

MICROPARASITE ASSEMBLAGES OF CONSPECIFIC SHREW POPULATIONS IN SOUTHERN CALIFORNIA

Juha Laakkonen*, Robert N. Fisher†, and Ted J. Case

Section of Ecology, Behavior and Evolution, Division of Biology, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0116. e-mail: juha.laakkonen@metla.fi

ABSTRACT: The microparasite component communities of 2 species of shrews, *Notiosorex crawfordi* and *Sorex ornatus*, were investigated for the first time in 2 isolated and 3 continuous landscapes in southern California. With microscopical examination, a total of 6 parasite species was found in *N. crawfordi* and 8 species in *S. ornatus*. The highest number (5) of parasite species was detected in the lungs. The corrected estimate of parasite species richness did not significantly correlate with the host abundance in either shrew species. Altitude, and also latitude in *N. crawfordi*, appeared to be significantly positively associated with the parasite species richness, but this could be due to a false association because of the rare occurrence of some of the parasites or the small altitude range (or both). No other landscape variable analyzed (location, size of the study site, disturbance) was significantly associated with the parasite species richness of the shrews. The parasite assemblages of the 2 shrew species were similar despite the fact that *N. crawfordi* has a lower metabolic rate than *S. ornatus*.

The fragmentation of native habitats around the world underlines the importance of ecological studies aimed at explaining spatial distribution of life-forms. Parasite studies in fragmented habitats are particularly important because, compared with free-living animals, parasite populations are remarkably spatial in their distribution (Kuris et al., 1980), and parasites may threaten the biodiversity in shrinking ecosystems (Holmes, 1996). The distribution and abundance of parasites is affected not only by their own biological requirements but also by the abundance (which is related to body size) and geographic distribution of their host and vector species (Simberloff and Moore, 1997), as well as by increasing habitat disturbance and contact with humans (Nasher, 1988; Ashford et al., 1990; Ol-lomo et al., 1997; Daszak et al., 2000; Remis, 2000). Several studies on intestinal worms, ectoparasites, and various microparasites have suggested that the parasite richness correlates with landscape or habitat characteristics (Kirner et al., 1958; Roberts et al., 1992; Mills et al., 1997; Poulin, 1997; Apanius et al., 2000; Behnke et al., 2001; Soliman et al., 2001). Although several studies have documented the parasite assemblages of island populations of animals (Dobson and Pacala, 1992; Hanley et al., 1998; Apanius et al., 2000; Fromont et al., 2001), the effects of habitat fragmentation on these have been little studied in any parasite group (Kozakiewicz, 1991; Stuart et al., 1993; Lutz and Kierdorf, 1997).

In the present study, we investigated the microparasite component communities of 2 species of shrews, *Notiosorex crawfordi* and *Sorex ornatus*, in fragmented and continuous landscapes in southern California. Despite their many physiological adaptations against desiccation (Lindstedt, 1980; Laakkonen, 2002), low abundance characterizes southern California shrew populations in all seasons and habitats (Laakkonen et al., 2001a). Soricinae shrews are particularly interesting for parasite richness studies because of their short longevity and high basal metabolism rate, which have been shown to correlate with parasite species richness (Morand and Harvey, 2000). Because parasite prevalence is often lowest at high altitudes and climatic

extremes (low temperature, low moisture; Mills et al., 1997), prevalence of most shrew parasites was predicted to be low in the arid habitats investigated in the present study.

Using microscopic endoparasite data from 5 sites, we analyzed the effects of host characteristics (species, sex, age, and host abundance) and landscape variables (location, disturbance, and the size of the habitat fragment) on the distribution and prevalence of parasites found in the major internal organs, blood, and feces of the 2 shrew species. Because of the differences in the life cycles and the mode of transmission of parasites, their distribution and abundance is predicted to vary depending on the host abundance and the location, size, altitude, and disturbance of the study sites (Kozakiewicz, 1991; Simberloff and Moore, 1997).

MATERIALS AND METHODS

The shrews were caught by pitfall trapping (for details of the trapping methods, see Laakkonen et al., 2001a) at 5 study sites (Table I) in San Diego and Riverside counties (California) from 1998 to 2000. For the density estimates used in the trapping had started already in 1996, see below. The boundaries of the mainly coastal study sites (Pt. Loma and Torrey Pines), representing isolated habitat fragments, are delineated by urban development. The 3 inland sites are characterized by more continuous and relatively undisturbed habitat. The climate of the region is characterized by long, dry summers and limited winter rainfall (an average of 250 mm/yr along the coast; National Weather Service).

The area of undeveloped landscape around the site (Table I) was determined by drawing a polygon around the trap arrays of a site, using the program Topo USA (DeLorme, Yarmouth, Maine), that extends to any man-made borders or barriers fragmenting the habitat landscape. The perimeter of this polygon was divided into 500-m segments, and each of these was then scored as intact (score 0), disturbed (score 1), or urban (score 3) habitat. These scores were then averaged to determine a weighted edge index for each site (for details, see Laakkonen et al., 2001a).

Only shrews caught between January and May were included in the present study because the majority of shrews were caught at this time of year, when all age groups are present in the population (Laakkonen et al., 2001a). The trap-success rate shows the number of individuals caught per 100 trap-nights (a trap-night equals 1 pitfall left open for 24 hr). It is used as a surrogate for the abundance of shrews. The shrew abundance estimates were based on 5-yr averages (1996–2000) to reduce the effect of trapping error in low-density populations (Laakkonen et al., 2001a). For the abundance estimates, shrews were trapped throughout the year every 6 wk.

The shrews examined for this study were found dead in traps. On necropsy, the species and sex of the animal were recorded, and shrews were classified as mature and immature according to the tooth wear and condition of the pelage (Crowcroft, 1957). Of a total of 155 individuals

Received 22 January 2003; revised 4 June 2003; accepted 4 June 2003.

* Present address: Finnish Forest Research Institute, P.O. Box 18, FIN-01301 Vantaa, Finland.

† U.S. Geological Survey, 5745 Kearny Villa Drive, Suite M, San Diego, California 92123.

TABLE I. The location and geographic variables of the study sites. The edge index was calculated by estimating the size of intact habitat in each site (see text for details). The trap–success rate shows the number of individuals caught per 100 trap–nights (a trap–night equals 1 pitfall left open for 24 hr) during 1996–2000 (see text).

Site	Coordinates	Area of the landscape (km ²)	Mean altitude (m)	Edge index	Trap–success rate	
					<i>Notiosorex crawfordi</i>	<i>Sorex ornatus</i>
Wild Animal Park, inland; coastal sage scrub, grassland	117.01, 33.09	397	200	0.75	1.00	0.43
Camp Pendleton, coastal; chamise chaparral, sage scrub	117.50, 33.34	>100*	320	0.5*	0.57	0.28
U. C. Elliott Reserve, inland; chamise chaparral, sage scrub	117.11, 32.89	120	190	0.92	0.20	0.06
Pt. Loma Reserve, coastal; maritime succulent, sage scrub	117.23, 32.67	5.5	55	0.38	0.86	0.00
Torrey Pines State Park, coastal; coastal sage scrub	117.24, 32.92	1.5	59	0.38	0.11	0.86

* Estimated values. Sample locations were spread throughout the habitat on site that includes a matrix of development impacts.

of *N. crawfordi* captured, 88 were males (25 mature, 63 immature) and 67 were females (25 mature, 42 immature). The 117 individuals of *S. ornatus* caught consisted of 85 males (44 mature, 41 immature) and 32 females (15 mature, 17 immature). Ectoparasites were preserved in 70% ethanol for later identification. A drop of blood was obtained from the heart for preparation of a thin blood smear, which was air-dried, fixed in methanol, and stained with Giemsa stain. Each smear was examined for 10 min at $\times 1,000$. Pieces of lung, heart, liver, spleen, and kidney were fixed in 10% buffered formalin to produce standard histological sections, which were stained with hematoxylin–eosin, Giemsa stain, and Grocott's modification of Gomori methenamine silver. The slides were examined by a light microscope at $\times 400$. Some of these slides had been used in previous studies on lung parasite (Laakkonen et al., 2001b, 2001c). Fecal samples (0.01 g) from the rectums were stored in 2.5% aqueous potassium dichromate (K₂Cr₂O₇) for analysis of *Eimeria* spp. parasites. After allowing the oocysts to sporulate at room temperature, the suspension was centrifuged for 3 min at 250 g and resuspended in a saturated magnesium sulfate (MgSO₄) flotation solution, and the sample was examined for oocysts by using a McMaster counting chamber. Because of the small amount of feces available from each host, no other technique was used to look for other intestinal protozoan parasites (e.g., *Cryptosporidium*). Because of the frequent fast deterioration of gastrointestinal worms after the death of the host shrew, intestinal worms were not examined. For the purpose of the present study, morphologically identical parasites were considered as 1 species. Because species within some parasite groups, e.g., *Bartonella* sp., are morphologically indistinguishable from each other, the actual number of parasite species could be higher.

We used logistic regression to analyze the effect of site, host species, sex, or age of the host species on the probability for the host being infected with a parasite species. Because parasite species richness has been shown to correlate with the number of individuals examined in many parasite groups (Poulin, 1995; Walther et al., 1995; Feliu et al., 1997) and because some of our sample sizes were small, we controlled this variable by using the residuals of a regression of species richness on host sample size as corrected estimates of species richness. We analyzed the correlations among parasite species richness, the landscape variables (Table I), and the abundance of shrews (sex and age groups pooled) with the Spearman rank correlation test, using site as a sample unit. Statistix® (Analytical Software, Tallahassee, Florida) for Windows, a statistical software package, was used in all the analyses.

RESULTS

All animals were normal on gross pathologic examination. We did not attempt to quantify the intensity of the infections, but in all infected animals, the number of organisms was low. A total of 6 parasite species were observed in 155 individuals of *N. crawfordi* and 8 parasite species were observed in 177 individuals of *S. ornatus* (Tables II, III). Some of the parasite species found are described in detail elsewhere (Laakkonen et al., 2001b).

The highest number (5) of parasite species was detected in

the lungs (Table II). *Pneumocystis* sp. was found at all study sites and in both species. Of the other fungi, 1 adiaspore of *Chrysosporium parvum* was found in an immature male *S. ornatus*, and yeastlike cells of *Histoplasma capsulatum* var. *capsulatum* were seen in bronchial areas of the lungs of 1 immature male *S. ornatus* from Camp Pendleton. Pieces of the pulmonary nematode, *Angiostrongylus* sp. (*Stefanskostrongylus*; Drozd, 1970) (*Metastrongyloidea*; see Lankester and Anderson, 1966; Ash, 1967), were found in the bronchioles of 1 mature male *S. ornatus* from Torrey Pines and from 1 mature male *N. crawfordi* from Wild Animal Park. Meronts of *Hepatozoon* sp. were found in the lungs of *N. crawfordi* at all sites and from *S. ornatus* in 2 of the 4 sites where this host species occurs. In 2 cases, meronts were also found in the liver of an infected shrew.

The intestinal coccidia, *Eimeria palustris* (Hertel and Duszynski, 1987), were found in at least 1 of the shrew species at all sites (Table III). Another coccidium, *Sarcocystis* sp., was detected in the cardiac muscle of 1 mature male *N. crawfordi* from Wild Animal Park and from 1 mature female *S. ornatus* from Camp Pendleton (Table III). The only parasite forms found in the blood were the rod-shaped bacteria resembling *Bartonella* spp. from erythrocytes of shrews at 3 of the study sites (Table III).

Of the ectoparasites, fleas, *Malaraeus telchius*, were detected on 2 individuals of *N. crawfordi*, and *Orchopeus leucopus* was detected on 1 individual of *N. crawfordi* from Pt. Loma. *Ixodes soricis* were found on 5 individuals of *S. ornatus* from Torrey Pines. Because only a few individual ectoparasites were found, they were excluded from the following analyses.

Because of the consistently low abundance of shrews in our study sites, the sample sizes were too small for seasonal and annual comparisons, and the data were pooled for all analyses. The corrected estimate of species richness did not correlate significantly with the host abundance in *N. crawfordi* ($r_s = 0.00$) or in *S. ornatus* ($r_s = -0.40$). In *N. crawfordi*, altitude ($r_s = 1.00$) and latitude ($r_s = 1.00$) were significantly ($P < 0.05$) associated with parasite species richness. Altitude correlated significantly ($P < 0.05$) with the species richness in *S. ornatus* ($r_s = 1.00$). None of the other landscape variables was significantly associated with the parasite species richness (not shown). The 2 most common parasites (*Pneumocystis* sp. and *E. palustris*) were found in all sites, including the small, isolated sites (Pt. Loma and Torrey Pines).

Logistic regression showed that host species ($P = 0.003$) and site ($P = 0.009$) were the variables that best explained the prob-

TABLE II. Microparasites in the lungs of *Notiosorex crawfordi* and *Sorex ornatus* at 5 study sites in southern California.

Host species*	Lung				
	<i>Pneumocystis</i> sp.	<i>Chrysosporium parvum</i>	<i>Histoplasma capsulatum</i>	<i>Angiostrongylus</i> sp.	<i>Hepatozoon</i> sp.
Camp Pendleton					
<i>N. crawfordi</i> (N = 30)	6 (20)	0 (—)	0 (—)	0 (—)	1† (3)
<i>S. ornatus</i> (N = 32)	1 (3)	1 (3)	1 (3)	0 (—)	1 (3)
U. C. Elliott Reserve					
<i>N. crawfordi</i> (N = 23)	2 (9)	0 (—)	0 (—)	0 (—)	1 (4)
<i>S. ornatus</i> (N = 8)	4 (50)	0 (—)	0 (—)	0 (—)	0 (—)
Pt. Loma Reserve					
<i>N. crawfordi</i> (N = 54)	12 (22)	0 (—)	0 (—)	0 (—)	1 (2)
Torrey Pines State Park‡					
<i>S. ornatus</i> (N = 63)	5 (8)	0 (—)	0 (—)	1 (1.5)	0 (—)
Wild Animal Park					
<i>N. crawfordi</i> (N = 48)	19 (40)	0 (—)	0 (—)	1 (2)	1 (2)
<i>S. ornatus</i> (N = 14)	1 (7)	0 (—)	0 (—)	0 (—)	1† (7)

* N = number of shrews examined. The numbers indicate the number of positive individuals found (and their percentages).
 † Microparasites found in liver.
 ‡ The few *N. crawfordi* captured at Torrey Pines were alive and were not examined for parasites.

ability of being infected with *Pneumocystis* sp. Infection was more prevalent in *N. crawfordi* than in *S. ornatus*, and the highest prevalence were found at sites with high abundance of *N. crawfordi*. The effect of site was significant ($P = 0.039$) in explaining the occurrence of *E. palustris*. Site, species, sex, or age of the host did not significantly explain the occurrence of any of the other parasites detected ($P > 0.21$ for all variables).

DISCUSSION

The disturbance or size of the habitat was not significantly associated with the occurrence of parasites in southern California shrews. Because most of the parasites examined in the pre-

sent study are not directly transmitted and they showed no dependence on host abundance (see below), the edge effect could not disrupt the transmission of parasites even in isolated, disturbed fragments. Previous island studies indicate that there is no simple relationship between area and numbers of parasite species (Dobson and Pacala, 1992; Apanius et al., 2000). Insular host populations generally have low parasite species richness due to losses during the colonization process rather than to any consequence of the island habitat (Fromont et al., 2001). Because the relictual shrew populations in Pt. Loma and Torrey Pines were isolated owing to recent habitat fragmentation, it can be expected that relatively few parasite species have been

TABLE III. Microparasites in the intestines, blood, and heart of *Notiosorex crawfordi* and *Sorex ornatus* at 5 study sites in southern California.

Host species*	<i>Eimeria palustris</i> (intestine)	<i>Sarcocystis</i> sp. (heart)	<i>Bartonella</i> sp. (blood)
	Camp Pendleton		
<i>N. crawfordi</i> (N = 30)	2 (6.7)	0 (—)	1 (3)
<i>S. ornatus</i> (N = 32)	1 (3)	1 (3)	1 (3)
U. C. Elliott Reserve			
<i>N. crawfordi</i> (N = 23)	0 (—)	0 (—)	0 (—)
<i>S. ornatus</i> (N = 8)	1 (12)	0 (—)	0 (—)
Pt. Loma Reserve			
<i>N. crawfordi</i> (N = 54)	5 (9)	0 (—)	1 (2)
Torrey Pines State Park†			
<i>S. ornatus</i> (N = 63)	1 (1.6)	0 (—)	0 (—)
Wild Animal Park			
<i>N. crawfordi</i> (N = 48)	6 (13)	1 (2)	1 (2)
<i>S. ornatus</i> (N = 14)	6 (43)	0 (—)	1 (7)

* N = number of shrews examined. The numbers indicate the number of positive individuals found (and their percentage).
 † The few *N. crawfordi* captured at Torrey Pines were alive and were not examined for parasites.

lost. The apparent correlation between parasite richness and altitude (and in *N. crawfordi* also the latitude) may reflect the habitat requirements of some of the parasites (fungi) or may be a false association due to the rare occurrence of many of the parasites detected or the small altitude range (or both). Larger data sets are needed to disentangle the effect of these factors.

Because of the small number of suitable sites available for this study, we could not use multivariate methods (Poulin and Morand, 1999) that allow for controlling the effect of geographical distance on the composition of parasite communities. However, because the landscape and climatic characteristics of our study sites vary most dramatically from the coast toward the inland, the effect of distance on the parasite assemblages of shrews is likely to be not only a matter of distance but also the direction of that distance. Of other factors possibly affecting the observed parasite assemblage of shrews, year and season often play a significant role in the occurrence of parasites (Bajer et al., 2001). Despite intensive trapping (Laakkonen et al., 2001a), the number of shrews was too low for annual and seasonal comparisons.

In contrast to many previous studies (Watve and Sukumar, 1995; Morand and Poulin, 1998; Morand and Harvey, 2000), parasite richness was not associated with host abundance in either shrew species. Because a perfect zero sample correlation is unusual, even in situations where there is no relation, the lack of correlation may be attributed to the method used and is not an indicator of correlation. The association between host abundance and parasite richness may also be obscured by the broad range of microparasites (with different modes of transmission) included in the present study. When analyzed separately, the prevalence of at least 1 of the fungi (*Pneumocystis* sp.) was associated positively with host abundance (Laakkonen et al., 2001c). In contrast, many fungi are facultative parasites with environmental forms capable of widespread transmission in the absence of direct contact with the host.

Comparative analyses between isolated populations of directly transmitted parasites with broad host specificity (Arneberg et al., 1998; Moro et al., 1999; Apanius et al., 2000; Fromont et al., 2001) are likely to produce more significant differences between sites, depending on the host densities and site characteristics, because many such parasites (especially viruses) may not survive in low-density populations.

At Pt. Loma, where only *N. crawfordi* occurs, the prevalence of its most common parasites was similar to those found in sites where both shrew species are present. The 2 parasite species (*Angiostrongylus* sp., *Sarcocystis* sp.) missing from Pt. Loma were also absent from some of the other sites. *Sarcocystis* spp. are rare in shrews in general (Grikiėnienė and Mažeikyte, 2000), possibly because shrews are not the preferred prey of most predators (Korpimäki and Norrdahl, 1989).

The fungal parasite fauna of *S. ornatus* appeared to be more diverse than that of *N. crawfordi*, but the limited data available from *Sorex* species indicate that these fungi are rare and random in shrews (Dvořák et al., 1966; Doby et al., 1971; Zlatanov and Genov, 1975; Laakkonen et al., 1997). The interspecific difference in the occurrence of *Pneumocystis* sp., on the other hand, is well documented (Laakkonen, 1998; Laakkonen et al., 2001b). Although the life cycle of this fungus is not completely understood, its prevalence in wild hosts appears to be correlated

with host density (Laakkonen et al., 1999, 2001c; this study) but not with the habitat characteristics of the site (see above).

The reason for the significant effect of the site on the occurrence of *E. palustris* is not known. Of the 2 shrew species, only 8% had eimerian oocysts in their feces. This is low compared with the prevalence of *E. palustris* found in several other species of *Sorex* (Hertel and Duszynski, 1987) and may be due to the limited survival of eimeria oocysts in an arid environment.

Of the hemoparasites, only bacteria similar to *Bartonella* spp. (molecular studies are needed to confirm the identification) were found in erythrocytes, and meront forms of *Hepatozoon* sp. were detected in the lung and liver tissues. Trypanosomes, which have been reported from 1 individual of *S. ornatus* from Alameda County, California (Davis, 1952), were not found in either shrew species in the present study. Sympatric rodents had more blood parasite species than the shrews in our study sites, but of the possible vectors of blood parasites, 2 species of fleas, *Malaraeus telchius* and *Orchopeus leucopus*, were found both in shrews and in rodents (data not shown). It should be noted that the low ectoparasite numbers were probably not due to lack of ectoparasite abundance in shrews but to the fact that collections were conducted on dead hosts. Ectoparasites often leave the host shortly postmortem, once the core body temperature drops to ambient levels.

The present study constitutes the first comprehensive examination of southern California shrews for microparasites. As predicted, the prevalence of most parasites was low in both shrew species at our sites, which represent extreme habitats for Soricinae shrews. However, the diversity of the parasite assemblages was similar to those of Soricinae from more mesic environments (Laakkonen et al., 1997; Laakkonen, 2000). Interestingly, the parasite assemblages of the 2 shrew species were similar despite the fact that *N. crawfordi* has a lower metabolic rate than *S. ornatus* (Lindstedt, 1980). There is little previous information on the parasite fauna of *S. ornatus* (Henry, 1932; Holdenried et al., 1951; Davis, 1952; Hertel and Duszynski, 1987; Duszynski and Upton, 2000) or on that of *N. crawfordi* anywhere in its large distribution area (Fisher, 1941).

ACKNOWLEDGMENTS

We thank Michael W. Hastriter for identifying the flea species. This project was funded by the Academy of Finland (43542 for J.L.), National Park Service, and USFWS-NAFTA program, and it was carried out under the Californian Department of Fish and Game permits 803001-04, 803034-01, and 801048-05 and the University of California San Diego Animal Subjects Committee approved protocol.

LITERATURE CITED

- APANIUS, V., N. YORINKS, E. BERMINGHAM, AND R. E. RICKLEFS. 2000. Island and taxon effects in parasitism and resistance of lesser Antillean birds. *Ecology* **81**: 1959–1969.
- ARNEBERG, P., A. SKORPING, B. GRENFELL, AND A. F. READ. 1998. Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society Biological Sciences, Series B* **265**: 1283–1289.
- ASH, L. 1967. *Angiostrongylus michiganensis* sp. n. (Nematoda: Metastrongyloidea), a lungworm occurring in the shrew, *S. cinereus cinereus*, in Michigan. *Journal of Parasitology* **53**: 625–629.
- ASHFORD, R., G. REID, AND T. BUTYNSKI. 1990. The intestinal faunas of man and mountain gorillas in a shared habitat. *Annals of Tropical Medicine and Parasitology* **84**: 337–340.
- BAJER, A., A. PAWELCZYK, J. M. BEHNKE, F. S. GILBERT, AND E. SINISKI. 2001. Factors affecting the component community structure of hae-

- moparasites in bank voles (*Clethrionomys glareolus*) from the Mazury Lake District region of Poland. *Parasitology* **123**: 43–54.
- BEHNKE, J. M., C. J. BARNARD, A. BAJER, D. BRAY, J. DINMORE, K. FRAKE, J. OSMOND, T. RACE, AND E. SINSKI. 2001. Variation in the helminth community structure in bank voles (*Clethrionomys glareolus*) from three comparable localities in the Mazury Lake District region of Poland. *Parasitology* **123**: 401–414.
- CROWCROFT, P. 1957. The life of the shrew. Max Reinhardt, London, U.K., 199 p.
- DASZAK, P., A. CUNNINGHAM, AND A. HYATT. 2000. Emerging infectious diseases of wildlife—Threats to biodiversity and human health. *Science* **287**: 443–449.
- DAVIS, B. S. 1952. Studies on the trypanosomes of some California mammals. University of California Publications in Zoology **57**: 145–250.
- DOBSON, A. P., AND S. W. PACALA. 1992. The parasites of *Anolis* lizards the northern Lesser Antilles. II. The structure of the parasite community. *Oecologia* **92**: 118–125.
- DOBY, J. M., M. T. BOISSEAU-LEBREUIL, AND B. RAULT. 1971. L'adspiromycose par *Emmonsia crescens* chez les petits mammifères sauvages en France. *Mycopathologia et Mycologia Applicata* **44**: 107–115.
- DROZDZ, J. 1970. Révision de la systématique du genre *Angiostrongylus* Kamensky, 1905 (Nematoda: Metastrongyloidea). *Annales de Parasitologie et Humaine Comparee* **47**: 597–603.
- DUSZYNSKI, D., AND S. UPTON. 2000. Coccidia (Apicomplexa: Eimeriidae) of the mammalian order Insectivora. Special Publication of the Museum of Southwestern Biology **4**: 1–67.
- DVOŘÁK, J., M. OTČENÁŠEK, AND J. PROKOPIČ. 1966. Adiaspiromycosis in *Sorex*. *Mycologia* **58**: 645–647.
- FELIU, C., F. RENAUD, F. CATZEFELIS, J.-P. HUGOT, P. DURAND, AND S. A. MORAND. 1997. Comparative analysis of parasite species richness of Iberian rodents. *Parasitology* **115**: 453–466.
- FISHER, H. I. 1941. Notes on shrews of the genus *Notiosorex*. *Journal of Mammalogy* **22**: 263–269.
- FROMONT, E., L. MORVILLIERS, M. ARTOIS, AND D. PONTIER. 2001. Parasite richness and abundance in insular and mainland feral cats: Insularity or density? *Parasitology* **123**: 143–151.
- GRIKIENIENĖ, J., AND R. MAŽEIKYTE. 2000. Investigation of sarcosporidians (*Sarcocystis*) of small mammals in Kamasta landscape reserve and its surroundings. *Acta Zoologica Lituonica* **10**: 55–68.
- HANLEY, K. A., K. PETREN, AND T. J. CASE. 1998. An experimental investigation of the competitive displacement of a native gecko by an invading gecko: No role for parasites. *Oecologia* **115**: 196–205.
- HENRY, D. P. 1932. Observations on coccidia of small mammals in California, with descriptions of seven new species. University of California Publications in Zoology **37**: 279–290.
- HERTEL, L. A., AND D. W. DUSZYNSKI. 1987. Coccidian parasites (Apicomplexa: Eimeriidae) from insectivores. III. Seven new species in shrews (Soricidae: Soricinae) from Canada, Japan, and the United States. *Journal of Parasitology* **73**: 172–183.
- HOLDENRIED, R., F. C. EVANS, AND D. S. LONGANECKER. 1951. Host-parasite disease relationships in a mammalian community in the central coast range of California. *Ecological Monographs* **21**: 1–18.
- HOLMES, J. C. 1996. Parasites as threats to biodiversity in shrinking ecosystems. *Biodiversity and Conservation* **5**: 975–983.
- KIRNER, S. H., K. R. BARBEHENN, AND B. V. TRAVIS. 1958. A summer survey of the parasites of two *Microtus pennsylvanicus pennsylvanicus* (Ord) populations. *Journal of Parasitology* **44**: 103–105.
- KORPIMÄKI, E., AND K. NORRDAHL. 1989. Avian and mammalian predators of shrews in Europe: Regional differences, between-year and seasonal variation, and mortality due to predation. *Annales Zoologici Fennici* **26**: 389–400.
- KOZAKIEWICZ, M. 1991. Intestinal helminth groupings in open and patch bank vole population—The role of habitat isolation. *Bulletin of the Polish Academy of Sciences Class II* **39**: 379–385.
- KURIS, A. M., A. R. BLAUSTEIN, AND J. J. ALIÓ. 1980. Hosts as islands. *American Naturalist* **116**: 570–586.
- LAAKKONEN, J. 1998. *Pneumocystis carinii* in wildlife. *International Journal for Parasitology* **28**: 241–252.
- . 2000. Microparasites of three species of shrews from Finnish Lapland. *Annales Zoologici Fennici* **37**: 37–41.
- . 2002. Relative medullary thickness of shrews from arid environments: Intraspecific spatial analysis, and comparison to arctic shrews and tropical tenrecs. *Annales Zoologici Fennici* **39**: 249–255.
- , R. N. FISHER, AND T. J. CASE. 2001a. Effect of land cover, habitat fragmentation, and ant colonies on the distribution and abundance of shrews in southern California. *Journal of Animal Ecology* **70**: 776–788.
- , ———, AND ———. 2001b. Pneumocystiasis in small mammals from California. *Journal of Wildlife Diseases* **37**: 408–412.
- , ———, AND ———. 2001c. Spatial analysis on the occurrence of *Pneumocystis carinii* in the shrew *Notiosorex crawfordi* in fragmented landscape in southern California. *Journal of Eukaryotic Microbiology* **48**: 111S–112S.
- , V. HAUKISALMI, AND J. E. MERRITT. 1997. Lung parasites of *Sorex cinereus*, *Sorex fumeus*, and *Blarina brevicauda* from Pennsylvania. *Journal of Wildlife Diseases* **33**: 285–289.
- , H. HENTTONEN, J. NIEMIMAA, AND T. SOVERI. 1999. Seasonal dynamics of *Pneumocystis carinii* in the field vole, *Microtus agrestis*, and in the common shrew, *Sorex araneus*, in Finland. *Parasitology* **118**: 1–5.
- LANKESTER, M. W., AND R. C. ANDERSON. 1966. Small mammals as paratenic hosts of lung worms. *Canadian Journal of Zoology* **44**: 342–343.
- LINDSTEDT, S. L. 1980. Energetics and water economy of the smallest desert mammal. *Physiological Zoology* **53**: 82–97.
- LUTZ, W., AND H. KIERDORF. 1997. Parasite loads on roe deer (*Capreolus capreolus* L.) from neighbouring habitats with different intensities of recreational traffic. *Zeitschrift fuer Jagdwissenschaft* **43**: 251–258.
- MILLS, J. N., T. G. KSIAZEK, B. A. ELLIS, P. E. ROLLIN, S. T. NICHOL, T. L. YATES, W. I. GANNON, C. E. LEVY, D. M. ENGELTHALER, T. DAVIS, D. T. TANDA, W. FRAMPTON, C. R. NICHOLS, C. J. PETERS, AND J. E. CHILDS. 1997. Patterns of association with host and habitat: Antibody reactive with Sin Nombre virus in small mammals in the major biotic communities of the southwestern United States. *American Journal of Tropical Medicine and Hygiene* **56**: 273–284.
- MORAND, S., AND P. H. HARVEY. 2000. Mammalian metabolism, longevity and parasite species richness. *Proceedings of the Royal Society Biological Sciences, Series B* **267**: 1999–2003.
- , AND R. POULIN. 1998. Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**: 717–727.
- MORO, D., M. L. LLOYD, A. L. SMITH, G. R. SHELLAM, AND M. A. LAWSON. 1999. Murine viruses in an island population of introduced house mice and endemic short-tailed mice in western Australia. *Journal of Wildlife Diseases* **35**: 301–310.
- NASHER, A. 1988. Zoonotic parasite infections of the Arabian sacred baboon, *Papio hamadryas arabicus*, in Asir province, Saudi Arabia. *Annales de Parasitologie Humaine et Comparee* **63**: 448–454.
- OLLOMO, B., S. KARCH, P. BUREAU, N. ELISSA, A. GEORGES, AND P. MILLET. 1997. Lack of malaria parasite transmission between apes and humans in Gabon. *American Journal of Tropical Medicine and Hygiene* **56**: 440–445.
- POULIN, R. 1995. Phylogeny, ecology and the richness of parasite communities in vertebrates. *Ecological Monographs* **65**: 283–302.
- . 1997. Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology and Systematics* **28**: 341–358.
- , AND S. MORAND. 1999. Geographical distances and the similarity among parasite communities of conspecific host populations. *Parasitology* **119**: 369–374.
- REMIS, M. 2000. Preliminary assessment of the impacts of human activities on gorillas *Gorilla gorilla gorilla* and other wildlife at Dzanga-Sangha Reserve, Central African Republic. *Oryx* **34**: 56–65.
- ROBERTS, M., A. RODRIGO, B. MCARDLE, AND W. A. G. CHARLESTON. 1992. The effect of habitat on the helminth parasites of an island population of the Polynesian rat (*Rattus exulans*). *Journal of Zoology* **227**: 109–125.

- SIMBERLOFF, D., AND J. MOORE. 1997. Community ecology of parasites and free-living animals. In *Host-parasite evolution. General principles and avian models*, D. H. Clayton and J. Moore (eds.). Oxford University Press, Oxford, U.K., p. 174–197.
- SOLIMAN, S., A. J. MAIN, A. S. MARZOUK, AND A. A. MONTASSER. 2001. Seasonal studies on commensal rats and their ectoparasites in a rural area of Egypt: The relationship of ectoparasites to the species, locality, and relative abundance of the host. *Journal of Parasitology* **87**: 545–553.
- STUART, M. D., K. B. STRIER, AND S. M. PIERBERG. 1993. A coprological survey of parasites of wild muriquis, *Brachyteles arachnoides*, and brown howling monkeys, *Alouatta fusca*. *Journal of the Helminthological Society of Washington* **60**: 111–115.
- WALTHER, B. A., P. COTGREAVE, R. D. PRICE, R. D. GREGORY, AND D. H. CLAYTON. 1995. Sampling effort and parasite species richness. *Parasitology Today* **11**: 306–310.
- WATVE, M. G., AND R. SUKUMAR. 1995. Parasite abundance and diversity in mammals: Correlates with host ecology. *Proceedings of the National Academy of Sciences of the United States of America* **92**: 8945–8949.
- ZLATANOV, ZL., AND T. GENOV. 1975. Isolation of *Emmonsia crescens* Emmons et Jellison 1960 from small mammals in Bulgaria. *Mycopathologia* **56**: 1–3.