Infection strategies of retroviruses and social grouping of domestic cats

Emmanuelle Fromont, Franck Courchamp, Marc Artois, and Dominique Pontier

Abstract: It is thought that parasites may exert selective pressure on the social structure of host populations. We compared the impact of feline immunodeficiency virus (FIV) and feline leukemia virus (FeLV), two retroviruses commonly found in domestic cats (Felis catus). Because of low transmissibility and virulence, both infections have a worldwide distribution and low prevalence. Transmission modes differ: FIV is transmitted only through biting, while FeLV transmission occurs by biting, licking, grooming, and sharing food and from mother to fetus. FeLV is also more pathogenic than FIV. We compared FIV and FeLV prevalence and risk factors within five populations of cats. FIV infection occurred almost exclusively among adult male cats fighting to acquire and maintain dominant status. Classes at risk for FeLV infection included sexually intact cats allowed to roam freely. The impact of FeLV on host population growth was greater than that of FIV but varied among populations. Our results show that FIV is favored by individual aggressiveness and a hierarchical social system, while FeLV is more prevalent among socially active cats. FeLV may constitute a source of selective pressure against numerous amicable contacts, particularly in urban cat populations, where aggression among individuals is reduced.

Résumé: Les parasites sont susceptibles d'exercer une pression de sélection sur la structure sociale des populations hôtes. Nous avons comparé l’impact du virus d’immunodéficience féline (FIV) et du virus leucémogène félin (FeLV), deux virus courants du chat domestique (Felis catus). En raison de leur transmissibilité et de leur virulence faibles, les deux infections ont une répartition mondiale et une prévalence faible. Leur mode de transmission diffère: le FIV est transmis seulement par morsure, alors que la transmission du FeLV se produit lors de morsure, léavage, toiletage, partage de plats de nourriture et de la mère au foetus. Le FeLV est également plus pathogène que le FIV. Nous avons comparé la prévalence et les facteurs de risque de FIV et du FeLV dans cinq populations de chats. L’infection par le FIV était rencontrée presque exclusivement chez les mâles adultes, qui se battent pour acquérir et maintenir un statut dominant. Les classes à risque pour l’infection par le FeLV étaient les chats non castrés autorisés à vagabonder. L’impact du FeLV sur l’accroissement des populations hôtes était plus important que celui du FIV mais plus variable selon les populations. Ces résultats montrent que le FIV est favorisé par l’agressivité entre individus et par un système social hiérarchique, alors que le FeLV est plus fréquent chez les chats actifs socialement. Le FeLV pourrait constituer une pression de sélection contre les relations amicales fréquentes, notamment dans les populations urbaines où l’agressivité entre chats est réduite.

Introduction
The impact of parasitism on host social structure and social interactions was recently reviewed by Loehle (1995), who proposed that “social barriers” divide host populations into risk groups that support different levels of parasitic infection according to behavioural or social characteristics. Few behaviourally structured populations of animals have also been assessed for parasite impact. Populations of domestic cats (Felis catus) provide an opportunity to test Loehle’s hypothesis, since the spatial and social structure of cats varies considerably among populations (Liberg 1981; MacDonald et al. 1987; Natoli and De Vito 1988; Pontier et al. 1995). Moreover, as a domestic species, cats are particularly accessible, and most important parasites have been studied extensively.

In their effect on host population growth and structure, microparasites (viruses, bacteria, protozoan) share many points with macroparasites (parasitic helminths and arthropods; Anderson 1979). Here we deal with two feline retroviruses, feline immunodeficiency virus (FIV) and feline leukemia virus (FeLV), which have been the subjects of particular study, owing to interest in animal models of human retroviral infections. Both viruses primarily attack the immune system, producing an immunosuppressive syndrome. FeLV also causes tumoral disorders. Clinical signs of the two infections include similar symptoms: fever, anemia, lymphadenopathy, and weight loss (Yamamoto et al. 1988; Braley 1994; Brandon 1995). Complete recovery is uncommon for FeLV and does not occur for FIV, but a long asymptomatic period precedes the appearance of the disease. Mean life expectancy after infection is 1 year for cats infected with FeLV and around 5 years for those infected with FIV (Hoover and Mullins 1991; Pedersen and Barlough 1991). Thus, FeLV is more virulent than FIV and is thought to be a more important cause of death in cat populations.
Fromont et al. also suggest that FeLV has a greater impact on host population growth than FIV (Courchamp et al. 1995; Fromont et al. 1997); thus, FeLV may be able to exert stronger selective pressure than FIV.

Both FIV and FeLV have an ancient origin and worldwide distribution (Benveniste et al. 1975; Olmsted et al. 1992). For both viruses, males are at higher risk than females and adults are infected more often than kittens. Among pet cats, free-roaming individuals are more at risk than cats living indoors (reviews in Braley 1994; Courchamp and Pontier 1994).

Despite their obvious similarities, FIV and FeLV exhibit distinct features. FeLV is transmitted via the saliva or blood, particularly through direct cat-to-cat contact: biting, grooming, or sharing food, or from mother to fetus during pregnancy (Francis et al. 1977). In contrast, FIV is only transmitted by biting; thus, the rate of transmission of FIV is expected to be low compared with that of FeLV (Spargher 1993; Courchamp et al. 1995a). As a consequence of the different transmission routes and virulences, we expect FeLV to have a stronger impact than FIV on host population growth. We also expect FIV and FeLV to be in different risk classes, leading to a different effect on host population structure. However, these differences have not been previously assessed, since published data concerning FIV and FeLV prevalence and risk factors were mainly obtained from veterinarians and were not representative of the whole cat populations (Courchamp and Pontier 1994).

The goal of our study was to compare the magnitude of the estimated depression of population growth due to each virus, which requires measurement of the proportion of infected individuals (prevalence) in each population. We also wanted to assess the selective pressure FIV and FeLV may exert on distinct categories of cats. For this purpose, we searched for variables having a statistical link with infection risk (risk factors), because high-risk classes are supposed to be counterselected by the corresponding virus. The prevalence and risk factors for the two viruses were measured in five populations for which demography and some spatial and social characteristics were known. The variables associated with each infection were distinct, which led us to hypothesize that either FIV or FeLV is favoured by local practices in the husbandry of cat populations, and that the impact of these two viruses differs between rural populations, where cats are widely spaced around human habitations, and urban populations, where cats live as large groups clustered around food sources.

### Materials and methods

#### Study areas

The five cat populations were located in central France, either in rural areas (Saint-Just Chaleyssin, Aimargues, and Barisey-la-Côte) or in the city of Lyon (Lyon-Croix Rousse and Lyon-Jardin). Cat density was lower in rural than in urban areas (Table 1), as is usually observed in cat populations. In rural areas, most cats were pets and lived in small groups associated with human dwellings. Urban populations consisted of a single large group of stray cats fed by voluntary caretakers (Liberg 1981; Liberg and Sandell 1988; Pontier et al. 1995). A detailed description of the populations has been presented elsewhere (Fromont et al. 1996).

#### Populations and sampling

The demographic and epidemiological characteristics of the five populations are summarized in Table 1. Demographic monitoring of rural populations showed that their size, sex, and age structures have been stable for over 10 years (Pontier 1993). The demographic stability of the urban populations was not assessed because study periods were shorter. Each year we selected a sample representing 16–100% of the cats in each population. Exhaustive sampling was performed once (all 47 cats living in Barisey-la-Côte in 1993 were sampled). Pet cats were caught by hand and free-roaming cats were captured with baited cages. Samples of captured cats were assessed for sex- and age-structure representativeness and the proportion of neutered cats (Fromont et al. 1996).

Potential risk factors were recorded as variables that included two to four categories, defined in accordance with risk classes previously found in the literature (Hosie et al. 1989; Braley 1994): number of cats in the population and age structure of the population (Courchamp et al. 1995). The demographic structure of the urban populations was not assessed because study periods were shorter. Each year we selected a sample representing 16–100% of the cats in each population. Exhaustive sampling was performed once (all 47 cats living in Barisey-la-Côte in 1993 were sampled). Pet cats were caught by hand and free-roaming cats were captured with baited cages. Samples of captured cats were assessed for sex- and age-structure representativeness and the proportion of neutered cats (Fromont et al. 1996).

### Table 1. Demographic and epidemiological characteristics of the cat populations studied.

<table>
<thead>
<tr>
<th>Population</th>
<th>Saint-Just Chaleyssin</th>
<th>Aimargues</th>
<th>Barisey-la-Côte</th>
<th>Lyon-Croix Rousse</th>
<th>Lyon-Jardin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population size (no. of cats)</td>
<td>300</td>
<td>200</td>
<td>60</td>
<td>50</td>
<td>45</td>
</tr>
<tr>
<td>Population density (no. of cats/ km²)</td>
<td>250</td>
<td>120</td>
<td>200</td>
<td>1500</td>
<td>7800</td>
</tr>
<tr>
<td>Location</td>
<td>Rural</td>
<td>Rural</td>
<td>Rural</td>
<td>Urban</td>
<td>Urban</td>
</tr>
<tr>
<td>Birth rate</td>
<td>2.4</td>
<td>2.4</td>
<td>2.4</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Rate of increase</td>
<td>0.64</td>
<td>0.64</td>
<td>0.64</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>D (%)</td>
<td>FIV</td>
<td>2.61</td>
<td>1.78</td>
<td>2.70</td>
<td>nd</td>
</tr>
<tr>
<td></td>
<td>FeLV</td>
<td>18.73</td>
<td>5.75</td>
<td>0</td>
<td>nd</td>
</tr>
</tbody>
</table>

**Note:** D is the depression of the cat population size due to the virus considered (see the text for the calculation). nd, not determined.
Retrovirus prevalence

Blood samples were obtained at each capture, from which FIV and FeLV status was assessed as positive or negative. FeLV antigen and FIV-specific antibodies were sought through ELISA, confirmed by Western blotting for FIV (Lutz et al. 1983; Yamamoto et al. 1988). FIV and FeLV prevalence was calculated from yearly samples and compared between years. Because prevalences were low, 95% confidence intervals were obtained from tables giving exact values for a binomial distribution (Thrusfield 1995). Yearly samples were pooled, since no time effect was detected (see Results). For individuals sampled repeatedly, a single blood sample was randomly selected. Overall prevalences were compared among populations with χ^2 exact tests.

Measuring disease incidence is preferable to measuring prevalence when infection risk is studied (Thrusfield 1995). However, incidence rates of retroviral infections are often so low that statistical investigations are not possible. Here we found population structures and virus prevalence to be stable (Pontier 1993; this study). Absolute values of incidence rate (i) can be obtained from prevalence (p) through the relationship

\[ i = \frac{p}{d} \]

where d is the duration of infection (Thrusfield 1995). Here, recovery is not possible; thus, d corresponds to the mean life expectancy after infection: 5 years for FIV and 1 year for FeLV (Hardy 1980; Pedersen and Barlough 1991). Thus, for FeLV, \( i = \frac{p}{5} \) year and for FIV, \( i = \frac{p}{2} \) year. In our results, only prevalence is given.

Risk factors

The individuals sampled were described using 26 categories belonging to 9 variables (FIV status, FeLV status, group size, body mass, age, fertility, movements, sex, and origin). Our first aim was to assess the relative importance of variables associated with infection risk (risk factors) and compare the risk factors for FIV and FeLV. Risk factors were first analyzed using multiple correspondence analysis (MCA; Tenenhaus and Young 1985). MCA is a multivariate analysis that searches for associations among individuals (rows) through categorical variables (columns). Based on χ^2 distances, the algorithm computes linear combinations of variables (factorial axes) maximizing discrimination between individuals. The relative importance of factorial axes is given by the eigenvalues of the analysis. A visual representation of the individuals for each category of each variable is provided for each axis retained. This representation is interpreted through correlation ratios, which measure the importance of each qualitative variable in the definition of the axes. The association between categories belonging to different variables is simply indicated by their proximity on the same axis. This allowed us to assess whether FIV and FeLV positivity was associated with the same risk factors and to select the most important risk factors for FIV and FeLV. MCA was performed with A.D.E. software (Thioulouse et al. 1995).

Subsequently, we assessed the significance of each possible risk factor by calculating the relative risk, that is, the ratio of risks between high- and low-risk categories. The significance of relative risks was tested using χ^2 exact tests, performed with StatXact software (StatXact-Turbo, Cytel Software Corp., Cambridge, Mass., U.S.A., 1992). One-tailed tests were performed for sex, since male cats were expected to be infected more often than females (Hosie et al. 1989; Braley 1994). Risk factors were first assessed for each population. Results were pooled after checking that there was no qualitative difference (no interaction between population and risk factors) between populations.

Intragroup transmissibility

We compared prevalence between exposed cats (living in the same dwelling as another infected individual) and non-exposed cats (Hosie et al. 1989). The relative risk of FIV and FeLV was calculated for exposed animals and significance was tested as above.

Quantitative impact

The depression of host population size due to FIV and FeLV, \( D \), was estimated following the method of McCallum and Dobson (1995):

\[ D = \left(\frac{\alpha + a(1 - f)}{r}\right) \phi \]

where \( a \) is the birth rate of uninfected hosts, \( r \) is the intrinsic rate of increase of the host population, \( \alpha \) is the death rate of infected animals, \( f \) is the effect of disease on host fecundity (from 0 (infected animals sterile) to 1 (no impact)), and \( \phi \) is the prevalence of the pathogen. The values of \( a \) (2.4 per year) and \( r \) (0.64 per year) for rural populations were estimated from the monitoring of cats in Saint-Just Chaleyssin (Table 1). The estimate of 0.64 for \( r \) was obtained using the basic demographic equation \( \Sigma l_e = \Sigma e^{-\alpha} = 1 \) (e.g., Stearns 1992). Maximal age-specific fecundity and survival rates for rural cats were obtained from Pontier (1984) and did not take into account the strong density-dependence exerted through elimination of kittens by owners. We also calculated \( r \) from data concerning the cat population introduced in the archipelago of Kerguelen. In 1960, 10 cats escaped a trial of eradication and produced an estimated 7700 cats in 1974 (Wetzel et al. 1982). In this case, \( r = 0.51 \), which is in accordance with \( r = 0.64 \) in rural populations. Considering that mean life expectancy after infection, \( a \), was estimated to be 0.5 and 0.13, respectively (Hardy 1980; Pedersen and Barlough 1991). The effect of FIV infection on fecundity is thought to be negligible (Pedersen and Barlough 1991), whereas FeLV-positive females may abort or give birth to infected kittens that rapidly develop fatal immunodepression (Hoeve et al. 1983). Thus, \( f \) was estimated at 1 for FIV and 0.8 for FeLV. Depression of host population size was calculated only for rural populations for which demographic parameters and FIV and FeLV prevalence remained steady from 1991 to 1995.

Comparison of FeLV/FIV ratios between countries

Since FIV is transmitted through biting, we expected it to be favoured in populations where frequent aggressive contacts occur. In contrast, FeLV should be more prevalent where amicable contacts such as licking and sharing food sources are frequent. We hypothesized that human practices towards cats may differ geographically and may have favoured one virus over the other. We searched for geographic differences in the FeLV/FIV ratio using data from a large-scale retrovirus survey performed in eight countries in Europe and North America by the IDEXX Corporation (IDEXX Corp. 1991, 1992a, 1992b, 1992c, 1994a, 1994b; Braley 1994). Similar sampling and testing methods were used in each country: healthy pet cats were selected by veterinarians and tested for both viruses. For each country, we calculated the ratio of FeLV prevalence to FIV prevalence. We also noted within-country variability in the FeLV/FIV ratio when additional data collected in the same countries with comparable methods were compared.

Results

Retrovirus prevalence

Of the 566 cats sampled, 75 (13.25%) were positive for FIV and 41 (7.24%) for FeLV. Ten individuals (1.77%) were infected by both viruses, a proportion that was higher than...
Fig. 1. Prevalence of FIV and FeLV in five cat populations between 1991 and 1996. Bars show 95% exact confidence intervals. Numbers in parentheses are sample sizes.

Fromont et al. 1997

(45) (53) (49) (43) (41)

Saint-Just Chaleyssin

(30) (38) (47) (34) (20)

Barisey-la-Côte

(43) (27) (66) (28)

Lyon-Croix Rousse

(42) (55) (56) (58) (53) (55)

Aimargues

(33) (17)

Lyon-Jardin

Year

the expected prevalence based on single-virus infection (0.59%, χ² = 4.77, df = 1, P = 0.035).

Examination of confidence intervals showed no significant year trend in any of the populations (Fig. 1). FIV prevalence did not differ significantly between populations (χ² = 7.02, df = 4, P = 0.134). In contrast, FeLV prevalence differed between populations, either considering all five populations (χ² = 25.00, df = 4, P < 0.001) or excluding the population of Barisey-la-Côte, where the virus was absent (χ² = 12.64, df = 3, P = 0.005).

Risk factors

The eigenvalues of MCA led us to retain the first three axes, which took into account 32.9% of the total inertia. The other axes revealed only associations between two variables and were not retained. The first axis, F1 (Fig. 2), described associations between group size, body mass, age, fertility, and movements and showed the contrast between urban street cats and rural pet cats (see legend of Fig. 2). The second axis showed the association between FIV, heavy body mass, male sex, and immigrant status. The third axis indicated that FeLV-positive cats were most often intact pet cats allowed to roam freely. Since different axes show independent correlates, these results also mean that FIV status and FeLV status were independent of each other and of the difference between urban and rural cats.

There were distinct correlates between FIV and FeLV infection and certain classes of the cat population (Fig. 3). Classes significantly at risk for FIV were individuals weighing more than 4 kg (relative risk (RR) compared with cats ≤2 kg = 6.58, P = 0.001), those aged 6 years or more (RR compared with cats aged 0–1 year = 3.46, P = 0.001), males (RR compared with females = 1.91, P = 0.017), and immigrant cats (RR compared with natives = 2.48, P = 0.004). Group size, fertility, and movements had no significant effect (P = 0.177, P = 0.387, and P = 0.482, respectively). FeLV-seropositive cats were aged 4–5 years (RR compared with cats aged 0–1 year = 3.08, P = 0.005). Other variables had no significant effect, but FeLV-infected cats tended to be intact (RR compared with neutered cats = 2.07, P = 0.128) and allowed to roam freely (RR compared with indoor cats = 4.09, P = 0.086). Group size, body mass, sex, and origin were not linked to FeLV positivity (P = 0.807, P = 0.572, P = 0.295, and P = 0.231, respectively).

Intragroup transmissibility

The relative risk of exposed versus non-exposed cats was twice as high for FeLV (RR = 3.80, P < 0.001) compared with FIV (RR = 1.93, P < 0.001).

Quantitative impact

Estimates of virus-induced depression of host population size (D) varied from 1.78 to 2.70% for FIV and from 5.75 to 18.73% for FeLV, except in Barisey-la-Côte, where FeLV was absent (Table 1). In all populations where both viruses were present, the depression due to FeLV was greater than that due to FIV, whatever the relative prevalences of the two viruses. More generally, using the demographic parameters of our rural populations, the depression due to FeLV, "FeLV" should be higher than the depression due to FIV (0.19θFIV) if the FeLV/FIV prevalence ratio is higher than 0.136.

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Fig. 2. Distribution of the factorial coordinates of individuals on factorial axes F1, F2, and F3 for each category of the nine variables of MCA (modelled as Gauss curves). Correlation ratios are given in the upper left-hand corner of each graph. When the value of the correlation ratio is high, the categories associated on the axis are shaded. The F1 axis shows the contrast between urban street cats (intact, feral, and living in groups of more than 20 individuals, including many kittens) and rural pet cats with alternative characteristics. F2 and F3 are representative of FIV and FeLV status, respectively. FIV positivity was associated with a heavy body (>4 kg), male sex, and immigrant status; FeLV was associated with intact status and a free-roaming lifestyle.

Comparison of FeLV/FIV ratios between countries
FeLV/FIV prevalence ratios calculated from the largest survey allowed us to classify countries into “FIV areas” (Italy) and “FeLV areas” (Switzerland, Austria, United Kingdom, Germany, U.S.A, France, and Denmark; Fig. 4) according to whichever virus was predominant. The FeLV/FIV prevalence ratio varied from 0.39 in Italy to 6.28 in Switzerland. Other published data are consistent with the hypothesis that FIV is more frequent than FeLV in Italy but less frequent in Switzerland, Germany, and U.S.A. The FeLV/FIV prevalence ratio was higher than 0.136 in all the studies.

Discussion
Qualitative and quantitative impact of FIV and FeLV
Most of the previous studies on FIV and FeLV epidemiology have considered each risk factor and disease separately (e.g., Braley 1994). Group size, age, breed, health status, move-
Fromont et al. 1999

Fig. 3. FIV and FeLV prevalences for each category of the seven possible risk factors. Numbers in parentheses are sample sizes.

<table>
<thead>
<tr>
<th>Risk Factor</th>
<th>FIV Prevalence (%)</th>
<th>FeLV Prevalence (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group Size</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>2.5</td>
<td>2.0</td>
</tr>
<tr>
<td>6-20</td>
<td>2.1-3</td>
<td>1.4</td>
</tr>
<tr>
<td>&gt;20</td>
<td>0-1.3</td>
<td>0-1.3</td>
</tr>
<tr>
<td>Body Mass (kg)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;2</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>2.1-4</td>
<td>3.1-4</td>
<td>3.1-4</td>
</tr>
<tr>
<td>&gt;4</td>
<td>4.5-6</td>
<td>4.5-6</td>
</tr>
<tr>
<td>Age (years)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-1</td>
<td>1.0-3</td>
<td>1.0-3</td>
</tr>
<tr>
<td>2-3</td>
<td>2.0-5</td>
<td>2.0-5</td>
</tr>
<tr>
<td>&gt;3</td>
<td>4.0-7</td>
<td>4.0-7</td>
</tr>
<tr>
<td>Fertility</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neutered</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Intact</td>
<td>5.0</td>
<td>5.0</td>
</tr>
<tr>
<td>Movement Pattern</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Indoor</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Outdoor</td>
<td>3.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Home-Range Size</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>4.0</td>
<td>4.0</td>
</tr>
<tr>
<td>Medium</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Sex</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Female</td>
<td>3.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Immigrant</td>
<td>1.0</td>
<td>1.0</td>
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<td>Origin</td>
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<tr>
<td>Same</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Other</td>
<td>3.0</td>
<td>3.0</td>
</tr>
</tbody>
</table>

ment pattern, and sex were found to be linked to seropositivity of both viruses (Hosie et al. 1989; Braley 1994; Brandon 1995), but the relative importance of risk factors was not studied (review in Courchamp and Pontier 1994).

Individuals at risk for FIV were aggressive cats likely to be bitten during fights; a heavy body and an age of 4-5 years are associated with dominant status in male cats (Liberg 1981; Yamane et al. 1996). Dominance is acquired and maintained through fights with challengers. The strength of the association between FIV positivity and dominant status was illustrated by the high values of all relative risks of FIV infection. It is noteworthy that FIV-positive cats were found to have the characteristics of dominant cats, which means that they maintained their status during the long asymptomatic period. Moreover, FIV status is related to home-range size. FIV-positive males defending large home ranges (Courchamp 1996). Defense of territory provides numerous occasions for FIV to be transmitted from a dominant cat to challengers.

FeLV-infected individuals showed a less typical profile. Young adults were often infected. Free-roaming movements and intact status showed a nonsignificant association with FeLV. Cats living in the same household as an infected individual were particularly at risk, as is expected for any contagious disease. However, the relative risk was twice as high for FeLV than for FIV, which confirms the previous finding that intragroup transmission is important for FeLV (Mammerickx 1987; Braley 1994). Contrary to our findings for FIV, we did not define individuals at risk for FeLV, but groups. This is not surprising, since large groups are composed of kin-related cats (Macdonald et al. 1987) with strong social relationships, often sharing food dishes and litter boxes, all situations that enhance FeLV transmission (Francis et al. 1977).

Estimation of the quantitative impact of parasitism on host population size must take into account the demographic parameters of the host population (McCallum and Dobson 1995). Our results showed that the impact of FeLV is stronger than that of FIV, given that the FeLV/FIV prevalence ratio is higher than 0.136, which was observed in all published surveys (Fig. 4). More generally, if the same prevalence was observed for both viruses, the depression of host population size due to FeLV would be 7.35 times higher than the depression due to FIV.

Finally, owing to different modes of transmission, the two viruses are likely to act as opposite selective pressures and, because of higher morbidity, FeLV exerts a stronger constraint on host populations than FIV. By infecting aggressive cats, FIV may act as a selective pressure against aggressiveness. In contrast, FeLV transmission is favoured by numerous amicable contacts.

Urban stray cat populations may provide an example of the cost of parasites to social life. After being domesticated in rural areas, cats have colonized towns, where they form large and dense social groups with reduced intragroup aggression (Liberg and Sandell 1988; Natoli and De Vito 1988, 1991; Pontier et al. 1995). Because of the numerous social contacts that occur within urban cat populations and because of high FeLV mortality, we expect FeLV to constitute a strong selective pressure against the numerous social contacts prevailing in urban cat populations. Continued monitoring will allow us to test whether urban populations are more severely depressed by FeLV infection than are rural populations.

Spatial distribution between populations

FeLV prevalence varied between populations. It is noteworthy that among rural sites, the smallest population was free from FeLV, whereas, of the urban populations, Lyon-Jardin, where density was particularly high, was more infected...
Fig. 4. Ratio of FIV prevalence to FeLV prevalence in domestic cats in various countries, measured as log(FeLV prevalence / FIV prevalence). Data from IDEXX Corp. (IDEXX) (1991) for U.S.A., n = 15,374; IDEXX (1992a) for Germany, n = 2,613; IDEXX (1992b) for France, n = 4,456; IDEXX (1992c) for the United Kingdom, n = 624; IDEXX (1994a) for Italy, n = 740; IDEXX (1994b) for Denmark, n = 513; Braley (1994) for Switzerland, n = 1,660, and Austria, n = 400) are indicated by open squares. Other data (solid squares) are from Grinnell et al. (1989), n = 83 (U.S.A.); Hosie et al. (1989), n = 1,007 (United Kingdom); Knowles et al. (1989), n = 198 (United Kingdom); Neu et al. (1989), n = 96 (Germany); Perucchini et al. (1989), n = 54 (Italy); Peruccio et al. (1989), n = 142 (Italy); Shelton et al. (1989), n = 361 (U.S.A.); Lutz et al. (1990), n = 860 (Switzerland); Moraillon (1990), n = 629 (France); Rodgers and Baldwin (1990), n = 194 (U.S.A.); and Bo et al. (1993), n = 648 (Italy).

Possible interaction between FIV and FeLV
FIV and FeLV are two immunosuppressive viruses favouring the development of other diseases (Yamamoto et al. 1988). The replication of FIV during the primary stages is enhanced by the presence of FeLV (Pedersen et al. 1990; Torten et al. 1990), as is also observed with the homologous human viruses HIV-1 and human T-cell lymphotropic virus type 1 (HTLV-1; Siekevitz et al. 1987). Because of this pathogenic interaction, and although the risk factors for HIV-1 and HTLV-1 differ, increased prevalence of HTLV-1 has been observed in HIV-1-positive patients (Cohen et al. 1989, 1990). The same type of interaction may explain the positive association between FIV and FeLV infections, despite distinct risk factors (Cohen et al. 1990). Such an association has been observed in diseased cats (Cohen et al. 1990; Moraillon 1990), but this is the first study to analyze samples representative of the overall cat population. The influence of a FIV/FeLV interaction on the epidemiology of both viruses and on host–parasite relationships remains to be determined.

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