Influence of oestrus synchronization on male reproductive success in the domestic cat (*Felis catus* L.)

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Previous studies have predicted that the availability over time of females in oestrus influences the variance of male reproductive success in a given year. When females are spatially aggregated, they represent a potentially defendable resource for each male when oestrus is asynchronous, and the most competitive males are expected to gain priority of access to receptive females. When females breed synchronously, a single male, even when highly competitive, is not able to prevent them from mating with other males. This hypothesis was tested in a large multimale–multifemale group of domestic cats, *Felis catus*, which was monitored for three years. The results support the prediction that the variance in male reproductive success was four times greater in years when females bred asynchronously, and dominant males sired the highest proportion of offspring. We conclude that the temporal availability of mates plays a role in the adoption of reproductive tactics in the domestic cat.

Keywords: reproductive success; breeding synchrony; alternative tactics; microsatellites; domestic cat; *Felis catus*

1. INTRODUCTION

Physical and behavioural qualities of males are expected to influence reproductive success because males of lower quality can be excluded from mounting fertile females (Altman 1962; Clutton-Brock 1989). For species in which competition between males leads to the establishment of a dominance hierarchy, some empirical studies have found evidence for a relationship between dominance status and reproductive success, while others have found no such correlation (for a review in primates see Takahata *et al.* 1999). High-ranking males could be unable to monopolize access to receptive females in a wide variety of situations. Molecular data have shown that subordinate or peripheral males that use alternative mating tactics can sire offspring, in spite of a low frequency of mounting, and that females may play a more active role than previously thought by engaging in mate choice, mating with more than one male and selecting genetic partners that may differ from social partners (Reynolds 1996). Moreover, a relationship between dominance and mating could also be indirectly affected by the characteristics of reproductive biology (Bernstein 1981; Takahata *et al.* 1999). When females are abundant and spatially aggregated, the temporal distribution of female oestrus is thought to influence the way males compete and the intensity of female monopolization (Emlen & Oring 1977; Ims 1989). When females enter oestrus asynchronously, males with high competitive ability may potentially sire a greater proportion of offspring. When female oestrus occurs synchronously, less-competitive males may mate with females, exploiting the fact that more-competitive males are involved in courting and mating elsewhere. Hence, an increase in the synchronization of female oestrus is predicted to decrease the variance of male reproductive success (Ims 1989).

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Few empirical studies have analysed the relationship between reproductive success among males and synchronization of female oestrus in mammals in natural conditions. Here, we examined the effect of synchronization of female oestrus on the reproductive success of males in a natural population of feral domestic cats (*Felis catus* L.) living at high density. In this species, males actively search for females and compete among themselves to acquire sexual partners (Liberg 1981). At high density (more than 1000 cats km^{-2}), cats live in large social multimale–multifemale groups (Izawa *et al.* 1982; Natoli & De Vito 1991) with a promiscuous mating system (Natoli & De Vito 1991; Say *et al.* 1999). Multiple mating by females is common, but no evidence of female mate choice has been found (Natoli *et al.* 2000). In these large groups, although the existence of a linear dominance hierarchy is controversial (Liberg *et al.* 2000), males can undoubtedly be assigned to different rank classes (Natoli & De Vito 1991). We tested, first, whether the variance of male reproductive success increased with increasing asynchronization of female oestrus, and second, whether high-ranking males had the highest reproductive success when female oestrus was not synchronized.

2. METHODS

The study was conducted over a three-year period (1996–1998) at the Croix-Rousse hospital park (7.2 ha) in Lyon, France. Good cover is provided for females by the dense vegetation and many basements that are accessible to them. Cats are completely dependent on the food that is distributed in bulk every day by hospital staff at five feeding sites. This population has been monitored since 1992. We could recognize all individuals by sight from their coat colour pattern and hair length, or a coloured collar. The studied population was a large multimale–multifemale group with an even sex ratio, containing 50 adults and their offspring. The sex and age structure of the adult cat

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population did not vary significantly across years (Say *et al.* 1999). Every six months, 70–80% of cats were trapped using double-door traps (before and after the reproductive period). During each trapping session we took hair samples for genetic parentage analysis.

(a) *Determination of female oestrus*

Female cats are induced ovulators and accept males only when they come into oestrus (Stabenfeldt & Shille 1977). They generally have one or two litters per year. A first peak of oestrus occurs in January–February, when day length (hours of light) begins to increase (Liberg 1981). The second peak is less marked: some females who lost the first litter immediately after their birth come back into oestrus before females who must rear their first litter. The first day of female oestrus was clearly identifiable from typical behavioural patterns (Beaver 1977). The study area was visited daily from the beginning to the end of the breeding season in all three years (1996–1998) to record the first day of each female's oestrus. It was estimated that the fertile period of females lasted for four days (Bosse *et al.* 1990).

(b) *Social rank*

The social position of males more than ten months old was determined by the directionality of aggressive and submissive behaviours (for a description of recorded behaviours see Natoli & De Vito (1991)). Data were collected for 19, 21 and 18 males in 1996 (84 h), 1997 (114 h) and 1998 (124 h), respectively. We used the focal-animal-sampling method (Altmann 1974) during both reproductive and non-reproductive periods, but not feeding activities. We did not record the male–male interactions of males courting females in oestrus because in these situations the females in oestrus were always the focal animals. Outcomes of aggressive interactions and, separately, submissive behaviours 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 $I = N_a/(N_a + N_b) \times 100$, where N_a is the number of encounters won and N_b is the number of encounters lost (Martin & Bateson 1993). Males with the highest I values were considered dominant.

(c) *Parentage analysis*

Using microsatellite genotyping, we assigned paternity for 157 kittens (49 in 1996, 70 in 1997 and 38 in 1998). Nine hypervariable microsatellite loci were amplified by polymerase chain reactions for each kitten, mother and putative fathers (for more details see Say *et al.* 1999) and run on a Pharmacia sequencer. Data collection and analysis, as well as the automatic sizing of bands, was done using Fragment Manager software supplied with the sequencer. The mean number of alleles per locus was 7.89 (range of 5–11) and the mean observed heterozygosity was 0.67 ± 0.10. The paternal alleles were identified by comparison with the maternal genotype for each offspring. In most cases, only four microsatellite loci were useful for ascertaining paternity without ambiguity. The other five microsatellite loci were used for verification.

The reproductive success of males was estimated from the number of kittens that they sired. Four kittens were not sired by resident males. Two types of litters occurred: litters with only one father, and litters with at least two different fathers.

(d) *Data analysis*

Synchronization of oestrus periods was assessed on the basis of the number of receptive females per week, from January to August, in each year. To test whether oestrus periods were more or less synchronized in different years, we compared the distribution of the number of females in oestrus each week across years using Kolmogorov tests. Since the annual reproductive success of males and the social dominance index, I, were not normally distributed, we analysed the relationships between the number of young sired annually by each male and their social rank using non-parametric tests. We estimated the mean number of kittens sired by males in each year, and compared their variances between years using Fisher's tests. To assess the influence of synchronization of female oestrus on male reproductive success, we looked for a correlation between the I value and the annual reproductive success of each successful male using Spearman's rank correlation. Lastly, we used logistic regression to determine the relationship between the proportion of litters in which males sired at least one kitten and the variables year and social rank. For social rank, we considered high-ranking males ($I > 0.7$) and others ($I \leqslant 0.7$) (see §3). We used Statview 4.5 and GLIM (Francis *et al.* 1995) for statistical analyses.

3. RESULTS

(a) *Distribution of receptive females*

We recorded the beginning of oestrus for 27, 30 and 29 females in 1996, 1997 and 1998, respectively. Females were receptive more than once per year. Altogether, 86% of oestrus periods were recorded between February and June. A first peak occurred during February, followed by a smaller peak in April–May (figure 1). Consequently, some females can appear more than once in the analysis. Up to ten females were receptive on the same day.

In 1996 and 1998, oestrus was more concentrated (12 and 11 weeks, respectively, between January and August) than in 1997 (20 weeks during the same period) (figure 1). The difference was statistically nearly significant between 1996 and 1997 ($\chi^2 = 6.87$, d.f. = 2, $p = 0.07$), significant between 1997 and 1998 ($\chi^2 = 8.64$, d.f. = 2, $p = 0.03$), but not significant between 1996 and 1998 ($\chi^2 = 0.42$, d.f. = 2, $p = 1.00$).

(b) *Dominance and reproductive success*

The mean number of agonistic behaviours of males (s.e.m.) was 26.95 ± 3.05 in 1996, 16.86 ± 2.50 in 1997 and 51.67 ± 4.90 in 1998. Each male interacted with, on average, 8.95 ± 0.68 other males in 1996, 6.38 ± 0.63 in 1997 and 7.72 ± 0.67 in 1998. The I values obtained using aggressive and submissive behaviour patterns were correlated (Spearman's rank correlation, $\rho = 0.626$, $p = 0.008$ in 1996; $\rho = 0.792$, $p = 0.004$ in 1997; $\rho = 0.866$, $p = 0.004$ in 1998). Because agonistic relationships were essentially determined by submissive behaviour (ranging from 80% to 85% per year), we used the I values estimated from submissive behaviour. The mean value of I was similar across years (0.38 ± 0.09 in 1996, 0.37 ± 0.08 in 1997, 0.35 ± 0.08 in 1998), indicating that the pattern of social relationships did not change across years.

The mean ($\pm$ variance) number of kittens sired per male was similar across years (2.42 ± 4.14 in 1996, 3.33 ± 14.73 in 1997, 2.00 ± 3.06 in 1998). However, the variance of male reproductive success was significantly higher in 1997 than in the other two years ($F = 1.355$, $p = 0.53$ between 1996 and 1998; $F = 0.281$, $p = 0.0082$
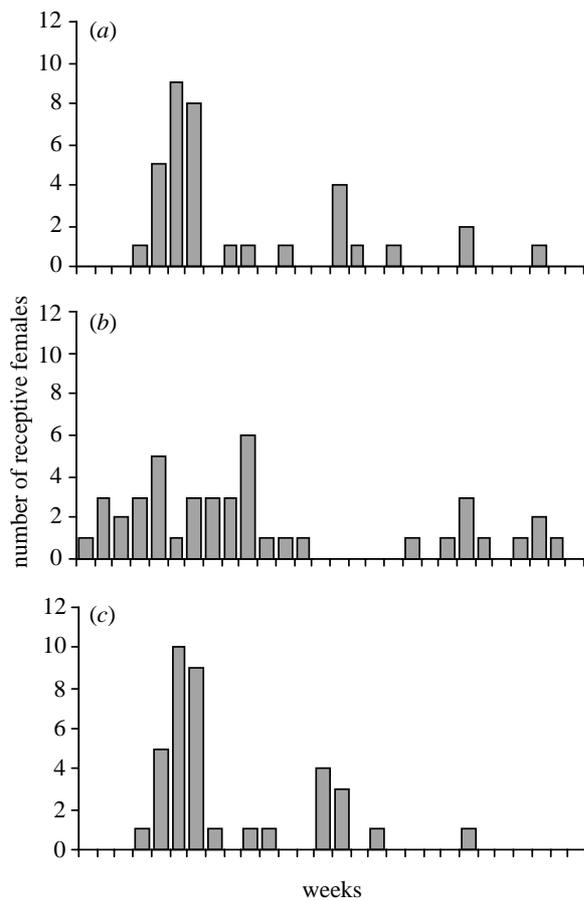
Figure 1. Distribution of receptive females between January and August, (*a*) 1996, (*b*) 1997 and (*c*) 1998.

between 1996 and 1997; $F = 4.817$, $p = 0.0015$ between 1997 and 1998).

The proportion of males who successfully reproduced was similar across years (15 out of 19 in 1996, 15 out of 21 in 1997, 15 out of 18 in 1998; $\chi^2 = 2.45$, d.f. $= 2$, $p = 0.29$). The number of kittens sired by successful males was correlated with I in 1997 ($\rho = 0.79$, $p = 0.003$) but not in 1996 ($\rho = 0.18$, $p = 0.22$) or 1998 ($\rho = 0.20$, $p = 0.54$) (figure 2). The proportion of litters sired by more than one father was similar across years (78% in 1996, 82% in 1997, 72% in 1998; $\chi^2 = 4.91$, d.f. $= 3$, $p = 0.17$). The proportion of litters for which high-ranking males ($I > 0.7$, figure 3) sired at least one kitten differed across years ($\chi^2 = 6.13$, d.f. $= 2$, $p = 0.047$). High-ranking males sired at least one kitten in a larger proportion of litters in 1997 (29.41 ± 6.35 versus 10.16 ± 2.11) than in the other two years (1996, 16.67 ± 3.21 versus 11.15 ± 3.10; 1998, 19.44 ± 8.33 versus 20.64 ± 5.10). Across all the years combined, the probability of a kitten being sired by a high-ranking male was higher when the number of females in oestrus during the week of the kitten's conception was low (logistic regression with litter size as covariate, $\chi^2 = 6.13$, d.f. $= 2$, $p < 0.0001$; figure 4).

4. DISCUSSION

As predicted by Emlen & Oring (1977) and Ims (1989), the variance in male reproductive success was four times greater, and dominant males sired the highest percentage
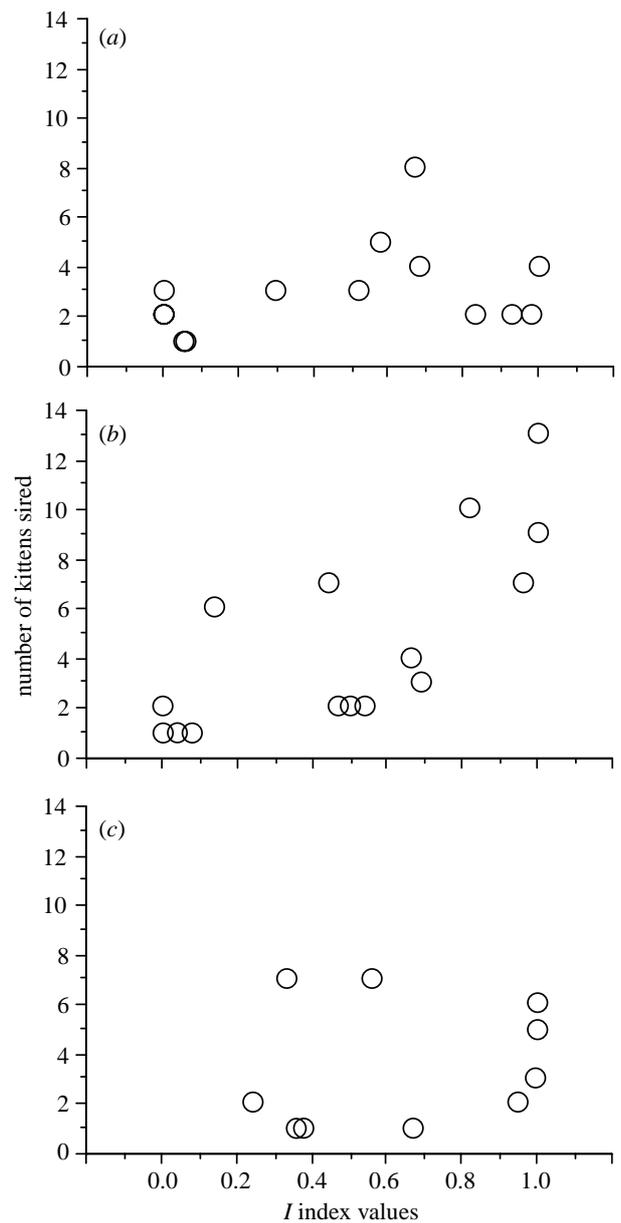

Figure 2. Relationship between annual reproductive success of males and dominance (I), (*a*) 1996, (*b*) 1997 and (*c*) 1998.

of offspring, when female oestrus was asynchronous. Asynchronization of female oestrus increases the number of reproductive males per receptive female (Emlen & Oring 1977; Grant *et al.* 1995) resulting in an increase in male–male sexual competition (Emlen & Oring 1977). In these conditions, as observed in other species (Höglund 1989; Elmberg 1991), the most-competitive males have higher reproductive success.

However, in this study, dominant males failed to monopolize access to reproductive females when the degree of oestrus synchronization was greater, whereas they are able to do so in rural cat populations where the density is 100 times lower (Pontier & Natoli 1996; Say *et al.* 1999). Thus, the particular mating tactic chosen by dominant males depends upon local circumstances (Say *et al.* 1999). Although the percentage of multiple paternities did not change between 1996 and 1998, the proportion of litters in which high-ranking males sired at least one kitten
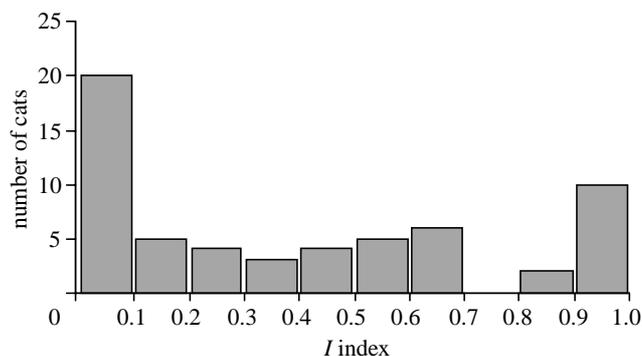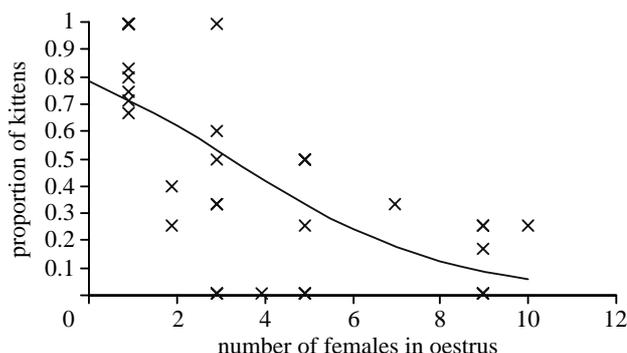
Figure 3. Distribution of males' *I* values.

Figure 4. Proportion of kittens sired by high-ranking males as a function of the number of females in oestrus during the week of the kittens' conception (all years combined). Solid line, curve predicted by logistic regression; crosses, observed values.

increased when female oestrus was asynchronous. A possible interpretation of these results is that when high-ranking males are not in contact with several females in oestrus, they use a tactic that enhances their own chance of siring the highest number of kittens. The cat is an induced ovulator, requiring a coital stimulus for ovulation (Stabenfeldt & Shille 1977). Repetition of the coital stimulus is necessary for ovulation in most females and ovulation does not occur until 24–50 h after copulation (Stabenfeldt & Shille 1977). This feature of female reproduction favours multiple copulations and the mixing of sperm from multiple males. This is reinforced by the absence of any real mate guarding of females by males (Natoli & De Vito 1991).

Hence, since high-ranking males have priority of access to females, they have to balance defending the female they are courting until the end of her oestrus with leaving to find a new female. When females are in oestrus asynchronously, high-ranking males can invest more time in courting and mating with a single female, achieving a high rate of copulations and increasing their probability of siring kittens. When many females come into oestrus at the same time, other competitors in the group may attempt to mate with the females. High-ranking males in these circumstances 'make the best of a bad job' by shortening the time spent with each receptive female, thereby lowering the probability of successful fertilization. On nine occasions, we observed three different high-ranking males ($I > 0.9$) copulating with the same female up to four times consecutively, when female oestrus was asynchronous (1997). However, we never observed this mating pattern in 1996 or 1998 when female oestrus was synchronous.

To conclude, when several females enter oestrus simultaneously, a single male cannot monopolize all copulations and prevent competitors from mating with those females with which he has copulated. Large social cat groups are generally characterized by synchronous breeding (Natoli & De Vito 1988; Yamane *et al.* 1996). Given that the ancestral cat probably lived solitarily (Leyhausen 1988), synchrony of reproduction could be advantageous to group-living females for several reasons. It favours communal care of offspring (Macdonald *et al.* 1987) and increases the probability of copulating with most of the males who inhabit a territory. Multiple mating stimulates female reproduction, ensuring that all ovules are fertilized (Eaton 1978). Females may also gain an advantage from mixing paternity, by reducing male

aggression and the risk of infanticide. Infanticide has not been described in high-density cat populations (Natoli & De Vito 1991), whereas it has been reported in low-density cat populations (Pontier & Natoli 1999). Moreover, harassment may be particularly pronounced in high-density cat populations, and hence females may copulate with all the males that court them since this is probably less costly than trying to reject them (Natoli *et al.* 2000). Thus, the significance of dominance from a functional perspective in domestic cats living in social groups has to be questioned since, by definition, obtaining a high social rank is costly. These costs include an increased chance of being injured, with consequent exposure to disease or parasites. In the group of cats studied here, Courchamp *et al.* (2000) showed that dominant cats are more likely to be infected by the feline immunodeficiency virus when it is transmitted during male–male combats (Courchamp & Pontier 1994). Given that food is not a limiting factor in the urban environment (Haspel & Calhoon 1989), in this context the function of dominance in males is not strictly linked to access to trophic resources. Nevertheless, the most important benefit of being of high rank in the urban environment remains reproductive advantage, but, as demonstrated here, only when females breed asynchronously. Further research into the factors that provoke asynchrony of female oestrus and the frequency of occurrence of such factors may throw some light on the costs and benefits of engaging in aggressive competition.

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