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Source: Journal of Wildlife Diseases, 36(1) : 71-78

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-36.1.71

Journal of Wildlife Diseases, 36(1), 2000, pp. 71–78

DETECTION, IDENTIFICATION, AND CORRECTION OF A BIAS IN AN EPIDEMIOLOGICAL STUDY

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ABSTRACT: The relative lack of epidemiological studies of natural populations is partly due to the difficulty of obtaining samples that are both large enough and representative of the population. Here, we present the result of an epidemiological study (December 1992–August 1995) of feline immunodeficiency virus (FIV) in a free-roaming population of domestic cats (*Felis catus*), with a special emphasis on sample bias. Over five trapping periods, the prevalence of FIV in sampled cats steadily declined. Across these samples we consistently achieved a very large sampling fraction (approximately 60% of the population), the sex ratio, age and weight distributions remained stable with time in the samples, and the sex ratio was similar in the samples and the population. These indices would normally indicate that our samples were representative, suggesting the decline in FIV prevalence to be real. However, a concomitant ecological study of the whole population revealed an important bias in the samples, with an initial high probability of capturing a few individuals, which appeared significantly more likely to be FIV-infected, and then a lower probability of recapturing them. Since our protocol resulted in a non-random sampling, subsequent trappings were designed to avoid this bias, by also capturing individuals who had previously learned to escape capture. This modified capture regime revealed that FIV prevalence was in fact constant in the population. This study shows how samples of large size, which are stable and appear representative of the population, can still be biased. These results may have major implications for other studies based on trapping.

Key words: Epidemiology feline immunodeficiency virus, response to capture, sampling bias, trapping, trap-shy.

INTRODUCTION

The last decades have seen a growing contention that parasitism may act as a major force shaping the evolution and ecology of communities (e.g., Dobson and Hudson, 1986; Holt, 1993; Gulland, 1995; Grenfell and Gulland, 1995). However, despite their alleged importance in evolutionary ecology (e.g., Anderson, 1994; Ewald, 1994); behavioural ecology (e.g., Keymer and Read, 1991), population dynamics (e.g., Anderson and May, 1982) and conservation biology (e.g., Scott, 1988; McCallum and Dobson, 1995), empirical epidemiological studies remain strikingly scarce. This might be due to two complementary causes. First, epidemiological studies imply interdisciplinarity, with competence and interest in both ecology (at a broad level) and veterinary sciences. The basic ecology of most species is often not known well enough to spend time on the "special case" of diseases. Indeed, diseases often remain viewed as a malfunction in the ecosystem, being considered for studies only when their abnormal manifestations (epidemics) threaten the host species or the ecosystem equilibrium (Gregory and Keymer, 1989). A second cause is that epidemiological studies of natural populations of most animals are difficult to conduct, for three main reasons. First, one often needs a very large sample for parasites to be detected. This is the case for most macroparasites characterised by an aggregative distribution (Dobson and May, 1986) or for microparasites with low prevalence when they are endemic, or at the early stages of an epidemic. Even when the sample is large enough to allow parasite detection, the number of infected individuals must be sufficiently high to allow study of the effects of individual characteristics. Second, these samples must be representative of the study population, at least for the studied parameters. This implies some knowledge of the total population to check sample representativity, since sample size is rarely a guarantee by itself. Third, understanding of the dynamics of parasite transmission often requires long term studies, which may be too time consuming or costly, especially when there is no apparent threat to the host population.

Domestic cats (*Felis catus*) are ideally suited for epidemiological study. A good knowledge of infectious agents in cat and induced pathology exists, and cats are common and easy to study in their natural populations. Using these advantages, we studied the epidemiology of feline immunodeficiency virus (FIV) in a natural population of cats. We show how three precautions to ensure a reliable estimate of FIV prevalence ((1) five samples over 3 yr; (2) very large sampling fractions; (3) study of the population structure and sample representativity for the only parameter available for the population) were not sufficient to avoid an important sampling bias. Only the knowledge of the population, and especially of cats individually, eventually enabled us to detect, identify, and correct this bias.

METHODS

We monitored a population of feral domestic cats living in the grounds of Croix-Rousse hospital in Lyons (46°47′N, 4°54′E), France during a 7 yr period (1992–98). One of the aims of this study was to obtain unbiased epidemiological data for feline immunodeficiency virus in a natural population. For this, the population was monitored on a continuous basis, and cats were trapped twice a year. The different trapping periods lasted 4 to 10 days, during which up to 17 standard baited two-door traps were deployed over the whole area, both above and below ground, especially in areas where cats were known to live or to feed. The traps were of four different designs (Sanitservice 140 × 25 × 30 cm; Aimargues, France, ref 01-48039 140 × 30 × 32 cm; Kettner, Metz, France, St-Hubert 20 × 30 × 100 cm; Palmero, La Festinière, France, handmade by hospital staff 30 × 40 × 10 cm). Captured cats were kept in individual cages (Atlas 69 × 51 × 48 cm; Kettner, Metz, France) after processing, and released at the end of the trapping period. This provided data on individual characteristics (such as sex, age, morphology and behavioural profiles), as well as data on the population dynamics and the spatial, social and genetic structure. Each individual of the population was known by sight and its profile recorded in a database. Detailed results of the epidemiological study of this population are available elsewhere (Courchamp, 1996).

Blood samples were collected from trapped cats (when older than 3 mo), and were screened for antibodies for FIV, using the ELISA method, which is considered "the most sensitive and desirable" for screening tests (Bendinelli et al., 1995): 98.3% sensitivity and 100% overall specificity (O'Connor et al., 1991). To avoid false positives, all positive sera were confirmed by Western Blot (Lutz et al., 1988). For details on FIV, see reviews by Pedersen and Barlough (1991), Courchamp and Pontier (1994), Elder and Phillips (1994), Miyazawa et al. (1994), Bendinelli et al. (1995) and Hartmann (1998).

We used StatView IV software (Abacus Concepts, Inc. Berkeley, California, USA) to perform Mann-Whitney, Chi Square, and *t*-tests. Prevalence data were analysed using a Logistic Regression Test with GLIM (NAG, Oxford, UK) in order to take into account the time order of the years (Agresti, 1990). Following the convention, we chose a value of 0.05 for the Type I error α (Sokal and Rohlf, 1995). Percentages are given as integers, because of the small sample sizes.

RESULTS

Detection of the bias

Details are only given for the first 3 yr of this study, since the bias was corrected at the end of this period by adapting our trapping method (see below). The population size increased during the 3 yr period, from 30 individuals at the beginning to 73 at the end. However, we believe that part of this change is due to the seasonal presence of kittens and juveniles, mostly absent from the first census. The structure of the population did not change significantly.

Despite the increase in the number of cats present (Fig. 1), the trapping efficiency remained high for the five first trapping periods ($\bar{X} \pm SE = 60 \pm 2\%$), owing to an improved knowledge of the area and of the population with time, an improved trap-

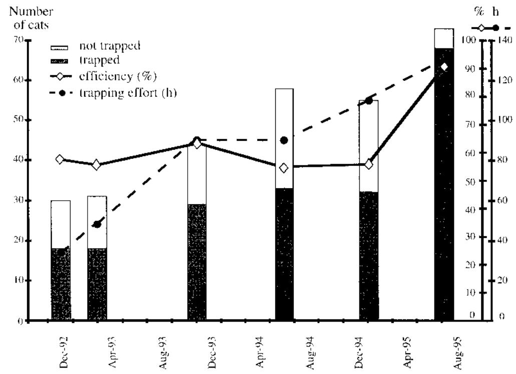

FIGURE 1. Quantitative trapping effort for the six trapping sessions in hours of presence (black circles), to be compared with the population size (bars) and the trapping efficiency in percent of the population trapped (white diamonds). Despite an increased effort, the trapping efficiency remained stable for the first five trapping sessions because of population growth. The increase in trapping efficiency in the last session is also due to increased qualitative trapping effort (use of a new type of traps).

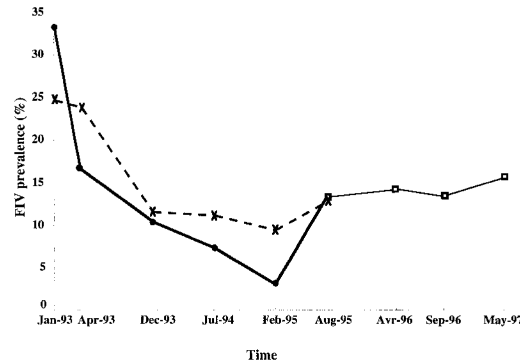

FIGURE 2. Evolution of FIV prevalence with time, as measured from the samples (plain line). The first five sessions are shown by a black circle; they correspond to sampling with a bias in the trapping. The white squares represent the four last trappings where the bias was corrected. The crosses linked by a dashed line represent the corrected prevalence, taking into account untrapped individuals known to be present during the captures, and for which FIV status was known from previous (positive cats) and/or subsequent (negative cats) captures.

ping experience and a constantly increasing trapping effort. Over the 3 years, 138 cats were present during at least one trapping period and only one individual was never captured. Of these, 98 were old enough to be sampled for blood. For the whole period, the total trapping efficiency was 99%. Recapture was more difficult.

The prevalence of FIV (Fig. 2) significantly decreased during the first five trapping periods, from a third of the population at first to about 10 times less (33%; 17%; 10%; 7%; 3%; Logistic Regression Test: $\chi^2 = 9.891$; df = 4; $P = 0.04$). A bias was suspected as this point, because no explanation was available for this dramatic decrease. The difference between the prevalence and the trapping is due to seven cats that were too young to be blood sampled.

Identification of the bias

Since the above decrease was unexpected and difficult to explain, we checked for potential problems due to sampling before the sixth trapping session. No trend in age, sex ratio or weight of individuals was found for the five different samples (Fig. 3).

Because we knew the sex of all individuals in the population, we could test for representativity of the samples based on this parameter. The sex structure of the total population was non-significantly biased in favour of males (56%; $\chi^2 = 1.210$; df = 1; $P = 0.27$), a tendency which also was found in the samples (51%; $\chi^2 = 0.729$; df = 1; $P = 0.39$), suggesting they were indeed representative (see Fig. 3). Overall, males were as likely to be trapped as females, with 79% of males trapped in total, against 75% of females ($\chi^2 = 0.471$; df = 1; $P = 0.49$). However, comparison of recapture rates (kittens excluded) indicated that males were less likely to be recaptured: females were trapped 1.98 ($\pm$0.20) times on average, versus 1.61 ($\pm$0.12) for males (see Fig. 4). Although the difference is not significant ($t = 1.87$; df = 98; $P = 0.07$), this implies that some males were more difficult to recapture than others. Since we corrected for it (by removing cats which disappeared immediately after their first capture), this is not due to the early disappearance of many juvenile males, probably by dispersal (which may account for a significant part of the

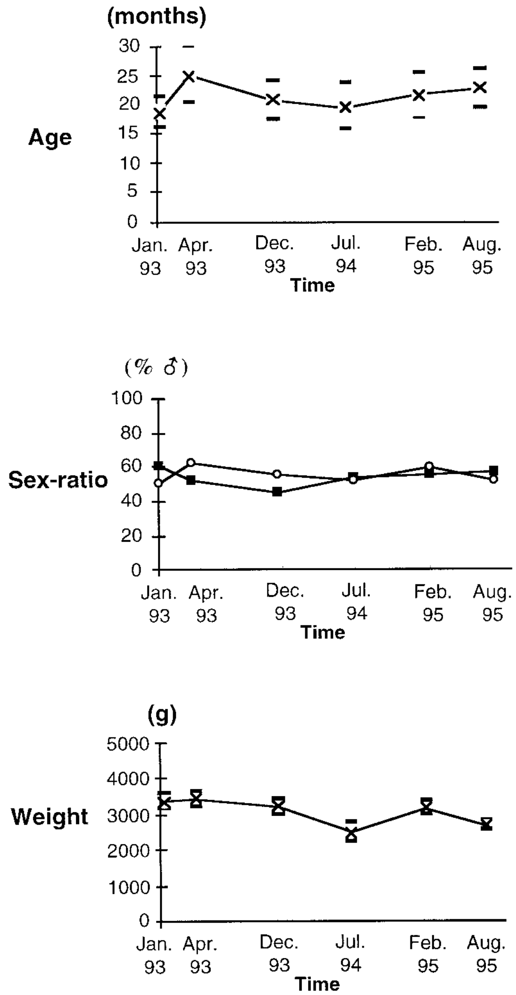

FIGURE 3. Evolution of the average age and weight and of the sex ratio (circles) for the first six samples, and of the sex ratio for the whole population (squares). Sex-ratio, which is the only parameter also known for the whole population, shows no significant difference between population and sample (but see Fig. 4). The remarkably stable values for the three parameters, and the seemingly representativity of the samples for sex-ratio suggested consistency in the population representativity of the samples throughout time.

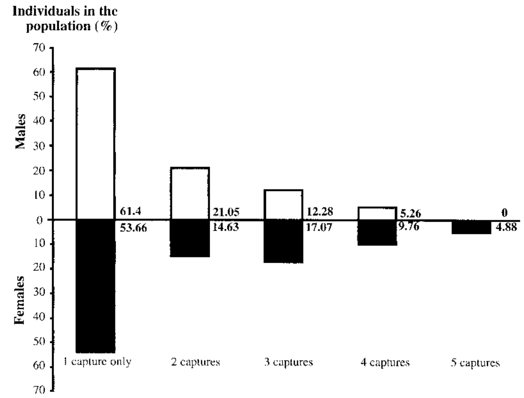

FIGURE 4. Distribution of the number of captures for males and for females. Despite an equilibrated sex ratio, more males are captured once or twice, whereas females are, more often than are males, trapped three, four or five times. Because males are more difficult to recapture (0.75 recapture in average) than females (1.07 recapture in average), there is a bias in the samples, which increases with additional capture sessions.

shorter life expectancy of males). Concerning the age structure of the samples, data were too few to test statistically for a potential bias (the age of most uncaptured cats was unknown), preventing comparisons. However, except for one case, individuals known to regularly escape recapture were mature adults (>2-yr-old), and it was clear from field experience that trapping was much easier for younger cats. Since trapping sessions were conducted once every 6 mo, and given the low degree of precision of age estimates and the small size of the samples, it was not possible to test the effect of age on recapture rates.

In addition, we knew for each trapping period which cats were present in the population but escaped capture. From previous or subsequent captures, we were able to determine the serological status of many cats at the time they escaped capture and thereby correct our prevalence estimate (Fig. 2). Our knowledge of the behaviour of individuals and of the social structure of the population also indicated that cats that were less easily trapped were the heavy adults with larger home ranges (see Courchamp, 1996). Due to its nature (individuals escaping recapture), the bias in the samples increased with time.

Even if a few individuals (<10 of 60 cats) were systematically missed, the decrease in FIV prevalence could not be explained unless these individuals were more often infected by FIV than expected on the basis of the prevalence of the total population. In order to check for a potential capture bias concerning FIV infection, we tested for a difference in the distribution of the number of recaptures for infected individuals and for uninfected individuals. For each individual, we recorded the number of trapping sessions when it was present and the number of times when it was actually trapped. We compared the number of possible recaptures divided by the number of actual recaptures. Results show that infected individuals were recaptured less often than other cats ($t = 2.60$; df $= 10$; $P < 0.03$), which explained the decrease of the FIV prevalence with time.

Correction of the bias

In order to trap these few individuals, we extended the trapping effort, mainly by increasing the number of traps and the trapping session (135 hr of presence over 7 days, see Fig. 1) for the sixth session. We also developed a new kind of trap, directly inside the dog kennels where cats were usually fed. These new traps were baited every day, but were not engaged before the last 2 nights, to allow suspicious cats to see others visiting them without harm. This increased effort resulted in an increase of the trapping efficiency, with only five individuals escaping capture (93% efficiency). Four of these five cats were pregnant females, which were extremely cautious and did not approach any trap. Their serological status can be deduced only for two of these, which were subsequently tested negative, the others have not been captured since. On the last two nights, nine cats were trapped, eight of which were in the two new traps; all eight were large trap-shy males. Of these eight individuals, four were positive for FIV, compared to three of the 45 cats blood sampled in the remaining sample. This difference is highly significant ($\chi^2 = 6.83$; df $= 1$; $P < 0.01$). Of the four infected cats in the new traps, one was a new capture and two had seroconverted since their last capture. FIV prevalence is stable when this new trapping session is added to the five first (13%: $\chi^2 = 9.95$; df $= 5$; $P = 0.08$). Moreover, since on the last trapping session we were able to trap almost all individuals, we have an estimate as close as possible to the actual prevalence in the whole population. The boundaries can be calculated by setting the five remaining individuals as all negative (12%) or all positive but two subsequently tested negative (18%). If the same prevalence as in the sample (13%) is given to these five individuals, taking into account sex and age or not, then zero or one individual is positive, setting the prevalence no higher than 14%. The three next trapping sessions since this study, which are believed to be as free of bias as possible, gave 14%, 14% and 16%, respectively. The stability of FIV prevalence is confirmed when these three samples are taken into account ($\chi^2 = 10.27$; df $= 8$; $P = 0.25$).

DISCUSSION

This paper reports evidence of a bias in an epidemiological study of a behaviourally transmitted disease conducted on an intensively studied population of domestic cats. Samples represented a very large part of the total population, compared to most epidemiological studies, with 60% of the individuals included being captured. The characteristics of these samples remained stable over time (33 mo) for three available parameters (sex-ratio, age, weight distributions). Moreover, the samples were representative of the population for the only parameter we could confirm from the population (sex-ratio). Together, this suggested that the five first samples were likely to be representative of the population.

Despite these suggestions of good sampling protocol, two parallel studies suggested that the dramatic decrease recorded in the FIV prevalence might be an artefact of the sampling. First, a modeling study of the dynamics of FIV within populations of cats predicted an endemy of the disease with steady prevalence (Courchamp et al., 1995). Second, from an ecological study of the population, we could not find a plausible explanation for a 10 fold prevalence decrease in such a short period of time on the basis of the empirical study (Courchamp, 1996): the tests were all performed at the same time, there was no evidence of increased mortality due to FIV in the population (before or during the study), and we could not explain why the transmission rate would decrease. In fact, mortality by FIV seemed very low in our population: only 4 infected cats disappeared over three years, two of which at least presumably from the infection.

Once the bias was suspected, a knowledge of all individuals in the population allowed us to identify those individuals escaping recapture. The unique opportunity to have access to a large panel of data concerning the whole population, allowed us to see consistencies among these few trap-shy cats and to realize that our trapping was non-random. The analysis of individual capture and recapture rates showed a relationship between the probability of being trapped and parameters linked to infection by FIV, with dominant adult males both more likely to escape recapture and more likely to be infected (Courchamp, 1996).

Since most carriers of FIV are asymptomatic for several years, the bias came only from a difference in behaviour of FIV infected cats. Cats are generally suspicious when approaching a trap, seeming to detect or recognise a potential danger (e.g., Jackson, 1981; see also Veitch, 1985). In our study, dominant cats were not only cautious (after the first capture), but also learned how to walk into the traps without triggering them off, and/or how to get the bait while staying out of the traps (see Courchamp, 1996 for details). In addition, they were often seen sitting close to a trap, watching younger cats entering the trap. These cautious cats were captured by the traps specifically designed for them in the last capture session, revealing that they were indeed significantly more often infected by FIV than others.

Infected animals can, for different reasons, be more difficult to sample than other individuals, leading to possible bias in epidemiological data (Wiger, 1977). This is especially the case for debilitating diseases, or diseases inducing high mortality rates, because infected individuals die too quickly to be captured. Trapping may induce a stress, which may affect subsequent captures, either because the survival of trapped animals decreases (Parmenter et al., 1998), or because they become trap-shy. The bias affecting our study is due to a non-random sampling which resulted in the loss of follow-up of a specific group within the study population (unfortunately consisting of individuals disproportionately at-risk for the studied virus). This type of bias can thus arise in any study based on trapping, when the subject of the study (be it epidemiological or not) is linked to behaviour (which may not be known before the study) and when capture probability can be affected by behaviour (which may be difficult to predict). Using very different kinds of traps from the start would have helped to capture all categories of individuals in our study. By definition, the population is often not known before the study. Therefore, the only possible way to detect (and correct) this type of bias may be to conduct long term studies and check for representativity (and consistency) of social classes in the samples, mostly of those characterised as at-risk for the infection in the early stages of the study. This may not be feasible in many cases. It is also noteworthy that a theoretical study of the epidemiology (e.g., through mathematical modelling) may help to detect abnormalities in the observed pattern.

Aside from potential bias, it is important to conduct epidemiological studies over several years, and if possible in the long term. It is only the last capture which allowed us to conclude stability of the prevalence (this was then confirmed by three subsequent trapping sessions). Also, it seems very probable that in our study the prevalence was overestimated in the first sample. Indeed, dominant individuals were not yet trap-shy (we trapped most of them) and, because of a lack of knowledge of the terrain, we found relatively few subordinate adult cats (naturally more shy than dominants), but many juveniles, which were very curious and not wary. In addition, the sample size was the smallest. Had this study lasted only one sample, the estimated prevalence would have been almost three times as high as it really is. Had it stopped before we realised a sampling problem, we would have concluded a decreasing prevalence, down to a third of the actual prevalence.

There are very few species which can be studied well enough to allow a quasi-exhaustive knowledge of several population parameters, from large sampling fractions. This study on the domestic cat provides such an opportunity, and illustrates the difficulties associated with producing an unbiased epidemiological study on a natural population, and the even greater difficulties in detecting and defining any bias. The main differences between our study population and more classical wildlife populations are a small size and a high density. However, a similar epidemiological study on a larger (ca. 300–340 cats) and less dense population provided the same results (Courchamp et al., 1998). We hope that the main message of this paper, that individual differences can influence both the studied parameters and the probability of being sampled, will be enough to promote its usefulness for other epidemiological studies. We believe that the exceptional nature of the animal model we used here does not prevent extrapolation to possible bias in other species, even if we acknowledge the differences with more conventional populations. Feral domestic cat populations are natural in the sense that there is no human constraint on the nature and frequency of the contacts between individuals. In this regard, the spread of pathogens within and between populations is classical and the main difference between this type of populations and more classical ones is the advantages conferred by the feral cat model. Indeed, because domestic cat populations are natural (even in urban environment), yet accessible and relatively easy to study, because their pathology and immunology are among the best known, and because their populations present a wide variation of structure, they are a good model for epidemiological studies of less accessible species which bear more importance for research on wildlife diseases. Indeed, the best studies of wild species, especially on large populations and/or at low densities, cannot easily provide as large a sampling fraction (with individual identification) that our animal model allowed us here, meaning that a similar bias can be difficult to spot. This may have major implications for the conclusions obtained by similar epidemiological studies on other diseases, but also for many other ecological studies based on trap sampling.

ACKNOWLEDGMENTS

The authors thank the many field helpers who contributed to the success of this study, especially S. Beretoni, S. Bernoud, A. Bladier, C. Delhumeau, D. Grandclément, R. Guillermet, P. Laviec, E. Le Gall, S. Mesnager, C. Mion, C. Montoloy, Y. Ropert-Coudert, S. Rose, and P. Saladin. We also thank E. Fromont, M. Artois and E. Cain for blood samples and FIV testing, and S. Rose for the construction of the Data Base. We are grateful to H. Lutz who taught the Western Blot technique to F. Cliquet, and provided us the necessary antigen, and to A. Young, P. Brotherton, J. O'Riain and E. Fromont for helpful comments on the manuscript. We thank the Croix-Rousse Hospital staff and their director, A. Raisin-Dadre, for their permission, understanding and help for the "field" work. Financial support was provided by the French Ministry for Research and Higher Education and by a Marie Curie fellowship from the European Community.

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Received for publication 6 January 1999.