Izawa *et al.*, 1982). In central New York, Calhoon & Haspel (1989) demonstrated that shelter abundance and distribution were crucial for determining cat spacing pattern.

Male home range size

The variation in range size between different areas is just as large for males as for females (see Table 7.3). When plotted over density, the male range regression line has an almost identical slope with that of females in Figure 7.1, but lies on a higher level. On average, male ranges are three times larger than those of females. Energetically this increase in range size corresponds to a body weight more than four times that of females. As males rarely are more than 1.5 times as heavy as females (Liberg, 1981), we interpret this as a clear indication that food is not determining range size for males, at least not directly.

According to our hypothesis, males compete for access to females. From that we predict that the primary factor determining male range size is female density and distribution. We expect males to maximise access to females, and this means that male ranges generally will be larger than those of females. We will return to this point, but first two other aspects supporting our original hypothesis have to be considered.

The first concerns dominance categories in males. In most polygynous species both dominant breeding males, and subordinate males, that are partly or totally excluded from breeding, occur. When such a situation exists in a cat population, we would expect breeding males to have larger ranges than non-breeding males, if they are living under otherwise similar conditions. Unfortunately most authors have not distinguished between these categories.

Liberg (1981, 1984) recognised different categories of adult males, based on dominance and ecological status (house-based or feral). He found that no male cat reached dominant status ('breeder') before reaching 3 years of age. In house-based dominant males, ranges were 350–380 ha, whereas ranges of house-based subordinate males were around 80 ha, or not much larger than those of females. Turner & Mertens (1986) also found that the male they presumed to be the 'breeder' of their small Swiss rural population had the largest male range in the study. Langham (1992), too, found larger ranges in dominant males in his study of New Zealand farm cats, and in spring, dominant males showed a significant increase in movement compared with subordinates. In an Australian suburban area, the largest home range among ten radio-tracked house cats was found in the only mature, sexually intact male cat in the study, although one castrated male and one female also had similarly sized ranges (Barrat, 1997).

We believe the reason subordinate males generally have smaller ranges than dominants is that they gain little by travelling widely in search of females. However, under certain circumstances they can have even larger ranges. In the Swedish study some subordinate males were driven out of their primary homes by dominant rivals and assumed a feral status (Liberg, 1980, 1981). These males (termed 'outcasts') had larger ranges than the house-based dominant males, partly because they were no longer fed by humans and had to subsist on hunting, and partly because they were 'pushed around' by dominanat males during the breeding season (Liberg, 1984). To a certain extent these males corresponded to the male lion category that Schaller (1972) called 'nomads'.

The second aspect concerns seasonality. If breeding is seasonal we would expect female density and dispersion to be important for male range extension only during the mating season. At other times of the year breeder male ranges might be determined by the same factors as those of females and subordinate males. As mentioned earlier, there are few studies that have presented data on differences in range size between mating and non-mating seasons. However, Mirmovitch (1995) found a non-significant increase of male ranges during the mating season, and Corbett (1979) showed graphically that male ranges in his Hebrides study were largest in early spring, when presumably mating activities were at their highest, and then declined as the year proceeded. He did

Table 7.3. Range characteristics of male and female domestic cats. References as in Table 7.1

			Female ranges					Male ranges			
						Overlap/Exclusive					
Study no.	Location	Density (no./km^2)	Mean size (ha)	Range (ha)	n	Within groups	Between groups /unrel. females	Mean size (ha)	Range	n	Overlap/ Exclusive
Group-living females											
1	Jerusalem	>2000	0.27	0.12–0.47	10	O(83%)	O(36%)	0.75	0.32–2.0	16	O
2	Japan	>2000	0.51	0.06–1.8	6	O	E	0.72	0.31–1.7	6	O
5, 7	Canberra	High	2.34[a]	1.38–3.30	5	O	E	3.03	1.59–4.46	2	O
6	Portsmouth	300	0.84	0.03–4.24	68	O	E	8.40	0.08–24.0	32	O
9	Cornwall	30	4.04	0.7–15	5	O	–				
14	Switzerland	14	6.0	1.2–17.8	6	O(55%)	E(4%)	7.2	0.8–16.0	3	O
18	Illinois	6	112	4.8–185	7	O	–	228.00	109–528	4	O
20	Sweden	3–7	50		15	O	E	370	84–990	18	O
23	Hastings, N.Z.	3.5	57	22–110	9	O	E	86	19–156	4	E
Solitary females											
4	New York	300–500	1.77	0.06–6.76	47		O	2.62	0.08–10.33	48	O
12	Dassen I.	30	19	11–32	3		O	44	32–63	5	O
16	Avonmouth	12.5	10.3	2.6–17.6	13		O	15	0.9–56	13	O
22	Monach I.	4	42	24–60	2		–	–	–	–	–
24	Galapagos	2–3	82	21–220	4		O	304	35–760	10	O
25	Victoria	1–2	170	70–270	2		–	620	330–290	2	–
26	Po Delta	1.4	147	62–254	4		O	394	149–639	2	–
27	Orongorongo	1.1	80	20–170	5		O	140	50–130	4	O
28	Netherlands	0.9	113	50–180	3		E	367	320–420	3	O

[a] Nocturnal ranges

not present separate data for breeding versus non-breeding males. Nor did Izawa *et al.* (1982), who also showed that male ranges were larger in the mating season than during the rest of the year. In an unpublished study in the Revinge area of southern Sweden, we (O.L. and M.S.) found that breeding males had significantly larger ranges during the mating season than in the autumn when females were anoestrous (Table 7.4). We also found that breeding males had larger ranges than non-breeding males during the mating season, but similar-sized ranges during autumn, although these latter findings could not be confirmed statistically.

Table 7.4. *Range sizes (hectares) for dominant and subordinate males during the mating and the non-mating seasons respectively, in the Revinge area, Sweden, 1984*

	Mating season			Non-mating season		
	$\bar{x}$	Range	n	$\bar{x}$	Range	n
Dominant males	218	158–326	4[a]	44	21–63	3
Subordinate males	10	1–18	2	85	2–169	2

[a] p <0.05, Mann–Whitney *U*-test.

The range size ratio males:females

Even if male ranges generally are larger than those of females, the male:female range size ratio among the different studies varies from almost 1:1 to 10:1. We believe one important reason for this variation is female distribution which causes different responses in the male spacing pattern. It is, however, surprising that both the lowest and the highest ratios are found in populations where females live in groups and intermediate values are from populations with solitary females. We must therefore ask more specifically under what conditions we would expect a low or a high range size ratio.

Again we start with the assumption that males strive for access to as many females as possible. We further assume that males visiting many different female groups or 'clumps' will have larger ranges relative to females, than those visiting just one or a few groups. When female groups are large and widely dispersed it may not pay for a male to include more than one such group in his range, in which case he would not need a larger home range than any of the females living in that group. This seems to be the situation in the Swiss study, where the lowest male:female range size ratio of all was found. There, no fewer than eight females lived on four closely situated farms, which is in effect just one clump. The dominant male visited all four farms, and therefore did not have to cover more ground than the most mobile of the females (Turner & Mertens, 1986). Thus, the first condition, many females in the 'group', was met. The question is whether the second, widely dispersed groups, was met. The next 'clump' of females was not more than about 500 metres away (D. C. Turner, personal communication), but that obviously was enough to deter this male from including it. In the Japanese study where at least one of the groups was of the same size as in the Swiss study, the groups were no more than 100–200 m apart, and at least some of the males visited several groups. Kerby (1987), although not giving range sizes, presented data which indicate that distance between groups is more important than group size in determining whether dominant males shall stay with just one group, or include more (see the section on Mating system, below).

The conditions favouring a high male:female range size ratio are just the opposite of those favouring a low ratio, namely small female groups that are evenly distributed and not too far apart. This was the situation in the Portsmouth dockyard, and here the highest ratio of all was found (Dards, 1978). Although a few males stayed with only one female group, most males wandered widely and incorporated many groups in their ranges (Dards, 1983). In the Revinge area in Sweden female groups were also small, but here they were more widely spaced (Liberg, 1980). Breeding males incorporated on the average five female groups in their ranges, with a maximum of nine. The range size ratio here was still fairly high at about 7:1. This again indicates that female group size might be more important than distance between groups in determining how many groups a breeding male will visit.

In populations with solitary females, our prediction is that the ratio would increase the more exclusive, and therefore dispersed, the female ranges are. This holds true for some of the areas with dispersed females, but not for all (Table 7.3). The reason for this is unclear, but confounding factors might be involved here (see below).

Liberg (1984) showed that variation in range size was much higher than variation in number of female cats included in the ranges for breeding males; the opposite was true for subordinate males, where range size was more constant than number of females included. It is plausible that breeding males simply visit and check as many females as they have time to, and that this figure is rather constant for all males in a given area; heterogeneity in female distribution would then cause a larger variation in the area covered while performing these visits.

A confounding factor here is that different studies have incorporated different proportions of dominant and subordinate male cats. The larger the proportion of subordinate males in the sample, the smaller we expect the size ratio between male and female home ranges to be. In the Canberra study (Barrat, 1997), for example, the ratio between male and female ranges in a sample of suburban cats was only 1.19 to 1, and in a nearby farm colony 1.29 to 1. In the suburb sample however, only one of the six males was sexually intact and he also had the largest range of all (when 100% of the radio points were included), and in the farm sample both of the two males were immature, i.e. approximately one year old. The Avonmouth dockyard study (Page, Ross & Bennett, 1992) also had a low ratio between mean range sizes of males and females, but again there was a large variation among the males, and the authors also demonstrated a significant positive correlation between male weight (which is related to dominance: Liberg 1981) and male range size. The largest male range (56 ha) was more than three times larger than the largest female range (17 ha).

Spatial distribution

Living in groups or alone

Most wild felids are solitary-living, at least in the sense that they are not forming social groups of adult animals. Females might be accompanied by their young for varying periods, which in the larger species might extend for most of a year or even more, e.g. European lynx, *Lynx lynx* (Haglund, 1966), tiger, *Panthera tigris* (Schaller, 1967), cougar, *Puma concolor* (Hornocker, 1971) and leopard, *Panthera pardus* (Bailey, 1993), but adult females never live or even stay temporarily together. The notable exception from this pattern is the lion, which is a true social animal, living in female kin groups (Schaller, 1972). A large literature treats the possible reasons for this deviation from the general felid pattern, including benefits when hunting large prey, defence of killed prey against competitors (see also Chapter 6), defence of cubs and benefit of group territory (e.g. Schaller, 1972; Caraco & Wolf, 1975; Rodman, 1981; Pulliam & Caraco, 1984; Van Orsdol, Hanby & Buggett, 1985; Packer, Scheel & Pusey, 1990).

Domestic cats are very flexible regarding their ability to live solitarily or in groups, and there seems to be a clear correlation with food dispersion (Table 7.1). Female cats that live on dispersed natural prey typically live alone (e.g. Corbett, 1979; Konecny, 1983; Fitzgerald & Karl, 1986; Genovesi *et al.*, 1995). A possible exception to this pattern is the claim by van Aarde (1978) that at least some adult cats lived in small groups in his feral population on subantarctic Marion Island, and that one reason for this might be heat preservation when several cats curl up together to rest. But this interpretation was based on just a few sightings and further documentation is required before any firm conclusion can be drawn. Such a pattern was never observed on the subantarctic Kerguelen Island: adult cats were always observed alone (D. P. Pontier, personal observation).

A large number of studies have reported female cats living in groups, which sometimes also include adult males. Group living is seen in either one of two typical situations. One is groups of cats living in households, often but not necessarily farms, where they are fed regularly by the residents (e.g. Laundré, 1977; Liberg, 1980; Turner & Mertens, 1986; see also Table 7.5) or have access to some other regular rich food source such as forage spillovers (Kerby, 1987). The second is an anthropogenic concentration of food that is frequently refilled, usually in urban or village areas, such as one or several closely situated food waste dumps (Izawa *et al.*, 1982; Mirvovitch, 1995) or a cat lover feeding station (Tabor, 1983; Natoli, 1985) (Table 7.5). Common to both situations where groups of cats establish is thus a central place where food is provisioned more or less continuously.

There are, however, several studies that report solitary cats in spite of a relatively rich food supply in urban areas, e.g. feral cats in the streets of central Brooklyn (Calhoon & Haspel, 1989) and in the English dockyard of Avonmoth (Page *et al.*, 1992). Typical of both study areas were numerous scattered food sources, that together provided a large amount

Table 7.5. *Characteristics of cat groups in the different studies*

Study no. and place	Environment and the food resource	Group size (ad. fem.)	Number of groups studied	Group structure and kinship of females in group	Female group relation to males
1 Jerusalem	Large garbage bins in residential city area	3–7	4	Core group with stable membership, a few more loosely attached females. Kinship unknown	Males visit several groups
2 Japan	Fish dumps in village	4–8	2 (5)	Female kin group with stable membership	Males born in group leave before age of 5. Several adult males attached to each group.
3a Rome	Daily provision in city park by cat lovers	15	1	Stable membership, kinship unknown	Males occurring irregularly
3b Rome	Cat lover provision, market refuse	37	1	Core group of 37 females, but other loosely attached females also occurred. Kinship unknown	Many males occurred regularly in the group, but might also visit other groups. Transient males occurred
5 Canberra	Farm; daily provision of cat food, scrapes, rodents	>5	1	Stable membership, kinship unknown	No adult males premanently in group
6 Portsmouth	Dockyard; refuse and cat lover provision	2–9	20	Female kin group with stable membership	Males born in group leave at age 1–2. Adult males visit several groups, sometimes one male more permanently attached
8 Oxford	Pig farms, *ad lib.* provision of pig food	3–15	2	Stable membership. Kin groups, but several 'lineages' might occur	Younger males more attached to natal group. Older males visit several groups
9 Cornwall	Dairy farm, regular provision of milk, cattle feed	5	1	Female kin group with stable membership. One immigrating female	Males loosely attached

Table 7.5. *continued*

11 Wisconsin	Dairy farm, regular provision of milk, cattle feed	6	1	Female kin group with stable membership. One immigrating female	Males loosely attached
14 Zürich	Three closely located farms; regular provision	2	3	Female kin groups with stable membership. Some kinship also between farms	Males visiting several groups
18 Illinois	Farming and non-farming rural residences, regular provision, natural prey	x = 1.6	16–26	No data	No data
19 Devon	Dairy farm, milk provided	3	1	Experimentally started group with 3 related females introduced to new farm	One adult male in the group
20 Sweden	Rural non-farming residences, regular provision, natural prey	1–7	20	Female kin groups with stable membership	Males born in group leave at age 1–3. Dominant males visited several groups
23 Hastings, N.Z.	Field barns, no human provision, natural prey	1–2	3	Related females share barn, except during breeding, no communal feeding observed	Dominant males visited several barns

References to studies as in Table 7.1.

of food overall, but a moderate provision from each one. For example, in the Brooklyn study, 'sector A' covered 16 ha of residential area, where 80 cats were feeding from no fewer than 17,500 open containers distributed all over the area.

The solitary habit of some cats in Avonmouth dockyard is also interesting considering that another English dockyard, Portsmouth, was the scene for one of the earliest scientific studies of group-living feral cats (Dards, 1978, 1979). The cat density in Portsmouth, however, was 20 times larger than in Avonmouth, indicating a quite different food situation there.

On the other hand, there is one study that reports up to three related females living together in a group-like manner with no concentrated food resource (Langham & Porter, 1991; Langham, 1992). The females shared field barns to rest and find refuge during the day, when farm workers and their dogs were active in the area around the barn, and emerged only in the evening when the people and dogs had left. The social bonds here were less tight however, as 'related females preferred to give birth and nurse their kittens in separate locations before associating with relatives and their offspring' (Langham, 1992).

In all cases where kinship between the cats in groups has been possible to check, the group members are closely related on the matrilineal side (Dards, 1978; Liberg, 1980; Izawa *et al.*, 1982; Turner & Mertens, 1986; see also Chapter 6). Typically groups are founded by a single female cat, and the group then grows and is maintained through philopatry of female offspring (Liberg, 1980, 1981; Yamane, Doi & Ono, 1996). Male cats born into the group normally leave it some times after adolescence (Liberg, 1980; Dards, 1983; Yamane, Ono & Doi, 1994). Groups might vary in size from just several, to more than 30 adult females (Table 7.5), but kinship in the largest groups is not completely kown (Natoli, 1985).

We propose that it is the utilisation and communal defence of a concentrated and stable food resource large enough to support more than one individual that causes adult female cats to live in groups (but see also Macdonald *et al.*, 1987; Kerby & Macdonald, 1988, and Chapter 6). All reported cases of true group-living, where females also breed together, include this condition. The case described by Langham and Porter (see above), however, also shows that other concentrated resorces, such as refuge places, might lead to at least a loose form of group living.

Since cats living on only natural prey do not form groups, we assume that behavioural advantages such as communal care and cooperative defence of kittens are not responsible for the appearance of group-living in the domestic cat, as has been proposed in the past (e.g. Macdonald & Apps, 1978). Such behavioural patterns are secondary benefits of living in groups, once these groups have arisen as an effect of resource distribution. The Langham study where cats shared barns, but did not breed and nurse together, also supports the hypothesis that the shared resource is the key factor that starts group-living and that co-operation comes later (Langham & Porter, 1991; Langham, 1992). We thus conclude that the ultimate factor determining whether cats will live solitarily or in groups is food dispersion, in support of our primary hypothesis.

But are these cat colonies true social groups or are they mere aggregations around food concentrations? Most data point to the former. All studies that have relevant data report that female membership in the group is stable over time. In most cases it has also been documented that female membership is based on kinship, which is an effect of philopatry and internal recruitment of female offspring coupled with hostility towards strange females (e.g. Liberg, 1980; Turner & Mertens, 1986; Kerby 1987). There is also some evidence that individual bonds develop between different cats within groups, and persistent hostility (although usually at a low level) occurs towards others (Kerby & Macdonald, 1988; see also Chapter 6). As mentioned earlier, female group members also interact cordially when rearing offspring (Macdonald & Moehlman, 1982; Macdonald *et al.*, 1987).

Males usually have a much looser attachment to groups, which also is in accordance with our hypothesis. In several studies the majority of males dispersed from their natal groups after attaining sexual maturity (see e.g. Liberg, 1980; Dards, 1983; Warner, 1985; Pericard, 1986), and only a few ever reached breeder status there (Liberg, 1981; Dards, 1983). In the large groups at fish dumps in Japan no female transfer between groups was observed, but an occasional male transfer occurred (Izawa *et al.*, 1982). It seems that adult males manage to visit strange groups more easily than females; the reason for this will be discussed below in connection with mating behaviour. In any case, given the pattern of dispersion in this species (females are philopatric, males disperse), juvenile or subadult males manage to enter strange groups much more easily than females. The reason for this will also be discussed below.

Range overlap

Degree of range overlap or exclusiveness tells something about how animals in a population distribute resources among themselves. A low degree of range overlap can be the result either of mutual avoidance and an equal sharing of resources and space at low population densities, or of animals defending their ranges from which they exclude conspecifics, at least of their own sex. The latter case is called territoriality and we adhere to the more restricted definition of this, requiring active defence of the range (Maher & Lott, 1995).

There is a large asymmetry between the data needed to show range overlap and exclusive ranges. Data on two adult individuals of the same sex can be sufficient to show range overlap, whereas the documentation of exclusive ranges requires either a high degree of confidence that all animals within the study area are monitored, or that a number of animals with adjacent ranges are followed simultaneously. Since it is often uncertain that all individuals in an area are monitored, the latter alternative is advantageous for demonstrating the presence of exclusiveness. We consider three of four adjacent ranges showing a mean of less than 10 per cent overlap (measured on 'convex polygons') as a convincing indication of exclusive ranges.

Range overlap in females

Throughout this review we have assumed that food is the most critical resource for female cats. Group-living females utilise a food source that is predictable in time and clumped in rich, concentrated patches. Predictability is considered an important condition for defendability, whereas a clumped distribution generally is not, at least not when the clumps are very rich (Davies & Houston, 1984). The latter is true, however, only when the defender is a single individual and the clump contains more food than an individual can utilise by itself. A stable and rich clump can be defended by a group of individuals, and this is what we think the group-living female cats do. Within groups home ranges overlap extensively, especially at the primary feeding place, be it a farm, a refuse dump or the corner of a city park where 'cat lovers' regularly place food. Between groups there is little range overlap (see Table 7.3). This was very nicely illustrated by Izawa and colleagues (1982, 1984) in their work with feral cat groups subsisting on fish waste dumps. And in their small Swiss farmer village Turner & Mertens (1986) measured degree of range overlap quantitatively within and between groups and found it to be, on average, 55 and 4 per cent respectively.

There is no published evidence of active defence of ranges or core areas by group-living females, but the complete lack of female transfer between groups (Liberg, 1980; Izawa *et al.*, 1984; Natoli, 1985; Natoli & De Vito, 1991) does point to some kind of repulsion of strange females. In contrast, foreign males might be able to become established in female groups (Liberg, 1980, 1981; Izawa *et al.*, 1982). The reason why males, but not females, manage to do this could be greater physical strength (although females can unite to drive away a strange male when they have small kittens: Macdonald & Moehlman, 1982; Liberg, 1983), sexual relationships, or simply because males pose a lower competitive threat than strange females, making it less worthwhile for females to exclude them. An invading female would not only compete herself for food, den sites, etc., but might also start a new matriarchal line in the group. This would pose a much more serious threat to the future reproduction of the established females than would an invading male. The situation directly parallells pride-living lions, where strange females are kept away by the pride females, but males are not; but male lions are certainly more capable of parasitising the pride females than male cats are (Schaller, 1972; Bertram, 1978).

The discussion above about territoriality of course also applies to solitary females, which likewise have easily defendable, predictable food patches: their primary homes. The situation for solitary feral females which subsist on natural prey is different. Their food is usually more dispersed and less predictable than that of house-based and other group-living cats.

Generally we expect exclusive ranges when the food resource is stable and evenly distributed, whereas variations in space and time give rise to a system of overlapping ranges (for a detailed discussion, see Waser & Wiley, 1979). Food distribution is notoriously difficult to record, and most researchers do not even mention the characteristics of the food resource; therefore the following analysis will have to be a very rough one.

Fitzgerald & Karl (1986) worked with a low density population (one cat per km²) that subsisted on a patchily distributed food source, and they recorded large overlap between female ranges. A high density population (30 cats per km²) was studied by Apps (1986). These cats lived partly on a rich and patchy food resource (ocean bird colonies), and the females had overlapping ranges. Thus, density *per se* does not have much influence on range overlap. Langeveld & Nievold (1985) reported exclusive female ranges in a population with a low density of about one cat per km². Since they radio-tracked three adjacent females simultaneously and were also able to record the replacement of one of these females by another, still with exclusive ranges, they seem to have good indications of exclusiveness. Unfortunately, the food distribution in their study area was not reported, but we predict an even prey distribution.

Range overlap in males

When discussing the spatial organisation of male ranges, we again have to be aware that the pattern may differ between seasons and that different categories of males may show different patterns. In our unpublished study (O.L. and M.S.) referred to above, the dominant males showed almost complete overlap during the mating season (Figure 7.2), whereas their smaller ranges during the non-mating season were completely separated. The ranges of subordinate males were covered by those of the dominant males all year round. Once again this demonstrates that one has to know the social status of the subjects investigated, and the influence of seasonality in the area, to understand the data obtained in a study of spatial patterns.

The reason we get these differences in male range overlap between seasons and social categories are the same as those discussed in the section on male range size. During the non-mating season food is the most important resource for both males and females, and a similar spacing pattern can be expected for both sexes. During the breeding season food is still the most important resource for females and no change in their spatial organisation is expected or found. For breeding males the most important resource is receptive females, and if that resource has different spatial and

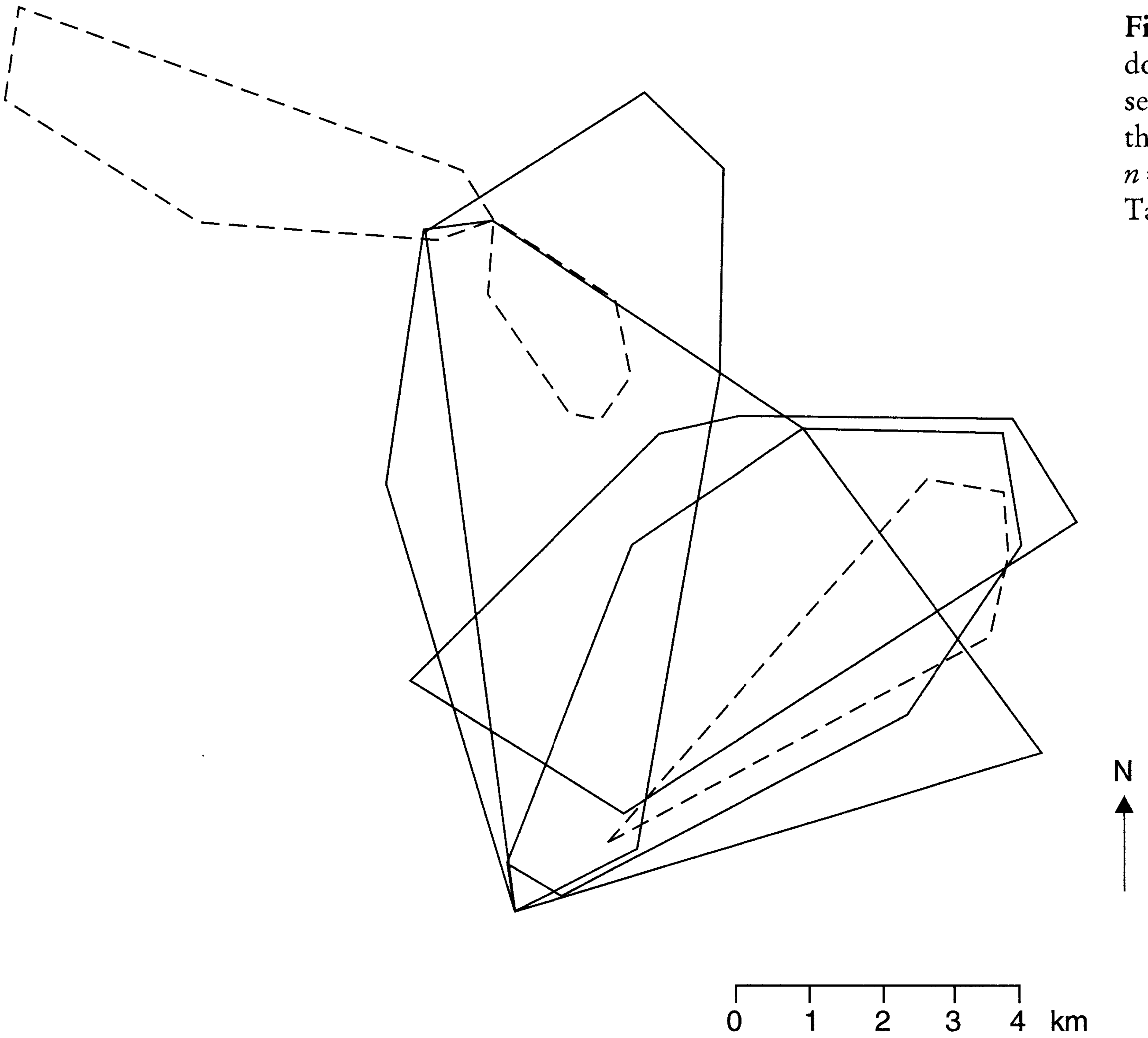

Figure 7.2. Spatial organisation of dominant males during the mating season (solid lines, $n = 4$) and during the non-mating season (broken lines, $n = 3$) in the Revinge area, 1984 (cf. Table 7.4).

temporal characteristics than food, then a different tactic has to be used to exploit it and this will give rise to a different spatial organisation (Sandell, 1989).

The male spacing pattern during the mating season will be determined by the tactic used by the dominant males to achieve matings. There are two alternatives for a male; to stay in a relatively small area trying to defend and monopolise a number of females during the breeding period, or to roam over a large area competing for receptive females as they are encountered, i.e. to stay or to roam. We suspect that the former system is only possible when it is in the interest of all dominant males in the population. It is then maintained through a mutual interest in exclusivity. It is probably impossible to defend a territory against other dominant males if they are not also interested in having exclusive areas. As soon as a roaming tactic is more rewarding for some dominant males, the whole system of exclusivity will break down (Sandell & Liberg, 1992).

If females are clumped, it may pay for a male to stay with one female group if it is very large; but then it will probably be impossible for him to monopolise the whole group, since the females are not always close together. If groups are smaller, it would probably be more rewarding for a dominant male to check several groups, thereby increasing the potential number of matings, than to defend one group, again resulting in a roaming tactic. The only case where we expect exclusive areas in males is when females are dense and evenly distributed (see above).

Given these predictions, there are very few populations of domestic cats where we would expect exclusive ranges in dominant males. Female domestic cats are seldom evenly distributed, and if they are, the population densities are low. As shown in Table 7.3, all studies, except one, with data on male spatial organisation have reported overlapping male ranges. The male overlap in the studies of Langeveld & Niewold (1985) and Fitzgerald & Karl (1986) thus is expected considering the low density of females. The female density was higher in Konecny's (1987) study, and even more so in that of Apps (1986), but still the males' ranges overlapped, possibly because the distribution of females in these studies was patchy.

The male range overlap found in all studies of group living females, was expected (see Table 7.3), and even the prediction of more than one male staying with large female groups was supported (Kerby, 1987; Natoli & de Vito, 1991, Yamane *et al*., 1996). We will come back to this in somewhat more detail in the section on Mating system, below.

The only study where exclusive male ranges were observed was that of Langham & Porter (1991) in a New Zealand rural area where the females were feral and lived alone or in very small groups that were rather well spaced. Density was intermediate (3.7 cats per km^2). This is not the situation in which we would expect exclusive male areas. Actually, the density and distribution of females resembled that of the Revinge area in Sweden (Liberg, 1981, 1983), where dominant males had overlapping ranges during the breeding season. For the time being the results of this study therefore remain somewhat puzzling.

Natal dispersal

Natal dispersal is defined as movement of a young animal from the place where it was raised to a new area where it establishes a new stable home range and starts breeding (Greenwood, 1980). Female cat dispersal in this sense seems to be infrequent as it is rarely mentioned, even in reports where male dispersal is described or mentioned (Natoli, 1985; Warner, 1985; Langham & Porter, 1991). In fact, female groups are built up and maintained because of philopatry in young females (Liberg, 1980; Panaman, 1981; Izawa *et al*., 1982). However, Liberg (1980) gave details of a few cases of female dispersal in a population of rural house cats. In all cases the dispersing young female left a residence where there were other adult females, and settled at a new household, where she was accepted by the human residents, and where there were no other female cats. The disperser moved to the nearest suitable residence, no movement was greater than 1.5 km. Yamane *et al.* (1996) also mention a case where two sibling females left their maternal group and started a new breeding group at a newly established refuse site. As mentioned above, dispersing females rarely are accepted into a foreign, established female group (in a 7-year study of approximately 20 groups, this was never seen: Liberg, 1980), but Laundré (1977) and Panaman (1981) each report one such case in their studies of single farm groups.

Male dispersal seems to be more frequent, and is described both in group-living populations (Liberg, 1980; Izawa *et al*., 1982; Dards, 1983; Natoli, 1985; Warner, 1985), and in solitary cats (Langham & Porter, 1991; Genovesi *et al*., 1995). In group-living cats males might either switch between groups

(Liberg, 1980; Izawa *et al.*, 1982) or establish themselves as loners (Liberg, 1980; Dards, 1983). Dards reported that all males dispersed from their natal groups between the age of 1 and 2 years, and that it was rare for a male cat to maintain contact with its family group after becoming sexually mature.

Liberg (1980) reported that males generally dispersed substantially further than females, but as this has not been studied anywhere else, it is not known whether this a general rule. None of the studies gives figures on dispersal distances in the two sexes, but a general impression from the literature is that males on average disperse greater distances than females .

In the Revinge area it was also found that young males allowed inside the houses of their owners, and thereby enjoying at least some protection against harassing dominant males which visited or lived in their maternal group, dispersed significantly later, or even managed to stay on, compared with their non-protected counterparts (Table 7.6) (Liberg, 1981). When comparing this with dispersal in females, which only seemed to occur when a good opportunity appeared, and considering that survival and future reproductive success of dispersing males was much lower than in philopatric males, while no such difference could be seen in females (O. L., unpublished), it was concluded that dispersal in females seems to be voluntary and related to the food situation, while in males it seems to be enforced and related to sexual competition. Again, this supports our main hypothesis that the spacing pattern in females is shaped by competition over food resources, while that in males is shaped by competion for mates.

Table 7.6. *Differences in natal dispersal between young male housepet cats that are at least partly protected from harassment by more dominant male cats, and corresponding barn cats that are exposed to the same type of harassment, in the Revinge area (Liberg, 1981 and unpublished)*

	Protected	Exposed
Dispersed 2nd or 3rd year of life	7	16
Dispersed later, or stayed	12	3
	$\chi^2 = 7.05; p < 0.01$	

Mating system, mate choice, and correlates of mating success

Throughout this review we have seen that mating tactics and other sexually related behaviour are important determinants of the spacing system of cats, especially for males. We have touched upon these issues whenever relevant, but there is also a need for a more complete overview of the sexual life of the cat in one context. In this section we will therefore summarise what is known about mating system and sexual selection in cats.

Included traditionally in the term 'mating system' are the manner of mate acqusition, number of mates acquired (in a relative sense), and presence and characteristics of any pairbonds (Emlen & Oring, 1977; Davies, 1991). As the form and extent of parental care of each sex is important in relation to the way the two sexes compete for mates, this aspect is normally also included, which is why Reynolds (1996) prefers the term 'breeding system' over mating system. Before trying to characterise domestic cats according to mating system classifications described, we thus have to look a little closer into these aspects of the cat's life. We will also attempt to assess which factors determine the mating success of individual males and, likewise, see whether females perform any active mate choice. After all, the mating system of a species is 'the outcome of the reproductive strategies used by individuals' (Clutton-Brock, 1989) or, to emphasise also the importance of external factors, 'the outcome of a battle among competing interests, with opportunities and constraints set by the environnement' (Reynolds, 1996).

Detailed investigation of mating behaviour and sexual selection in cats have been performed in only a few studies. Even so, variation on the theme seems bewildering. To illustrate this, we will give a brief summary of these studies, before attempting to make some generalisations on male mating tactics. We also take a brief look at female behaviour and the possible existence of female mate choice. Correlates of female reproductive success other than mating behaviour are not dealt with here (see Kerby, 1987; Macdonald *et al.*, 1987, and Chapter 6). The section ends with a short synthesis on mating system in domestic cats.

Intra-male competition for access to mates: five case histories

Unfortunately, none of the studies of mating behaviour in domestic cats concern populations characterised purely by solitary females, and therefore our picture of the mating system in cats is biased towards group-living populations. However, one of the most detailed studies of mating behaviour and sexual selection in cats so far, the 8-year Revinge study in Sweden (Liberg, 1980, 1981,1983, 1984a, b, c) was performed on a mixed population in this respect. The females in the rural study area occurred as house cats, alone or in small groups (1–6 adult females per cat-holding residence, mean 2.2) at variously spaced residences. Each dominant male included several female cat residences in his range. There was a large overlap between different dominant male ranges, but relative dominance varied from place to place. At each residence with female cats there was only one male holding the 'Breeder' position, but other males (including males that were 'Breeders' in other female residences) also visited the place regularly, presumably in search of unattended females, and occasionally also to test the dominant male. Hardly any Breeder restricted himself to only one female residence. The system was dynamic, with occasional changes in the dominance order even within the same breeding season, although the latter was rare. The average dominant male included 4.4 female residences (range 1–9) in his home range, of which he held Breeder status in 2.5 (range 1–5). The number of sexually mature females in his home range was 11 (7–15) and in the residences where he held Breeder status it was 7 (4–8).

Females in oestrus were often courted by more than one male (maximum four) simultaneously, but the local Breeder, when present, always kept the position closest to the female. When the Breeder was absent, other males took over this central position. Only central position males performed copulations. That Breeders obtained most of the matings in the groups where they were dominant, and had a high reproductive success relative to subordinate males, was confirmed through a 'paternity index' that was constructed from the combination of behavioural data and the inheritance of coat colours. Reproductive success in males was significantly and positively correlated to dominance, measured as the proportion of 'victories' in male–male aggressive interactions (Liberg, 1981). Dominance was also correlated with age and body weight.

This study also demonstrated how a dominant male might solve the optimisation problem between staying and guarding the female he is courting until the end of her oestrus, and leaving to find a new female. In one case a dominant male (male A) showed varying behaviour towards receptive females as the breeding season progressed. Early in the season he guarded one female for two days, and none of the other males in the area showed any interest in the female before or after that. During the peak mating season the top male stayed less than one day with a receptive female, and that same female was courted by male C (third in the hierarchy) before, and by male B (second in the hierarchy) after male A took her over. Thus, the dominant male showed dynamic behaviour as the mating season progressed. The other categories of males also showed changes in their behaviour: when male A guarded during the whole oestrus, the other males did not remain in the vicinity, but when he just took over the female for a while, they remained close by (Liberg & Sandell, 1988, and unpublished).

In the Portsmouth dockyard feral cat population (Dards, 1978, 1983), most females lived in groups that also were larger than in the Swedish study (2–9, mean 5.4). Also here 'mature males' visited several groups, and there was range overlap between these males, so that many if not most groups were visited by more than one mature male. In this study, however, some males appeared more permanently attached to just one group 'like a pride lion'. In at least one case it was reported that such a stationary male (which also was unusually large) had 'almost exclusive control over one group' (Dards, 1983, p. 150). Dards also noted that females in oestrus often were courted by several males (up to six) simulataneously. She never saw any open aggressions between males in this situation, and assumed the reason for this was a dominance hierarchy, although she had no direct evidence for that. Dards also indicated that size and age were important factors determining dominance, and presumably mating success.

On Ainoshima Island, Japan, the earlier study of Izawa (1984) and Izawa *et al.* (1982), was resumed from 1989 onwards (Yamane *et al.*, 1994, 1996, 1997). The female groups Yamane and co-workers were studying were of about the same size as in Portsmouth (26 females distributed over 5 groups, mean 5.2: Yamane *et al.*, 1996), but the food resource was probably richer and more concentrated. A remarkable feature of this population was that there were almost twice as many adult males (48) as females (26), and most of these males were permanently attached to one female group, but not to the one they were born in. Males courted predominantly females in their own group, but none managed to monopolise a whole group, and many (but not all) of them also courted females in other groups (Yamane *et al.*, 1996).

Also in this study several males aggregated around a female in oestrus (up to 11), and there was a correlation between male position and copulation success, but not as strong as in the Swedish study (Liberg, 1983). In 18 of 23 cases where multiple courtship was observed, the male with the shortest mean distance from the female (the 'courtship distance', measured over the whole oestrus) was seen to copulate; in the other five cases it was number two or three. Mean 'courtship distance' of copulating males was 0.57 m and of non-copulating males 1.53 m. More than one male copulating with the same female was seen in only two of the 23 cases. Body weight was found to be one of the most important factors influencing fighting ability, courtship rank and mating success. The latter two were also correlated with age. However, it was interesting to note that group membership also had an influence; males were more successful in their own groups than in foreign groups. Fighting ability was not found to correlate significantly with age, but this might be because males 5 years old and older were pooled, and this class might have contained some very old males. Copulations were only observed by males at least 4 years old. On the other hand, Yamane (1998) found that 50 per cent of offspring born in the group studied were sired by males strange to the group.

Kerby (1987) investigated the cat groups at two pig farms in different parts of Oxfordshire, England. One group was large with 8–16 adult females and around 10 males, and the other smaller, with 3–5 adult females and 4–6 males. Kerby was not able to determine individual correlations between the mating success of males and other characteristics such as age and weight, but she made interesting observations of the relationship between male mating success and affiliation to the study group. She categorised males as 'Central' or 'Peripheral', based upon their attendance record in the group. In the large group Peripheral males were more aggressive and scored a higher mating success than Central males, while in the smaller group it was the other way round. Kerby argued that the larger group had other female cat groups nearby, and the most dominant breeding males split their time between the different groups. Central males were generally younger and less competitive and therefore were sticking to their natal group. The smaller group, on the other hand, was several kilometres away from the next place with female cats. There dominant breeders chose to stick to just one (the study-) group, thereby forcing subordinate males to a more peripheral status.

The largest cat group ever investigated for sexual behaviour lived in a market square in central Rome and contained 81 residential cats (37 adult females, 4 subadult females, 32 adult males and 8 subadult males) (Natoli & De Vito, 1988, 1991). Most of the males 'showed sign of sexual maturity' and were courting females in their own group, but only 19 were seen to copulate. Eleven of these males stood out for displaying frequent sexual behaviour. Visits by males not belonging to the group were also observed, but it was not reported whether these ever participated in courtship. Whether the resident males also courted females in other groups was unknown, but the authors presumed that this might have been the case.

This study differed in many respects from the others reported here. Male aggregations around females in oestrus were extremely large, with up to 20 males courting a particular female during her oestrus and up to 16 males doing so simultaneously (Natoli & De Vito, 1988). There was no correlation between courtship distance and copulation frequency, as found in Liberg (1983) and Yamane *et al.* (1996). The authors found indications of a linear dominance hierarchy among the males, but they failed to find any correlation between dominance and measures of mating success such as courtship distance, number of females courted or copulation frequency. Courtship seemed more to be like a queue of equals where some males were so eager that they tried 'even to mount the male mounting the female', rather than an ordered hierarchy where only the top males were successful. Nevertheless, there was one male with an outstanding conflict score: he was involved in 38 of the 64 conflicts observed and he won all but two of them. This male was also outstanding with respect to the mean number of successful copulations. Still, he was observed to tolerate subordinate males mating females in his presence, and also to be replaced by other males during mounting attempts.

Male mating tactics: some generalisations

Here we attempt to make some generalisations about male mating tactics based primarily on the collective findings of the five studies reported above (unless otherwise stated and without repeating references).

Male cats compete for females singularly. The unusual degree of sociality in domestic cats, expressed in their ability and tendency to live in groups whenever favoured by resource distribution, has – as far as we know – never resulted in any male coalitions, such as seen in lion (Schaller, 1972) and cheetah (Caro & Collins, 1987). Mating success of male cats is strongly correlated with dominance which in turn is correlated with age and body weight, but also to location. Males residing in a particular female group might be dominant over outsiders, even if they are younger and/or smaller. In these respects cats are similar to most polygynous mammals (Clutton-Brock, 1989).

As predicted from theory (see the Range overlap section, above), males in almost all cases fail to maintain exclusive mating territories, although this might occasionally occur (see Dards, 1983; Langham & Porter, 1991). An extreme case of male exclusion and monopolisation of a number of females was reported by Pontier & Natoli (1996): during one season, one male cat managed to sire 95 per cent of the 18 litters delivered by 10 females belonging to five different residences. His mating success was confirmed through inheritance of a rare coat colour gene that only he possessed. However, this case must be regarded as exceptional.

Not having exclusive mating ranges does not mean that male cats can not hold exclusive mating priorities. In areas with many small female groups, one specific male can hold a monopoly on mating in one or several of these groups, depending on how widely they are scattered. In larger groups it becomes increasingly difficult for just one male to exclude rival males from 'his group(s)', and here we observe a transition to multimale groups, but still with the possibility that males might try to breed in more than one group. Regardless of group size, pairbonds – other than during courtship – do not seem to occur in domestic cats.

There is variation regarding degree of male attachment to one particular female group. Here probably resource abundance and distribution is more important than female group size. In the Revinge rural residences and in the Portsmouth dockyard, some males spent a large portion of their time in just one residence (group) and could thus be regarded as resident there; but many others roamed freely among them. In comparison, in the Japanese fishing village with its large fish dumps, almost every individual male had one 'feeding group' to which he belonged. Resident males are, however, free to also court females in other groups. Whether they do so or not probably depends more on the distance to these other groups than on the size of the groups, as was demonstrated by Kerby (1987).

What are the options for a subordinate young male in this system? In a population of dominant roamers, roaming would be useless, as he would not be able to take over any of the receptive females he encounters, and he would be more susceptible to harassment from dominants during his movements. Therefore the best tactic for a subordinate male would be to stay at home, where he might be able to mate with receptive females in his group when no dominant males are present (e.g. Liberg, 1981, 1983; Kerby, 1987). Thus, if roaming is the tactic employed by the dominant males, staying will be the best tactic for subordinate males until they are old and strong enough to establish themselves as dominant roamers. When staying is the dominant male tactic, roaming will be the best alternative for subordinates as was indicated by Kerby (1987). Their only chance to achieve matings in that situation is to encounter females with no dominant male present.

A spectacular element in cat reproductive behaviour is the occurrence of large aggregations of courting males around oestrus females. These probably have no specific function in themselves, but are an inevitable consequence in situations where many males live close together and females come into oestrus one after the other in a location that is predictable. In small groups and/or low density areas, where the courting male aggregations are small, the most dominant male keeps a mating monopoly as long as he is present; but at times his optimal choice might be to leave a particular female, even if that means his subordinate rivals will have a chance to mate that female.

One of the most remarkable things with these aggregations is that the degree of open competiton seems to decline with the size of the aggregation. In the largest group almost all structure in the competition collapsed; still the most dominant male had the most successful matings, although he did not manage to monopolise females in any way. The reason for this lack of open aggression and the upheld correlation between dominance and mating success in these large male aggregations could be either that most of the competition occurs at the sperm level, or that the situation is so artificial, and in an evolutionary sense so recent, that the cats simply have not had enough time to adapt to it (Natoli & DeVito, 1991).

In other mammal species with large multi-male groups, such as in lions and in some primates and ungulates, it is common that a male gains temporary dominance over his rivals while he is consorting with a female, and often the consorting couple isolates itself from the rest of the group. In cats, this works with small groups, but obviously not when groups exceed a certain size.

Female mate choice

Do female cats choose their mates? The answer is not straightforward. At a first and superficial glance female cats seem rather indiscriminant and appear to mate willingly with most males competitive enough to reach a mating position. However, several authors have reported that female cats under some circumstances might prefer 'familiar males' which would give stationary males competitive advantages (e.g. Leyhausen, 1979; Dards, 1983; Natoli *et al.*, 1999). Unfortunately, no hard data how this is expressed and realised have ever been presented.

But there are other subtle ways in which the female might influence the paternity of her offspring, for example through inducing increased competition between courting males. A female courted by a number of males sometimes makes quick rushes, which might break up a 'locked' dominance situation between males in a courtship aggregation, and force the dominant male to re-establish his central position again from scratch (Liberg, 1983). Or she might induce competition by increasing scent-marking during oestrus which will attract more males to her (cf. Janetos, 1980).

Female cats have a high copulation frequency (15–20 times per 24 h) during their 4–5 days of oestrus (Leyhausen, 1979; Eaton, 1978; Liberg, 1983). Functional aspects of multiple matings in females have received an increasing amount of attention in recent years, and a large number of possible benefits to the female of this behaviour have been proposed (see e.g. Halliday & Arnold, 1987; Hunter *et al.*, 1993; Reynolds, 1996) and discussed (Eaton, 1978; Liberg, 1983), but never tested.

Another aspect of mate choice concerns avoidance of inbreeding. The detrimental effects of inbreeding in domestic cats are not known, but close kin matings are not uncommon; six out of 17 matings in the Revinge study area were with related females from the males' natal group (O.L. and M.S., personal observations). There was, however, a tendency for females with males in their groups to leave home more often during oestrus than females without males in their groups (Liberg, 1983). This is possibly a behaviour selected to avoid inbreeding. Unfortunately, these as well as most other aspects of female reproductive tactics remain unexplored.

The mating system in domestic cats

Although mating tactics and system have not been investigated in low density domestic cat populations with solitary females, it is likely that this is the original situation in which the reproductive behaviour of the ancestors of domestic cats evolved. The mating system to be expected in that situation is promiscuity in both sexes, with 'roaming' (or 'roving') being the dominant male mating tactic (*sensu* Clutton-Brock, 1989), or a 'scramble competition polygyny' (*sensu* Davies, 1991). This basic pattern can be discerned also in group-living cats. Males are reluctant to limit their mating activities to just one female group, even if the group is large. We rarely find 'uni-male' or 'multi-male polygyny' in the sense normally conveyed by these terms, meaning that one or a group of males keeps control over one particular female group (Davies, 1991), as seen, for example, in lions (e.g. Bertram, 1975), many primates (e.g. Harcourt, 1979; Andelman, 1986; Wrangham, 1987) and some ungulates (Klingel, 1975; Clutton-Brock, Guinness & Albon, 1982; Berger, 1986). The reason for this discrepancy might be the artificial food resource situation in domestic cats, which allows different female groups to live in close proximity. In situations where female groups live far apart, reflecting a more natural situation, male cats indeed tend to stick to just one group. Thus, it is probable that basic mating behaviour in cats has not changed much with domestication, only that cats show phenotypic plasticity in their adaptation to new situations created by human interference.

Spatial organisation in other felids

All of the above-mentioned difficulties in studying free-roaming domestic cats apply to an even greater extent to studies of wild felids, and in many cases it is just as difficult to interpret the data on their spatial organisation. Most wild felids live at low densities in rough terrain and are very hard to spot; radio-telemetry is the only reliable method of securing data on spatial organisation. Again, data on at least two adult individuals of the same sex is the absolute minimum required to study spacing patterns, which means we have a rather small number of studies on only a handful of the 37 wild species (Table 7.7).

The negative correlation between density and home range size found in domestic cat is also present in wild felids, both for all species combined ($r = -0.94$, $n = 12$, $t = 8.88$, $p < 0.01$) and separately for the cougar ($r = -0.96$, $n = 5$, $t = 6.02$, $p < 0.01$, data from Hemker, Lindzey & Ackerman, 1984) and bobcat ($r = 0.98$, $n = 5$, $t = 7.60$, $p < 0.005$, data from McCord & Cardosa, 1982). As discussed above we think both of these variables are influenced by prey biomass (the total weight of prey in the area). For lions a correlation was indeed found between range size and lean-season prey biomass, and between the latter and measures of density (van Orsdol, Hanby & Bygott, 1985). A negative correlation between home range size and prey density has been reported for the bobcat (Litvaitis, Sherburne & Bissonette, 1986). Increasing range size with decreasing prey density and vice versa have been reported from several studies on Canadian lynx (Ward & Krebs, 1985; Poole, 1994). A number of studies have demonstrated the close correlation between lynx density and changes in density of its main prey, the snowshoe hare (Elton & Nicholson, 1942; Brand, Keith & Fisher, 1976; Ward & Krebs, 1985; Poole, 1994; O'Donoghue *et al.*, 1997) . Thus, both density and home range size in wild felids are strongly influenced by prey biomass, and this explains the correlation between the two variables.

For the same reason as discussed for domestic cats, female spacing pattens in wild Felidae should also be determined by the characteristics of the food resource. Exclusive ranges are expected when food is dense, evenly distributed and stable, while in all other situations we expect overlap. Reliable data from wild felids are so scarce that these predictions cannot be properly tested, and even when data on overlap are given, they still have to be regarded with care due to methodological problems (see e.g. Breitenmoser *et al.*, 1993). These restrictions have to be kept in mind in the following discussion.

Female tigers in Royal Chitawan National Park, Nepal, had a rich, stable and evenly distributed food source, and they had exclusive ranges (Smith, McDougal & Sunquist, 1987). In the Idaho wilderness ungulates show seasonal migrations between high and low elevations. Female cougars there had almost totally overlapping ranges in winter when the ungulates were concentrated at lower elevations (Seidensticker *et al.*, 1973). During summer, when prey were more evenly spread out, the ranges were larger, but overlap was greatly reduced. In a habitat with patches of variable prey density, female lynx had overlapping ranges and several animals utilised the same high density patch (Ward & Krebs, 1985). With evenly distributed prey female bobcats also had exclusive ranges (Bailey, 1974).

However, density of the felid population itself also influences overlap. In a newly introduced population of European lynx with low density, females had exclusive ranges (Breitenmoser *et al.*, 1993) while in another population of the same species, where prey density and distribution was similar but the lynx population was saturated and 4–5 times more dense, the range overlap in females was also higher. In Candian lynx, female ranges overlap at peak densites, but are exclusive during phases with low densities, although the ranges then are larger.

The only wild felid where females live in stable social groups is the lion (Schaller, 1972). The function(s) of group living in lions have been discussed at length. The earlier work stressed the advantage of group hunting (Caraco & Wolf, 1975), possibly modified by kin selection (Rodman, 1981; Giraldeau & Gillis, 1988) and risk avoidance (e.g. Clark, 1987). These explanations have little bearing for domestic cat groups, as cats do not hunt cooperatively. However, in an elaborate analysis, Packer *et al.* (1990) point out that hunting efficiency is not enough to explain group-living in female lions. Instead they provide data and arguments that communal defence of cubs against incoming infanticidal males and communal defence of territory against competing female groups might be more important advantages for group-living in female lions. The former reason seems questionable since it should apply to many solitary carnivores where infanticide has been demonstrated as well. But the latter reason also has strong implications for

Table 7.7. *Range characteristics of wild solitary felids*

			Female ranges				Male ranges				
Species	Place of study	Density n/100 km²	X km²	Range	*n*	Overlap/ Exclusive	X km²	Range	*n*	Overlap/ Exclusive	Reference
Geoffroy´s cat	Chile	–	4.3	2.3–6.5	3	O	9.2	3.9–12.4	5	E	Johnson & Franklin 1991
Canadian lynx	Minnesota	–		51–122	?	O		142–243	?	E?	Mech 1980
	Alaska	0.9	70	51–89	2	–	783		1	–	Bailey *et al.* 1986
	Canada	27–30	14	7–36	21	O	23	3–68	25	E	Poole 1994, 1995
	Canada	2–5	63	34–91	2	(E)	44	30–58	2	(E)	Poole 1994, 1995
Bobcat	Idaho	5	19	9–45	8	E	42	7–108	4	E	Bailey, 1974
	Minnesota	4–5	38	15–92	6	E	62	13–201	16	O	Berg, 1979
	California	5	43	26–59	4	O	73	39–95	3	O	Zezulak & Schwab 1979
	Tenessee	–	26		3	O	77		2	O	Kitchings & Story 1984
	Alabama	77–116	1.1		6	E	2.6		6	E	Miller & Speake 1979
European lynx	Poland	3–5	133	74–147	4	O	248	190–343	5	O	Schmidt *et al.* 1997
	Jura Mts	0.9	168	71–243	4	E	264	237–281	3	–	Breitenmoser *et al.* 1993
Cougar	Idaho	1.4	268	173–373	4	O	453		1	–	Seidensticker *et al.* 1973
	Utah	0.3–0.5	685	396–1454	4	O	826		1	–	Hemker *et al.* 1984
	California	3.5–4.4	94	54–119	3	O	178	78–277	5	O	Sitton *et al.* 1976
	California	1.5–3.3	66	57–74	2	–	152	109–238	4	O	Kutilek *et al.* 1980, cited in Hemker *et al.* 1984
	Alberta	3–5	140	62–318	21	O	334	221–438	6	E/O	Ross & Jalkotzy 1992
Jaguar	Brazil	4–8	30	25–34	2	(O)					Schaller & Crawshaw 1980
	Brazil	1.5	>10		2	–	33	28–40	5	O	Rabinowitz & Nottingham 1986
	Brazil		140	97–168	4	O	152		1	–	Crawshaw & Quigley 1991
Tiger	Nepal	3	21	10–51	11	E	54	19–151	?	E	Smith *et al.* 1987

domestic cats, especially when one considers the preconditions the authors gave explaining why group defence of a feeding territory would be selected for only in lions, and not in other felids: 'First, lions live at higher density than any of the other large cats, and high population density can lead to the shared defense of a communal territory . . . Second, the relative large size of the lion's prey may result in a pattern of resource renewal that permits group foraging in a common territory' (Packer *et al.*, 1990). Both these conditions apply to group living domestic cats as well: high density (because of the abundant and predictable food source) and a renewal rate of the resource that permits group foraging. Perhaps the reasons why lions and domestic cats live in groups are not so different after all, and this is substantiated by the calculations of Macdonald *et al.* in Chapter 6.

Whereas female spacing patterns are determined by a single resource, food, males have two decisive resources: food and receptive females. Also for wild felids, male ranges are larger than those of females, probably for the same reason as discussed above for domestic cats. For all species pooled in Table 7.7, mean male:female ratio in range size was 2.0 (SD= 0.35, $n = 11$; only studies where at least three animals of each sex had been radio-tracked were included in this calculation). Outside the mating season, there should not be any notable differences in male and female spatial organisation. Some supporting evidence was found during a snowshoe hare decline in the Yukon, where both male and female lynxes showed the same response to the declining food resource (Ward & Krebs, 1985). In the European wild cat males and females had about the same monthly range sizes during winter, but when the mating season started, the males increased their ranging behaviour substantially (Corbett, 1979).

In situations where males have exclusive breeding areas they might have to maintain them throughout the year. Unfortunately there are no data to test this; data on range sizes analysed separately for breeding and non-breeding seasons are sorely needed. In species where breeding occurs at any time of the year the males will of course employ their breeding tactic throughout the year.

In wild felids different categories of males might also exist, including roamers. Even when the authors in many studies mention non-resident males, they usually disregard them as 'transients', assuming that only the resident males take an active part in breeding (e.g. Seidensticker *et al.*, 1973; Bailey, 1974; but see Breitenmoser *et al.*, 1993). From studies of other carnivores there are indications that wide-ranging, 'transient' males perform most of the matings (e.g. Mills, 1982; Sandell, 1986). Thus, we have reason to suspect that 'transient' males in many felid species play an important role in the breeding of the population.

As predicted for domestic cats, wild male felids should also have exclusive ranges when females are dense and evenly distributed, whereas a patchy distribution and/or low female densities would favour a roaming male tactic. Indeed we find exclusive ranges in males when females are evenly spaced and have ranges of less than about 20 km^2, i.e. when density is rather high (see Table 7.7; Bailey, 1974; Miller & Speake, 1979; Sunquist, 1981). But large female ranges seem to cause overlap among the males, even if the females are evenly spaced (see Table 7.7; Berg, 1979). When female ranges overlap, we need to know whether there are patches of high female density with low density areas in between, or if there is an even distribution. The former situation would resemble the female group pattern in domestic cats (see above), resulting in overlapping male ranges, independent of density. An even distribution of overlapping female ranges would be equivalent to the situation with exclusive female ranges, and should give rise to exclusive male ranges at high densities and overlapping male ranges at low densities. In this case we would expect to find a threshold density at which the system changes from exclusive to overlapping male ranges. This value will of course differ between species, but we believe the change would take place in a rather narrow density interval. The data needed to test these predictions in wild felids are unfortunately lacking.

We conclude that there are no great discrepancies between domestic cats and wild felids regarding the principles of their spatial systems and the factors influencing them. We therefore believe that future studies on domestic cats have great potential, not only for increasing our understanding of that species in itself, but also to gain further insight into felid behavioural ecology generally.

Concluding remarks

We have seen that domestic cat population density varies by three orders of magnitude, from less than one cat, to more than 2000 cats per square kilometre.

Density level is determined by food abundance. Home range size also varies by three orders of magnitude; in females from 0.1 to almost 200 hectares, in males up to almost 1000 hectares. Female range size is determined by food abundance and distribution. Males have ranges that are on average three times larger than those of the females. Male ranges are larger during the mating season, and dominant males have larger ranges than subordinates. The size of dominant male ranges is determined by female density and, even more so, by female distribution.

Group living in cats depends on human subsidies, and is an effect of rich food concentrations, like dairy farms or city refuse depots. The groups are stable and consist of female kin, with males usually being loosely attached. Most young males disperse from their natal groups, while young females are philopatric. The home ranges of group-living females overlap very little with those of females from other groups. Solitary females show range overlap when living on patchily distributed prey. Male home ranges overlap extensively, especially during the mating season. Males perform a roaming mating tactic, even when females live in large groups. This pattern of spatial organisation in the domestic cat is also found in various wild felids, making the former a handy 'model' species for studies of general patterns in felid behavioural ecology.

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