



# Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season

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**Abstract.** The relative effects of host species identity, locality and season on ectoparasite assemblages (relative abundances and species richness) harboured by four cricetid rodent hosts (*Akodon azarae*, *Oligoryzomys flavescens*, *Oxymycterus rufus* and *Scapteromys aquaticus*) were assessed across six closely located sites in Buenos Aires province, Argentina. Relative abundances of ectoparasites (14 species including gamasid mites, an ixodid tick, a trombiculid mite, lice and fleas), as well as total ectoparasite abundance and species richness, were determined mainly by host species and to a lesser extent by locality (despite the small spatial scale of the study), whereas seasonal effect was weak, albeit significant. The abundances of some ectoparasites were determined solely by host, whereas those of other ectoparasites (sometimes belonging to the same higher taxon) were also affected by locality and/or season. In gamasids, there was a significant effect of locality for some species, but not for others. In fleas and lice, the effect of locality was similar in different species, suggesting that this effect is related to the characteristic life history strategy.

**Key words.** Ectoparasites, host species, locality, rodents, season, species composition.

## Introduction

The relative effects of host, locality and season have been studied for communities of various parasites harboured by a number of hosts (Kisielewska, 1970; Bush & Holmes, 1986; Carney & Dick, 2000; Calvete *et al.*, 2003, 2004; Behnke *et al.*, 2008; Bordes & Morand, 2008). The species composition of parasite communities varies across hosts, localities and seasons (Arneberg *et al.*, 1997; Krasnov *et al.*, 1997; Carney & Dick, 2000; Poulin, 2003; Calvete *et al.*, 2004; Foata *et al.*, 2006) and, consequently, some species in a parasite community encountered in an individual host are determined by the host, whereas other species are determined by the specific location or time (Kennedy & Bush, 1994).

The majority of these studies considered intestinal helminths. A host presents an ultimate habitat for these parasites,

providing them with a site for living, foraging and mating. It is, therefore, not surprising that the main finding indicated that the host is a major determinant of parasite community structure (including species composition, abundance and diversity). Communities of ectoparasites have been less studied [but see Krasnov *et al.* (2006a, 2006b, 2008)]. Ectoparasites are influenced not only by host characters, but also by characters of the off-host environment, although the extent of these effects differs among ectoparasite taxa [see Marshall (1981) for review]. The off-host environment may also affect endoparasites (especially those that are not directly transmitted), at least during certain periods of their lifecycles. However, local and seasonal effects on the structure of communities of ectoparasites are expected to be stronger than for endoparasites (Krasnov *et al.*, 1997). Studies of ectoparasites have demonstrated that although the identity of the host species has the strongest effect

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on community composition, the effects of locality and season are also pronounced (Krasnov *et al.*, 2005). However, investigations into the effect of locality on the structure of ectoparasite assemblages have mainly been carried out on large spatial scales, such as across localities that differ substantially in environmental conditions (e.g. across distinct geographic regions) (Krasnov *et al.*, 2006a, 2008; Gomez-Diaz *et al.*, 2008). It is unclear whether the patterns found on a large spatial scale also occur on a small spatial scale, or whether ectoparasite communities respond to subtle variations in the environment. Another limitation of earlier studies of ectoparasite communities is that individual studies focused on one ectoparasite taxon [fleas in Krasnov *et al.* (2006a) and gamasid mites in Krasnov *et al.* (2008)]. The relative effects of host identity, locality and season on relative abundances of the different species that comprise the entire ectoparasite community on terrestrial hosts have not been studied. Ectoparasites belonging to different higher taxa differ in their life histories and in the degree of their association with hosts and thus may differ in their sensitivity to spatial or temporal variations in the environment. As a result, the relative effect of locality and/or season is expected to be weaker in parasites that are closely associated with their hosts (e.g. lice) and stronger in parasites that spend most of their lives off-host (e.g. ticks).

The relative effects of host species, locality and season on relative abundances and species richness of ectoparasites harboured by rodent hosts were studied in closely located sites within the same ecogeographic region (marshland) in northeast Buenos Aires province, Argentina. We sought to establish whether: (a) the effect of locality on the structure of the ectoparasite community is apparent on a small spatial scale, and (b) how the relative roles of host, locality and season differ among ectoparasite species belonging to different higher taxa.

## Materials and methods

### Study area

Rodents were sampled and ectoparasites were collected at six localities in Buenos Aires province, Argentina. Ramallo (33°32' S, 59°52' W) is situated along the banks of the Paraná River, whereas Hudson (34°45' S, 58°06' W), Punta Lara (34°47' S, 58°01' W), Palo Blanco (34°53' S, 57°50' W), Balneario Bagliardi (34°54' S, 57°48' W), and La Balandra (34°56' S, 57°42' W) are located along the banks of the La Plata River. Distances between these locations range from a minimum of 4 km between Palo Blanco and Balneario Bagliardi to a maximum of 42 km between Hudson and La Balandra. Hudson and Punta Lara are nature reserves. The entire study area is situated in the biogeographic province of La Pampa (Morrone, 2001), which constitutes the southern border of the South American subtropical humid forest. The climate is temperate humid–mesothermal, with moderately hot summers and dry winters that cannot sustain snow cover. The landscape in Punta Lara, La Balandra and Hudson represents a mixture of graminoid swamps and forested wetlands, whereas Palo Blanco and Balneario Bagliardi consist of frequently flooded scrublands. Ramallo is dominated by xeromorphic and riparian

marshland along the river banks. Sampling was carried out in 1990–1991 and 1994–1996 in Punta Lara, in 1995–1996 in Hudson, Palo Blanco, Balneario Bagliardi and La Balandra, and in 2000–2001 in Ramallo. Detailed descriptions of the sites may be found elsewhere (Nava *et al.*, 2003; Beldoménico *et al.*, 2005; Lareschi *et al.*, 2007).

### Rodent sampling and ectoparasite collection

Rodents were captured using wire mesh live-traps (7.5 × 15 × 8 cm) baited with bread dipped in oil and arranged in grids of either 10 × 10 m (10 m apart) or 8 × 10 m (3 m apart). In total, we carried out 58 one-night trapping sessions (ranging from two to 15 trapping sessions per locality). Trappings in the same locality were carried out at least 1 month apart. Each locality was sampled between one and 14 times during both the cold, dry season (May–September, hereafter referred to as winter; mean monthly air temperature 9.8–13.4 °C, mean monthly precipitation 38.8–58.9 mm) and the warm, wet season (October–April, hereafter referred to as summer; mean monthly air temperature 16.5–23.3 °C, mean monthly precipitation 99.2–127.0 mm). The designation of these seasons was related to: (a) the difference in air temperature and precipitation (see above); (b) the occurrence of various parasite species (Lareschi, 2006), and (c) the reproductive patterns of rodents (Bonaventura *et al.*, 1990; Cueto *et al.*, 1995a). Numbers of captured rodents ranged from 39 to 245 per locality and from one to 27 per trapping session. Rodents were killed with sulphur ether, placed in individual pre-marked plastic bags and transferred to a laboratory where each animal was identified, sexed and weighed (to estimate age). The fur of each animal was systematically examined under a stereoscopic microscope and all ectoparasites seen were removed. Ectoparasites were placed in 96% ethanol and identified using conventional techniques. Acari were identified following Cooley & Kohls (1945), Strandmann & Wharton (1958), Furman (1972), Krantz (1978) and Marques *et al.* (2004); fleas were identified according to Smit (1987), and lice according to Johnson (1972). Counts of ticks included larvae and nymphs. Counts of gamasid mites and lice included nymphs and adults. Counts of trombiculid mites included only larvae, and counts of fleas included only adults.

Seven rodent species (Rodentia: Cricetidae) were captured, including: the pampas mouse, *Akodon azarae* (Fischer); Kemp's grass mouse, *Deltamys kempii* Thomas; the Brazilian marsh rat, *Holochilus brasiliensis* (Desmarest); the yellow pygmy rice rat, *Oligoryzomys flavescens* (Fischer); the black-footed pygmy rice rat, *Oligoryzomys nigripes* (Olfers); the red hociendo, *Oxymycterus rufus* (Waterhouse), and the Argentine swamp rat, *Scapteromys aquaticus* Thomas. *Holochilus brasiliensis*, *D. kempii* and *O. nigripes* were found either in only one locality or in low numbers and were not included in further analyses. From all animals combined, 26 ectoparasite species were collected. Voucher specimens of ectoparasites and rodents were deposited in the collections of the Departments of Entomology and Vertebrate Zoology, respectively, Museum of La Plata (MLP), La Plata, Argentina. The sampling protocol

used in this study accorded with the regulations and policies of the Dirección de Administración y Difusión Conservacionista del Ministerio de Asuntos Agrarios, Buenos Aires, Argentina.

#### Data analysis

The analyses referred to adult host individuals that were infested by at least one ectoparasite, host species that were found in more than three localities and of which at least 10 individuals were captured and ectoparasite species of which at least 30 individuals were collected.

To construct composite variables describing ectoparasite species composition on each individual host, we used counts of each ectoparasite on each host individual as input data for principal component analysis (PCA). Prior to PCA, these counts were (log +1)-transformed and weighed by the overall abundance of ectoparasites on this host. New variables produced by PCA (also referred to as principal components or axes of ordination space) were linear combinations of counts of each parasite species. Principal components represented the main directions of change in ectoparasite species composition among individual hosts and were obtained independently of host species, locality and season of sampling. In addition, the total abundance and diversity of ectoparasites were calculated as the total number of ectoparasite individuals and species, respectively, collected from an individual rodent. To test for the relative effect of host species, locality and season on species composition, abundance and diversity of ectoparasite assemblages, we carried out repeatability analyses following Arneberg *et al.* (1997). In these analyses, each of the aforementioned principal components, total ectoparasite abundance or ectoparasite diversity (= species richness) were analysed using Model II main effects analyses of variance (ANOVAS) with host species, locality and season as independent factors to test whether a measure was repeatable within a host species, locality or season (i.e. varied less among individuals of the same host species captured in the same locality or during the same season than among host species, localities or seasons).

The proportion of the total variance originating from differences among host species, localities or seasons, as opposed to within species, localities and seasons, was estimated following Sokal & Rohlf (1995). Then, the ectoparasite assemblages of each individual rodent were ordinated according to host species or locality or season in the space of the two principal components that explained the most variation in ectoparasite species composition among host species, localities or seasons.

#### Results

In total, data on four common host species (457 individuals; 32 rodent individuals harboured no ectoparasites) and 14 common ectoparasite species (17 121 individuals) were included in the analyses. Ectoparasites included seven species of gamasid mites (Acari: Laelapidae and Macronyssidae), one species of tick (Acari: Ixodidae), one species of trombiculid mite (Acari: Trombiculidae), two species of fleas (Siphonaptera: Rhopalopsyllidae) and three species of lice (Anoplura: Hoplopleuridae). Basic information on the intensity of infestation and the prevalence of each of these ectoparasites in each common host in each locality is presented in Tables 1 and 2, respectively.

Principal component analysis of ectoparasite counts from each individual rodent demonstrated that the first five principal components explained 68.9% of the total variance in species composition (Table 3). The contribution of the first principal component to the segregation of ectoparasite assemblages was approximately two to three times greater than the cumulative contribution of the remaining principal components. Each of the principal components corresponded to a change in the abundance of three to four ectoparasite species across hosts, localities and seasons. Furthermore, principal components correlated with abundances of parasites belonging to both different and the same higher taxa (Table 3). For example, the first principal component represented the change in abundance of three gamasids and a louse, the second principal component referred to a gamasid and a louse, and the third principal component pertained to a gamasid, a trombiculid and a flea.

**Table 1.** Mean  $\pm$  standard error intensity of infestation (mean number of parasites per infested host) of each of four host species by each of 14 ectoparasite species across six localities.

Parasite		Host			
Higher taxon	Species	<i>Akodon azarae</i>	<i>Oligoryzomys flavescens</i>	<i>Oxymycterus rufus</i>	<i>Scapteromys aquaticus</i>
Acari	<i>Androlaelaps fahrenheiti</i> (Berlese)	0.53 $\pm$ 0.20	0.19 $\pm$ 0.15	2.14 $\pm$ 0.45	1.59 $\pm$ 0.45
	<i>Androlaelaps rotundus</i> (Fonseca)	4.51 $\pm$ 0.48	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01	0.002 $\pm$ 0.002
	<i>Gigantolaelaps wolffsohni</i> (Fonseca)	—	1.61 $\pm$ 0.61	—	0.02 $\pm$ 0.01
	<i>Laelaps manguinhos</i> Fonseca	0.01 $\pm$ 0.01	1.18 $\pm$ 0.65	0.01 $\pm$ 0.01	23.03 $\pm$ 4.78
	<i>Laelaps paulistanensis</i> Fonseca	0.02 $\pm$ 0.20	1.00 $\pm$ 0.32	0.05 $\pm$ 0.02	0.02 $\pm$ 0.02
	<i>Mysolaelaps microspinosus</i> Fonseca	—	2.51 $\pm$ 0.43	—	—
	<i>Ornithonyssus bacoti</i> (Hirst)	0.03 $\pm$ 0.03	0.01 $\pm$ 0.01	4.05 $\pm$ 1.38	1.07 $\pm$ 0.76
	<i>Eutrombicula alfreddugesi</i> (Oudemans)	0.08 $\pm$ 0.07	0.07 $\pm$ 0.06	14.84 $\pm$ 7.48	13.22 $\pm$ 9.19
	<i>Ixodes loricatus</i> Neumann	1.10 $\pm$ 0.30	0.09 $\pm$ 0.06	0.06 $\pm$ 0.03	0.14 $\pm$ 0.08
Anoplura	<i>Hoplopleura aitkeni</i> Johnson	7.68 $\pm$ 4.33	—	—	—
	<i>Hoplopleura scapteromydis</i> Ronderos	—	—	—	11.30 $\pm$ 3.54
	<i>Hoplopleura travassosi</i> Werneck	—	13.43 $\pm$ 6.21	—	—
Siphonaptera	<i>Polygenis atopus</i> (Jordan & Rothschild)	0.02 $\pm$ 0.02	0.27 $\pm$ 0.15	0.18 $\pm$ 0.09	0.64 $\pm$ 0.23
	<i>Polygenis massoi</i> Del Ponte	—	0.03 $\pm$ 0.03	0.24 $\pm$ 0.14	0.005 $\pm$ 0.005

**Table 2.** Ectoparasite prevalence on each of four host species across six localities.

Parasite		Host			
Higher taxon	Species	<i>Akodon azarae</i>	<i>Oligoryzomys flavescens</i>	<i>Oxymycterus rufus</i>	<i>Scapteromys aquaticus</i>
Acari	<i>Androlaelaps fahrenheitzi</i>	19.1 ± 7.5	8.1 ± 5.7	21.0 ± 9.8	39.3 ± 10.1
	<i>Androlaelaps rotundus</i>	66.0 ± 9.3	0.8 ± 0.8	0.8 ± 0.8	0.2 ± 0.2
	<i>Gigantolaelaps wolffsohni</i>	—	64.0 ± 6.8	—	1.7 ± 1.1
	<i>Laelaps manguinhos</i>	1.2 ± 1.2	19.2 ± 5.2	1.8 ± 1.2	76.5 ± 2.0
	<i>Laelaps paulistanensis</i>	0.7 ± 0.7	30.2 ± 5.3	1.0 ± 1.0	1.4 ± 1.4
	<i>Mysolaelaps microspinosus</i>	—	56.4 ± 10.8	—	—
	<i>Ornithonyssus bacoti</i>	1.5 ± 1.5	0.4 ± 0.4	44.8 ± 7.1	58.6 ± 26.3
	<i>Eutrombicula alfreddugesi</i>	3.0 ± 2.2	5.4 ± 4.9	20.8 ± 13.4	33.6 ± 8.8
	<i>Ixodes loricatus</i>	44.1 ± 12.9	9.1 ± 5.9	3.6 ± 2.1	8.7 ± 4.9
Anoplura	<i>Hoplopleura aitkeni</i>	34.9 ± 10.6	—	—	—
	<i>Hoplopleura scapteromydis</i>	—	—	—	42.2 ± 11.3
	<i>Hoplopleura travassosi</i>	—	84.0 ± 5.5	—	—
Siphonaptera	<i>Polygenis atopus</i>	1.5 ± 1.5	19.0 ± 10.6	5.2 ± 3.1	28.6 ± 9.8
	<i>Polygenis massoia</i>	—	2.9 ± 2.9	7.0 ± 4.2	0.5 ± 0.5

**Table 3.** Summary of principal component analysis of the ectoparasite counts on each individual host for four rodent species in six localities.

Principal component		1	2	3	4	5
Eigenvalue		3.29	2.09	1.71	1.56	1.01
Percentage of variance explained		23.47	14.91	12.23	11.14	7.19
<i>r</i>	<i>Androlaelaps fahrenheitzi</i>	0.14	0.10	0.04	-0.75*	-0.20
	<i>Androlaelaps rotundus</i>	0.06	-0.90*	-0.08	0.08	-0.05
	<i>Gigantolaelaps wolffsohni</i>	0.91*	0.01	0.05	0.02	0.12
	<i>Laelaps manguinhos</i>	-0.11	0.23	0.73*	0.09	-0.30
	<i>Laelaps paulistanensis</i>	0.80*	0.00	0.04	-0.01	-0.10
	<i>Mysolaelaps microspinosus</i>	0.93*	-0.02	0.02	0.05	0.12
	<i>Ornithonyssus bacoti</i>	-0.23	0.06	0.23	-0.74*	0.16
	<i>Eutrombicula alfreddugesi</i>	-0.36	0.29	-0.71*	0.13	0.39
	<i>Ixodes loricatus</i>	-0.07	-0.28	0.15	-0.02	-0.79*
	<i>Hoplopleura aitkeni</i>	-0.08	-0.90*	-0.10	0.08	-0.08
	<i>Hoplopleura scapteromydis</i>	-0.23	0.40	-0.22	0.19	-0.91*
	<i>Hoplopleura travassosi</i>	0.92*	-0.02	-0.01	0.06	0.11
	<i>Polygenis atopus</i>	0.10	0.03	0.80*	-0.03	0.18
	<i>Polygenis massoia</i>	-0.04	-0.02	-0.21	-0.82*	0.10

\*Indicates coefficient of correlation >0.7.

*r*, linear correlation between an ordination axis and number of individuals of each ectoparasite on a host individual.

Repeatability analyses (i.e. ANOVAs) of each principal component demonstrated a strong significant effect of host species on all five principal components (Table 4). Host identity explained 20.5–74.2% of the variation in relative abundances of ectoparasites among, as opposed to within, host species, independent of locality and season. The effect of locality on relative abundances of ectoparasites was significant for four of five principal components. The same was true for the effect of season. However, locality explained little (6.9–17.9%) of the variation in relative abundances of ectoparasites among localities, as opposed to within locality, and season explained even less (1.9–6.6%) of the variation in relative abundances of ectoparasites among, as opposed to within, seasons, independent of host species and locality (Table 4).

Total abundance and species richness of ectoparasites on an individual rodent were repeatable mainly within host species and less within locality, but not within season (Table 4). Indeed, locality explained 5.9% and 13.9% of variation in

total ectoparasite abundance and species richness, respectively, among, as opposed to within, locality, whereas the proportions of variation in total ectoparasite abundance and species richness explained by differences among, as opposed to within, host species were 17.0% and 23.0%, respectively.

The ordination of ectoparasite assemblages according to host species suggested that hosts differed in the extent of variation in the relative abundances of their ectoparasites (Fig. 1). Relative abundances of ectoparasites of *O. flavescens* and *A. azarae* varied among localities and seasons more than those of the other two hosts. Moreover, infracommunities of *O. flavescens* differed among samples, mainly as a result of differences in the abundances of three gamasids, *Gigantolaelaps wolffsohni* (Acari: Laelapidae), *Laelaps paulistanensis* (Acari: Laelapidae) and *Mysolaelaps microspinosus* (Acari: Laelapidae), and a louse, *Hoplopleura travassosi* (Anoplura: Hoplopleuridae). The infracommunities of *A. azarae* also differed, mainly as a result of differences in abundances of a

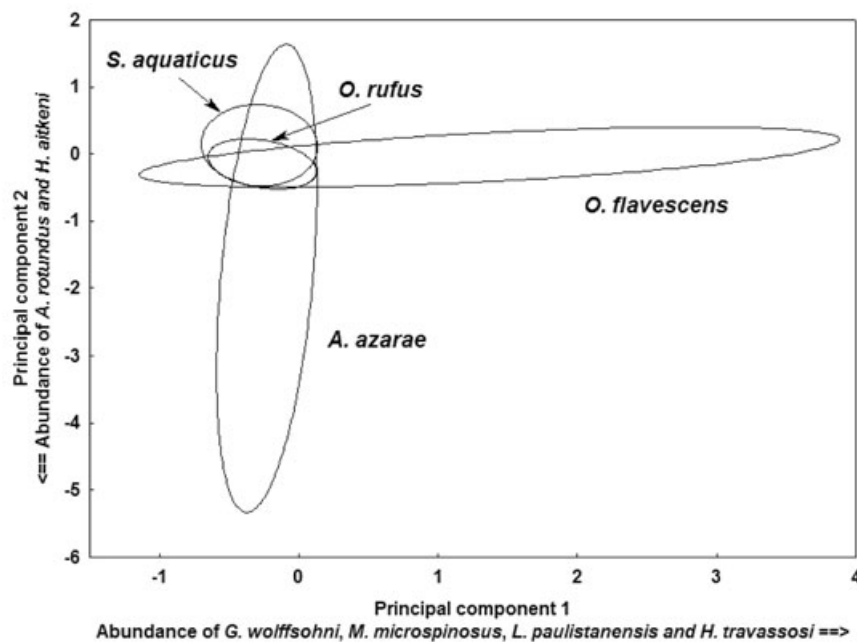
**Table 4.** Summary of repeatability analyses (ANOVAs) of the effect of host species identity, locality and season on ectoparasite species composition (via the principal component scores).

Scale	Host species effect		Locality effect		Season effect	
	F	V	F	V	F	V
PC 1	287.7‡	74.2	1.5	—	16.1‡	6.6
PC 2	219.3‡	68.6	5.6†	7.1	9.2†	3.7
PC 3	45.5†	30.8	14.1‡	17.9	0.1	—
PC 4	26.4†	20.3	7.8‡	10.2	9.9†	6.5
PC 5	26.7‡	20.5	6.3†	6.9	5.1*	1.9
Total ectoparasite abundance	21.4‡	16.9	5.6†	5.9	0.2	—
Ectoparasite species richness	30.8‡	23.0	10.7‡	13.9	0.8	—

\* $P < 0.05$ ; † $P < 0.005$ ; ‡ $P < 0.0005$ .

V, Proportion of the total variance originating from differences among hosts, localities or seasons as opposed to variance within hosts, localities or seasons, respectively.

PC, principal component.



**Fig. 1.** Ordination diagram showing 95% confidence ellipses for ectoparasite assemblages from each host individual according to host species in the space of two first principal components. *A. azarae*, *Akodon azarae*; *O. flavescens*, *Oligoryzomys flavescens*; *O. rufus*, *Oxymycterus rufus*; *S. aquaticus*, *Scapteromys aquaticus*; *G. wolffsohni*, *Gigantolaelaps wolffsohni*; *M. microspinosus*, *Mysolaelaps microspinosus*; *L. paulistanensis*, *Laelaps paulistanensis*; *H. travassosi*, *Hoplopleura travassosi*; *A. rotundus*, *Androlaelaps rotundus*; *H. aitkeni*, *Hoplopleura aitkeni*.

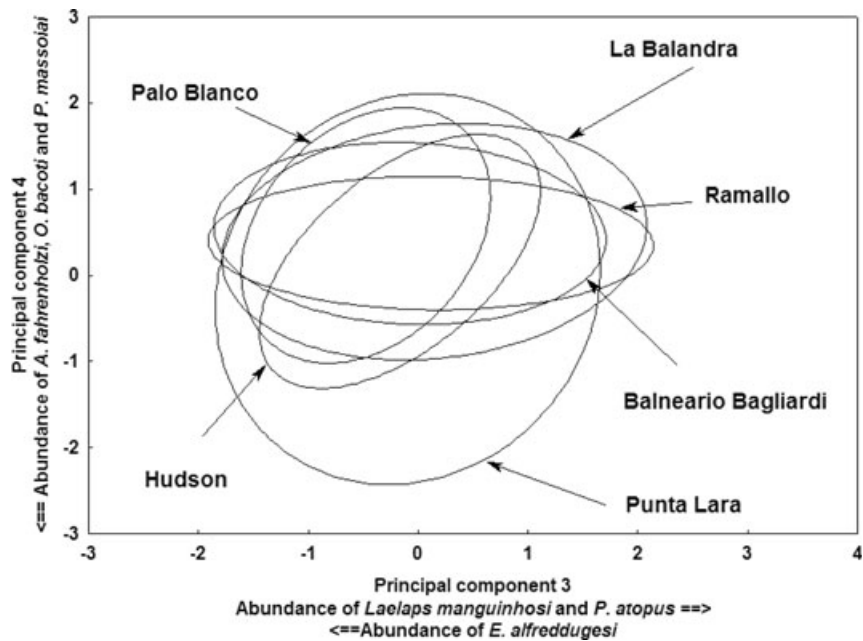
gamasid, *Androlaelaps rotundus* (Acari: Laelapidae), and a louse, *Hoplopleura aitkeni* (Anoplura: Hoplopleuridae). The ordination of ectoparasite assemblages according to locality demonstrated that relative abundances of ectoparasites varied similarly (in terms of extent and direction) among individual hosts in the majority of localities, except in Punta Lara, where ectoparasite assemblages differed mainly in terms of the relative abundance of two gamasids, *Androlaelaps fahrenheitzi* (Acari: Laelapidae) and *Ornithonyssus bacoti* (Acari: Macronyssidae), and a flea, *Polygenis massoi* (Siphonaptera: Rhopalopsyllidae) (Fig. 2). Ordination of seasonal ectoparasite assemblages suggested that they were more variable in winter than in summer, mainly as a result of changes in

abundances of five gamasids (*G. wolffsohni*, *L. paulistanensis*, *M. microspinosus*, *A. fahrenheitzi* and *O. bacoti*), a louse (*H. travassosi*) and a flea (*P. massoi*) (Fig. 3).

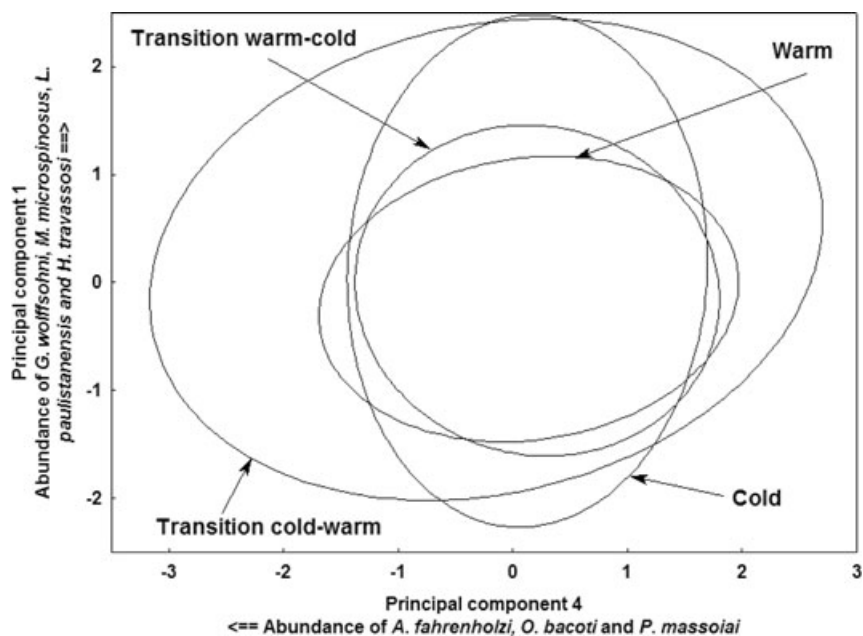
## Discussion

### Effect of host species

The strong effect of host species on the ectoparasite community structure found in this study supports numerous earlier studies of a variety of host–parasite associations (Carney & Dick, 2000; Poulin & Valtonen, 2002; Poulin, 2003; Krasnov



**Fig. 2.** Ordination diagram showing 95% confidence ellipses for ectoparasite assemblages from each host individual according to locality in the space of the third and the fourth principal components. *L. manguinhosi*, *Laelaps manguinhosi*; *P. atopus*, *Polygenis atopus*; *E. alfreddugesi*, *Eutrombicula alfreddugesi*; *A. fahrenholzi*, *Androlaelaps fahrenholzi*; *O. bacoti*, *Ornithonyssus bacoti*; *P. massoi*, *Polygenis massoi*.



**Fig. 3.** Ordination diagram showing 95% confidence ellipses for ectoparasite assemblages from each host individual according to season in the space of the first and the fourth principal components. *A. fahrenholzi*, *Androlaelaps fahrenholzi*; *O. bacoti*, *Ornithonyssus bacoti*; *P. massoi*, *Polygenis massoi*; *G. wolffsohni*, *Gigantolaelaps wolffsohni*; *M. microspinosus*, *Mysolaelaps microspinosus*; *L. paulistanensis*, *Laelaps paulistanensis*; *H. travassosi*, *Hoplopleura travassosi*.

*et al.*, 2005). The abundance of a parasite on members of the same host species was consistent and differed from that on other host species, independent of the locality and season. A significant effect of host species found for each of five principal

components indicated that the limits of abundance for each parasite were dependent on which host species the parasite exploited. If all else (e.g. microclimate) is equal, the abundance of a particular ectoparasite on a particular host is the result of

two opposing forces: successful parasite performance (feeding and reproduction) on the host, and host behavioural and/or immunological defensiveness against the parasite. The feeding of a parasite may differ among host species for a variety of reasons, such as the morphology of mouthparts that can penetrate the skin of some hosts, but not others (Marshall, 1981). The fecundity of a parasite often varies among host species, resulting in differences in the reproductive outputs of the same parasite exploiting different hosts (Krasnov *et al.*, 2004). Different hosts may have different abilities to defend themselves against the same parasite (Mooring *et al.*, 2000).

A significant effect of host species on total ectoparasite abundance and species richness suggested that, independent of ectoparasite species, some rodents had abundant and diverse ectoparasite assemblages, whereas other rodents harboured only a few ectoparasites. This supports earlier narrative descriptions of the abundance and diversity of various ectoparasites on rodents from our study area (Lareschi *et al.*, 2003, 2007). The reason for the among-host difference in the total abundance and diversity of parasites may be that some species-specific host properties constrain the number of individuals and species of ectoparasites harboured by an individual host. These constraints can be related to processes on the host body and/or to processes within a host burrow or nest that affect the pre-imaginal stages of some ectoparasites (e.g. fleas). For example, the abundance and diversity of ectoparasites can be limited by host body size (Morand & Guégan, 2000), host immune defence (Khokhlova *et al.*, 2004) and host antiparasitic behaviour (Mooring *et al.*, 2000).

An assemblage of ectoparasites of a given host is usually composed of two groups of species (Combes, 2001). Some parasite species are specific to the host, whereas other parasites are either generalists or spillovers that occasionally switch from one host species to another. However, the spatial and/or temporal stability of ectoparasite species composition may be driven not only by specialist parasites, but also by generalists because even a highly host-opportunistic parasite often varies in its abundance among host species and achieves higher abundance in hosts that are phylogenetically related to its ancestral principal host (Poulin, 2005). This suggests that the most variable portion of a host's parasite assemblage is represented by parasites switching from other hosts. One of the host-related reasons behind the high numbers and diversity of these parasites may be the breadth of a host's spatial niche. For example, hosts occurring in many different habitats are likely to have a higher probability of being attacked by various parasites than hosts that occupy a narrow habitat range. Indeed, the results of this study suggested that relative abundances of ectoparasites in assemblages harboured by *O. flavescens* and *A. azarae* were highly variable. Both these rodents have been found in a variety of habitats (Suarez & Bonaventura, 2001; Delfraro *et al.*, 2003) and seasonal habitat shifts have been reported for *A. azarae* (Suarez & Bonaventura, 2001).

However, data obtained via short-term sampling should be treated with a degree of caution because they may give only a 'snapshot' of the parasite assemblage occurring on each individual host. A wide range of other influences, including pathogens and endoparasites, may in fact determine the infracommunity of parasites on a host at any one time.

### Effect of locality

The species composition of ectoparasite assemblages varied to some degree across localities, indicating that it was influenced by some local factors. In other words, the abundances of some ectoparasites in the same locality were similar, independent of host species, and differed from those in other localities. The main reason for the effect of locality is that ectoparasites exploiting terrestrial hosts are exposed to the off-host environment, although the effect of environmental factors on some of them, such as lice, is likely to be minor. High sensitivity to environmental factors such as air temperature and relative humidity has been demonstrated in various ectoparasites [see Marshall (1981) for review]. The small spatial scale in effect in this study (i.e. the short distances between localities) suggests that some ectoparasites may respond to subtle differences in the environment. For example, in fleas, differential survivorship of the pre-imaginal stages was found at an air temperature difference as small as 3 °C (Krasnov *et al.*, 2001). In addition, biotic factors such as host density and diversity may also be important as determinants of variation in ectoparasite community structure. For example, higher host density may cause an increase in the frequency of intra- and interspecific contacts, thus promoting ectoparasite host-switching and leading to similar presences of ectoparasite species across different host individuals (Lareschi *et al.*, 2004; Krasnov *et al.*, 2006a).

Interestingly, in some higher taxa of ectoparasites, the significant effect of locality was found for some species, but not for others. Indeed, abundances of some gamasids (*G. wolffsohni*, *L. paulistanensis* and *M. microspinosus*; principal component 1) were similar across localities, whereas abundances of other gamasids (*Laelaps manguihosi*, *A. fahrenheiti* and *O. bacoti*; principal components 3 and 4) differed significantly. This difference between two groups of gamasid species may be linked to differences in their lifecycles that remain to be studied and may be related to differences in feeding mode (e.g. pre-emption, haematophagy and mixed diet) and degree of association with a host (facultative and obligatory parasitism) among gamasids (Radovsky, 1985). It is also possible that this difference (high between-locality variations in the abundance of some gamasids and low between-locality variations in the abundance of other gamasids) was a result of between-locality variations in the abundances of their preferred hosts. For example, the abundance of *L. manguihosi* is thought to be closely associated with the abundance of *S. aquaticus* (Lareschi, 1996; Lareschi *et al.*, 2003), whereas abundances of *A. fahrenheiti* and *O. bacoti* in the study area seem to be associated with the abundance of *O. rufus* (Lareschi *et al.*, 2007). Both these hosts are characterized by wide fluctuations in density across habitats (Cueto *et al.*, 1995a, 1995b; M. I. Sánchez López, 'Factores que Limitan la Abundancia de los Roedores Muridos en el Delta del Paraná', unpublished PhD thesis, National University of Buenos Aires, 1998).

Within other ectoparasite taxa, the effect of locality was similar in different species, which supports the suggestion that this effect is related to their characteristic life history strategy. For example, there was a significant effect of locality for fleas, *Polygenis atopus* and *P. massoi* (principal components 3 and 4, respectively). With few exceptions, fleas (including

*Polygenis*) alternate periods on the host with periods in its burrow or nest, whereas pre-imaginal stages are not parasitic. As a result, the effect of the off-host environment on both imaginal and pre-imaginal fleas is strong (Marshall, 1981). In the three species of lice (*H. travassosi*, *H. aitkeni* and *Hoplopleura scapteromydis*; principal components 1, 2 and 5, respectively), no or an extremely weak effect of locality on their abundances was found. This is likely to be related to the close association of lice with hosts during their entire lifecycle.

#### Seasonal effect

In general, the effect of season on relative abundances of ectoparasites was weak. This supports earlier findings that the same parasite species occur on their hosts in both winter and summer (Lareschi, 2006). In other words, seasonal assemblages of ectoparasites differed as a result of differences in their relative abundances, rather than as a result of species composition. Furthermore, relative abundances of ectoparasites in winter assemblages tended to be more variable across localities and hosts than those in summer assemblages. This variation mainly reflected higher within-winter fluctuations in the abundance of five gamasids (*A. fahrenheiti*, *G. wolffsohni*, *L. paulistanensis*, *M. microspinosus*, *O. bacoti*), a flea (*P. massoi*) and a louse (*H. travassosi*). The reasons for higher winter fluctuations in the abundance of these species have not been studied. Higher winter fluctuations in abundance may be related to low levels of new infestation coupled with unequal rates of survival of 'old' imago between hosts and localities. Another explanation may be that the probability of parasite exchange between at least some hosts is probably higher in summer than in winter because these hosts do not reproduce in winter (Bonaventura *et al.*, 1990; Cueto *et al.*, 1995a), so their summer density is likely to be higher. This may result in a less variable distribution of ectoparasites across different host individuals in summer assemblages.

In conclusion, this study demonstrates that the structure of ectoparasite assemblages is determined mainly by the identity of host species and to a lesser extent by locality (despite the small spatial scale of the study), whereas the effect of season, although significant, is much weaker. Furthermore, the abundances of some ectoparasites are determined solely by host identity, whereas other ectoparasites (sometimes belonging to the same higher taxon) are affected also by locality. Finally, the effect of locality appears to be similar in ectoparasites belonging to the same higher taxon if they have similar life history strategies.

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