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Ecologic Correlates of *Toxoplasma gondii* Exposure in Free-ranging Neotropical Mammals

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ABSTRACT: A serologic survey for *Toxoplasma* gondii in 18 free-ranging forest mammal species (n=456) in French Guiana was undertaken with a direct agglutination test. Serum antibody prevalence varied from 0–71%. The relationships between ecologic features of the species and seroprevalence were investigated. Terrestrial mammals were significantly more exposed to *T. gondii* than other mammals. This result is concordant with oral exposure to *T. gondii* related to ground dwelling behavior and/or carnivory.

Key words: French Guiana, neotropical mammals, serologic survey, Toxoplasma gondii.

Toxoplasma gondii is an apicomplexan parasite with worldwide distribution. The life cycle includes the felids as definitive hosts: the parasite replicates in their digestive tract and oocysts are excreted in feces. Contaminated ground and water may be a source of infection for many mammal species in which tissue cysts form in various organs. Another form of transmission for predators is by ingestion of tissue cysts in prey (Dubey, 1994). Human toxoplasmosis is of increased medical importance in French Guiana with severe cases recently described (Carme et al., 2002a). The objectives of the current study were to determine antibody prevalence in a wide number of forest mammals from French Guiana, excluding felids, and to assess relationships between seroprevalence and some ecologic features of hosts, including density, life span, vertical use of space, and feeding behavior.

Blood samples of most species except peccary (*Tayassu tajacu*) were collected in 1994–95 during a wildlife rescue operation at the Petit Saut hydroelectric dam site, French Guiana (Vié, 1999). Sera were stored at -80 C before testing. Peccary carcasses were purchased in the same re-

gion from hunters in December 2000. Blood or serosanguinous fluid was collected within 3 hr after death and was centrifuged within 6 hr. Tests were conducted within 24 hr by the direct agglutination method (Desmonts and Remington, 1980) following manufacturer's recommendations (Toxo-Screen DAR©, Biomérieux SA), on a total of 456 free-ranging mammals of 18 species. Briefly, formalin-treated T. gondii agglutinate in the presence of diluted serum (dilution 1:40) containing specific antibodies; non-specific agglutination is abolished by use of a dilution buffer containing 2-mercaptoethanol. Analysis of variance (P < 0.05 considered significant) was used to study correlations between ecologic patterns and arcsine-transformed seropositivity of species. The following parameters were considered 1) diet: strictly herbivore (i.e., folivore, frugivore, or granivore), strictly carnivore or insectivore, or omnivore; 2) vertical use of space: arboreal, terrestrial, or both; 3) densities: low $(<10 \text{ individuals/km}^2)$, intermediate, and high $(>20 \text{ individuals/km}^2)$; and 4) life span. Because life span data in the wild are not available for most of species, we used last reproduction age as an indicator, and we classified life span as short (last reproduction age<5 yr), intermediate, and long (last reproduction age>15 yr). Data and references used are given in Table I.

Each ecologic pattern was tested alone in order to assess its relationship to the serologic response and then patterns with greatest contributions (on the base of R^2 and P values) were fitted together in the final model. To avoid small sample sizes in the analysis, the coati (*Nasua nasua*) and the tayra (*Eira barbara*) were considered

Order, species (n)	Diet ^b	Vert- ical ^c	Den- sity ^d	Long- evity ^e	Seroprevalence
Marsupiala					
White eared opossum, <i>Didelphis albiventris</i> (15)	0	AT	Ι	L	20
Common opossum, D. marsupialis (34)	0	AT	Ι	L	15
Brown four-eyed opossum, Metachirus nudicaudatus (13)	0	Т	Ι	\mathbf{L}	8
Xenarthra					
Two-toed sloth, Choloepus didactylus (50)	V	Α	L	Н	0
Nine-banded armadillo, Dasypus novemcinctus (50)	Α	Т	Η	Ι	44
Collared anteater, Tamadua tetradactyla (13)	Α	AT	Ι	Н	39
Rodentia					
Paca, Agouti paca (37)	V	Т	Η	Ι	60
Brazilian porcupine, Coendou prehensilis (19)	V	Α	Η	Ι	0
Red-rumped gouti, Dasyprocta agouti (45)	V	Т	Η	Ι	18
Acouchy, Myoprocta acouchy (26)	V	Т	Ι	Ι	4
Carnivora					
Kinkajou, Potos flavus (10)	0	Α	Ι	Ι	10
Tayra, Eira barbara and coati, Nasua nasua (7)	0	AT	L	Ι	72
Artiodactyla					
Brocket deer, Mazama spp. (15)	V	Т	L	Ι	40
Collared peccary, Tayassu tajacu (22)	V	Т	Ι	Ι	68
Primate					
Red howler monkey, Alouatta seniculus (50)	V	Α	Ι	Н	4
Golden-handed tamarin, Saguinus midas (50)	Ο	Α	Ι	Ι	0

TABLE 1. Summarized ecologic patterns and seroprevalence to Toxoplasma gondii in free-ranging mammals, French Guiana.^a

^a References used: Bodmer et al., 1997; Robinson and Redford, 1986a, 1986b; de Thoisy, 2000; E. Taube, pers. comm. (Xenarthra data), A. Lavergne, pers. comm. (Marsupiala data).

^b Diet: V=vegetal, A=animal, O=omnivore.

^c Vertical (vertical use of space): A=arboreal, T=terrestrial, AT=both terrestrial and arboreal.

^d Density: L=low, I=intermediate, H=high (see text).

^e Longevity: L=low, I=intermediate, H=high (see text).

together, and the two brocket deer species (*Mazama americana* and *M. gouazoubira*) together as *Mazama* spp.

Results of serologic tests are presented in Table I. Among orders, mean prevalences were lower in primates (2%) and Marsupialia (15%). Xenarthra and Rodentia showed intermediate prevalences (24%), whereas Carnivora and Artiodactyla exhibited higher Toxoplasma exposure rates (35 and 57%, respectively). These differences are statistically significant (P < 0.001). Prevalences also varied significantly (P < 0.001)between species, ranging from 0-71%. The best analysis of variance model ($R^2=0.585$, P=0.033) fit vertical use of space (P=0.031) and longevity (P=0.096); terrestrial and/or terrestrial and arboreal species were more prone to be infected than others. Contributions of other ecologic features were not significant. However, this model remains insufficient; some strictly terrestrial species such as marsupials and the acouchy (Myoprocta acouchy) has less evidence of exposure than would be predicted by the statistical analysis.

Felids are definitive hosts of *T. gondii*. Because domestic cats are absent in neotropical French Guianan forests, wild felids may serve as definitive hosts although this has not been confirmed (Carme et al., 2002b). A similar wild cycle of *T. gondii* transmission has been reported in Alaska (USA; Zarnke et al., 2001).

Our serologic survey of a wide number of species from various orders and with distinct ecologic patterns underlines the importance of the risk of *T. gondii* infection in the vertical use of space for food foraging. Most hosts are either carnivorous or carrion-eaters, or those that accidentally consume oocysts while foraging for food on the ground. Felids could be exposed by consuming infected animals; this may be the case for humans, since many of species with high seroprevalence are major game species (de Thoisy and Vié, 1998). Although both partially terrestrial and omnivorous, all three marsupial species had little evidence of exposure. In Australian species, low seroprevalences are explained by high sensitivity and mortality of infected marsupials (Obendorf et al., 1996). A similar pattern could occur in neotropical marsupial species, and their short life span (about 2 yr) may reduce the opportunity for exposure. In our model, life-span does not significantly contribute to variation in seroprevalence, but the calculated P value is very close to the significant threshold. Unfortunately data for life-span was speculative for some species and may have biased that analysis. Within species, as observed in humans (Carme and Tirard-Fleury, 1996), prevalence may increase with age. Unfortunately, our sample did not allow analysis with consideration of age classes because most animals tested were adult.

The low prevalence of antibodies in other terrestrial species such as the agouti (Dasyprocta agouti) and the acouchy is discordant with the model result. These two rodents are strictly granivorous and highly selective foragers, therefore they probably ingest much less soil than other species such as peccary and armadillo (Dasypus novemcinctus). More detailed analysis of the influence of behavior and habitat use may be required. For instance, within terrestrial species, microhabitat use may vary: the acouchy is more frequently observed in dry areas at higher elevations and the paca (Agouti paca) is often located in lower elevation wet grounds (de Thoisy, unpubl. data) where oocysts may be more concentrated due to water flows. Finally, a specific sensitivity to T. gondii infection may explain part of the variation. Phylogenetically and ecologically closely related

species may exhibit different parasite infection levels (de Thoisy et al., 2000, 2001).

The natural history of most viral and parasitic zoonoses in South America are poorly investigated. Difficulties in obtaining samples and insufficient knowledge of the biology, ecology, and ethology of potential reservoirs limit these investigations. Nonetheless, they will be a major part of the understanding emerging diseases (Nielsen, 2001).

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