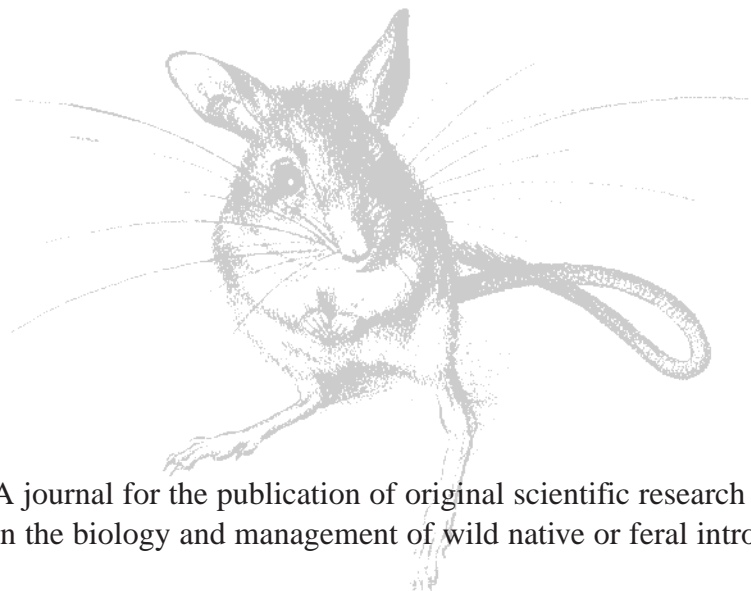

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Transmission of Feline Immunodeficiency Virus in a population of cats (*Felis catus*)

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Abstract. The increasing awareness of the ecological impact of domestic cats (*Felis catus*) as wildlife predators has given rise to much effort in research on cat control, but studies related to the spread of pathogens in natural populations remain almost non-existent. We aimed to determine the infection strategy of Feline Immunodeficiency Virus (FIV) in a natural population of cats, focusing on qualitative and quantitative aspects of its transmission. FIV is a lethal retrovirus infecting cats world-wide, transmitted by bites. It has an interesting potential as a control agent for this species. We studied an urban population of stray cats over three years, monitoring its epidemiology and its social and spatial structures. Despite a high cat density, both transmission rate and prevalence of FIV were relatively low. Socially dominant males were more likely to be infected. In addition, males of the study population were less often infected than in another population, where a polygynous mating system involved more fights. Infected individuals lived long enough to acquire the virus and infect another cat. Because they were subordinates, non-infected cats had a shorter life expectancy, which would not have permitted the spread of FIV. Thus, FIV infected predominantly at-risk individuals whose social ranking allowed a high probability of retransmitting the virus.

Introduction

The impact of introduced domestic cats (*Felis catus*) in many parts of the world is widely recognised as very detrimental to many small endemic vertebrate species. In addition to entire continents, domestic cats have successfully invaded at least 118 of the 131 major island groups (Atkinson 1989). In island ecosystems they exert a high pressure on indigenous fauna and are one of the most important causes of past extinction and current endangerment of endemic species (Atkinson 1989; King 1985; Lever 1994; Dickman 1996; Boitani 2000). Of all introduced carnivore species, the cat is often considered to be by far the most dangerous for native animals, as much for its wide prey spectrum as for its efficiency in rapidly extirpating entire populations (Boitani 2000).

Classical control methods, including shooting, poisoning and trapping, are poorly cost-effective for feral cats, especially when accessibility is limited (Bester and Skinner 1991; Hone 1994). Although it may not be the most suitable solution for some problem populations, such as those on mainland Australia and New Zealand where owned cats would be at risk, biological control is considered a promising alternative for remote or uninhabited islands (Courchamp and Sugihara 1999; Cleaveland *et al.* 1999). Success in controlling the Marion Island cat population by releasing feline panleucopaenia (van Rensburg *et al.* 1987) has provided an excellent stimulus for studies to improve this control method. In partic-

ular, the choice of optimum pathogens is of crucial importance, calling for empirical studies on the epidemiology of natural cat populations (Courchamp and Sugihara 1999). Such studies are strikingly absent from the literature, despite the strong advocacy of biological control (Dobson 1988), and the evident need to better understand the pattern of spread and control potential of the more than 30 parasitic species naturally harboured by cats (Lever 1994).

Among these parasites, Feline Immunodeficiency Virus (FIV) has recently been considered a potential candidate for biological control of cats introduced onto oceanic islands (Courchamp and Sugihara 1999). FIV is a lentivirus that induces feline AIDS in domestic cats (Pedersen 1993). Different strains of this virus infect other felid species (Courchamp and Pontier 1994), but there is no external disease reservoir for *Felis catus*. This virus is functionally analogous to its human homologue, the Human Immunodeficiency Virus (Bendinelli *et al.* 1995; Willett *et al.* 1997; Hartmann 1998), apart from its transmission mode, which is mainly through bites during aggressive interactions (Yamamoto *et al.* 1989; Courchamp and Pontier 1994; Courchamp *et al.* 1998). There is no vertical transmission (from mother to offspring). FIV infection leads to lifelong antibody (and virus) carriers. The clinical staging of FIV infection is very similar to that of the Human Immunodeficiency Virus infection, with a short acute stage, a

long asymptomatic period (lasting up to several years, in which the cat is healthy), a Persistent Generalised Lymphadenopathy, an AIDS-Related Complex associated with chronic infections, and finally AIDS. As in humans infected by HIV, feline AIDS is characterised by a loss of immunological defences, allowing subsequent opportunistic infections. Therefore, cats infected with FIV may die from micro-organisms that would not normally harm them. The cat is infectious during all five stages of infection, which have been estimated to last an average of five years in laboratory conditions (experimentally infected cats: Pedersen and Barlough 1991). There is no recovery nor immunity to FIV, either natural or artificial. For further details on FIV, see the complete reviews published on various aspects (molecular: Elder and Phillips 1994; genetic: Miyazawa *et al.* 1994; immunological: Lin 1992; clinical: Pedersen and Barlough 1991; serological: Courchamp and Pontier 1994; general: Bendinelli *et al.* 1995; Hartmann 1998). Epidemiology remains the one aspect where FIV knowledge is completely lacking. Some at-risk parameter classes have already been defined, involving an effect of age (old cats) and sex (males) for the probability of acquiring FIV infection (Courchamp *et al.* 1998; see also Courchamp and Pontier 1994 for a review of serological surveys), but most epidemiological features of this disease remain unknown. As an example, no estimation of FIV transmission rate in natural populations has yet been made. Similarly, the life-expectancy of naturally infected individuals is unknown. Qualitative aspects of FIV transmission, such as the identification of at-risk individuals, also need further study.

The aim of this paper is to characterise the epidemiological pattern of FIV infection. This we do by testing four predictions: (i) FIV prevalence should be relatively low in natural populations (because the virus is transmitted by bites during fights, which are infrequent: Liberg 1981; Kerby and Macdonald 1988); (ii) high-ranking individuals are expected to be more exposed and thus more often infected by FIV (because they are more involved in aggressive interactions than low-ranking ones: Liberg 1981; Kerby and Macdonald 1988); (iii) FIV prevalence in males should be higher than in females, and higher in polygynous populations than in promiscuous populations (because polygynous males are involved in more intensive competition and aggressive encounters with other males than promiscuous males: Liberg 1981; Natoli and De Vito 1991); (iv) assuming a low transmission rate (because physical confrontations leading to bites are rare), life expectancy of infected cats should be high, otherwise FIV would not persist.

To test these predictions, we continuously monitored an urban population of stray cats for three years. We tested the association between FIV infection and social status (assessed by body size, home-range size and by a range of typical behaviours); we also compared an estimate of the average life span of infected individuals with that of uninfected individuals, and then to an estimate of FIV transmission rate; we then tested the effect of social structure of cat populations on FIV

prevalence by comparing results from this population with that of a population with a polygynous mating system (Courchamp *et al.* 1998).

Material and Methods

The natural population of cats used for this study inhabits the 7.5-ha site of a hospital situated in the centre of Lyons, France. Data presented here are from December 1992 to August 1995 (33 months). Cats were located by direct observation, and observed during the day and at dawn and dusk, periods previously determined to be the most important in terms of activity for this population. Individual characteristics and behavioural data were collected in the field and were recorded later into a computerised database, which was used for the analyses. During the study, cats were observed at least once a week, for varying duration (1 h at least), using focal, scan and *ad lib* data collection. Data were pooled for a preliminary analysis of the behavioural and home-range size differences between infected and uninfected individuals (4590 observations in total). Four different behaviours were analysed for this study: walking, marking and resting, which are associated (the latter negatively) with territory vigilance or defence, and mounting of females by males, which can be associated with dominance (Yamane *et al.* 1996). In all, 48 cats, with 20–335 observations each, were used for these analyses. All behaviours were considered for each cat as a percentage of activity, in order to compare between cats (by a *t*-test).

To complete our analysis of whether infected and uninfected cats differ in their social status, observations were also carried out throughout the year to collect information on the home range of each individual. In feral and stray domestic cats, high-ranking individuals are known to be usually bigger and have larger home ranges than low-ranking individuals (Liberg 1981; Konecny 1983). For each observation, the position of the cat was plotted on a digitised map. We determined home-range size using the 95% Minimum Convex Polygon method, from the RANGE IV program (Kenward 1990).

Full census and trapping sessions were conducted twice a year. Cats were individually trapped in baited cages, and then tranquillised (see details in Courchamp *et al.* 1998, 2000). The trapping protocol had no noticeable effect on the social interactions in the population. Control observations were carried out before and after the captures. We individually marked each cat and recorded its sex, age, weight, and health condition in addition to several morphometric features including the length, width and height of the head. Sex of individuals was estimated by primary and secondary sexual characteristics, and confirmed when cats were trapped. Precise age was known for cats born during the study (58.3% of all cats) but was estimated (on the basis of the condition of the teeth) for older cats or for cats immigrating from outside of the study population. Following Natoli (1985), cats were allocated to one of four age categories: kittens (<6 months old), juveniles (<12 months), sub-adults (<18 months) and adults (≥ 18 months). A blood sample was taken for serological analysis of the presence of FIV antibodies from cats older than 3 months old (see details in Courchamp *et al.* 1998). Captured cats were kept in individual cages where they were fed until release at the end of the trapping session (after 10 days at most).

The database was constructed and used in 4e Dimension; statistical analyses were carried out using Statview IV. For a detailed description of the rural population with which we compare the present population, see Courchamp *et al.* (1998).

Results

Population

In total, 145 cats were present during the period of study, the population at any one time varying between 30 and 73 individuals, with a significant increase over the six censuses of

the study (Spearman rank correlation test: $r_s = 0.94$, $n = 6$, $P = 0.005$). Such a change is partly due to the seasonal presence of kittens and juveniles, which were mostly absent from the first census. Depending on the time of the year, 33–56% of all cats were adults. The sex ratio was non-significantly biased towards males (54% males, $\chi^2 = 1.847$, d.f. = 5, $P = 0.870$). Probably owing to good conditions such as regular feeders among the hospital staff, the density of the cat population was high: 345–2485 cats km⁻², depending on the place and the time of the year. The average density was 733 cats km⁻². These estimates are based on the whole hospital site; if sub-areas where cats were never seen are excluded, the actual density was on average 1100 cats km⁻² and increased to 3650 cats km⁻². Details of the population characteristics are available elsewhere (Courchamp 1996, see also Courchamp *et al.*, 2000); we therefore present only information that is directly relevant to the epidemiological study.

FIV prevalence and transmission rate

FIV prevalence was stable during the years of the study (Fig. 1; $\chi^2 = 9.952$, d.f. = 5, $P = 0.077$). Censuses made after the period presented here confirm this stability ($\chi^2 = 10.27$, d.f. = 8, $P = 0.247$, see Courchamp *et al.* 2000). In addition, as all cats were identified individually, it was possible to estimate a corrected prevalence in the population, by adding the few non-captured individuals that were known to be present during the captures and for which FIV status was known from previous (positive cats) and/or subsequent (negative cats) captures (see Fig. 1). For the last capture, only 5 individuals escaped capture (93.2% efficiency), allowing a more precise estimate of the prevalence: between 12.28% (if all 5 non-trapped cats were uninfected) and 21.05% (if they were all positive). If this group of 5 cats has the same prevalence as the rest of the population (taking into account the sex-ratio of this subgroup), then the total prevalence is no higher than 14.04%. This is to be compared with a prevalence of *c.* 20%

in a population with a polygynous mating system (see Courchamp *et al.* 1998).

We estimated the transmission rate in the population to be one new infection every 190–316 days (at least 3–5 new infections in 33 months). Only four individuals were potential transmitters at the time of each new infection: other infectious cats had disappeared from the population before the seroconversion of new infected cats. If we assume an equivalent transmission rate from all infectious individuals, the transmission rate is therefore at most one new infection per infected individual every 760–1264 days.

Social status

Of the 12 infected individuals in total, 8 were males. Males were not significantly more infected than females (13.3% of males were infected *v.* 10.0% of females: $\chi^2 = 0.253$, d.f. = 1, $P = 0.615$), because of a slightly higher number of males in the population. This differs from the results obtained in another population of free-roaming cats, where we found a significantly higher infection rate in males (23.8% in males *v.* 9.6% in females: Courchamp *et al.* 1998). That other population had a polygynous mating system, where males strongly compete for females, in contrast to the present population, which is promiscuous (Say *et al.* 1999). The prevalence in females was similar in both populations ($\chi^2 = 0.004$, d.f. = 1, $P = 0.949$). In contrast, it was almost double for males in the rural population (23.8% *v.* 13.3%), although this is not significant ($\chi^2 = 2.219$, d.f. = 1, $P = 0.136$). Interestingly, FIV-infected males performed most mountings of females observed in the urban population (see below). It is also worth noting that no serious fight (that could involve bites) was ever directly observed since the beginning of the study in late 1992, confirming that fighting (with bites) is an infrequent behaviour in this population.

The body size of individuals was estimated using both body mass and an estimate of head size (length \times width \times

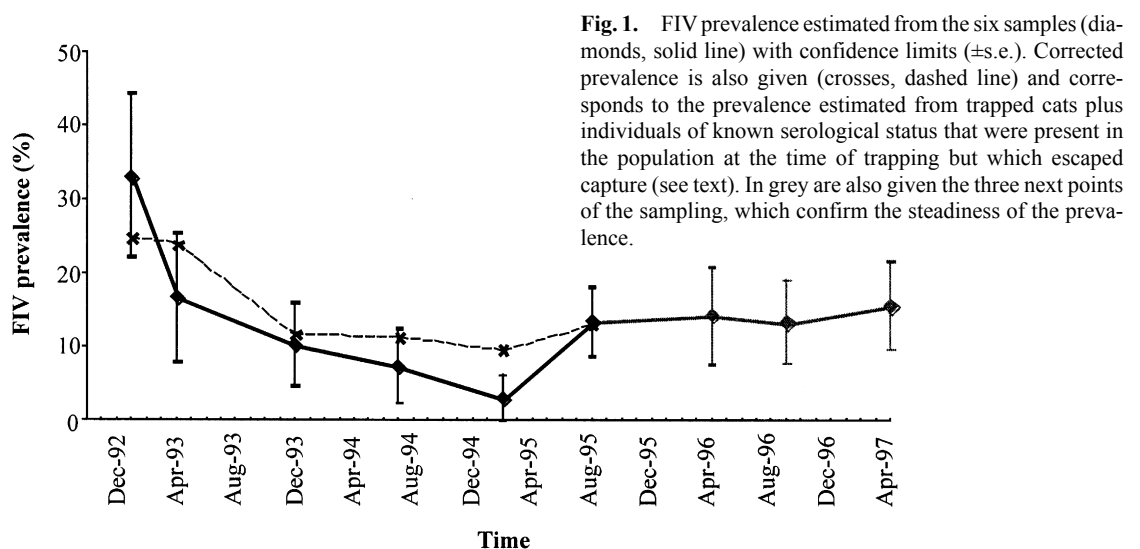


Fig. 1. FIV prevalence estimated from the six samples (diamonds, solid line) with confidence limits (\pm s.e.). Corrected prevalence is also given (crosses, dashed line) and corresponds to the prevalence estimated from trapped cats plus individuals of known serological status that were present in the population at the time of trapping but which escaped capture (see text). In grey are also given the three next points of the sampling, which confirm the steadiness of the prevalence.

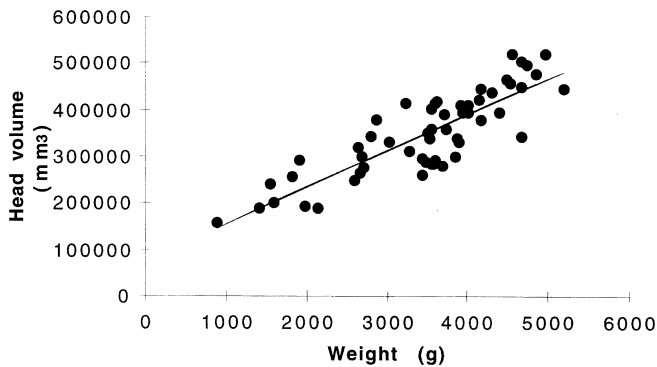


Fig. 2. Correlation between volume of the head and body mass.

height). Body mass was significantly correlated with this estimate of head size ($n = 55$, $r = 0.85$, $P < 0.0001$; Fig. 2). However, body mass varied according to the time of year and with breeding condition of females. We therefore first checked that infected individuals had the largest heads ($t = 2.257$, d.f. = 68, $P = 0.027$) and then, because of allometric relations, we used the residual of a weight *v.* head volume regression to control for the correlation between these two parameters. We then tested for a difference between this measure of cat size and the infection status of individuals. For four infected cats, at least one of the five variables we used for this analysis was missing; the animal therefore had to be removed from that analysis. Infected individuals had a significantly larger body size than uninfected cats ($U = 190$, $P = 0.036$; see Fig. 3), showing that they had the largest skull, regardless of their current body weight. Since they were also among the heaviest cats in absolute terms, this analysis shows

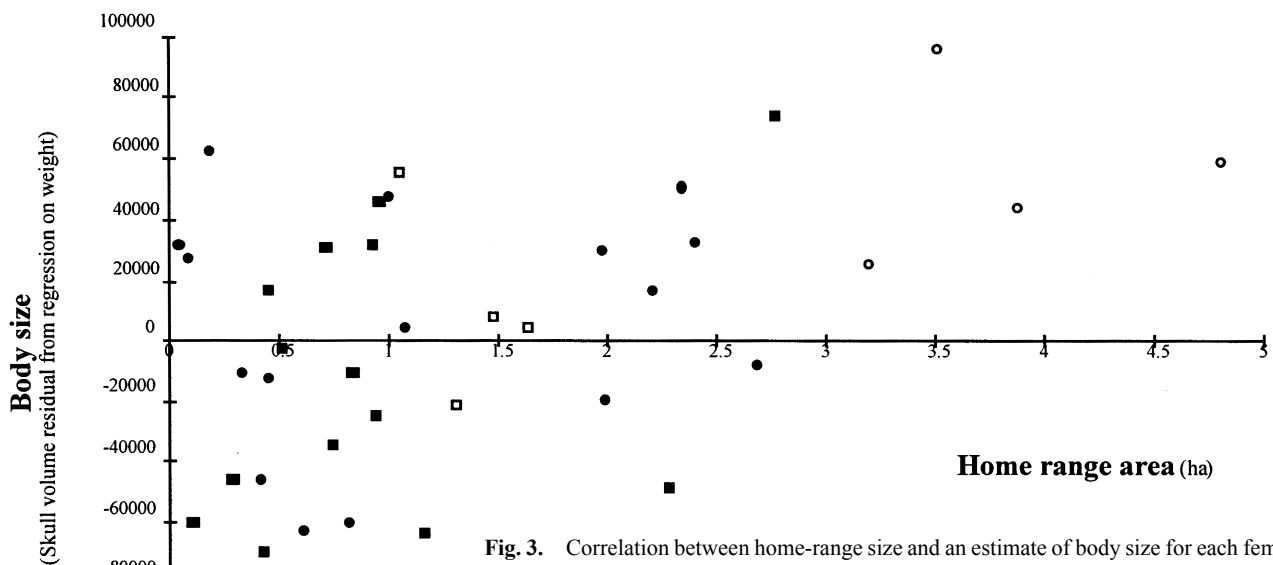


Fig. 3. Correlation between home-range size and an estimate of body size for each female (squares) and male (circles) for which these data and FIV status (infected: open shapes, uninfected: solid shapes) were known. The estimate of body size is the residual of the linear regression between body weight and skull volume (length \times height \times width). Individuals with positive residuals are 'large' individuals: they have a large body size regardless of their weight (see text).

that infected cats were among the largest and heaviest individuals in the population, and therefore likely to be dominant.

Sufficient data on home range was available for 40 cats. Home ranges of males were nearly twice as large as those of females (1.57 ± 0.27 ha *v.* 0.85 ± 0.11 ha: $t = 2.585$, d.f. = 51, $P = 0.013$), whereas home ranges of adults were, on average, three times larger than those of juveniles (1.87 ± 0.24 ha *v.* 0.66 ± 0.11 ha: $t = 4.8721$, d.f. = 49, $P < 0.0001$). For both sexes, there was a significant trend for individuals with a larger home-range size to be infected by FIV (males: $U = 80$, $P = 0.002$; females: $U = 91$, $P = 0.009$; Fig. 4). Fig. 3 shows that body mass alone cannot explain the larger home range of infected cats.

FIV-infected individuals were significantly more often observed walking around their home range ($t = 3.601$, d.f. = 46, $P = 0.0089$) or marking it ($t = 4.861$, d.f. = 46, $P < 0.0001$) than uninfected individuals. In contrast, infected cats were significantly less often observed resting ($t = -3.131$, d.f. = 46, $P = 0.0030$). FIV-infected cats also performed most of the mountings of females, although data were too few to allow a meaningful statistical test: five out of a total of seven (the other two were, however, performed by a young male who became positive for FIV shortly afterwards). These results show that individuals displaying typical dominant cat behaviour, territory defence or vigilance and mounting, were more often infected by FIV than were others (Fig. 5).

Life expectancy

It is difficult to assess the life expectancy of cats in natural populations. Although most cats born in our population were discovered within weeks, dead individuals were often hidden, and disappearances could seldom be unambiguously

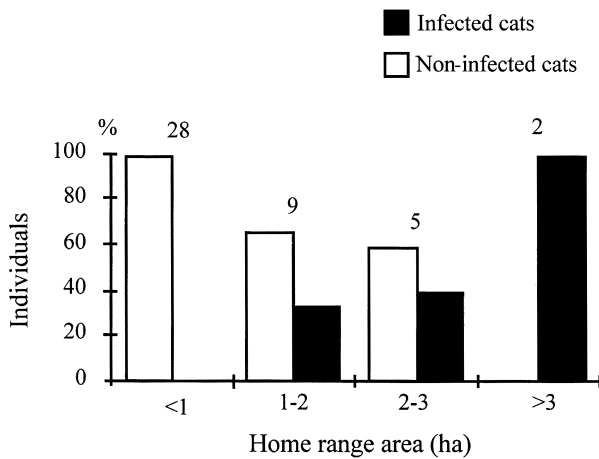


Fig. 4. Class of home-range size according to the serological status for FIV infection: uninfected (open bars) and infected (solid bars). On average, infected cats have a significantly larger home range. Sample size is given above the bars.

attributed to death. Moreover, the life expectancy of cats is too high to be adequately studied in a natural population within a few years: many cats were born before the start of the study and many others will die after its end. We therefore used the observation period (time between the first and the last observation in the population) of infected and uninfected cats. Whilst not an accurate estimate of life expectancy, we assume that observation and life spans are correlated, because the disappearance of regularly seen individuals is most likely to be due to mortality and because we generally discovered litters very rapidly, at least those that were to eventually emerge. Moreover, our goal was only to compare our estimate of life expectancy between infected and uninfected cats. Since cats live, on average, longer than the 33 months of our study, we used five years of data. The study period covers the full five years, but only 33 months of data were used for most of this paper because of a change in protocol after 33 months (see Courchamp *et al.* 2000). We found that infected cats were present in the population significantly longer than uninfected cats: 788 days *v.* 242 ($U = 1241.5, P = 0.0002$). However, a likely explanation for this finding is the existence of an age effect on FIV infection (Courchamp and Pontier 1994; Courchamp *et al.* 1998): as older individuals are more likely to be infected, including juveniles in our calculation would lower the mean life span of uninfected cats. Owing to a high juvenile mortality, many juveniles were observed for less than a month. We thus removed from the sample all individuals younger than the youngest infected cat (322 days). We still found a significantly longer observation period for infected individuals (1085 *v.* 879 days: $U = 263.5, P = 0.040$). When sex is taken into account, our estimation of life expectancy does not differ significantly for infected and uninfected females ($U = 34, P = 0.413$), but is significantly higher (1250 *v.* 778)

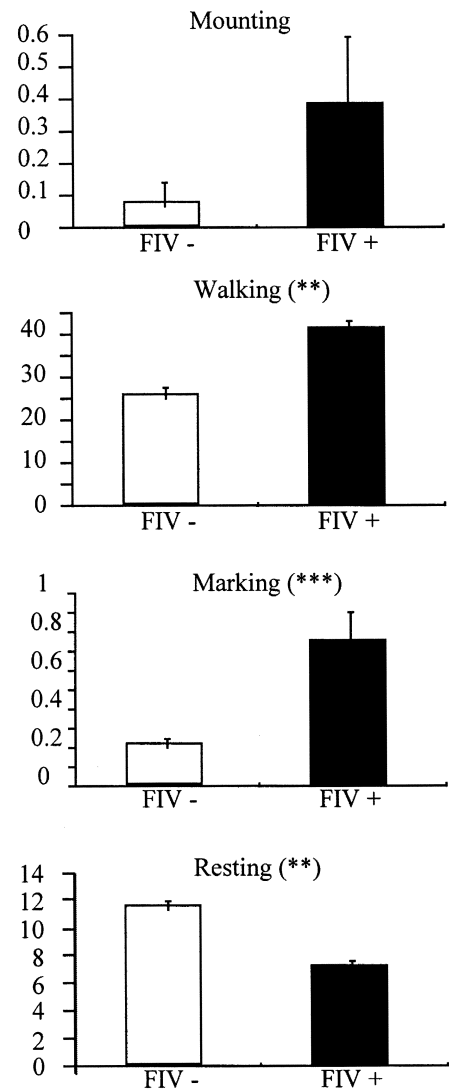


Fig. 5. Average percentage of activity (+s.e.) for four behaviours, for FIV-uninfected cats (open bars) and FIV-infected cats (solid bars): mounting of females (for males only), walking, marking and resting. All differences are significant (**, $P < 0.01$; ***, $P < 0.0001$), except for mounting, for which too few occurrences were observed (no test was performed). Infected cats show behaviours typical of higher social ranking (more mounting of females, walking and marking; less resting).

in infected males than in uninfected males ($U = 49.5, P = 0.014$). We can conclude that infected cats do not have a shorter life than uninfected cats. On the contrary, males that were observed longer in the population were more likely to be infected.

To be successfully transmitted at least once, the virus should infect individuals that live long enough to be infected and to infect at least one other cat. In order to avoid disappearing with the death of its host, the virus should therefore infect individuals with a total life expectancy of at least 1082 days, i.e. 322 (youngest age of infection in our population) plus 760 (because there is at most one infection every 760

days). This is strikingly close to our (under)estimate of 1085 days for infected individuals and well below the estimate obtained for infected males (1250 days). Since our method underestimates the actual life expectancy of all cats, these data suggest that infected cats are actually the most likely to live long enough to contract the virus and then transmit it back into the population.

Discussion

The aim of this study was to characterise the epidemiological pattern of Feline Immunodeficiency Virus (FIV). The two major features of its epidemiology, namely a long asymptomatic 'latency' period and a low-efficiency behavioural transmission, suggest a pattern where only a few individuals with at-risk behaviour would be responsible for most of the infections. We monitored the epidemiology and social and spatial structure of an urban population of domestic cats in order to better characterise FIV transmission pattern.

FIV prevalence was around 12.3–14% in the study population. The apparent decrease of the prevalence with time in the first samples is not significant and was due to an initially undetected difficulty in recapturing infected individuals (see Courchamp *et al.* 2000). This difficulty was corrected in the third year and the subsequent prevalence estimate was very precise (see Courchamp *et al.* 2000). Although we could not include them in the present study, because of protocol changes for some parameters, three additional samples (14.29%, 13.51%, and 15.79%) confirm the steadiness of FIV in our population. Stability of prevalence is to be expected in diseases with long infectious periods (as opposed to violent cyclic epidemics, such as measles). As predicted, this prevalence is not very high, given the facts that this virus is transmitted by contact, has a seropositivity period of several years during which cats are infectious, and has been present for several years in a very dense population (up to 3650 cats km⁻²). This is mainly because of a low transmission rate (see below). This result was also predicted by a mathematical model of FIV dynamics (Courchamp *et al.* 1995).

Our data also support the prediction that FIV transmission is mainly due to a particular social category of cats: the socially dominant males. Indeed, we showed that there is a correlation between the likelihood of being infected and three different measures of social ranking (see also Yamaguchi *et al.* 1996). First, infected individuals are larger than other individuals, and it has been shown that body size is a major factor in determining the social rank of cats (Liberg 1981, 1983; Yamane *et al.* 1996; Yamane 1998). Second, analysis of the spatial structure of the population indicates that infected individuals had the largest home ranges, which is a typical feature of dominant individuals in domestic cats (Liberg 1981). Third, infected cats displayed more behaviours typical of dominant individuals, such as more home range 'patrolling'

and marking, less resting (Natoli 1985; Kerby and Macdonald 1988) and more mountings of females by males (Yamane *et al.* 1996). Dominant cats are characterised by a better fighting ability (Kerby and Macdonald 1988; Yamane *et al.* 1996) and greater aggressiveness (Pontier *et al.* 1995, 1998), and are more likely to be involved in fights and therefore to acquire and transmit FIV. Since precise age was known for only a few individuals, we could not test our data for an effect of age. However, such an effect has already been highlighted by several authors (for a review, see Courchamp and Pontier 1994). Since dominant cats are often mature adult cats (young cats rarely fight seriously), such an effect of age is consistent with a higher probability of infection of socially dominant individuals.

If FIV transmission relies on relatively few at-risk individuals, these individuals should have more transmission opportunities and/or survive long enough to transmit the virus back, once infected. It seems that both compensation mechanisms actually occur in this system. Indeed, first we have seen that the dominant social status of infected cats is likely to result in a higher transmission rate, because of their more aggressive behaviour and better ability to fight. Second, we showed that infected individuals are those that stayed the longest in our population, and we suggest that this is because FIV mostly infects individuals who are likely to live longer in the population since they are dominants. Thus, the few at-risk individuals have, on average, both a higher probability of transmitting the virus and a longer life to do so.

Finally, as predicted, differences in the social structure of the population seem to be reflected by the prevalence of FIV. We found a higher FIV prevalence (19.6%) in a rural population (Courchamp *et al.* 1998), compared with 12–14% in this urban population (23.8 v. 13.3% for males only), although the result was not statistically significant. Urban domestic cat populations are characterised by a high density (1000–2000 cats km⁻²), a promiscuous mating system (Say *et al.* 1999 for this population), and generally less frequent aggressive behaviour (Natoli and De Vito 1991). In contrast, the lower density (<200 cats km⁻²) and the polygynous mating system (Pontier *et al.* 1995; Pontier and Natoli 1996; Say *et al.* 1999) in the rural population led to more frequent fights. Furthermore, in contrast to most other studies (reviewed in Courchamp and Pontier 1994; see also Courchamp *et al.* 1998), we found that females were no less infected than males in this population. When compared with the results found in a rural population (Courchamp *et al.* 1998), the lower FIV prevalence in the present study is entirely due to the marginally lower prevalence of males (13.3% v. 23.8% in the urban and in the rural population, respectively), the prevalence in females being similar in the two populations (10.0% v. 9.6%, respectively). These results support the current hypothesis that males infect males during fights, and females during mating (through the bite at the neck during the mount: Courchamp and Pontier 1994; Courchamp *et al.* 1998).

According to this hypothesis, sex differences in FIV prevalence should be more pronounced in polygynous populations, where access to females is achieved through intense competition among males. In contrast, all males have access to females in promiscuous populations (Kerby and Macdonald 1988; Natoli and De Vito 1991). The higher number of mates for females may counterbalance a lower FIV prevalence in males in the promiscuous population (Say *et al.* 1999), leading to similar prevalence in females in both types of population. Accordingly, these results would suggest that males have a more important role in spreading FIV within the population than do females. These results highlight the need to further investigate the role of mating systems in the spread of FIV. In particular, we need to elucidate the relationship between the number of sexual partners per female and FIV prevalence, as well as the respective role of males and females in the spread of FIV. The research for the main route of FIV transmission to females, which may be investigated experimentally, is of major importance in this context. It is noteworthy here that only one population of each type (promiscuous and polygynous) was compared in our study and that more replicates would be needed to unequivocally distinguish within-population variation from between-population variation.

Even though a complete analysis of the potential of this virus as a control agent would lead us beyond the scope of this study, the information provided by this work can be useful in generating a few preliminary reflections on this matter. For example, the impact of this virus is very unlikely to be brutal or high, mostly because of its low transmission rate and long seropositivity period. If these appear to be poor characteristics of a control agent, it should be recalled that virulent pathogens may trigger three kinds of problems: they may more easily select for a subpopulation of naturally resistant individuals, they may induce a rapid crash of the population and die out because of a shortage of hosts (allowing a demographic explosion of the surviving population), and they may be detrimental to the equilibrium of the trophic web, as shown by mesopredator releases set off by a too-rapid extinction of the top predator (Courchamp *et al.* 1999). A lower but longer-term impact may be more efficient in many cases (Dobson 1988). It is, however, worth noting that the impact of FIV, although probably higher on islands than on continental populations (see below), still remains quite low and may be below the optimum for population control. However, this virus has several advantages over others considered so far for biological control. One advantage is that FIV is a lethal virus, for which there is no natural immunity and no recovery. Another is that it is behaviourally transmitted, meaning that infections should occur as long as there are individuals to form a population. A third is that FIV persists for a long time before killing its host, allowing multiple transmissions of the viral strain during the life of the host. Moreover, the impact of this retrovirus should be higher on islands where cats may

live 2–3 times longer on average (Derenne 1976; Konecny 1983; Hayde 1992), allowing more transmissions than in mainland populations (Courchamp *et al.* 1995). The important result of the present study (that the life expectancy of most cats will be shorter than the seropositive period of FIV) may not hold on islands, where the much longer life of cats may drastically change the epidemiology of this virus. FIV is also considered to be a very specific virus, lowering the infection risk of non-target species (Bendinelli *et al.* 1995; Cleaveland *et al.* 1999). A further advantage of FIV as a control agent is that it predominantly infects individuals with high reproductive rates and survival probabilities (i.e. dominant individuals). Finally, in the light of the new concept of virus-vectored immunocontraception (Tyndale-Biscoe 1994; McCallum 1996) and of its potential interest for controlling feral cats on islands, it is noteworthy that the enormous number of studies recently conducted on the genetics, molecular biology and immunology of FIV could be of considerable help for the required genetic engineering (e.g. Bendinelli *et al.* 1995; Hartmann 1998). FIV could be considered for insertion of genes coding for proteins of the reproductive cells of cats, as well as for increased virulence or infectiousness. In this regard, it is interesting that FIV infects predominantly dominant males, that is, those who are likely to monopolise matings. If these could be rendered sterile, or infected so that they infect most females (and render them sterile), then the agent might be successful. The combination of advantages and disadvantages of FIV as a biocontrol agent could make it a good candidate for virus-vectored immunocontraception.

In conclusion, we have shown that FIV prevalence and transmission rates are low, and are mostly restricted to a subpopulation defined by a few individuals with at-risk behaviour, and which live long enough in the population to spread the infection further. The low quantitative impact of FIV seems to be the major drawback of this virus, and this alone may prevent its use for biological control based on increased mortality: very non-pathogenic agents generally make poor control agents. Its advantages are its good specificity, its behavioural transmission mode, its at-risk class (reproducers) and a good potential for genetic engineering.

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