Parasite richness and abundance in insular and mainland feral cats: insularity or density?

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(*Received 8 September 2000; revised 28 December 2000 and 16 March 2001; accepted 16 March 2001*)

SUMMARY

Hosts living on islands carry few parasite species, and the prevalence and intensity of directly transmitted parasites are often higher in insular than in mainland populations. However, it is unclear whether density or other features of insular populations can be responsible for the pattern observed. We compared the parasite richness, prevalence and intensity of parasites between 2 feral populations of cats living either at low density on an island (Kerguelen) or at high density on the mainland (Lyon). Parasite richness was higher in Lyon than in Kerguelen, where only *Toxocara cati* was found. *T. cati* egg prevalence was higher in Kerguelen (71·1%) than in Lyon (58·0%). Because cat density cannot explain this pattern, we propose that the low number of parasite species, the diet and/or immunity of cats act to increase prevalence in Kerguelen. Moreover, prevalence, intensity and variance-to-mean ratio increased with age and body mass in Kerguelen whereas, in Lyon, prevalence decreased with age and body mass. We hypothesize that the pattern of exposure differs between populations, and that density-dependent parasite mortality is lower in Kerguelen than in Lyon. We discuss the consequences concerning the influence of parasites on insular host populations.

Key words: epidemiology, parasite dynamics, insular populations, *Toxocara cati*, cat.

INTRODUCTION

The host–parasite relationship (here we use the term parasite in its broad sense, including micro- and macroparasites (Price *et al.* 1977)) is modified in the insular environment. Insular host populations generally experience low parasite species richness (Mas-Comá *et al.* 1987*b*). The low number of parasite species is generally attributed to loss during the colonization process, rather than to any consequence of the island habitat (Dobson, 1988; Font & Tate, 1994). Considering the distribution of parasites, several studies concluded that the proportion of hosts that are parasitized by a given parasite species (prevalence) and the number of parasites per individual host (intensity) were higher on islands than on the mainland (Lewis, 1968*a*, *b*; Gregory & Munday, 1976) and were highest in the smallest islands (Casanova *et al.* 1996; Miquel *et al.* 1996). This increase has been observed in cestodes and nematodes, and generally in macroparasites with direct life-cycles (but other macroparasite taxa showed different results, Mas-Comá *et al.* 1987*a*). however, it is not clear why parasites should have a high transmission rate within island host populations. According to Dobson (1988), 'this effect is most likely a consequence of increased transmission efficiency in the higher density host populations on the island'. The influence of host density on parasite prevalence and intensity has been clearly demonstrated among mainland populations (Arneberg *et al.* 1998). Combes (1995) also proposed that 'behavioural shifts' (e.g., small home ranges, low aggressiveness) influence parasite propagation. Otherwise, because of a reduced number of parasite species, the competition between parasitic species is reduced within hosts, probably allowing parasites to be more frequently found, and more numerous per host (Dobson, 1985). However, most studies compared populations living at higher density on islands than on the mainland (Lewis, 1969*a*, *b*; Gliwicz, 1980; Gulland, 1992). Hence there is confounding between the effects of host density and other levels of structure of host populations in determining the dynamics of parasites on islands.

We compared 2 populations of domestic cats: one population living on the subantarctic archipelago of Kerguelen, and the other being a urban feral population in Lyon, France. Contrary to insular populations studied previously, cats live at lower density in Kerguelen (1–3 cats/km^2; Say *et al.* unpublished data) than in Lyon (1000 cats/km^2, Say 2000). If the increase in parasite prevalence and

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DOI: 10.1017/S0031182001008277 Printed in the United Kingdom

intensity generally observed on islands was due to high density of insular host populations, we expected to observe a prevalence lower in Kerguelen than in Lyon.

Besides insularity and density, the 2 populations showed other differences that could affect the epidemiology of parasites. First, the Kerguelen population is derived from a few ancestors that were released in the 1950's (Derenne, 1976; Pascal, 1984). Several parasite species could have been lost during the colonization process, or the parasites never were brought to the island. In Kerguelen, low temperatures and high precipitation are unfavourable to parasite persistence and development in the environment, and thus may be a limiting factor for the propagation of parasites that need soil development. Moreover, due to the climate and isolation, vectors and intermediate hosts are lacking for several parasites (see below). We thus expected that the number of parasite species would be lower in Kerguelen compared to Lyon.

We also aimed to characterize the distribution of the parasites found. If few parasite species were present on Kerguelen, we expected that the competition for the exploitation of the resource (cats) would be lower in Kerguelen than in Lyon. Competition being one of the factors affecting the growth of parasites within hosts through density-dependent processes (Poulin, 1998), we expected that the minimal intensity (number of parasites per host) necessary for density-dependent processes to occur would be higher in Kerguelen than in Lyon. Thus parasite aggregation should be higher in Kerguelen than in Lyon.

A practical interest of this study is to provide insights into the control of insular cat populations by parasites. Because parasites often show high prevalence and intensity, they are supposed to have a strong negative effect on the growth of insular host populations and on the distribution of host species (Van Rensburg, Skinner & Van Aarde, 1987; Dobson, 1988; Berthier *et al*. 2000). In Kerguelen, however, we predict low prevalence, so the impact of parasites on the growth of the cat population should be low. Cats established on subantarctic islands represent a dangerous predator for native birds (Jouventin *et al*. 1984; Johnstone, 1985; Van Rensburg & Bester, 1988), thus it is of interest to check if the parasite species present could help controlling the growth of the cat population.

MATERIALS AND METHODS

Populations

The 2 populations studied experience no direct human intervention on cat movements, reproduction or parasitism. In Kerguelen (49° 21′S, 70° 14′E) located in the South Indian Ocean, we studied the population living on the main island of the archipelago. The climate is characterized by high precipitation and windy conditions. Temperatures range from a mean of 2·3 °C in July to 7·8 °C in February (MétéoFrance, Port-aux-Français). The cat population is estimated at around 6000 individuals. On the Courbet Peninsula where the cat population lives, cat density is 1–3 cats/km² (Say *et al*. unpublished data). Cats prey on rabbits, mice and many species of birds (Derenne, 1976; Pontier *et al*., unpublished data). The population of Lyon lives in the basements of the Croix-Rousse hospital. The population has been monitored since 1993, and included 30 to 73 cats (Courchamp, Say & Pontier, 2000*b*) living at a density of 1000 cats/km² (Say, 2000).

Sampling

In Kerguelen, sampled cats originated from 2 sources. Live individuals were captured (between December 1997 and March 1999) with baited traps in 5 sites distributed around the Courbet peninsula, at Port-aux-Français (PAF), Ratmanoff, Port-Jeanne d'Arc, Port-Couvreux and Sourcils Noirs. A second group of dead cats was examined after being killed in the area of PAF, between November 1994 and March 1999. In Lyon, all cats were captured between October 1997 and June 1999, with baited cages (Courchamp, Say & Pontier, 2000*a*). In the 2 populations, live cats were kept in captivity until faeces were obtained, and then released. None of the cats was resampled.

Clinical examination

We anaesthetized trapped cats with a mixture of ketamin chlorhydrate (15 mg/kg; Rhône Mérieux, Lyon, France) and acepromazin (0·5 mg/kg; Sanofi, Paris, France). Then we examined the cats clinically to search for signs of external parasitism, including mycosis and arthropods. We took samples of blood, faeces and hair for serological, coproscopic and mycological examinations.

For dead cats, fresh carcasses were examined immediately or frozen for later examination. We searched for signs of external parasitism, we opened the entire gastro-intestinal tract and examined the faeces grossly, counted the parasites found and searched for the presence of significant gross lesions.

Search for parasites and viruses

In the sera, we searched for Feline Leukemia Virus (FeLV) group-specific antigens and Feline Immunodeficiency Virus (FIV) antibodies using the ELISA method with a commercial kit (IDEXX, Cergy Pontoise, France). We also searched for serum-neutralizing antibodies against Feline HerpesVirus (FHV) and Feline CaliciVirus (FCV) by cell culture (Fromont, Artois, & Pontier, 1996).

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We collected fecal samples by maintaining cats in cages. Faeces were first suspended in a 35 % $MgSO_4$ flotation solution, with 5 g of faeces in 75 ml of solution. For the identification of parasite eggs, we placed a cover-slide over the tube into a centrifuge (5 min at 2500 rpm), then examined the slide by light microscopy. We examined hair samples for fungal colonies after incubation for 15 days either in a Sabouraud + chloramphenicol agar plate, or in a Sabouraud + chlorhexidin(cycloheximid) + chloramphenicol agar plate (Jungerman & Schwartzman, 1972).

We weighed and sexed all cats. In Kerguelen we classified cats as young (< 1 year) or adult ($\geqslant 1$ year) based on body size and teeth development. In Lyon, birth date was known for all cats studied, and we considered the same age classes.

Data analysis for prevalence

We analysed separately egg prevalence (the proportion of captured cats carrying eggs in their faeces) and worm prevalence (the proportion of necropsied cats carrying worms in their digestive tract or faeces). We searched for the relationships between prevalence and the population, site (in Kerguelen), sex, age and body mass of cats. We also tested the effect of interactions between the above factors when sample size was adequate. We used logistic regression (Breslow & Day, 1987), which relates the logit of the probability for a cat of being infected to the predictor variables: population, site, sex, age, body mass, or their interaction. We built all possible models including each variable, and interactions between significant variables. For each model we calculated its number of parameters and a measure of its goodness-of-fit, the scaled deviance. We searched for the model that fitted the data and did not include unnecessary terms using the Akaike Information Criterion (AIC). We selected the models with the lowest AIC value. When differences in AIC values between 2 or more models were < 1, we selected the most parsimonious model (Burnham & Anderson, 1992).

Data analysis for aggregation and intensity

We characterized parasite aggregation by adjusting the distribution of the number of parasites per host to random (Poisson) and aggregated (negative binomial) distributions. An aggregated distribution is expected if cats differ in their susceptibilities to infection, due to differences in immunology, behaviour or exposure among hosts (Poulin, 1998). We also tested a zero-inflated Poisson (ZIP) distribution. A ZIP distribution is expected if some cats are resistant, or not exposed to *T. cati* and if the parasites are distributed at random among other cats (Johnson & Kotz, 1969). We analysed parasite aggregation and intensity according to the sex, age and body mass of cats. In each class of cats we calculated mean intensity, variance, and variance/mean ratio (VMR, which gives a measure of the level of parasite aggregation; Pacala & Dobson, 1988). For this purpose we defined 3 classes of body mass: light cats ($\leqslant 2$ kg, kittens and juveniles), intermediate cats (from 2·1 to 3 kg, subadults and adult females) and heavy cats ($> 3{\cdot}1$ kg, adults). We tested the relationships between intensity and sex, age or body mass using non-parametric analysis of variance (Kruskall–Wallis test) or Mann–Whitney test (Sokal & Rohlf, 1995). Non-parametric tests were used to limit the influence of the non-normal distribution of parasites (Wilson, Grenfell & Shaw, 1996).

Logistic regressions were performed with program GLIM (Crawley, 1993) and other tests with program StatView IV (Abacus Concepts, 1992). We performed two-tailed tests and applied a significance level of 5 %.

RESULTS

Parasitic species found

In Kerguelen, we detected no specific external parasites on 104 live cats and 46 carcasses. Searches for fungal parasites were negative on the 15 samples of hair tested. We tested 104 cats for FIV antibodies and FeLV antigens, 98 cats for FHV antibodies, and 102 cats for FCV antibodies. All cats were negative. We calculated the probability of failure to detect a single case of infection if the viruses were present with prevalences similar to those observed elsewhere in the world. The average prevalence observed in previous studies is 10·0 for FIV (range: 9–33 %, Courchamp & Pontier, 1994), 5·3 % for FeLV (range 0–23 %, Fromont *et al*. 1997), 21·2 % for FHV (range: 11–50 %, Drapier, 1992), and 77·0 % for FCV (range: 59–89 %, Coman, Jones & Westbury, 1981). For FIV, the probability of failure to detect infection with a sample of 104 animals was $< 0{\cdot}001$ (Thrusfield, 1995). This probability was 0·006 for FeLV, and $< 0{\cdot}001$ for FHV and FCV.

In faecal samples, the only nematode was *Toxocara cati*. Fifteen cats (57·7 %) carried oocysts of several species of *Eimeria* sp. a coccidian probably originating in rabbits that were eaten by cats (Langlade, 1995). We found no lesions, indicating that *Eimeria* did not have a pathogenic effect on cats. Two individuals were found to carry *Cheyletiella* sp. (Acari: Cheyletidae). The species was not determined, it may be either *C. blackei* (parasite of cats) or *C. parasitivorax* (parasite of rabbits). However, the parasites were found in the digestive tract and in a faecal sample, suggesting that they could be originating from rabbits ingested.

In Lyon, previous studies of the same population showed that the 4 viruses studied were present: prevalence equaled 14 % for FIV (Courchamp *et al*. 2000*b*), 4·6 % for FeLV (Fromont *et al*. 1997), 38 %

https://doi.org/10.1017/S0031182001008277 Published online by Cambridge University Press

Table 1. Sample sizes per age and sex in each group studied for *Toxocara cati* epidemiology

	Kerguelen			Lyon
	Captured		Carcasses	
	PAF	Other sites	(PAF)	
Males < 1 year	12	0	8	28
Males ⩾ 1 year	11	4	25	14
Females < 1 year	9	6	8	19
Females ⩾ 1 year	6	4	11	20
Total	38	14	53*	81

* Age of 1 cat was not determined.

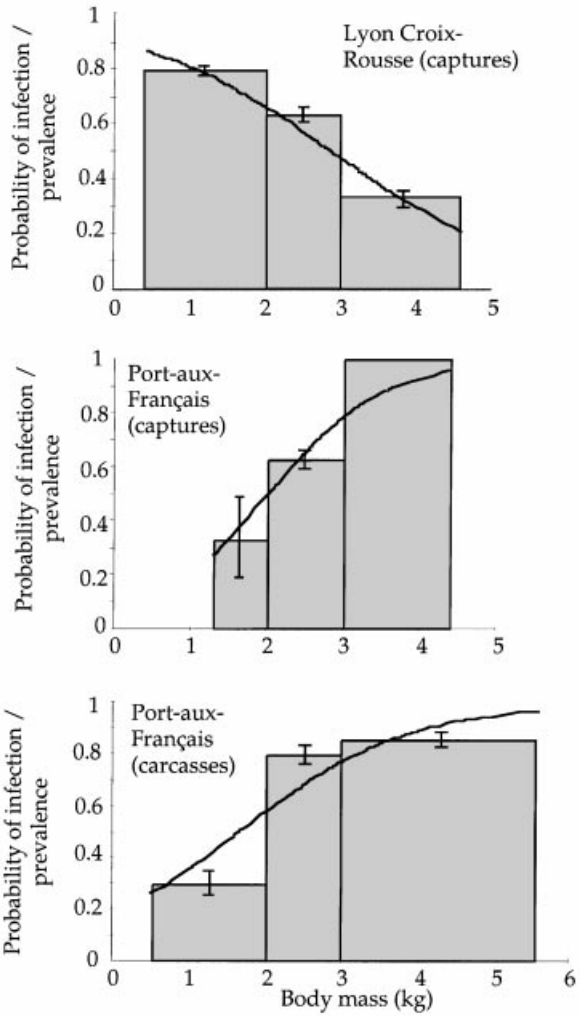

Fig. 1. Logistic regression lines showing the probability of being infected (p, estimated as egg prevalence in captured cats and worm prevalence in necropsied cats) as a function of body mass in cats captured in Lyon (adjusted function: logit p = 2·227–0·767* mass), cats captured in PAF (logit p = −2·682+1·321* mass) and cats necropsied in PAF (logit p = −1·478+0·8971* mass). Data used in logistic regressions were body mass and presence/absence of parasites in each cat. Raw data were grouped for graphical representation: superimposed bars represent prevalences in the 3 groups of body mass (±S.E.).

for FHV and 80·4 % for FCV (Fromont, Artois & Pontier, 1996). Faecal samples revealed the presence of *T. cati* and *Isospora felis*. During capture sessions, cats were observed with otacariasis (*Otodectes cynotis*), cat fleas (*Ctenocephalides felis*) and ticks (*Ixodes* sp.).

Egg prevalence of Toxocara cati

We studied *T. cati* in 52 cats captured in Kerguelen (38 in PAF and 14 in other sites), 81 cats captured in Lyon, 53 carcasses from PAF (Table 1).

In Kerguelen, coproscopic examinations showed that 28 of 52 captured cats were positive (prevalence: 53·9 %; 95 % Confidence Interval (C.I.): 40·3–67·4 %). In PAF, 27 of 38 cats (71·1 %) carried *T. cati*, while in other sites only 1 cat was positive out of 14 tested (7·1 %). The difference between PAF and other sites was significant ($P < 0·001$). In the subsequent analyses we only considered results from PAF in order to avoid introducing bias linked to site effect. In Lyon, 58·0 % (95 % C.I.: 47·3–68·77 %) of 81 cats carried eggs of *T. cati*. Prevalence in Lyon was not significantly different from PAF ($P = 0·172$).

Egg prevalence was independent of sex both in Lyon ($P = 0·202$) and in PAF ($P = 0·802$). The effects of age and body mass differed between the 2 populations. In Lyon, prevalence decreased with age (from 78·7 % in cats less than 1 year old to 29·4 % in older cats, $P < 0·001$) and decreased with body mass ($P = 0·001$, Fig. 1). On the contrary, in PAF, prevalence increased with age (from 57·1 to 88·2 %, $P = 0·036$) and increased with body mass ($P = 0·040$, Fig. 1). Because age and body mass were related (Mann–Whitney tests, $P < 0·001$ in each population) we hypothesized that the two variables had a confounding effect, i.e. that the effect of body mass was due to its relationship with age or reciprocally. In accordance with this hypothesis, in the 2 populations the model that best fitted the data included either age or body mass but not the two variables together (Table 2).

Worm prevalence

T. cati was the only parasite found during the 53 post-mortem examinations from PAF. Worm prevalence equaled 73·6 % (95 % C.I.: 61·7–85·5 %). Like egg prevalence in PAF, worm prevalence was independent of sex ($P = 0·583$) but increased with age (from 56·3 to 83·3 %, $P = 0·037$) and body mass ($P = 0·003$, Fig. 1). Logistic regression showed that body mass alone was the model that best explained the probability of being infected (Table 2).

Worm distribution and intensity

Among the 53 individuals studied, the mean number of parasites per host was 8·68, with a variance of 200·4. the VMR for *T. cati* intensity was 23·09,

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Table 2. Statistical models testing the effects of age (A) and body mass (B) on the prevalence of *Toxocara cati*

(The best models according to AIC are indicated in bold.)

Model	No. of parameters	Egg prevalence Lyon	Egg prevalence PAF	Worm prevalence PAF
		Deviance/AIC	Deviance/AIC	Deviance/AIC
Null model	1	106·28/108·28	44·32/46·32	58·48/60·48
A	2	**86·19/90·19**	**39·58/43·58**	54·37/58·37
B	2	95·75/99·75	**40·09/44·09**	**49·53/53·53**
A+B	3	85·99/91·99	38·90/44·90	49·42/55·42
Full model	4	85·91/93·91	37·83/45·83	47·47/55·47

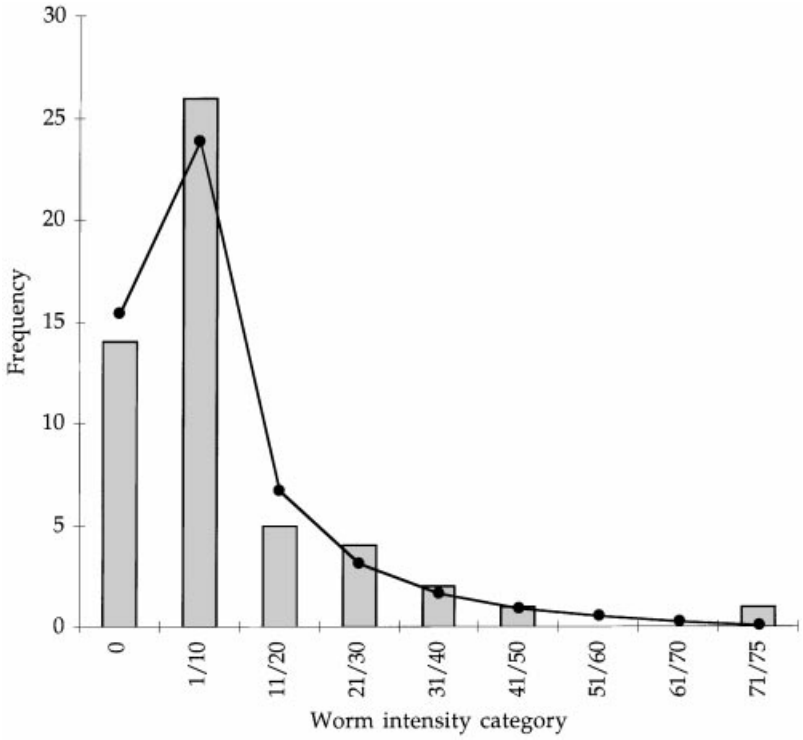

Fig. 2. Observed (bars) and negative binomial-adjusted distribution of the number of *Toxocara cati* per cat (intensity) in carcasses from PAF.

which indicated an aggregated distribution. *T. cati* intensity was first adjusted to a random (Poisson) distribution; however, the observed overdispersion was too large for the Poisson series ($\chi^2 = 201{\cdot}1$, 5 D.F., $P < 0{\cdot}001$). A ZIP distribution also did not fit the observed data ($\chi^2 = 49{\cdot}7$, 4 D.F., $P < 0{\cdot}001$). Then the series was adjusted to a negative binomial distribution, using the maximum likelihood method (Bliss & Fisher, 1953). We found a parameter k of 0·393, which confirmed the presence of aggregation at relatively high level ($k < 0{\cdot}5$) (Grenfell *et al.* 1995). The adjusted distribution fitted closely to the observed data ($\chi^2 = 3{\cdot}73$, 5 D.F., $P = 0{\cdot}589$, Fig. 2).

Mean intensity did not vary with sex (Mann–Whitney test, $P = 0{\cdot}567$). The relationship between intensity and age was close to significance (Mann–Whitney test, $P = 0{\cdot}076$), with intensity increasing from 5·88 in cats aged less than 1 year old (VMR = 17·23, $n = 16$) to 10·17 in older cats (VMR = 23·83, $n = 36$). Intensity depended on the class of body mass considered (Kruskall–Wallis test, $P = 0{\cdot}007$) but the only significant difference occurred between very light cats that had low intensity and VMR, and other cats showing higher intensities and VMR. Again we hypothesized that the effect of body mass was confounded with age. We could not test this hypothesis because all very light cats were aged less than 1 year old.

DISCUSSION

Parasite species richness

Our investigation of parasite species richness was limited by the methods we used: we did not search for microscopic forms other than dermatophytes, nor for internal non-digestive parasites. Moreover,

https://doi.org/10.1017/S0031182001008277 Published online by Cambridge University Press

in cats, coproscopic examination is of high value to detect nematodes – so we could expect coherent results between worm and egg prevalences for *T. cati* – but has low sensitivity and negative predictive value concerning cestodes (Martini & Poglayen, 1990). However, several parasite species that were present in the population of Lyon were absent from Kerguelen. These include viruses (FIV, FeLV, FHV, FCV), coccidia (*Isospora felis*) and external parasites (*Otodectes cynotis*, *Ctenocephalides felis* and *Ixodes* sp.). These findings support the prediction of a lower number of species in Kerguelen cats, at least for the limited number of species considered here. Parasites that need soil maturation could have been eliminated by cold temperatures (*I. felis*, *C. felis*). For other directly transmitted parasites (FIV, FeLV, FHV, FCV, *Otodectes cynotis*, *Ixodes* sp.), either the parasites were absent from the founder group, or the species were not able to persist, due to low density of cats at the beginning of colonization. Remarkably, however, numerous helminths commonly observed in cats (Pedersen, 1988) were absent from Kerguelen and also from Lyon. For example, parasites needing intermediate hosts (such as *Dipylidium caninum* and *Taenia taeniaformis*) could be absent from Kerguelen because intermediate hosts were absent, but they were also absent from Lyon where intermediate hosts (cat fleas and rodents, respectively) are present. Other mainland populations of stray cats were found to carry only few parasite species (Niak, 1972; Malloy & Embil, 1978). As a first conclusion, the loss of parasite species during colonization of Kerguelen would explain part, but not all the depletion of parasite species richness.

Prevalence of Toxocara cati

In contrast to our expectation, the prevalence of *T. cati* was not significantly different between the 2 populations. However, several replicates would be highly desirable to confirm this observation. If insular condition determines the pattern we observed, we expect that parasite intensity should be relatively high in any insular host population, whatever its density.

We cannot formally separate the effects of density and other features of insular populations. Nevertheless, even if host density probably acts to reduce prevalence (Arneberg *et al*. 1998), other factors counterbalance this effect. Three hypotheses can be proposed to explain the high prevalence in Kerguelen. (1) The low number of parasite species should result in low competition between parasitic species for host resources, and the availability of resources may allow parasites to be more abundant. This hypothesis could be tested experimentally, by comparing parasite burden in cats infected by a given number of parasitic species. (2) *T. cati* can be transmitted through ingestion of embyonated eggs, through ingestion of paratenic host or by transmammary passage (Overgaauw, 1997). The ingestion of embyonated eggs should be lower in Kerguelen than in Lyon because no development of *Toxocara* larvae occurs below +10 °C (O'Lorcain, 1995, Overgaauw, 1997). In Kerguelen, the mean daily temperature reaches +10 °C only on 26·4 days each year, on average (MétéoFrance, Port-aux-Français). Moreover, cats live at low density, thus the probability of encountering contaminated faeces should be generally low in Kerguelen. On the contrary, the ingestion of paratenic hosts should be an important route of infection in Kerguelen, because mice constitute the most common paratenic host of *T. cati* (Dubinsky *et al*. 1995), and larva migrans has also been described in rabbits (Lautenslager, 1972). Whether paratenic hosts are sufficient to explain the high prevalence in Kerguelen remains to be tested by extending our investigations to sites where one or two species of paratenic hosts are absent. Finally, the transmammary route occurs after ingestion of eggs but not after ingestion of paratenic host, thus we expect that transmammary infection should be less frequent in Kerguelen than in Lyon. (3) Another factor potentially explaining the high prevalence in Kerguelen is that cats could be particularly susceptible to infection, as the result of the founder effect (Meagher, 1999). A recent assessment showed that no more than 4 cats are at the origin of the current cat population (Pontier *et al*., unpublished data). Only experimental infestation of mainland and insular cats in controlled conditions may bring information on this hypothesis.

The most striking difference between Kerguelen and Lyon was the pattern of infection with age. In PAF, the prevalence of eggs (in live cats), the prevalence, intensity and VMR of worms (in necropsied cats) were higher in cats aged more than 1 year than in younger cats, and increased with body mass. On the contrary, in Lyon, prevalence decreased with age and body mass. It is noticeable that, compared to Lyon, the prevalence in PAF was both lower in young cats (57·1 %, *versus* 78·7 % in Lyon) and also higher in older cats (88·2 % *versus* 29·4 % in Lyon). In other mainland populations, the prevalence of *T. cati* also decreased with age, generally after 3 months (Malloy & Embil, 1978; Visco, Corwin & Selby, 1978) and peaked or decreased with body mass (Dubey, 1966, Niak, 1972). Intensity also decreased with age (O'Lorcain, 1994). Variations in prevalence among age classes can be interpreted in relation with exposure to parasite. In high-density urban populations such as Lyon, both males and females are philopatric and live in large multimale–multifemale groups (Natoli, 1985; Say, Pontier & Natoli, 1999). Thus exposure to *T. cati* eggs is expected to be high all through life. The high prevalence in kittens suggests that they were exposed to parasite contamination soon after birth, either through the trans-

https://doi.org/10.1017/S0031182001008277 Published online by Cambridge University Press

mammary route, or through ingestion of eggs. The lower prevalence in adults may be due to elimination of parasites through acquired immunity (Overgaauw, 1997). In PAF, exposure to *T. cati* seems to increase with age. The low prevalence in kittens suggests that, as predicted, the transmammary route of infection is infrequent. Cats may acquire infection only when they begin to eat prey. Moreover, adults are solitary, with both males and females defending their own territory; kittens stay on their mother's territory until they disperse to search for a new territory (Pascal, 1980). If some *T. cati* eggs were able to mature in Kerguelen, cats could be exposed to embryonated eggs when sniffing the faeces of other cats during dispersion. An alternative explanation for the high prevalence in older cats is that cats from Kerguelen do not show efficient acquired immunity, either because the founder cats showed deficient immunity, or because the immune system is not activated by the low-level infection. All mechanisms could play together.

Intensity and aggregation of Toxocara cati

The distribution of parasites among necropsied cats in PAF followed an aggregated distribution, as in other studies on mainland populations, concerning either *T. cati* (Enbaek, Madsen & Larsen, 1984; O'Lorcain, 1994) or other helminths (Crofton, 1971; Grenfell *et al*. 1995). The value of k (0·393) here was in the same range as the value (0·554) observed by Engbaek *et al*. (1984) in urban stray cats from Denmark, indicating a high degree of aggregation. Aggregation may be caused by heterogeneity in host exposure, due to spatial and temporal distribution of hosts and parasites and/or heterogeneity in host susceptibility to parasites, due to genetic or non-genetic factors (Anderson & Gordon, 1982; Wakelin, 1985; Poulin, 1998). The importance of genetic predisposition to parasites as a mechanism generating heterogeneity in the field has been discussed (Munger, Karasov & Chang, 1989; Quinnell, Medley & Keymer, 1990). In Kerguelen, we could expect cats to have rather similar predisposition to parasitism because of their relative genetic relatedness (Pontier *et al*. unpublished data). However, we observed a high level of aggregation, which means that either the founder effect was not sufficient to render cat homogeneous as for their immune response, or genetic factors are only a minor cause of parasite aggregation in *T. cati*. The high level of aggregation we observed may also be a consequence of the low level of intraspecific density-dependent parasite mortality, because density-dependent parasite mortality and parasite-induced host mortality are the main mechanisms that could decrease parasite aggregation (Poulin, 1998).

Helminth aggregation generally decreases with host age (Pacala & Dobson, 1988), and this decrease is interpreted to be a result of density-dependent effects, such as density-dependent parasite mortality and fecundity (partly due to immunity) or parasite-induced host mortality (Anderson & Gordon, 1982; Poulin, 1998). The decrease of prevalence with age in Lyon suggests that within-host density-dependent processes occur. On the contrary, in Kerguelen, intensity and aggregation seem to increase with age. Thus we hypothesize that in Kerguelen, the density of parasites within cats does not reach the threshold for density-dependent effects. This hypothesis can be tested (see Marcogliese (1997) for a method to estimate parasite fecundity). We expect that within-host parasite density should not affect parasite fecundity in insular populations, contrary to mainland populations.

In conclusion, the result we observed of high prevalence in a low density host population was not expected, and should be confirmed in other populations and/or host species. However, several hypotheses can be proposed and will be testable in the near future in the system we studied or in other hosts.

A consequence of the possible low density-dependence in Kerguelen is the low impact of the parasite on the growth of the host population. In mainland populations, the morbidity due to *Toxocara* occurs mainly in kittens and the mortality is uncommon (Overgaauw, 1997). On Kerguelen, adults are more often parasitized than kittens. Since mortality due to *T. cati* is probably lower in adults than in kittens, the effect of *T. cati* on growth of the cat population should be even lower on Kerguelen than in mainland populations.

The authors thank C. Dekeyser and M. Castellazzi for help in collecting data and F. Courchamp and W. G. King for comments on the manuscript. Two referees raised a number of stimulating points and contributed to improve the manuscript significantly. This work is part of program 279 of the French Polar Institute I.F.R.T.P.

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