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Spacing pattern in a social group of stray cats: effects on male reproductive success

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Reproductive consequences of male spacing patterns have received relatively little attention in nonterritorial mammals, in particular in group-living species, where most studies have focused on the relation between social rank and reproductive success. We investigated the effects of spacing pattern on male reproductive success within a social, nonterritorial, promiscuous population of stray cats, *Felis catus*. Male home ranges overlapped home ranges of many females, consistent with a promiscuous mating system. Furthermore, males with the largest home ranges included the most female home ranges; they successfully reproduced with these females and had the highest reproductive success. Home range size predicted male reproductive success even when controlling for the effect of social rank. However, males also reproduced with females whose home range did not overlap their home range, suggesting that males can make quick excursions outside their home range to find new mating opportunities. We conclude that, in group-living situations, a male's ability to maintain a large home range may be one of the principal causes of variation in mating success in the stray cat.

The distribution of females is expected to be determined largely by the distribution of resources, because access to resources, including food or shelter, affects female reproductive success. Alternatively, when males are free from parental care, their distribution, as well as their ability to copulate with receptive females and to monopolize access to more than one female, should depend on the size and ranging patterns of females, the degree of synchrony of female receptivity to mating and the size and stability of female groups (Emlen & Oring 1977; Wittenberger 1981; Clutton-Brock 1989; Sandell 1989; Ostfeld 1990). To increase their reproductive success, males can use two basic categories of spacing behaviour, territorial or nonterritorial. In general, territorial tactics appear when female movements are predictable, their ranges are small or they require a resource that can be easily monopolized. Such territorial behaviour is then assumed to prevent reproductive competitors from gaining access to females living on the area defended by the male (Emlen & Oring 1977; Clutton-Brock 1989). If females cannot be easily monopolized (e.g. females' ranges are too large to be defended, or females range widely, have unpredictable movements or form large groups), males may adopt several types of nonterritorial tactics. In particular, they may attempt to follow and defend their access to a group of females, establish dominance relationships or simply follow females and mate opportunistically (Emlen & Oring 1977; Clutton-Brock 1989). In this last case, the attributes that influence mating success the most will be the searching ability and home range size of males (Fisher & Lara 1999). Female behaviour may nevertheless influence the relative importance of searching behaviour to male mating success (Davies 1991). Prolonged advertisements, conspicuous movements or increase in home range size may permit females approaching oestrus to increase the probability that several males find them, therefore inciting conflict or multiple matings (Lott 1991; Jarman 1991).

Although spacing patterns are a common form of reproductive competition among male vertebrates, the exact reproductive consequences of this behaviour are often poorly understood (Lacey & Wieczorek 2001). Relations between spacing behaviours and reproductive success, that is, male copulatory and fertilization success, has mainly focused on territorial species, mostly when males and females form explicit social bonds. In many of these studies, genetic paternity analyses have revealed that male defence of a territory does not preclude the females resident on that territory from copulating with other males (e.g. Birkhead & Møller 1992; Morin et al. 1994; Hoogland 1995; Goosens et al. 1998; Lacey & Wieczorek 2001). In comparison, reproductive consequences of male

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spacing patterns have received relatively little attention in nonterritorial mammals, in particular in group-living species, where most studies have focused on relations between social rank and reproductive success (e.g. McCann 1981; Dewsbury 1982; Cowlishaw & Dunbar 1991; Pereira & Weiss 1991; Haley et al. 1994; Ellis 1995). Some of these studies reported a lower than expected correlation between the social rank of a given male and his reproductive success (e.g. Natoli & De Vito 1991; Pereira & Weiss 1991; Berard et al. 1993; Inoue et al. 1993; Say et al. 2001). Those results suggest, then, that social ranking should be regarded, not as a comprehensive description of male reproductive success, but rather as one of the many axes along which males compete for access to reproductive females. Male spacing patterns could be another important axis. In particular, roaming over large areas could increase access to potential mates (Gaulin & Fitzgerald 1986, 1989).

The domestic cat, *Felis catus*, provides an ideal opportunity to investigate the effects of spacing pattern on male reproductive success within a social, nonterritorial population. In urban, high-density environments, stray cats form large multimale–multifemale groups (Liberg et al. 2000). A dominance hierarchy exists between males (Natoli & De Vito 1991; Liberg et al. 2000; Say et al. 2001). Nevertheless, with many competitors attempting to mate with females, male cats are unable either to monopolize females (Natoli & De Vito 1991) or to ensure their paternity (Yamane 1998; Say et al. 1999). Consequently, social rank only partially explains the number of kittens sired by each male (Say et al. 2001). Rather than defend females with whom they have copulated, males adopt a searching strategy to gain access to as many females as possible (Say et al. 2001). In spite of the absence of aggressive defence of home ranges and the large overlap in home ranges, males also pass much of their daytime patrolling and marking their home range (Liberg et al. 2000; Say 2000). Maintaining these spatial behaviours could be explained if the spacing pattern of males is a form of reproductive competition in nonterritorial male cats. In particular, patrolling large home ranges may allow males to obtain many copulations with different females and thus to increase their reproductive success.

To test this hypothesis, we assessed the spacing pattern of both sexes over 3 years in a social group of stray cats. We examined whether reproductive males expanded their home range during the breeding season to include more females within their home range and whether males with the largest home ranges had the highest reproductive success (as previously determined by paternity analysis: Say et al. 1999). We predicted a positive correlation between home range sizes, the number of female home ranges overlapped and male reproductive success (Gaulin & Fitzgerald 1986, 1989).

METHODS

Study Area and Population

We studied a population of feral cats in the park surrounding the Croix-Rousse hospital in Lyon, France. The study site was a typical urban habitat for stray cats (Rees 1981; Tabor 1983; Natoli et al. 1999; Liberg et al. 2000). The park was isolated from other suitable habitats (e.g. parks, cemeteries, individual gardens, small waste grounds) by highways and buildings. It provided good cover for females, and large quantities of food were provided daily at 1200 hours by hospital staff at five feeding sites. This population has been monitored since 1993. All cats were individually recognizable by sight from their coat colour pattern and hair length or from coloured collars. Typically, the 7.2-ha park was inhabited by 25–28 adult males (>10 months old, the age of the youngest successfully reproductive males within the population; Say et al. 1999) and 25–38 adult females (>8 months old; Say 2000), with a density of 7–9 adults/ha. Females in oestrus show typical behavioural patterns characterized by prolonged vocal advertisements and conspicuous movements (Beaver 1977). A clear period of reproduction occurs between January and July with a peak of oestrus in February (Say et al. 2001), when daylength increases. Females' oestruses are synchronized (Liberg et al. 2000). No evidence of female mate choice has been found (Natoli et al. 2000).

Each year, from 1996 to 1998, we assessed the dominance hierarchy in males (Say et al. 2001). Briefly, we used the focal animal sampling method (Altmann 1974) to record agonistic behaviours of males (Natoli & De Vito 1991). Outcomes of agonistic interactions allowed us to construct a dominance matrix (Martin & Bateson 1993) based on the direction rather than the number of interactions. For each male, we calculated a dominance index (Martin & Bateson 1993), in which males with the highest index values were considered dominant. Male cats were then categorized into three social classes (high, medium or low social status) by dividing the scale of rank into three equal sections to have the same number of individuals in each social class. The reproductive success of males was estimated from the number of kittens that they sired each year, based on paternity analysis using microsatellite genetic markers (Say et al. 1999). Paternity analysis identified a high rate of multiple paternities in litters (80% of litters were sired by more than one male; Say et al. 1999) and a weak relation between the social rank of males and their reproductive success. High-ranking males did not sire more kittens than did medium-ranking individuals (Say et al. 2001).

Home Range Estimation

To document the spatial distribution of males and females during both the mating and nonmating periods, we used direct observations to delineate the areas occupied by cats resident on the study site between 1996 and 1998. A transect of 25 min covering the whole park was walked once or twice each day (mean = 1.2 times per day) during daylight hours and from 11 to 23 days per month (mean = 16 days). We allowed a minimum of 5 h between successive transects to avoid nonindependence in the data. Every time a cat was observed, its position was plotted on a digitalized map of the study area and converted to *X* and *Y* coordinates. We used the 95% minimum convex polygon estimator to calculate home ranges (Mohr & Stumpff 1966) using Ranges V software (Kenward 1990). The polygon convex method was chosen because cats used the whole of their home range rather than a limited number of core areas interconnected by a network of narrow pathways. We excluded from analysis the 5% of data points furthest from an animal's centre of activity (defined as the arithmetic mean of the X and Y coordinates), because the low frequency of extreme outlying points (resulting, for example, from occasional excursions from the home area) would otherwise considerably expand the home range. The relation between home range size and the number of available locations, as well as the percentage of overlap between areas occupied by different cats, was also generated using Ranges V (Kenward 1990).

Data Analysis

To verify whether home range size changed between years for a given individual, we used generalized mixed models (GLMMs). In this analysis we used individuals that did not change reproductive or social status during the period of study. Sex differences in ranging pattern can decrease outside the breeding season (Gaulin & Fitzgerald 1986, 1989), so we used paired t tests to test whether home range size changed between the periods of breeding (January–July) and nonbreeding (August–December) for adult cats. We then performed one-way analyses of variance (ANOVAs) to test for the effects of sex and adult status on home range size.

To investigate whether increasing home range was an efficient way to increase the number of females encountered (estimated by the number of females who shared a part of their home range with that of a given male), we used a linear regression to analyse whether the number of females included in a male's home range depends on male home range size. To examine whether home range size affected reproductive success (estimated from the mean annual number of kittens sired) independently of social rank, we applied an analysis of covariance (ANCOVA). Only reproductive males of high or medium social ranking were taken into account in the ANCOVA. Low-ranking males were excluded because their home range size was not in the same range of values as the high and medium social classes. Statistical analyses were performed with R software (StatSci Mathsoft, Ihaka & Gentleman 1996).

RESULTS

Home range size in both sexes did not differ between years (GLMM: $F_{2,70} = 0.30$, $N = 36$, $P = 0.74$) or between the breeding and nonbreeding periods (paired t test: males: $t_{24} = 1.53$, $P = 0.14$; females: $t_{34} = -0.49$, $P = 0.63$), so we pooled all observations regardless of the reproductive period and year to estimate the home range size of each cat as well as the percentage of overlap between areas occupied by different cats. In cases where an animal changed in status (e.g. becoming reproductive or dominant) during the period of study, we calculated one home range size for each corresponding status and used the home range estimated from the largest number of fixes in the analysis.

We defined home range size and overlapping ranges for 60 cats ($N = 35$ females, 22 of which were adults, and 25 males, 18 of which were adults). For all these individuals, curves representing the relation between the number of locations and home range size estimation reached an asymptotic value. The number of visual fixes per animal used in our analyses ranged from 53 to 395.

The mean ± SE area occupied by a male was 0.80 ± 0.20 ha, four times larger than the area occupied by females (0.19 ± 0.02 ha; ANOVA: $F_{1,58} = 4.67$, $P = 0.03$). Mean home range size of sexually mature females did not differ from those of younger females (0.18 ± 0.03 ha, $N = 13$ versus 0.21 ± 0.08 ha, $N = 22$; $F_{1,33} = 1.02$, $P = 0.28$). However, sexually mature males occupied areas, on average, 10 times larger than those of nonreproductive males (1.51 ± 0.30 ha, $N = 18$ versus 0.15 ± 0.10 ha, $N = 7$; $F_{1,23} = 9.63$, $P = 0.005$).

The mean ± SE percentage overlap between areas occupied by adjacent females was 45.48 ± 2.79%. Females used, in general, only one of the five sites where food was delivered daily. The mean overlap between females using the same feeding site ± SE was as high as 83.79 ± 3.90%. Males did not show such fidelity to a particular feeding site and used indifferently up to three sites. The mean ± SE percentage overlap between areas occupied by adjacent males was 51.53 ± 1.56%.

The number of females for which the home range was totally or partially included in the home range of a given male varied strongly (range 1–18, 8.89 ± 1.22, $N = 18$ males). The number of females per male home range was related to home range size (linear regression: $R^2 = 0.86$, $N = 18$, $P < 0.001$; Fig. 1) suggesting that occupation of more habitat increased the number of a male's potential mates.

Say et al. (1999) determined the genetic father of 192 kittens ($N = 42$ litters) born in this population using nine microsatellite loci. Between 1996 and 1998, the 18 males for which a spacing pattern had been described had sired between them 107 kittens. The annual reproductive success of these 18 males varied from zero to six young (Fig. 1). Male reproductive success was normally distributed

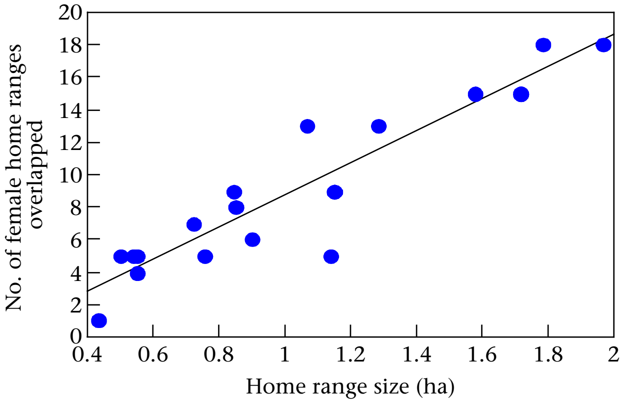

Figure 1. The relation between male home range size and the number of females with overlapping home ranges.

(Kolmogorov–Smirnov test: $D = 0.17$, $N = 18$, $P = 0.5$) and increased significantly as home range size increased even when social rank was taken into account (ANCOVA: $F_{1,8} = 20.69$, $P = 0.002$; Fig. 2). Thirty kittens (28%) were sired by males whose recorded home range did not overlap that of the mother of the kittens.

DISCUSSION

Males had home ranges that overlapped the home ranges of many females and other males, a pattern that is consistent with the promiscuous mating system described in this population (Say et al. 1999) and in other, similar urban populations (Natoli & De Vito 1991; Yamane 1998). The sizes of occupied areas found here were within the range found for other urban, social, group-living populations of cats (reviewed in Liberg et al. 2000). Female home ranges were organized around a unique feeding station. Adult male home ranges included up to three of the five permanent feeding sites, even though all cats could meet their energy requirements by visiting just one site, supporting the hypothesis that in the domestic cat the spacing pattern of males is a response to the distribution of reproductive females (Liberg et al. 2000).

As predicted, we found that males capable of ranging more widely increased their reproductive output. Although this mating tactic considerably decreases the probability of siring all the kittens of a litter (Say et al. 2001), the occupation of a large area appeared to increase fertilization success by allowing a male to mate with more females (Sandell 1989). The relation between reproductive success and home range size was the same independent of social class. As in bridled nailtail wallabies, *Onychogalea fraenata* (Fisher & Lara 1999) and in contrast to what has been found, for example, in red-necked wallabies, *Macropus rufogriseus* (Johnson 1989) this result suggests that competitively superior males did not exploit the uneven distribution of females by establishing small home ranges concentrated around feeding sites in area of higher density.

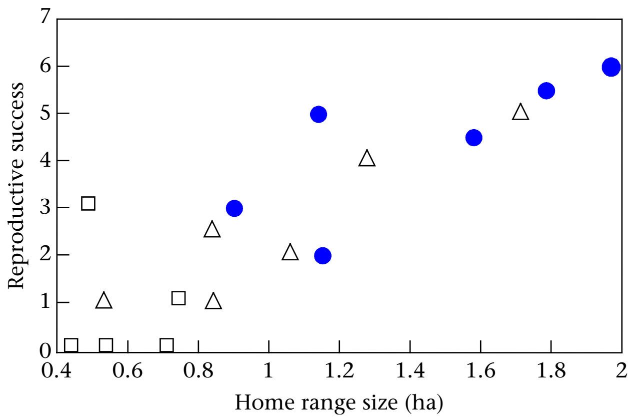

Figure 2. The relation between male home range size and reproductive success estimated from the mean number of kittens sired per year (●: high-ranking males; △: intermediate-ranking males; □: low-ranking males).

Female cats behave in ways that promote conflict between males. Females approaching oestrus increase the probability that several males find and then compete for them with typical vocalizations and small rushes, i.e. running fast over small distances (Beaver 1977). Although small rushes may result from harassment by males (Poole 1989; Michener & McLean 1996), females may also attract males and incite male–male competition (Lott 1991; Fisher & Lara 1999). In high-density populations, several males will then find and simultaneously court a single female (Natoli & De Vito 1991). When the number of male candidates increases, the cost of defending the female becomes too high, and most of the males copulate with the female regardless of their social rank or body weight (Natoli et al. 2000), leading to a high rate of multiple paternity (Say et al. 1999).

Females can also increase their home range around the time of oestrus to promote conflict between males (Lott 1991), but this did not appear to be the case in our study. Males are also expected to increase their home range during the breeding period in polygynous or promiscuous populations (e.g. Farentinos 1979; Webster & Brooks 1981; low-density, rural cat populations: Corbett 1979; Liberg et al. 2000). However, males in our population did not decrease their home range size during the nonbreeding period. This result is surprising, because patrolling over a large area might increase energetic costs and mortality risk from road accidents (a main cause of mortality in this population; Courchamp 1996), as well as the probability of injury or exposure to disease from a high encounter rate (Courchamp et al. 2000). Nevertheless, maintaining large home ranges during the whole year may reinforce the dominance status of males over other males in their range, thereby avoiding costly repeated fighting and maybe ensuring priority of access to the food or females (Yamane et al. 1997; D. Pontier, S. Devillard, E. Fromont & L. Say, unpublished data). Cats in this population are fed and home ranges are not large, so such a tactic could be less costly than decreasing home range size during the nonbreeding period and enlarging it again during the breeding period and winning back dominance status.

Another important component of the spacing pattern of male and female cats is quick excursions outside of their home range during the breeding period (Yamane et al. 1997). Such behaviour has been described for several territorial species (e.g. Birkhead & Møller 1992; Travis et al. 1995; Lacey & Wieczorek 2001), and it enables copulations with partners other than those usually encountered. In our population, 28% of kittens were sired by males whose recorded home range did not overlap. It was nevertheless unclear whether this behaviour was the result of males trying to increase their mating opportunities or females trying to copulate with new males, for example, to avoid inbreeding (Brooker et al. 1990; Anzenberger 1992) or to confer genetic benefits to the offspring (Kempenaers et al. 1992).

To conclude, few studies have reported relations between male fertilization success and both the size of their home range and the number of overlapped female home ranges for nonterritorial species or populations, and few have shown that enlarging the home range is an effective way of increasing individual fertilization success (e.g. bridled nailtail wallabies: Fisher & Lara 1999; water skink, *Eulamprus heatwolei*: Morrison et al. 2002). We found that competition for high social rank in a promiscuous colony of feral cats is not the only way for males to get access to reproductive females. Spacing behaviour and, more precisely, expanding home range size make an effective tactic to increase individual reproductive success, that is, male copulatory and fertilization success, in group-living stray cats.

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