Male Reproductive Success in a Social Group of Urban Feral Cats (*Felis catus* L.)

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Abstract

Dominance rank, morphological characteristics and reproductive success of adult males were measured in a multi-male multi-female group of urban feral cats (*Felis catus* L.). Paternity of nine litters (34 kittens) of the domestic cat from six females was determined through microsatellites analyses at nine loci. The percentage of multiple paternities in this social group was as high as 78%. A positive correlation was found between male size/body weight and dominance. The males who sired the highest number of kittens were the dominant ones. Additionally, dominant males were more likely to be infected by the feline immunodeficiency virus, a virus transmitted by bites through aggressive interactions. Thus this study demonstrates that rank and body weight were both important in predicting the annual reproductive success. However, it shows that the reproductive benefit associated to rank may be balanced by cost due to at-risk aggressive behaviour of dominant males.

Introduction

In mammals, where male–male competition for mating is intense, sexual selection has favoured larger male body size compared with females (Alexander et al. 1979; Clutton-Brock 1989). When male intrasexual competition leads to the establishment of a dominance hierarchy, it has been postulated that large male size promotes high ranking which, in turn, leads to high reproductive success (Altman 1962). Relationship between social rank and reproductive success has received considerable attention. But whereas some authors have reported the expected positive correlation between social rank and reproductive success (e.g. McCann 1981; Dewsbury 1982; Brown et al. 1988; de Ruiter et al. 1992; Haley et al. 1994; Ellis 1995), others have failed (e.g. Fedigan 1983; Rowell 1987; Cheney et al. 1988; Natoli & De Vito 1991). Dominant males are not always able to control the access to mates and both alternative tactics from subordinate males and mate choice from females can decrease the dominance effect (Gross 1996; Reynolds 1996). Moreover, both dominance rank and reproductive success can be affected by other factors than body size. In particular age has been found to be the main determinant of male social rank in different species (e.g. Thouless & Guiness 1986 in *Cervus elaphus*; Berdoy et al. 1995 in *Rattus rattus*). Other factors such as prior experience (e.g. Beaugrand et al. 1991) or prior possession of resources (e.g. Barnard & Brown 1982), as well as formation of male coalition (e.g. Harcourt & Stewart 1987) can also be involved. Consequently, relationship between social rank, body size and reproductive success cannot be assumed and has to be investigated (Haley et al. 1994). This is particularly true for species with medium size dimorphism and low rate of aggression among males as it is the case in urban population of feral cats (*Felis catus* L.).

Male domestic cats are, on average, 20% heavier than females (Pontier et al. 1995). In urban environment, feral cats live in multi-male multi-female social groups (Liberg et al. 2000). The social structure of males is organized around a dominance hierarchy (Natoli & De Vito 1991). Nevertheless, the hierarchy is not always markedly linear (Natoli & De Vito 1991; but see Natoli et al. 2001) and the frequency and intensity of aggressive behaviour by males is low throughout the year (Tabor 1983; Natoli & De Vito 1991). No obvious mate choice from females for copulation with high ranking males has been highlighted in cats (Natoli et al. 2000). Yamane (1998) found no relationship between male reproductive success and large body mass: males of medium body size sired more offspring than the heaviest males. We reported previously that dominance rank and annual reproductive success were correlated when females were asynchronous but we did not assess the relationship between social rank and body size of males (Say et al. 2001).

Here, we used DNA-based paternity analysis to examine whether body weight influences dominance rank and, in turn, the annual reproductive success in male domestic cats living in a social group in the urban environment. Furthermore, in addition to measuring benefits of dominance, we also tried to assess one of the costs reported for being highly competitive in male domestic cats (Courchamp et al. 1998, 2000), i.e. the risk of being infected by some diseases and, in particular, by the feline immunodeficiency virus (FIV). This virus acts slowly, while not having a strong action on the fertility or survival (Courchamp et al. 1998, 2000), the pathogen has consequences on host behaviour. Infected cats are weakened due to fever and neutropenia during the first stage of the infection (lasting 4–16 wk, Yamamoto et al. 1989) and thus healthy cats may take advantage of the weakened state of infected individuals. Because dominant males are involved in more intense competition and aggressive encounters with other cats, mainly from other colonies (Tabor 1983; Say 2000), we expect that dominant males should be more exposed to FIV than the other males since the predominant mode of transmission seems to be through bites inflicted during fights (Yamamoto et al. 1989; Ueland & Nesse 1992; Bendinelli et al. 1995; Pontier et al. 1998).

Methods

Colony Studied

The study was conducted over a 1-yr period (1999) at the Fori di Traiano (historical ruins in the centre of Rome). This colony has been monitored for management purpose since 1986. Cats are provided with food every day in bowls by cat lovers belonging to an Italian Association (Miciopolis). During the study period, the colony contained six reproductive females (from 8 mo to 6 yr old) and 14 reproductive males (from 12 mo to 7 yr old). We visually recognized all individuals by their coat colour pattern and hair length.

All cats but six adult males were trapped using double-door traps in December 1998 before the mating period (from January to April 1999). Captured cats were anaesthetized with an intramuscularly injection of ketamin chlorhydrat (Imalgène 1000 15 mg/kg; Rhône Mérieux, Lyon, France) and acepromazine (Vétranquil 5.5% 0.5 mg/kg; Sanofi, Paris, France). We measured body weight, as well as head width and length from all captured animals. Blood and fur samples were collected respectively for epidemiological and genetic parentage analyses. Age of the subjects was obtained from inquiries to the cat lovers or estimated according to Pascal & Castanet's (1978) method. Cats were then released. For three of the six uncaught males, hair samples could be collected by the cat feeders and thus be used for paternity analysis.

Social Rank

Data on the outcomes of aggressive interactions (striking with a paw, assuming a threatening posture, chasing, ritualized vocal and physical contests) (Natoli & De Vito 1991) were collected; for aggressive interactions we mean any interaction between two individuals where one male threats the other by means of one or more behavioural patterns listed above, clearly prevailing on the other. The latter either undergoes without reacting, or shows submissive behaviour. When the outcome was not clear (both were aggressive and no one was prevailing over the other), data of that particular interaction were not considered. Submissive interactions (crouching with the ear flattened, avoiding, retreat, fleeing, hissing at) were also collected. For submissive interactions, we mean any interaction between two individuals where one male performs one or more behavioural pattern listed as submissive behaviour, even without threats from the other. In other words, it is not taken for granted that the response to threat is submissive behaviour, thus in this work it was worthwhile collecting aggressive and submissive behaviour separately.

Data were collected during the breeding season for all the 14 reproductive males (445.30 h of observation; mean observation time per tom cat: 978.14 mn ± 207.51 SE), using the 'focal sub-group' and

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'all occurences' sampling methods (Altman 1974). The sub-group consisted of males courting and mating a female in oestrus within a 4 m radius circle, the centre of which was represented by the female itself. When a female cat came into oestrus, she advertised it with all the typical behaviour patterns (for a detailed description see Natoli et al. 2000). During the oestrus period, we followed each female for 4 h/day, for 4 d (or for the duration of the oestrus when <4 d). Since female cats have a high copulation frequency (15–20/24 h) during their 4–5 d of oestrus and it has not been reported that there are peaks of sexual activity during the 24 h (Liberg et al. 2000), the distribution of the 4 h daily observation periods was designed to evenly sample all available diurnal hours.

It was not possible to test statistically whether dominance hierarchy was transitive in this population, as suggested by Appleby (1983), because some males rarely or never interacted with other males. We used the approach of Jameson et al. (1999) developed from the work of Batchelder et al. (1992) and called Batchelder–Bershad–Simpson scaling method (BBS thereafter) that does not assume transitivity to ranking males in a hierarchy. Furthermore, we utilized submissive behaviour and not aggressive behaviour because, as it has already been shown in this and other species of mammals (Rowell 1974; de Waal & Luttrell 1985; Natoli et al. 2001), submissive behaviour is less ambiguous than aggressive behaviour. The BBS method is based on a mathematical model of paired comparisons so that an animal's scale position, concerning the agonistic interactions, depends on the proportion of wins in his encounters with other males, his proportion of losses, and the scale scores of the other males that he has met in agonistic encounters.

Pedigree Determination

Data on occurrence and length (number of days) of oestrus of females belonging to the group were collected: oestrus was generally asynchronous (first period of breeding season in 1999: 27 January to 9 March: seven oestrus asynchronized; second period of breeding season in 1999: 4 May to 19 June: two oestrus asynchronized). The birth of 34 kittens belonging to nine different litters (mean litter size: 4.4 ± 1.7) took place at the Fori di Traiano through the study period. Maternity was determined from field observation and, thereafter confirmed by genetic analysis. All of the 34 kittens, their mothers and their putative fathers, were successfully typed at nine dinucleotide repeat microsatellite loci *fca*8, *fca*23, *fca*37, *fca*43, *fca*45, *fca*77, *fca*78, *fca*90, *fca*96 (Menotti-Raymond & O'Brien 1995) using protocols described in Say et al. (1999).

Serological Status

The ELISA method (Cite-Combo, Idexx) was used to detect the presence of FIV-specific antibodies, which generally reveal virus carriers (Sparger 1993). Details of serological analysis for FIV are available in Courchamp et al. (1998).

Statistical Analyses

Age, body weight and body size are not independent variables in cats (Say 2000) such that older males are heavier and have larger size than younger males. Our sample is not sufficient to test for the relative effect of these three factors on the reproductive success (see Haley et al. 1994). To describe the morphological characteristic of each male living in our colony we then decided to construct a synthetic variable (called Index of Morphological Characteristics, IMC thereafter). This variable was the first factor F1 of the Principal Component Analysis (PCA) on weight, age, and head volume. Head volume was calculated by using the formula for the volume of an oblate spheroid: $V = [(\pi W^2 L):6]$ with W as the head width and L as the head length (Abbott & Hearn 1978). Principal Component Analysis was performed using ADE4 package (Thioulouse et al. 1995). Relationship between male reproductive success (estimated from the number of kittens that they sired) and, firstly, male dominance rank and, secondly, male morphological characteristics (using IMC) were then analysed by mean of Spearman rank correlation tests. We also carried out a separate analysis for body weight and reproductive success, to compare our results with those of Yamane (1998). Tests were performed using STATVIEW 4.5 software.

Results

Agonistic encounters between males were not frequent. Out of 237 agonistic interactions, 111 were aggressive and 126 were submissive. Relationship among males could be described as mutual tolerance (Table 1). Out of 90 pairs of cats, 63 or 70% were never observed together in any encounter. Some of males (PA, TE, NO, FK and TO) rarely appeared in the study area. Nevertheless, they were recognized as members of the colony studied since the other

Table 1: Matrix of submissive behaviour among the 14 males of the group studied

	BT	VO	BY	PA	GE	TE	DN	SN	GR	NO	FK	TO	CO	MZ	Total
BT		1													1
VO	2														2
BY	4	3							1	1					9
PA															0
GE	1	1	2	1											5
TE	1														1
DN	29			3		4		2							38
SN	13						2								15
GR	18	4	2		2		3								29
NO			2		1										3
FK	3						2								5
TO	4								2						6
CO							4	5							9
MZ							3								3
Total	75	9	6	4	3	4	14	7	3	1	0	0	0	0	126

resident cats did not react aggressively to their presence. Furthermore, while courting females of the subject colony, they rarely interacted with resident males. Thus, the dominance matrix for these cats is relatively sparse (see Table 1). Using the BBS method, the resulting scale in which no two males had the same score allowed us to rank all 14 tomcats (at the 15th recursion, Jameson et al. 1999) (Table 2).

Genetic diversity was relatively large: the mean number of alleles per locus ranged from 5 (for *fca*45 and *fca*96) to 11 (for *fca*8). The overall expected heterozygosity was 0.60 ± 0.13 (mean ± SE). This polymorphism permitted us to determine paternity of all kittens with a high level of confidence. In most cases, only five microsatellite loci were sufficient to ascertaining paternity without ambiguity. The other four microsatellite loci were used for verification. The father of three, out of 34, kittens was not identified. We can hypothesize either that the father was one of the three uncaught males of the colony studied, or that they were sired by a male that did not belong to it. The proportion of multiple paternity defined as the proportion of litters where at least two different males sired the kittens was as large as 78% (seven on the nine studied litters, Table 3) suggesting that males were unable to monopolize females.

The first factor F1 of the PCA on weight, age, and head volume explained 78% of the total variability observed among males. Males characterized by a high value on F1, were old males with large head and weight. These males were also individuals with the highest dominance rank ($n = 8$, $rho = 0.81$, $p = 0.03$, Fig. 1a) and males that sired the largest number of kittens ($n = 8$, $rho = 0.91$, $p = 0.02$, Fig. 1c). Reproductive success was also positively correlated with dominance rank ($n = 11$, $rho = 0.81$, $p = 0.01$, Fig. 1b). Correlation between reproductive success and weight is not significant ($n = 7$, $rho = 0.71$, $p = 0.08$); however, the correlation become significant ($n = 6$, $rho = 0.89$, $p = 0.047$) when male GE was excluded from the analysis. This male presented a great weight loss because he was in the AIDS phase, and died within the end of the year.

The prevalence of FIV in our colony was 20.0% (4/20). All infected cats were males, and males of high rank (BT, VO, PA and GE, see Table 2). No females were positive for FIV. Moreover, all kittens were tested for this virus, and none of them were infected.

Table 3: The occurrence of multiple paternity in the Foro Traiano cat colony in 1999

	Fathers						
Mothers	BT	VO	PA	GE	DN	?	Total
First litter of the year							
Ma	2				2		4
Se		2			1		3
Cy						3	3
Na	2	2					4
Ka							
Va							
Second litter of the year							
Ma	3	1					4
Se	1		2				3
Cy							
Na							
Ka		2			3		5
Va	4						4
Third litter of the year							
Ma							
Se	1			1	2		4
Cy							
Na							
Ka							
Va							34
Total	13	7	2	1	8	3	

Numbers indicate numbers of kittens.

Table 2: Dominance scale order for 14 tomcats, predicted by the Batchelder–Bershad–Simpson (BBS) method, convergent at iteration 15

Cats	BT	VO	PA	TE	GE	BY	NO	GR	DN	SN	TO	FK	MZ	CO
BBS	−1.29	−1.31	−1.43	−1.49	−2.75	−2.84	−3.59	−4.30	−4.51	−4.56	−4.59	−4.69	−6.30	−6.33

BBS scores in the table have to be multiplied by 10^{-2}.

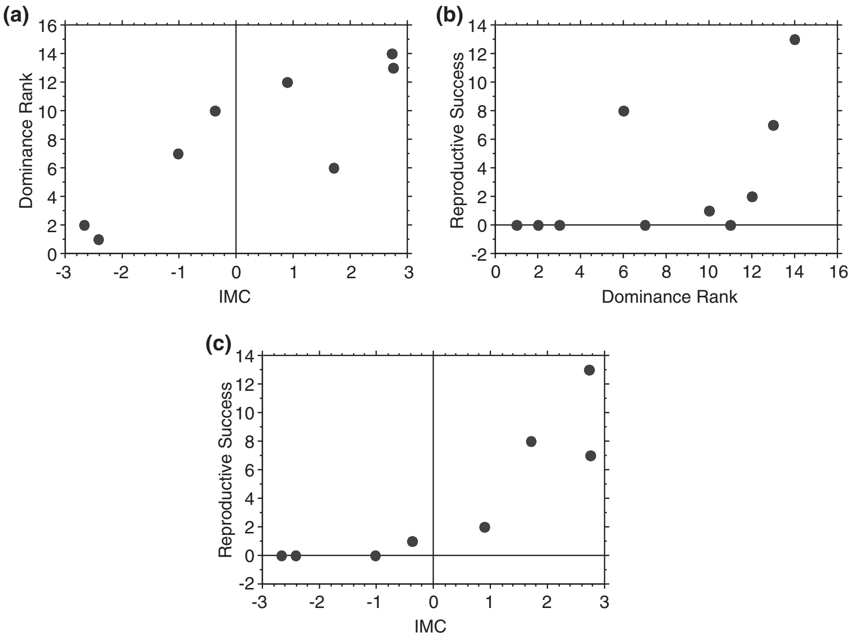

Fig. 1: Relationships between (a) IMC (Index of Morphological Characteristics) and dominance rank; (b) dominance rank and reproductive success (estimated as the number of kittens sired by a given male); and (c) IMC and reproductive success. Males are classified according to their dominance rank from the cat with the lowest dominance rank quoted 1 to the dominant male quoted 14

Discussion

Our results support the hypothesis that, in cats, male morphological characteristics (age, size and body weight) are an important determinant of dominance rank, and dominance rank is a major factor of reproductive success.

Nevertheless, acquisition of a high rank does not permit the entire control of receptive females. Although in our study the dominant male sired the highest percentage of kittens, he monopolized only one entire litter (out of nine) and co-sired the highest number of litters from five females. The percentage of multiple paternities in this colony was as important as 78%; a percentage exclusively found in urban feral cats living in high density social groups (Yamane 1998; Say et al. 1999).

In the urban environment, the number of competitors for reproduction is important and several females are generally in oestrus at the same time (Liberg et al. 2000). Furthermore, features of female reproduction – induced ovulation, long ovulation period, delayed ovulation after copulation (Stabenfeldt & Shille 1977) – favour multiple copulations and mixing of sperm from multiple males. Thus, the cost associated with the exclusion of all other males for the alpha male is consequently high. In fact, while the dominant male fights with some of them, other males could exploit the situation and mate successfully with the female. In this way, the dominant male would run the risk of being completely excluded from reproduction. The dominant male makes then 'the best of a bad job': he does not aggressively interact with other males, which simultaneously court the same receptive female (Natoli & De Vito 1991; Say et al. 1999, 2001) and share the paternity of litters with other males (Say et al. 1999, 2001).

Contrarily to this study, Yamane (1998) did not find any correlation between the body mass and the reproductive success in male domestic cats. The discrepancy between our results and those of Yamane (1998) indicates that some factors can modify the way with which body mass and social rank affect the reproductive success. In particular, Say et al. (2001) found that the temporal pattern of female oestrus is important in determining the reproductive tactics of dominant males in urban cats. For the population studied by Yamane (1998), females were synchronized within each colony. In our study females were asynchronous. In such conditions, the dominant male attained a higher reproductive success than lower ranking males through priority of access to females. This priority of access to females allowed him to be involved in copulations with more females than other males or to copulate several times with same females to insure their paternity (Say et al. 2001; Say & Pontier 2004).

Reproductive success and survival are pivotal to understanding the benefits and costs associated to dominance. If high dominance rank presents, on one hand, benefits in terms of annual reproductive success (this study) and priority of access to food (Yamane et al. 1996; E. Natoli et al. unpublished data), on the other hand it can be costly, for example, in terms of time invested in achieving and maintaining high rank positions, that result in higher risk of being injured. Another cost that has to be taken into account is the risk of being infected by some pathogens. As expected, we found that the individuals more exposed to the risk of being infected by FIV are the larger and fully mature males: they occupy the first, second, third and fifth places in the hierarchy (BT, VO, PA and GE). FIV infection is well known to be characterized by risk factors linked to aggressive behaviour (Courchamp et al. 1998, 2000; Pontier et al. 1998). Thus, if on one hand these results yield evidence that there is a fitness gain of being high ranking males, on the other hand they show clearly that among other costs, impact of disease transmission on survival also has to be considered (e.g. the case of male GE in this study). Future studies should be aimed at defining precisely the relationship between costs and benefits of being dominant, by means of the determination of lifetime reproductive success of males. The results would help to understand the ecological pressures that have influenced the evolution of social dominance in urban feral domestic cats.

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