

Toxoplasmosis in prey species and consequences for prevalence in feral cats: not all prey species are equal

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SUMMARY

Toxoplasma gondii is largely transmitted to definitive felid hosts through predation. Not all prey species represent identical risks of infection for cats because of differences in prey susceptibility, exposure and/or lifespan. Previously published studies have shown that prevalence in rodent and lagomorph species is positively correlated with body mass. We tested the hypothesis that different prey species have different infection risks by comparing infection dynamics of feral cats at 4 sites in the sub-Antarctic Kerguelen archipelago which differed in prey availability. Cats were trapped from 1994 to 2004 and anti-*T. gondii* IgG antibodies were detected using the modified agglutination test ($\geq 1:40$). Overall seroprevalence was 51.09%. Antibody prevalence differed between sites, depending on diet and also on sex, after taking into account the effect of age. Males were more often infected than females and the difference between the sexes tended to be more pronounced in the site where more prey species were available. A difference in predation efficiency between male and female cats may explain this result. Overall, our results suggest that the composition of prey items in cat diet influences the risk of *T. gondii* infection. Prey composition should therefore be considered important in any understanding of infection dynamics of *T. gondii*.

Key words: *Toxoplasma gondii*, epidemiology, feral cat, diet, sub-Antarctic environment.

INTRODUCTION

Toxoplasma gondii is a worldwide protozoan parasite that infects humans and a large variety of animal species. Felids, particularly domestic cats (*Felis catus*), are the only hosts that excrete the oocysts that infect intermediate hosts (Dubey and Beattie, 1988). The life-cycle of the parasite includes intermediate hosts such as small mammals and birds, which complete the life-cycle when they are eaten by cats. Besides predation, cats can be contaminated by vertical transmission or by ingesting oocysts. Vertical transmission, however, appears to be rare in laboratory and natural conditions (Dubey and Hoover, 1977; Afonso *et al.* 2006) and oocysts are less infectious than tissue cysts in cats (Dubey, 2006). Predation is therefore the major cause of infection in cat populations and differences in prevalence between domestic and stray cats are closely correlated with dietary levels of hunting (Tenter *et al.* 2000).

In cats that have access to prey the levels of infection should depend on the levels of infection in prey. Cats are opportunistic predators that can rapidly adapt their diet to prey availability (Turner and Bateson, 2000). The variability of prevalence in cats should thus also depend on the variability of infection in prey. Not all prey species have identical susceptibility (Gustafsson *et al.* 1997; Sedlak *et al.* 2001). Prey species also vary in exposure, because of the level of oocyst contamination in their habitat or differences in home-range size or energy requirements. Finally, infection accumulates with age, so that old individuals are more often infected than younger ones. Because life expectancy, home-range size and energy requirements are related to body size (Degen *et al.* 1998; Speakman, 2005; Ottaviani *et al.* 2006), body size may represent a good indicator of species risk.

The aim of this study was to provide information on *T. gondii* infection risk in feral cats according to their diet. We tested the prediction that cats exploiting different prey species would have different levels of *T. gondii* seroprevalence using data from a cat population living on the Kerguelen archipelago, one of the rare populations where cats survive exclusively through predation. We expected to find

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that seroprevalence in cats would vary between sites, according to availability of prey species.

MATERIALS AND METHODS

Body mass and prevalence in rodents and lagomorphs

We searched for reported *T. gondii* prevalence in rodent and lagomorph species, including studies with sample sizes of at least 30 individuals captured in non-anthropized environments. We used a linear model to describe the relationship between body mass and antibody prevalence and, to ensure linearity, we used the natural logarithm of body mass and the arcsine square root of prevalence values (Sokal and Rohlf, 1981). Because species are not independent, but are linked by phylogenetic history, we used the method of phylogenetically independent contrasts to correlate the two variables, taking into account non-independence of data (Felsenstein, 1985). We constructed a phylogenetic tree with data from Conroy and Cook (2000), Huchon and Douzery (2001), Michaux *et al.* (2002), Durish *et al.* (2004), Steppan *et al.* (2004), and Robinson and Matthee (2005), with all branch lengths set to 1. We first calculated the Pearson's correlation coefficient without contrasts then calculated the Pearson's correlation on contrasts with the ape package of the R 2.0.1 software (R Development Core Team, 2005).

Study area and population

The Kerguelen archipelago (49°20'S, 70°20'E) in the Southern Indian Ocean consists of 1 main large island partly covered by an icecap and about 300 small islands over a total surface area of 7200 km². The climate is characterized by high precipitation (mean 783 mm per year), low temperatures (mean annual temperature 4.8–11.9 °C, Météo France, Port aux Français) and windy conditions. Cats live at very low densities (1–3 cats/km²; Say *et al.* 2002a) and are mainly solitary (Say *et al.* 2002b).

Samples were collected from feral cats at 4 sites on the main island: (1) the French naval station, Port aux Français (PAF), (2) the farming settlement of Port Couvreur (PC), (3) the Norwegian whaling station of Port Jeanne d'Arc (PJDA), and (4) Cape Ratmanoff (RAT) on the Courbet Peninsula. Pairwise distances between sites range from 20 to 140 km and the 4 groups of cats appear to be genetically different and spatially independent (Pontier *et al.* 2005).

Rabbits (*Oryctolagus cuniculus*) are the most common prey consumed by cats at PAF, PC, and PJDA (about 90%), whereas in RAT, rabbits, mice (*Mus musculus*) and birds (*Pterodroma lessonii*, *Pachyptila desolata*, and *Procellaria aequinoctialis*) are all consumed (about 30% each; Pontier *et al.* 2002).

Cats were trapped between October 1994 and November 2004, using baited-traps. Captured cats were anaesthetized, weighed and sexed, and blood samples collected by jugular puncture. Cats were permanently marked at first capture with subcutaneous transponders. Age was estimated based on general appearance, body size, tooth development and marks from previous captures. Cats aged less than 1 year were aged by months, while age of adults was estimated in years (Pascal and Castanet, 1978). Blood samples were centrifuged and stored at –20 °C, sera were diluted 2-fold starting at 1:20 and tested for anti-*T. gondii* IgG antibodies using the modified agglutination test (Dubey and Desmonts, 1987).

Prevalence

We took 404 blood samples from 276 cats, with 74 cats captured several times (up to 4 captures per individual) and randomly selected 1 sample for each of the 276 individual cats. We then estimated seroprevalence as the proportion of cats having an antibody titre $\geq 1:40$ (Afonso *et al.* 2006).

Variables associated with antibody prevalence

We used logistic regression to relate the logit of the probability of being seropositive to predictor variables of site, year, cat sex and cat age. Comparisons were performed using the Akaike Information Criterion (AIC) since the model with the lowest AIC represents the best compromise between residual deviance and number of parameters (Burnham and Anderson, 1992). After taking into account the effect of age as a continuous variable, we then tested the effect of each variable (site, year and sex) with two-way interactions. We first included all variables and interactions that tended to influence antibody prevalence (using a Likelihood Ratio Test (LRT), $P < 0.2$) and then simplified the model using a backward approach. We retained the model with the lowest AIC and when AIC values of two models differed by less than 2, we selected the most parsimonious model. Coefficients in the final model were estimated by calculating adjusted odds-ratios and 95% confidence intervals to measure the strength of association between each variable and serological status. Overall fit of the final logistic equation was assessed using the Hosmer-Le Cessie test (Hosmer *et al.* 1997). All statistical procedures were performed using the R 2.0.1 software.

Estimation of the probability of infection

Assuming that incidence did not vary with time, we used age-specific prevalences to estimate the probability of a cat consuming an infected prey during 1

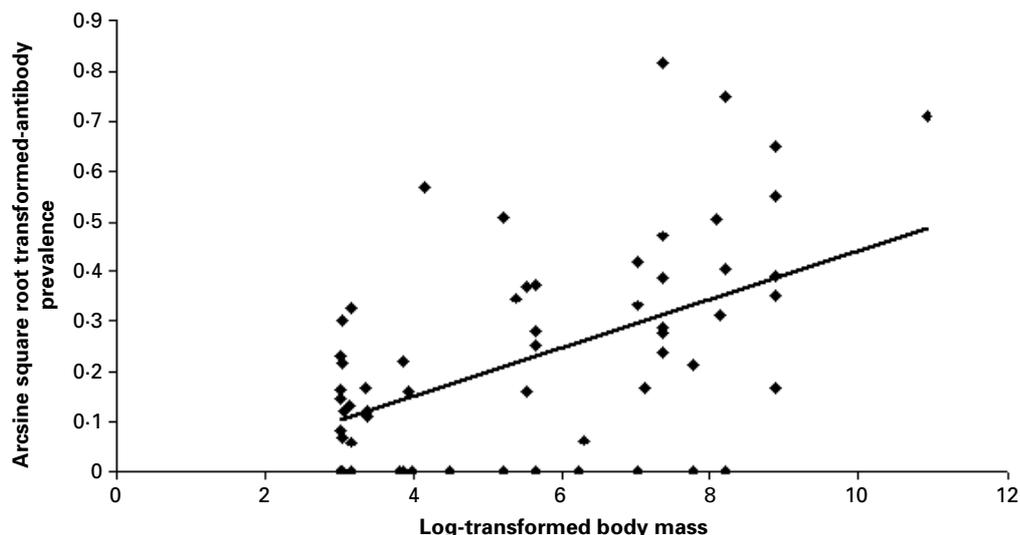


Fig. 1. Linear relationship between antibody prevalence for *Toxoplasma gondii* (arcsine square root-transformed) and body mass (log-transformed) in rodents and lagomorphs (data from Table 1). Each point represents the mean of at least 30 individuals captured in non-anthropized environments.

month (p). We considered that at age A (in months), the probability of being seronegative was the cross-product of the probabilities of encountering no infected prey ($1-p$) for A months. The probability of having antibodies at age A was thus $P(A) = 1 - (1-p)^A$. Using this relationship, we estimated p using maximum likelihood. For each age class, the age A was the median age of captured cats. Because prevalence differed between sites (see Results section), we performed separate estimates for RAT and other sites.

RESULTS

Body mass and seroprevalence of *T. gondii* in rodents and lagomorphs

A positive linear relationship was detected between body mass and *T. gondii* seroprevalence (Table 1, Fig. 1) with the largest species having the highest prevalences ($R^2=0.25$, $P<0.001$). After taking into account the phylogenetic relationships among species, prevalence was still positively related to body mass ($R^2=0.18$, $P=0.010$).

Prevalence

Of the 276 trapped cats, 103 were females and 173 were males. Approximately 36% (98/276) of cats were less than 1 year of age, and the median age was 1 year. In total, 151 cats were trapped at PAF, 23 at PC, 44 at PJDA and 58 at RAT.

Of the 276 cats tested, 141 had antibody titres of at least 40. Overall prevalence was thus 51.09% (95% CI: 45.22–56.93). Seroprevalence was 54.30% (95% CI: 46.35–62.04) at PAF, 60.87% (95% CI:

40.79–77.84) at PC, 54.55% (95% CI: 40.07–68.29) at PJDA, and 36.21% (95% CI: 25.05–49.07) at RAT.

Cats at the sites with the same diet (essentially rabbits at PAF, PC and PJDA) had similar *T. gondii* prevalences (Chi-2 test, $P=0.838$), while RAT cats had a significantly lower prevalence. We thus grouped sites according to cat diet and analysed RAT separately from OTHER sites (PAF, PC and PJDA combined).

Variables associated with antibody prevalence

T. gondii seropositivity was related linearly to age (LRT, $P<0.001$). Cats had a 2.43 times increased risk of acquiring toxoplasmosis for each year of life (95% CI: 1.77–3.33). In accordance with the hypothesis that vertical transmission is rare, none of the 11 individuals aged less than 3 months was positive (Table 2), while all cats of at least 4 years of age carried antibodies (Fig. 2).

After taking into account the effect of age, cats from RAT were less often seropositive than at OTHER sites (Table 3, LRT, $P=0.002$; odds-ratio of OTHER sites compared to RAT: 11.11, 95% CI: 2.13–50). Males were more often infected than females (LRT, $P=0.031$), and this difference was more pronounced in RAT, where males had a 5.00 times greater chance of having antibodies (95% CI: 0.88–28.3) than females. The interaction between site and sex was included in the model with the lowest AIC (332.76 versus 337.23 without the interaction), although the LRT was only close to significance (LRT, $P=0.051$). The variable year was not retained in the final model (LRT, $P=0.284$). The Hosmer-LeCessie goodness-of-fit

Table 1. Mean prevalence of *Toxoplasma gondii* antibodies and body mass of various rodents and lagomorphs

(Threshold of the serological tests is indicated in parentheses when specified by the authors.)

Order	Species	Country	Body mass ^a (g)	Seroprevalence (%)	N	Method ^b	Reference	
Rodentia	<i>Apodemus agrarius</i>	Korea	21.5	1.49	1008	ELISA	Jeon and Yong (2000)	
	<i>Apodemus flavicollis</i>	France	29.4	1.47	68	SFDT (/10)	Doby <i>et al.</i> (1974)	
	<i>Apodemus sylvaticus</i>	France	23.4	0.36	836	SFDT (/10)	Doby <i>et al.</i> (1974)	
			Scotland	23.4	10.20	98	SFDT (1/10)	Jackson <i>et al.</i> (1986)
			Sweden	23.4	0	136	SFDT (1/8)	Kapperud (1978)
	<i>Myodes [Clethrionomys glareolus]</i>	France (Ardennes)	20.8	4.69	64	MAT (1/25)	Afonso <i>et al.</i> unpublished data	
			France	20.8	0	243	SFDT (1/10)	Doby <i>et al.</i> (1974)
			Scotland	20.8	8.82	68	SFDT (1/10)	Jackson <i>et al.</i> (1986)
			Sweden	20.8	0.49	408	SFDT (1/8)	Kapperud (1978)
	<i>Cricetus cricetus</i>	France	506.67	0	42	SFDT (1/10)	Doby <i>et al.</i> (1974)	
	<i>Dasyprocta agouti</i>	Guiana (Petit Saut)	3265	23.26	43	DAT (1/40)	Carme <i>et al.</i> (2002)	
	<i>Eutamias amoenus</i>	USA (California)	48.25	0	34	HAI (1/64)	Franti <i>et al.</i> (1976)	
	<i>Eutamias quadrimaculatus</i>	USA (California)	88.45	0	44	HAI (1/64)	Franti <i>et al.</i> (1976)	
	<i>Hydrochaeris hydrochaeris</i>	Brazil	55000	42.28	149	MAT (1/25)	Canon-Franco <i>et al.</i> (2003)	
	<i>Lemmus lemmus</i>	Sweden	51.7	2.50	40	SFDT (1/8)	Kapperud (1978)	
	<i>Marmotta monax</i>	USA (Pennsylvania)	3413	9.36	545	MAT (1/25)	Stewart <i>et al.</i> (1995)	
	<i>Microtus agrestis</i>	France	46	0	44	SFDT (1/10)	Doby <i>et al.</i> (1974)	
		Sweden	46	0	46	SFDT (1/8)	Kapperud (1978)	
	<i>Microtus fortis</i>	China	63	29.03	124	MAT (1/20)	Zhang <i>et al.</i> (2004)	
	<i>Microtus nivalis</i>	France	54	0	52	SFDT (1/10)	Doby <i>et al.</i> (1974)	
	<i>Mus musculus</i>	France	20.5	0.68	295	SFDT (1/10)	Doby <i>et al.</i> (1974)	
		USA (Illinois)	20.5	2.09	1243	MAT (1/25)	Dubey <i>et al.</i> (1995)	
		Sweden	20.5	0	70	SFDT (1/8)	Kapperud (1978)	
	<i>Myocastor coypus</i>	France	7150	14.58	48	MAT (1/25)	AFSSA (2005)	
		France	7150	11.97	117	MAT (1/25)	AFSSA (2005)	
		Bulgaria	7150	2.70	37	Microagglutination	Arnaudov <i>et al.</i> (2003)	
		Italy	7150	36.58	41	DAT (1/8)	Bollo <i>et al.</i> (2003)	
		England	7150	27.27	110	SFDT (1/256)	Holmes <i>et al.</i> (1977)	
	<i>Ondatra zibethicus</i>	France	1135.8	10.71	56	MAT (1/25)	AFSSA (2005)	
		USA (California)	1135.8	0	38	HAI (1/64)	Franti <i>et al.</i> (1976)	
		USA (Missouri)	1135.8	16.67	42	SFDT (1/8)	Smith and Frenkel (1995)	
	<i>Oryzomys palustris</i>	USA (Florida)	47.67	4.84	62	IHAT (1/64)	Burridge <i>et al.</i> (1979)	
	<i>Peromyscus boylii</i>	USA (California)	28.7	2.70	37	HAI (1/64)	Franti <i>et al.</i> (1976)	
<i>Peromyscus gossypinus</i>	USA (Florida)	29	1.20	83	IHAT (1/64)	Burridge <i>et al.</i> (1979)		
<i>Peromyscus leucopus</i>	USA (Kansas)	23	1.74	115	MAT (1/25)	Brillhart <i>et al.</i> (1994)		
<i>Peromyscus maniculatus</i>	USA (Kansas)	20.5	5.36	56	MAT (1/25)	Brillhart <i>et al.</i> (1994)		
	USA (California)	20.5	2.60	269	HAI (1/64)	Franti <i>et al.</i> (1976)		
<i>Rattus norvegicus</i>	USA (Illinois)	280	6.31	95	MAT (1/25)	Dubey <i>et al.</i> (1995)		
	Egypt	280	13.33	60	HAI (1/64)	El Nahal <i>et al.</i> (1982)		
	Scotland	280	7.69	65	SFDT (1/10)	Jackson, Hutchison and Siim, 1986		
	India	280	0	186	HAI (1/64)	Mir <i>et al.</i> 1982		
<i>Rattus rattus</i>	USA (Florida)	246.5	13.16	38	IHAT (1/64)	Burridge <i>et al.</i> 1979		
	France	246.5	2.50	40	SFDT (1/10)	Doby <i>et al.</i> 1974		

Species	Country	Sample Size	Age (months)	Method	Reference
<i>Sciurus carolinensis</i>	USA (Florida)	540-33	0-38	IHAT	Burridge <i>et al.</i> 1979
	USA (Kansas)	185	0	MAT	Brillhart <i>et al.</i> 1994
	USA (Florida)	185	23-68	IHAT	Burridge <i>et al.</i> 1979
	Turkey	217	11-43	SFDT	Karatepe <i>et al.</i> 2004
<i>Stigmatopora hispidus</i>	USA (California)	2317	0	HAI	Franti <i>et al.</i> 1976
	France	2358	4-48	SFDT	Doby <i>et al.</i> 1974
	Bulgaria	3673-3	15-52	Microagglutination	Arnaudov <i>et al.</i> (2003)
	Australia	3673-3	0	IFAT	Cox <i>et al.</i> (1981)
<i>Spermophilus xanthophrynnus</i>	Germany	3673-3	46-23	SFDT	Frölich <i>et al.</i> (2003)
	Sweden	3673-3	0	ELISA	Gustafsson and Uggla (1994)
	Spain	1558-25	14-25	MAT	Almeria <i>et al.</i> (2004)
	France	1558-25	5-58	IFAT	Chalupsky <i>et al.</i> (1990)
<i>Lepus californicus</i>	Australia	1558-25	7-54	IFAT	Cox <i>et al.</i> (1981)
	Czech Republic	1558-25	53-01	SFDT	Hejlicek and Literak (1994)
	Sweden	1558-25	20-59	SFDT	Kapperud (1978)
	Chili (Juan Fernandez archipelago)	1558-25	8-00	IHAT	Stutzin <i>et al.</i> (1989)
<i>Lepus capensis</i>	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
<i>Lepus europaeus</i>	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
<i>Oryctolagus cuniculus</i>	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
<i>Sylvilagus palustris</i>	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)
	USA (Florida)	1233	2-70	IHAT	Burridge <i>et al.</i> (1979)

^a Data from Ernest (2003).
^b CIA, carbon immunoassay; DAT, direct agglutination test; ELISA, enzyme-linked immunosorbent assay; IFAT, indirect immunofluorescent antibody test; IHAT, indirect haemagglutination test; MAT, modified agglutination test; HAI, microtiter indirect agglutination test; SFDT, Sabin-Feldman dye test.

Table 2. Number of cats captured at less than 1 year of age and seropositivity for *Toxoplasma gondii* in Kerguelen sites

(Numbers in parentheses indicate sample sizes.)

	OTHER SITES	RATMANOFF
< 3 months	0 (10)	0 (1)
[3-5] months	7 (30)	0 (2)
[6-11] months	20 (44)	2 (11)

test showed a good fit of the final selected model ($P=0.935$).

Estimation of the infection probability

Using maximum likelihood, the probability of infection for 1 month (p) was estimated to be 0.023 (95% CI: 0.011-0.035) at RAT and 0.054 (0.044-0.064) in OTHER sites. These estimates provided accurate predictions of the age-prevalence relationship in both sites (Fig. 3).

DISCUSSION

We found that *T. gondii* seroprevalence in rodents and lagomorphs was correlated to body mass, with large species being more often positive than small ones. Because we compared seroprevalences estimated with various serological methods at various thresholds the variance in the relationship could be partially explained by differences in sensitivity, specificity and predictive values between tests.

Since prevalence of infection accumulates with age, large species that have longer life expectancies are likely to be more at risk than small ones. Several non-exhaustive factors could also modulate seroprevalence: susceptibility, home-range size and energy requirements. Susceptibility of hosts is variable and several species have been reported to be particularly susceptible to the parasite (*Lepus timidus*, Gustafsson *et al.* 1997; *Sigmodon hispidus*, Chinchilla *et al.* 1996). Also, small rodents could be very susceptible and might die soon after ingestion of the parasite leading to biases in the estimation of seroprevalence. Large species have high energy requirements and extended home ranges come in contact with large surface areas of contaminated resources (such as vegetation and soil). As a consequence of the direct relationship between body mass and seroprevalence in prey species, knowledge of the availability of different-sized prey should allow prediction of the infection risk of cats in specific habitats.

In Kerguelen feral cats, we observed a high seroprevalence (51.09%) compared to a dense urban cat population where predation is uncommon

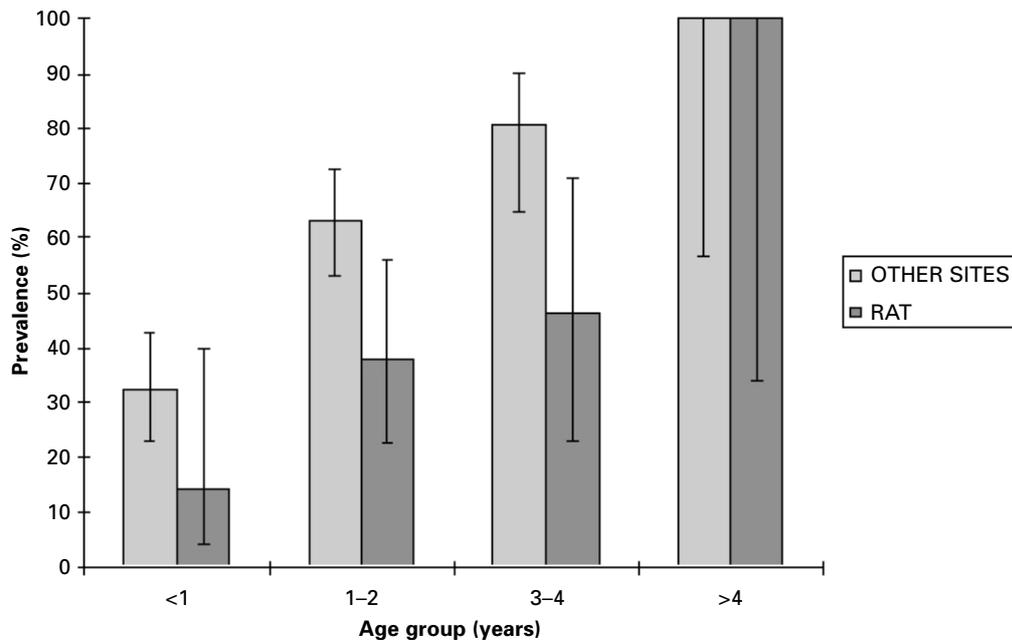


Fig. 2. Observed seroprevalence of *Toxoplasma gondii* in Kerguelen cats for 4 age classes. RAT = Ratmanoff.

Table 3. Variables associated with seropositivity for *Toxoplasma gondii* in Kerguelen cats

(RAT = Ratmanoff.)

Variable	Group	Adjusted odds-ratio	95% CI	P-value (Likelihood Ratio Test)
Age	—	2.43	[1.77; 3.33]	<0.001
Site	RAT	0.09	[0.02; 0.47]	0.002
Sex	Males	1.44	[0.79; 2.61]	0.031
Site: Sex	RAT: Males	5.00	[0.88; 28.3]	0.051

(18.6%, Afonso *et al.* 2006). In accordance with our hypothesis, the levels of infection were higher in sites where rabbits were the most commonly consumed prey item compared to sites where the diet included mice and birds as well as rabbits. Although genetic variability of the cat population is low, genetic differences can be detected among the 4 sites (Pontier *et al.* 2005), thus it is not possible to exclude the likelihood that cats from RAT are less susceptible than cats from OTHER sites. Cats from RAT also consume birds, but the low seroprevalence at RAT gave no indication that birds represent a major source of toxoplasmosis. More information on seroprevalence in different species of birds would help to define the role of birds as intermediate hosts of *T. gondii*. Studying prey species on Kerguelen, however, would raise practical difficulties. Although Kerguelen cats are exclusively predators, their risk of infection is relatively low (0.023 to 0.054 per month) and so seroprevalence in prey species is likely to be very low. The sampling effort required to

determine prey seroprevalence on Kerguelen would thus be extremely extensive. A study of other populations of predatory cats could help to confirm our hypothesis.

As expected, antibody prevalence was related to age, due to the accumulation of infection with age. Males were more often infected than females. Because adult males are larger and heavier than females, they are expected to consume more prey items (Niewold, 1986; Turner and Bateson, 2000) and to be more often exposed to infection. The difference between sexes was more pronounced in RAT, where several prey species were available. Diet may differ between males and females and it has been shown elsewhere that males tend to feed on lagomorphs, carcasses of large mammals and birds, whereas females prey mainly on small mammals (Niewold, 1986 in the Netherlands; Jones and Coman, 1981 in Australia). Liberg (1982) found that free-roaming males were more efficient at hunting voles (*Microtus* and *Arvicola*) and rabbits than females. Males may be more exposed to toxoplasmosis than females on Kerguelen, due to difference in their diets.

Toxoplasma gondii prevalence in cat populations is generally related to prey availability yet studies on cats rarely take into account the ecology of prey species. Our literature review suggested that different prey species represent unequal infection risks for predators. In addition, our study showed that different diets of Kerguelen cats led to different levels of infection. Because prey availability differs according to the environment, it is thus necessary to examine both predator habitat and diet in order to fully understand the spatial variability of *T. gondii* infection.

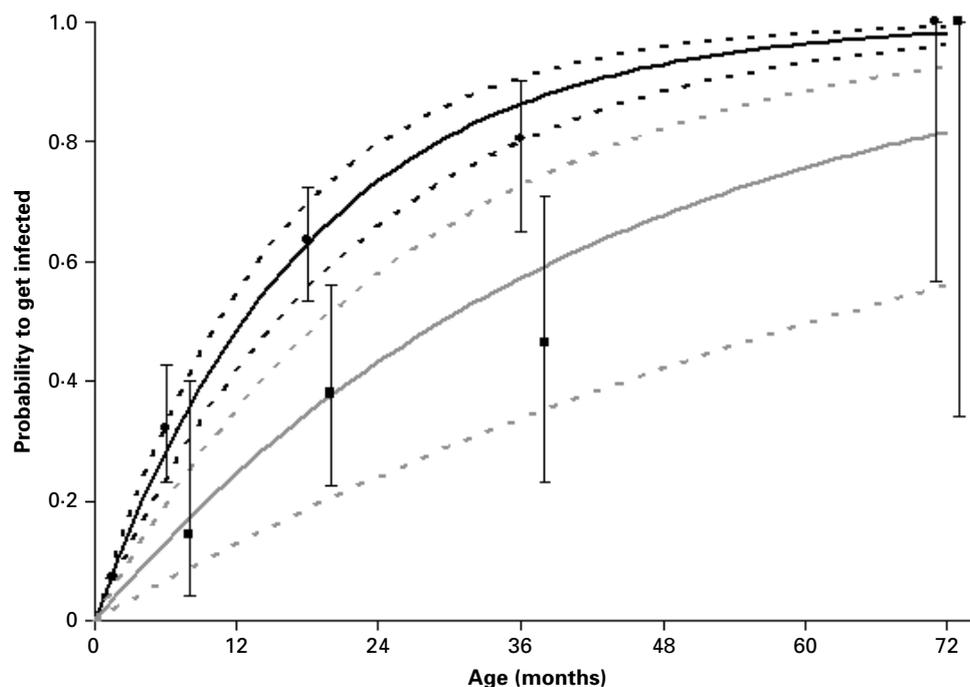


Fig. 3. Predicted relationship between age and seroprevalence at RATMANOFF (grey line) and OTHER sites (black line). Solid lines represent the mean prediction and broken lines represent the 95% confidence interval limits. Points represent the observed prevalence values for each age class, with confidence intervals drawn as whiskers: square points for RATMANOFF values and circular points for OTHER values. Prevalences are indicated for the median age observed at capture and are slightly displaced for better visualization.

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