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Review

Bold attitude makes male urban feral domestic cats more vulnerable to Feline Immunodeficiency Virus

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Abstract

Individual differences in behaviour are a phenomenon that is more and more attracting the attention of scientists. Among the other reasons, behavioural individuality occurs because selection favours the adoption of different tactics by individuals. It is now widely recognized that within many vertebrate species, individuals vary along an axis the extremes of which are represented by individuals 'bold' and 'shy', sometimes called 'proactive' and 'reactive'. Here we present the case of feral domestic cats (*Felis catus* L.) living in group in the urban environment where showing bold attitudes is linked to the benefit of a high annual reproductive success but, on the other hand, to a high probability to be infected by the Feline Immunoficiency Virus (FIV), a lethal disease caused by a retrovirus. In this species, natural selection has probably favoured proactive temperament in spite of the cost represented by getting the disease. In fact, proactive individuals, even if FIV positive, reproduce more than reactive individuals before the last stage of FIV-infection (AIDS) characterized by a loss of immunological defences and subsequent opportunistic infections. Evolutionary implications are discussed.

Keywords: Domestic cat; Urban environment; Temperament; FIV; Reproductive success

Contents

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1. Introduction

The number of studies aimed to explain behavioural individuality is steadily increasing, focusing on variations between individuals rather than between different age/sex classes of individuals. Behavioural individuality may vary with individual history, ecological context, sex, age, and many other variables but, still, even after having taken into account all variables, considerable inter-individual difference emerges. In human literature, these differences have been termed 'personality types' [1]. Scientists are still debating if the term 'personality' is suitable for non-human animals, and several other definitions have been suggested: the most important are 'coping style', 'tem-temperament' 'behavioural tendency', 'strategy', 'syn-syndrome', 'axe', 'construct' [2,3]. Whatever is the definition utilized, it is widely recognized that within vertebrate species, individuals vary along an axis the extremes of which are represented by individuals 'bold' and 'shy ' [4] or 'proactive' and 'reactive' [5]. Proactive individuals tend to be aggressively quicker to explore and try to manipulate the situation, even if the context is new; consequently they cannot be defined neophobic. They are less socially bound and, thus, more prone to disperse; on the other hand, they are more prone to form routine and less prone to innovate. On the contrary, reactive individuals are more cautious and more sensitive to external stimuli that they analyse trying to adjust to the situation. They are slower in taking decisions and, rather to manipulate the situation, they tend to adjust to it in a more passive way. In other words, proactive individuals manipulate or control their environments, while reactive individuals cope with their environments [3]. Given in this way, it seems that reactive individuals risk less. But, on the other hand, they are not less at risk. Empirical data have shown that reactive individuals show higher hypothalamic-pituitary-adrenal axis reactivity in response to stress, than proactive individuals (reviewed in [6]). This means that they result more vulnerable to stress-related disorders (reviewed in [7]) that represent one the cost of reactive temperament.

In this paper we present the case of feral domestic cats (*Felis catus* L.) living in group in the urban environment. According to their behaviour, we address the temperament of tomcats as proactive or reactive. Therefore we study the relationship between temperament, social rank and reproductive success of males. Finally we show that, contrarily to the usual balance costs-benefits found for the majority of other vertebrates where coping style was described so far, in domestic cats proactive temperament may increase the probability of being infected by the Feline Immunodeficiency Virus (FIV), a disease caused by a retrovirus analogous to the Human Immunodeficiency Virus.

2. Generality about the social organization of urban feral cats

In urban environment, feral cats live in multi-male multi-female social groups at very high local densities (up to 2000 cats/km^2, [8]) with a balanced sex-ratio. Cats have to share food and shelters that are provided by cat lovers in specific places like hospital parks, ruins, cemeteries and public gardens. Males and females live in small and largely overlapping home ranges [8,9]. The social structure of males is organized around a dominance hierarchy, which is not always markedly linear [10] (but see [11]). Aggressive interactions are not frequent between males belonging to the same social group and violent fights are not frequent [10] but, when they occur, tomcats can show deep wounds. Cats also fight in territorial defence against tomcats of neighbouring groups. Male morphological characteristics (age, size, body weight) are an important determinant of dominance rank. The highest ranking males are also the most aggressive individuals; they have the highest rate of spraying and explore the largest areas [12,9]. In that sense they can be considered as proactive individuals [5].

The mating system found in this environment is promiscuity [13,14]. During the oestrus period (from January to July in our latitude), several males can court and mate the same female with low levels of aggressiveness [10,13–15] between them. As a result, most litters are sired by more than one male. When females show synchronous oestrus, dominance rank [14,16] and male home range size [9] appear as two major components of reproductive success; the variability in male reproductive success is high and the dominant male sires the highest percentage of

kittens. No obvious mate choice from females for copulation with high ranking males has been highlighted in cats [17]. The absence of high aggressiveness and the possibility for all males to access to reproductive females leads to a very low dispersal rate with females dispersing over longer distances than males [18,19], a pattern of dispersal which is atypical in mammals.

3. Studied colonies

We monitored three different cat colonies typical of the urban environment: two were sited in Rome (Italy) [(1) Fori di Traiano, TR; (2) Garbatella, GA] and one in Lyon (France) (La Croix Rousse (LCR)) (see Table 1 for details). The functioning of LCR is well know and has been the object of several published works [13,19,20] synthesized here. Data reported for TR are actually submitted whereas data for GA are original. Tomcats are trapped regularly using double-door traps. They are anaesthetised 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). Blood and fur samples are collected, respectively, for epidemiological and genetic parentage analyses. Cats are then released.

4. Temperament and social rank

4.1. Behavioural data

Coat colour pattern and morphological characteristics were utilised to recognise individual cats in each colony. Behavioural patterns (see [17] for description) are recorded following the focal animal sampling method [21]. We recorded the six following behavioural categories: (1) aggressive behaviour (threating, vocal duel, real duel, chasing); (2) submissive behaviour (avoiding, leaving, crouching, flying, hissing); (3) affiliative behaviour (sniffing nose, passive contact, rubbing); (4) territorial behaviour (spraying, rubbing the cheeks); (5) display (scratching claws, rolling on the ground); and 6. mating behaviour (attempts to mount, false mounts, true mounts).

4.2. Temperament of tomcats

The temperament of male cats, for which behavioural data were sufficient, was determined by mean of a normed principal component analysis (PCA) that described the relationships between the individual cats and the six behavioural categories described previously. The basic goal of PCA is to reduce the dimensionality of a data set while retaining as much information as is possible. The analysis replaces the original correlated variables by new uncorrelated component variables called principal components. The analysis orders them, using as criterion the amounts of contribution to the sum of the variances of the original variables. So, a small number of principal components, linear combinations of the initial variables, is kept, explaining most of the variation in the data. The link between the original variables and these new ones is well described by the correlation circle. The first principal component (factor) is the combination of variables that accounts the maximum amount of variation. The second principal component accounts the next largest remaining amount of variation and is orthogonal to the first principal component. Here, the first factor which explained by itself more than 50% of the total variability, discriminated proactive (i.e. the most aggressive males that won the majority of encounters, marked frequently the territory but also that frequently showed affiliative behaviour towards members of the group) and reactive (i.e. individuals that often performed submissive behaviour to other members of the colony and that were rarely aggressive) temperaments (Fig. 1). The second factor of the PCA was more difficult to interpret because the behavioural patterns discriminated by this axis changed according to the cat colony. Cats characterised by a negative value on the first axis of the PCA were proactive whereas the temperament of cats with a positive value was rather reactive. Although similar, the pattern was less marked in TR because of two cats, DAM and SAN. They performed a lot of threats towards low ranking male but, at the same time, they showed a high number of submissive acts to high ranking males. DAM was a very competitive young male who was challenging high rank positions whereas SAN was a dominant male from another close colony which interacted with the males of the TR colony during the reproductive period.

Table 1
Principal characteristics of the three studied colonies

	Locality	Years of study	Cat density/km^2	No. of adults	Hours of observations	References
TR	Rome	1999	154.89	14 males, 6 females	445.30	[14]
GA	Rome	2001	2833	10 males, 7 females	557.41	Natoli et al, in preparation.
LCR	Lyon	1997	2091	21 males 25 females	229.00	[12,13,16]

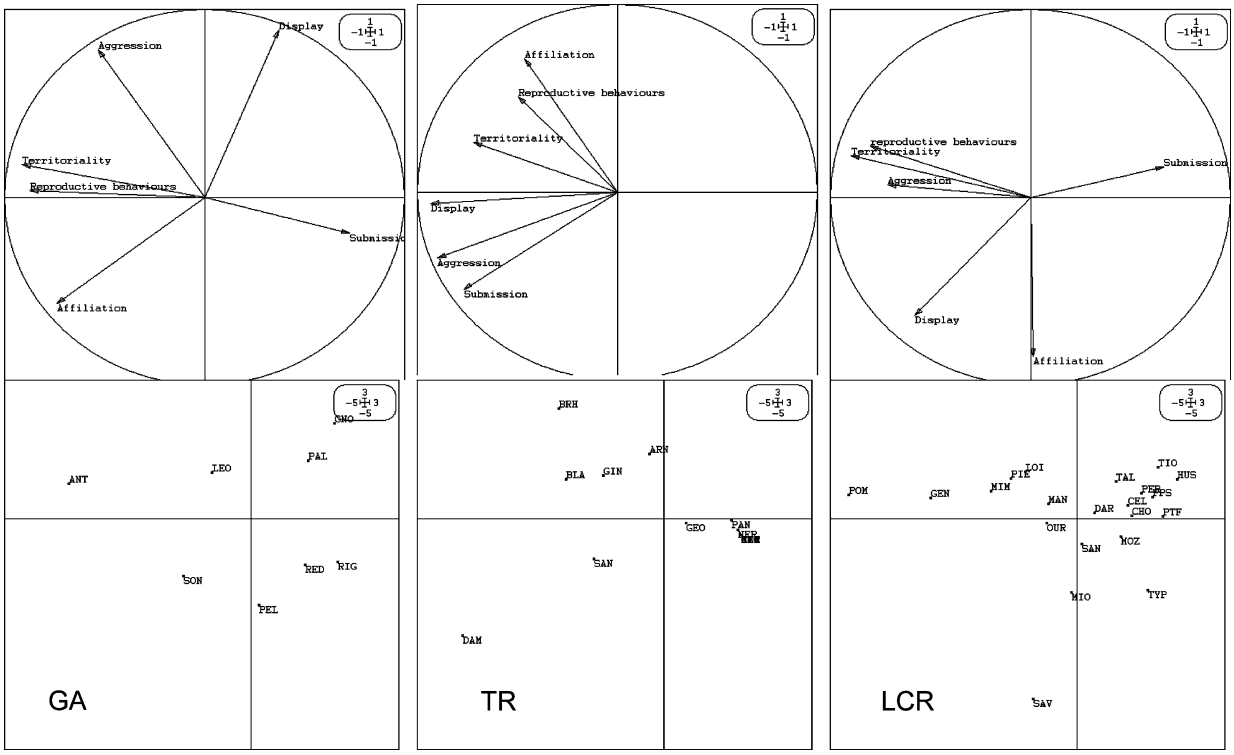

Fig. 1. Principal component analysis (PCA) on the six behavioural categories (see text) for the three studied colonies, TR, GA and LCR. Correlation circle and projection of the individuals onto the first two factors of the PCA analysis are presented. The circle shows the correlation between the initial variables and the new two first components. Only variables far from the centre are of interest for interpreting the meaning of each factor. The scatter plot shows the position of the cats on the plane and can easily be interpreted in relation to the corresponding position of the variables on the correlation circle.

4.3. Social rank

The scores of aggressive and submissive interactions were ranked in a squared matrix with winners on one axis and losers on the other cats [22,23] based on direction, not number of interactions. Social rank of males was determined by directionality of submissive behaviour since the squared matrix of the latter contained a lower number of inversions than the squared matrix of aggressive encounters. This method has been already utilised successfully in domestic cats [10,11,13,14,16].

4.4. Relationship between temperament and social rank

Proactive males, characterised by high negative values on the first axis of the PCA, were globally the males with the highest social rank in all colonies (Spearman rank correlation: $\rho = 0.71$, $P = 0.05$ for TR colony, $\rho = 0.67$, $P = 0.02$ for GA colony, $\rho = 0.77$, $P = 0.0006$ for LCR colony). Furthermore, high ranking males were also the oldest, the largest (for the head size), and the heaviest ones [14,24]. According to the definition of 'proactive' individuals [5], this result is not surprising since social rank is based on aggressive interactions between individuals. Nevertheless, some males of lower ranking behave as proactive. It is, for example, the case of DAM and SAN.

5. Temperament and reproductive success

Paternity of 34 kittens (belonging to 9 litters) and 70 kittens (belonging to 18 litters), respectively, for TR and LCR colonies was determined using nine microsatellites [13,14,16]. Results of paternity analyses showed a high proportion of multiple paternity (defined as the proportion of litter where at least two different males sired the kittens), ranging from 78% (in TR, [14]) to 83% (in LCR, [13]). This result suggests that males of high rank were unable to monopolize females. Nevertheless, when the oestrus of females was synchronised, high ranking males sired more kitten than males of lower social rank [16]. In accordance with these previous studies, tomcats with proactive temperament had the highest reproductive success (Spearman rank correlation, $\rho = -0.73$, $P = 0.008$ for TR colony; $\rho = -0.68$, $P = 0.002$ for LCR colony) (Fig. 2).

6. Pattern of Feline Immunodeficiency Virus (FIV) infection

The Feline Immunodeficiency Virus is a lethal lentivirus of the retroviridae family [25] with a worldwide distribution [26]. There is neither immunization nor natural cure for the FIV: after several years, 5 years on average in laboratory

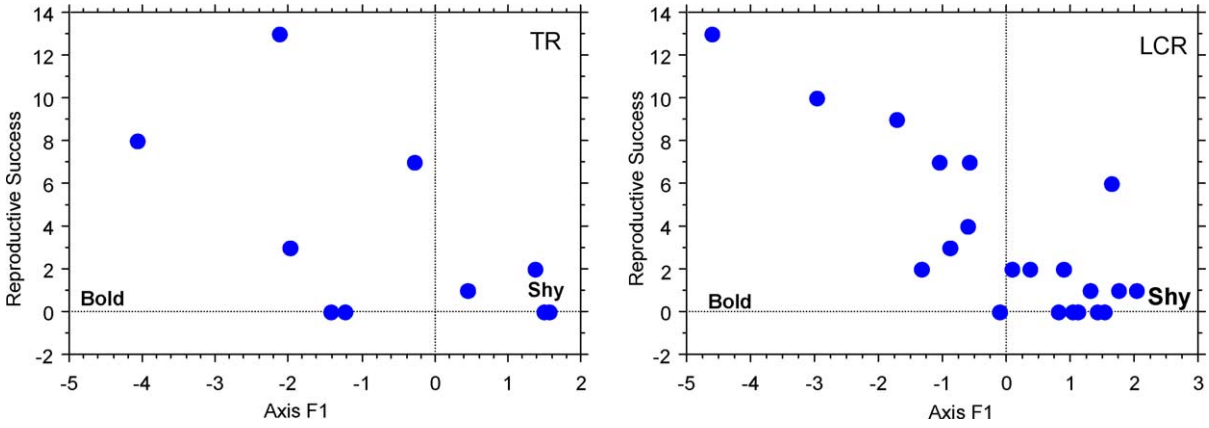

Fig. 2. Relationships between 1st factor of the PCA (that identifies "bold-shy" individuals) and reproductive success (estimated as the number of kittens sired by a given male) of cars belonging to the islomers studied.

conditions [27,28], individuals die from opportunistic diseases associated to the loss of immune defences in the last stage of FIV-infection (AIDS, [29]). Evidences tend to prove that the transmission of the FIV occurs through bite via saliva in natural populations [30–33], between males during fights (the female do not bite each other) and from male to female during coitus (when the male bites the female at the neck). No vertical transmission was observed in natural populations [33,34]. The highest prevalence is observed in sexually mature, non-neutered roaming males with the larger home range [32,33], i.e. in the most aggressive individuals [20,32,35]. Females are less infected than males [20,32,33].

We collected blood samples from male cats of the three studied colonies. We used ELISA method (Cite-Combo, Idexx) to detect the presence of FIV-specific antibodies and all positive sera were confirmed by Western Blot [36] to avoid false positives. Details of serological analysis for FIV are available in [32,33]. We found no positive cats in GA. The prevalence of FIV was, respectively, 28.6% in TR and 19% in LCR colony. Prevalence of FIV found here fall in the range of prevalence reported in other urban cats populations (from 0 to 30%, [37]). Absence of FIV in the GA colony can be explained by the very low probability of persistence of the virus in very small populations in the urban environment where the rate of dispersion among populations is weak [38]. All infected males were high ranking males (first BRH, second ARN, fourth PAN and fifth GEO in the hierarchy that included 14 males) in TR. With the exception of one male (GEO), these infected males were characterised as proactive individuals from the PCA. The serological status of one male among the highest ranks (POM, second in the hierarchy) was unfortunately unknown in the LCR colony; four males were infected (the first MIM, third LOI, fourth GEN and 12th TIO in the hierarchy that included 21 males). Our PCA analysis suggested that all males but TIO found FIV positive showed proactive temperament (Fig. 1).

7. Conclusion

The results of these studies show that in urban feral domestic cats living in group, the males with bold temperament are also those who obtain the highest annual reproductive success. Proactive temperament appears as the most successful strategy in urban feral domestic cats. Studies showing such an advantage of bold temperament in term of fitness are lacking. Nevertheless, several other works highlighted that proactive individuals are characterised by a lower basal and stress or social induced plasma corticosterone levels than the other males (e.g. in hens *Gallus gallus* [39], in mice *Mus musculus* [40]), in great tit *Parus major* [41]). Proactive individuals might then be less exposed to stress-related diseases (e.g. in pigs *Sus scrofa* [42], in minks *Mustela vison*, [43]). Unfortunately, in urban feral domestic cats nothing is known about levels of corticosterone as a response to both stress and social defeats.

FIV is an endemic cat disease [30–32]. The transmission of the FIV between males occurs through bite during fights for social rank establishment. Consequently, and at the opposite of results found in the studies previously quoted, cats characterised by a proactive temperament have a higher probability to be infected by FIV than shy individuals. Advantage of proactive strategy in cats is then under balanced by a higher risk to be infected by the FIV, which is a lethal lentivirus. Yet, natural selection has probably favoured proactive temperament in spite of the cost represented by getting this disease. Indeed, we observe that bold individuals, even if FIV positive, reproduce more than shy individuals during the asymptomatic period in which the cat is healthy. Moreover, the virus cannot be transmitted from mother to kittens in natural conditions [34], and very few individuals are infected by FIV before the sexual maturity (between 12 and 14 months of age in this environment, [33]). Consequently, the mortality rate of kittens sired by 'proactive' males (and then more likely infected by FIV) is not higher than the mortality of kittens

sired by other males. Furthermore, while proactive individuals are more at risk for the FIV-infection, their bold temperament may confer an advantage in delaying the apparition of symptoms because they are less sensitive to social stress. Indeed, a large variability of latency in FIV-infection has been observed between individual cats [26], and should reflect an undetermined variation in susceptibility to infection by the virus and eventual mortality. For example, individual differences in vulnerability to FIV could be due to the beginning of the decay of being the alpha male, i.e. to the detrimental effects of social defeats: when the dominant animals begins to loose encounters with members of its own group, he might develop the FIV opportunistic diseases and die quickly. This will be investigated in ongoing studies.

In evolutionary terms we might expect that natural selection takes, among several possibilities, one of two directions: the first is that proactive copers evolve stronger resistance to the development of the disease to have the longest period as possible of latency of the disease, to reproduce as much as they can before dying. The second possibility is the evolution of a 'medium' class of less proactive individuals that reproduce more than reactive individuals but do not elicit such a strong reaction from other proactive individuals to be involved in real fights.

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