

What determines testis size in the domestic cat (*Felis catus* L.)?

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Abstract: There is abundant evidence that the occurrence of sperm competition is associated with large testes across many taxa. Similar predictions have been made within mammal species but empirical data are scanty and results are not always consistent. Alternatively, it is argued that when the sperm competition is exceptionally intense within a species, game theory models suggest that there should be selection for decreased numbers of sperm transferred, which might select for decreased testis size. Additionally, males should produce low quantities of sperm when there is no competitor and highest when there is just one competitor. To test the sperm competition theory and Parker’s intensity model predictions, we compared relative testis size in 5 populations of feral cats (*Felis catus* L.) contrasted by the level of sperm competition the males encounter. As predicted by Parker’s intensity model, we found that males living in rural populations have larger testes than those living in extreme environments, where sperm competition is low, and than those living in urban populations, where sperm competition is higher.

Key words: sperm competition, mating tactics, cat, *Felis catus*

INTRODUCTION

Male reproductive success depends on both pre- and post-copulatory strategies in mammals (PRESTON et al. 2003). Contests for access to and control of receptive females are common and are responsible for the evolution of a large male body weight and/or conspicuous weaponry (ALEXANDER et al. 1979). However, males are often not able to exclude all other competitors and females can mate with 2 or more males. Competition among males will then continue in the form of a competition between the males’ ejaculates for fertilization of a given set of ova (PARKER 1998). Hypothesizing that the paternity probability depends on the number of sperm inseminated by each male (PARKER 1982), sperm competition could explain some behavioural and physiological adaptations observed in mammalian taxa, such as mate-guarding of receptive females, high copulatory frequencies, or evolution of larger testes, which would allow greater production, storage and, ultimately, ejaculation of sperm (MØLLER & BIRKHEAD 1989).

There is abundant evidence that the occurrence of sperm competition is associated with large testes across mammal species (e.g. HARVEY & HARCOURT 1984, KENAGY & TROMBULAK 1986, DIXON 1987, GOMENDIO & ROLDAN 1991, SCHWARZWEIG & SACHSER 1996, SACHSER et al. 1999). In contrast, there is currently a shortage of studies demonstrating that sperm competition affects also size of testes within a given mammal species in natural conditions. In accordance with the sperm-competition theory, PRESTON et al. (2003) and SCHULTE-HOSTEDDE & MILLAR (2004) reported respectively in Soay sheep (*Ovis aries*) and the yellow-pine chipmunk (*Tamias amoenus*), that males with larger testes had both higher copulation rates and higher siring success with increasing numbers of oestrus females, since dominant males can no longer control total access to them. Nevertheless, results are not always consistent (e.g. RISING 1987, RIBBLE & MILLAR 1992) and PARKER et al. (1996) argued that predictions from the sperm competition theory at an intra-specific level could differ from inter-specific predictions. In particular, they showed that in cases where there are exceptionally high levels of sperm competition within a species, game theory models suggest that there should be selection for decreased numbers of sperm transferred, which might select for decreased testis size. This arises because as the number of competitors increases, the benefit arising from a given unit of extra expenditure on sperm decreases (PARKER et al. 1996). Additionally, males should produce low quantities of sperm when there is no competitor and the highest quantities when there is just one competitor. Empirical studies attempting to measure sperm expenditure in relation to varying intensity of sperm competition again show contrasting results. Some support predictions of the intensity model of PARKER et al. (1996) (e.g. SIMMONS & KVARNERMO 1997, WEDELL & COOK 1999, PILASTRO et al. 2002), while others do not (e.g. FULLER 1998) and more studies are necessary to confirm the sperm-competition theory and the intensity model at the intraspecific level. An alternative approach to within-population-based studies, which need individual data on male characteristics, mating tactics and reproductive success that are available in very few natural populations, could be to compare testes size among populations of a given species that vary greatly in terms of sperm competition intensity.

The domestic cat (*Felis catus*) is a good candidate for such a study. In urban areas, the species reaches high population densities (up to 3000 cats per km², LIBERG et al. 2000). Both males and females live in small, largely overlapping home ranges (LIBERG et al. 2000, SAY 2000). Female estruses are synchronous (NATOLI & DE VITO 1991). Very low levels of aggression between males are described (TABOR 1983, NATOLI & DE VITO 1991, SAY 2000). The absence of monopolisation of female access by males leads to a high rate (around 80%) of multiple paternities, i.e. litters with more than one father (YAMANE 1998, SAY et al. 1999) generating a very high level of sperm competition. Lower-density populations (100-300 cats per km²) are found in the rural environment (LIBERG et al. 2000). In these populations, reproductive success of males is mainly dependent upon overt contest competition. Males live in large home ranges overlapping those of females (LIBERG et al. 2000). They enter into intense agonistic interactions with other males during the reproductive period to monopolise the access to the few receptive females living within their home range (LIBERG 1981). However, these females could also copulate with a peripheral male or a male from a neighbouring territory, resulting in a low rate of multiple

paternity (approximately 20%, PONTIER & NATOLI 1996, SAY et al. 1999). Lastly, very low densities (fewer than 5 cats per km², LIBERG et al. 2000, SAY et al. 2002b) are found in some extreme non-inhabited areas. Males or females live alone and defend large non-overlapping home ranges (DERENNE & MOUGIN 1976, JONES 1977, VAN AARDE 1979). No case of multiple paternity has been found there (SAY et al. 2002a), suggesting that the potential for sperm competition is extremely low.

To test that sperm competition is influential in determining testis size within a given species in natural conditions, we compared size of testes in 5 stray cat populations (2 urban, 2 rural and 1 in an extreme non-inhabited area), differing in density, social organisation and mating system. We addressed the following hypotheses: (1) relative testis size is comparable in the 2 urban populations and in the 2 rural populations; (2) according to the sperm-competition theory and the intensity model, the ejaculate expenditure should be maximized in slightly polyandrous rural populations (where the largest testes are expected) and then should decrease as the number of competitors increases in highly polyandrous urban populations (where smaller testes than in rural cats are expected); (3) cats living in the extreme environment should have the smallest testes as males that do not face sperm competition should invest a minimum quantity of sperm for each mating.

MATERIALS AND METHODS

Study populations

Five populations of feral cats were studied. Two urban populations were called CXR (situated in a hospital district of Lyon, France) and ROM (situated in a park in Rome, Italy). Two rural populations were called BAC (Barisey-la-Côte, North-Eastern France) and SJT (Saint-Just Chaleyssin, central France). The last population, called KER, inhabited the Kerguelen main island, 6600 km², partly covered by an ice-cap. The Kerguelen archipelago is in the sub-Antarctic area of the Southern Indian Ocean (49°20'S, 70°20'E). These populations of feral cats were monitored extensively for demography, spacing and social pattern, for several years.

Data

We visually recognized all individuals by their coat colour pattern and hair length or coloured collar. Cats were caught by hand or by using double-door traps once a year in September between 2 reproductive periods that occur from January to June on the continent and from December to April on Kerguelen Islands. Each cat was anaesthetised, with an intramuscular injection of ketamin chlorhydrat (Imalgène 1000 15mg/kg, Rhône Mérieux, Lyon, France) and acepromazin (Vétranquil 0.5% 0.5mg/kg, Sanofi, Paris, France). Cats were weighed to the nearest gram by using an "Emeraude 20" balance (manufactured by PRECIA). Testis width (W) and length (L) were measured with slide callipers (manufactured by MITUTOYO) and determined to the nearest 0.01 mm. Cats in the CXR, ROM, BAC and SJT populations were all first caught when they were kittens and, thus, were all of determined age. Only in the Kerguelen population, where most of the captured cats were of unknown age, age was estimated according to the method of PASCAL & CASTANET (1978).

All experiments were done with the permission of ethical commission.

Statistical analyses

We checked that all age classes were equally represented in cat samples of our 5 populations by using the χ^2 test. Three age classes were compared: 1–2 years, corresponding to young but physiologically sexually mature males (SAY et al. 1999); 3–5 years, corresponding to socially sexually mature males (SAY et al. 1999, LIBERG et al. 2000); and more than 5 years, corresponding to older males. We then compared the body weight in each sample by using an ANOVA. Size of testes was calculated by using the formula for the volume of an oblate spheroid $V=(\pi W^2L)/6$ (ABBOTT & HEARN 1978, HOSKEN 1998). Body weight and testis size were log-transformed for further analyses to take allometric relationships into account. To compare testes among the studied populations, we carried out an analysis of covariance (ANCOVA) by using *logarithm of testis size* as the independent variable, *logarithm of body weight* as the dependent variable, and *population* as the co-factor. Statistics were performed by R software (StatSci Mathsoft). This software permitted us to modify the matrix of contrasts of the ANCOVA and then to build specific tests of hypotheses.

RESULTS

Size of testes and body weight were determined in 7, 19, 26, 37 and 61 healthy, mature males aged from 1 to 8 years, in ROM, SJT, BAC, CXR and KER, respectively. Data and complete analyses are available at <http://pbil.univ-lyon1.fr/R/fichestd/tdr334.pdf>. The age structure of the cat samples did not significantly vary among sites ($\chi^2 = 8.03$, d.f.=8, $P=0.43$). Body mass between the 5 populations varied but not significantly ($F_{4,145}=2.40$, $P=0.05$). Males of the KER population were slightly less heavy (mean \pm SE: 3.72 ± 0.07) than cats of the other populations (4.27 ± 0.44 , 4.12 ± 0.13 , 3.85 ± 0.10 , 3.85 ± 0.13 , respectively for ROM, BAC, CXR and SJT). This result is probably a response to differences in environmental conditions between the studied areas. Cats have to prey to survive under difficult climatic conditions in the KER population (PONTIER et al. 2002), whereas cats in rural and urban populations use food and shelter provided intentionally or not by humans (PONTIER 1993). No significant between-population variation was highlighted for the relationship between testes size and body weight (comparison of slopes: $F_{4,140}=0.51$, $P=0.73$, Fig. 1). On the contrary, significant differences occurred in testis size among the populations (comparison of intercepts: $F_{4,140}=19.11$, $P<0.0001$). No pairwise difference in testis size existed between the rural populations SJT and BAC ($t=-0.03$, $P=0.973$). Testis size was smaller in ROM than in CXR ($t=2.18$, $P=0.03$), but also smaller in urban than in rural populations ($t=-6.34$, $P<0.0001$) and smaller in KER than in SJT and BAC ($t=4.54$, $P<0.0001$), than in CXR ($t=2.30$, $P=0.02$) but not significantly different from ROM ($t=-1.04$, $P=0.30$).

DISCUSSION

The results of this study show a large variation of relative testis size for males facing different levels of sperm competition, suggesting that some flexibility in sperm production is selected for in this species. Our results clearly support Parker's intensity model in that testis size is driven by the quantity of sperm ejaculated by males.

Cat density in KER is low (approximately 1.5 cats/km², SAY et al. 2002b). Males or females live alone and defend large non-overlapping home ranges but can form

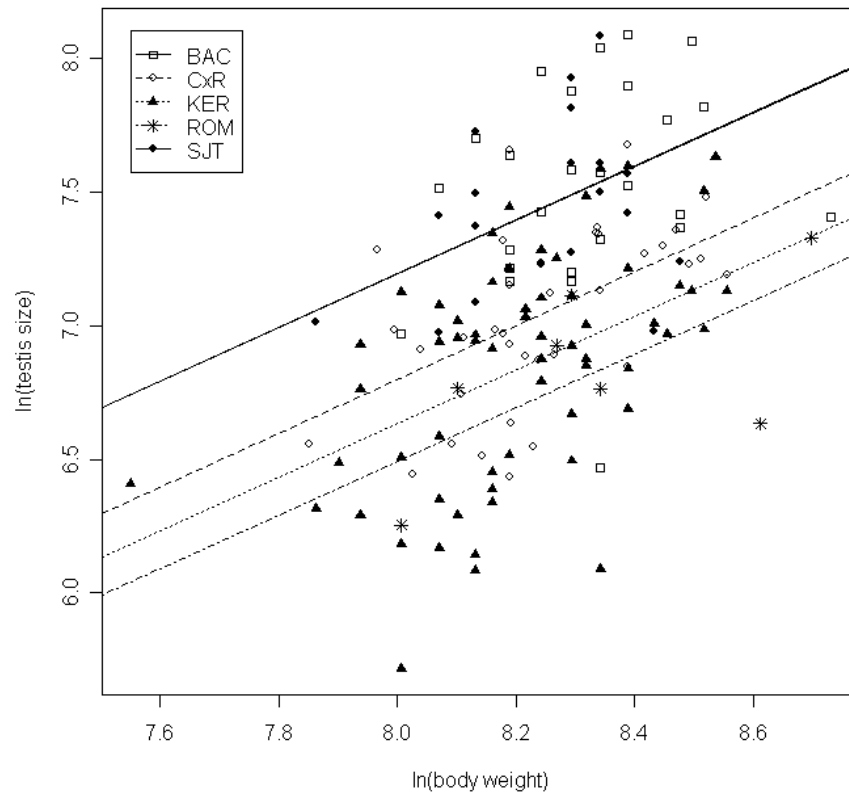


Fig. 1. Relationship between the logarithm of mean testis size and logarithm of body weight in 5 populations of feral cats (2 rural populations: BAC and SJT; 2 urban populations: CXR and ROM and 1 sub-Antarctic population: KER). We illustrated regression lines corresponding to the fitted ANCOVA model.

temporary social pair bonds during oestrus periods (PONTIER & SAY, unpublished data). Opportunities for females to copulate with several males are scarce there. DNA analyses of 13 litters from two sites on the main island of the Kerguelen archipelago revealed no case of multiple paternity (SAY et al. 2002a). In the KER population, sperm competition among males is not a factor and consequently, in accordance with the sperm competition theory and the intensity model of PARKER et al. (1996), they may invest a minimum quantity of sperm for each mating. This, in turn, may explain the small size of testes recorded in this population. Densities in BAC and SJT are respectively 140 and 260 cats/km² (SAY 2000). As described for other rural populations at similar densities, male cats defend access to the females living within their home ranges in BAC and SJT. Nevertheless, females can sometimes escape the vigilance of males and copulate with a peripheral male or a male of a neighbouring territory. The rate of multiple paternities in BAC and SJT was respectively 12% and 18%, but no litter with more than 2 different males has been found (SAY et al. 1999,

SAY 2000). Sperm-competition theory and the intensity model predict that males should produce more sperm in slightly polyandrous populations when there are at most 1-2 competitors. Maximization of the ejaculate expenditure could then explain why males living in rural populations (BAC and SJT) have larger testes than those living in extreme environments (KER), where sperm competition is low, and compared to those living in urban populations (ROM and CXR), where sperm competition is higher. Cat density is high in CXR (1900 cats/km²) and is similar in ROM (2000 cats/km²). In ROM and CXR, as in other urban populations, cats form social multimale and multifemale groups. While a dominance hierarchy exists among males, dominant male cats are unable either to monopolize females or to ensure paternity. During the reproductive period, several males may court a receptive female simultaneously. They do not interact aggressively and copulate with the receptive female one after the other. This behaviour leads to a rate of multiple paternities of 76%, with up to 5 different fathers in a litter of 6 kittens in CXR (SAY et al. 1999) and a rate of 78% in ROM (NATOLI et al. in press). In response to this extremely high sperm competition, male cats may reduce their sperm expenditure. Reduction of sperm expenditure may, in turn, lead to a reduction in testes size in comparison to that observed in rural populations. More intense sperm competition in ROM than in CXR could explain the extremely small testes size found in ROM. However, these results have to be viewed with caution since the dataset is smaller for ROM compared to CXR. ROM is a small colony with a sex-ratio biased in favour of males (only 6 adult females for 14 adult males) and competition across males for reproduction is probably more severe than in CXR, where the same number of males and females live (about 30 of each sex but varying between years).

While our results support Parker's intensity model expectations, sperm competition may not be the only selective pressure acting on testis size in cat. Mammalian testes produce not only sperm but also androgens, such as testosterone, and larger testes produce more testosterone (KAPLAN & MEAD 1994, ADAM & FINDLAY 1997). Testosterone can affect many physiological (SCHULTE-HOSTEDDE et al. 2004) and behavioural parameters, including individual aggressiveness (ALBERT et al. 1987, 1992). Thus, selection pressure acting not only on sperm production but also on androgen production may also determine testis size. Whether sperm competition or the level of aggressiveness is the major factor affecting size of testes in cats is debatable and requires further studies. Preliminary unpublished results (PONTIER, HUBERT, SAY & DUCHAMP) show that mean levels of testosterone found in male cats of BAC and SJT, where reproductive success of males is mainly dependent upon overt contest competition, are much higher than in CXR and KER populations. Sperm prudence and/or low levels of aggressiveness should be adaptive both in the sub-Antarctic and urban population, whereas large ejaculate expenditure and/or high testosterone production could have been selected for in rural populations.

In the future, it will be necessary to estimate testosterone production ability in relation to the ability to produce spermatozoa (i.e. proportion of spermatogenic and interstitial tissues) in each population to evaluate the relative importance of sperm competition and the level of aggressiveness in determining testes size in cats.

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