

# Fleas associated with non-flying small mammal communities from northern and central Chile: with new host and locality records

E. A. BAZÁN-LEÓN<sup>1</sup>, M. LARESCHI<sup>2</sup>, J. SANCHEZ<sup>2</sup>, G. SOTO-NILO<sup>1</sup>, I. LAZZONI<sup>1</sup>, C. I. VENEGAS<sup>1</sup>, Y. POBLETE<sup>1</sup> and R. A. VÁSQUEZ<sup>1</sup>

<sup>1</sup>Departamento de Ciencias Ecológicas, IEB, Universidad de Chile, Santiago, Chile and <sup>2</sup>Centro de Estudios Parasitológicos y de Vectores, CEPAVE (CCT La Plata-CONICET-UNLP), La Plata, Argentina

**Abstract.** Fleas associated with small mammals from seven localities from northern and central Chile were assessed. We captured 352 small mammals belonging to 12 species from which we obtained 675 fleas belonging to 15 different species. The most frequently captured flea species were *Neotyphloceras crassispina crassispina* ( $n = 198$ ) and *N. chilensis* ( $n = 175$ ). High values of flea species richness and diversity were found in Fray Jorge National Park (NP), a north-central Chilean site, whereas the highest values of mean abundance (MA) and prevalence were found in three diverse sites that include Los Molles River, a high altitude site located in north-central Chile, Fray Jorge NP and Dichato, in south-central Chile. On the other hand, high values of flea richness and diversity were found on two rodent species, *Abrothrix olivacea* and *A. longipilis*, whereas the highest values of MA and prevalence were found on *Oligoryzomys longicaudatus*, *A. longipilis* and *Phyllotis xanthopygus*. A total of three new host recordings, nine new localities and nine new host species and locality recordings are reported. Also, this study represents the first known record of *Tetrapsyllus (Tetrapsyllus) comis* in Chile and the first ecological analysis of *Neotyphloceras chilensis*.

**Key words.** *Neotyphloceras*, marsupial, parasite, rodent.

## Introduction

Parasites play important roles in the regulation of host populations and communities (Poulin, 2007; Combes, 2001; Koella & Turner, 2008), because they represent an important mortality factor (Degen, 2008). Some previous studies have showed that parasites have negative effects on life history traits and reproduction of their hosts (Møller, 1997; Fitze *et al.*, 2004), with relevant ecological and evolutionary consequences (Anderson & May, 1991; Poulin, 2007).

Fleas are hematophagous parasites of several vertebrate hosts (Marshall, 1981; see Fredes, 2008, for Chilean species). Given their potential as vectors, fleas could transmit several infectious diseases to birds, rodents and other mammal species,

including humans (Krasnov, 2008; see also Macchiavello, 1948, 1954, for Chilean species). Blanchard (1852) published the first report of Siphonaptera species in Chile, but it was not until the beginning of 1900s that the first species of Chilean fleas were described (see Rothschild, 1904, 1906, 1909a, 1909b, 1910). Between 1920 and 1950, some studies carried out in Chile focused on the epidemiological effects in order to identify taxonomically the vectors of the bubonic pest and murine typhus (Macchiavello, 1948, 1954). In the past 40 years, around 30 species of fleas have been described in Chile (see Smit & Rosicky, 1972; Jameson & Fulk, 1977; Beaucournu & Gallardo, 1978, 1989, 1991; Beaucournu & Torres-Mura, 1986; Beaucournu *et al.*, 1986, 1988; Beaucournu & Kelt, 1990; Hastriter, 2001). The majority of those species were collected from rodents (Beaucournu & Gallardo, 1991,

Correspondence: Rodrigo A. Vásquez, Departamento de Ciencias Ecológicas, Instituto de Ecología y Biodiversidad, Universidad de Chile, Las Palmeras 3425, Santiago, Chile. Tel.: + 56 2 29787385; Fax: + 56 2 22727363; E-mail: rvasquez@uchile.cl

1992), in studies carried out in central and southern Chile, with nil samples from northern Chile.

Thus, considering the potential medical importance of fleas and the relevance of small mammals as the main substrate for the investigation of these insects in Chile, the current study presents new host and locality records of fleas from northern and south-central Chile encompassing around 1700 km from north to south, from the Loa River in northern Chile at 21°25'S to Dichato in south central Chile at 36°31'S. Furthermore, although the ecology of fleas in different biogeographic regions has been studied (Krasnov *et al.*, 2008, 2010), this knowledge is still scarce in Chile. The present study shows an analysis of the prevalence and abundance for flea species as well as comparisons between localities and host species. The present study constitutes the first analysis of prevalence, abundance and diversity of fleas associated with small mammals in Chile.

## Materials and methods

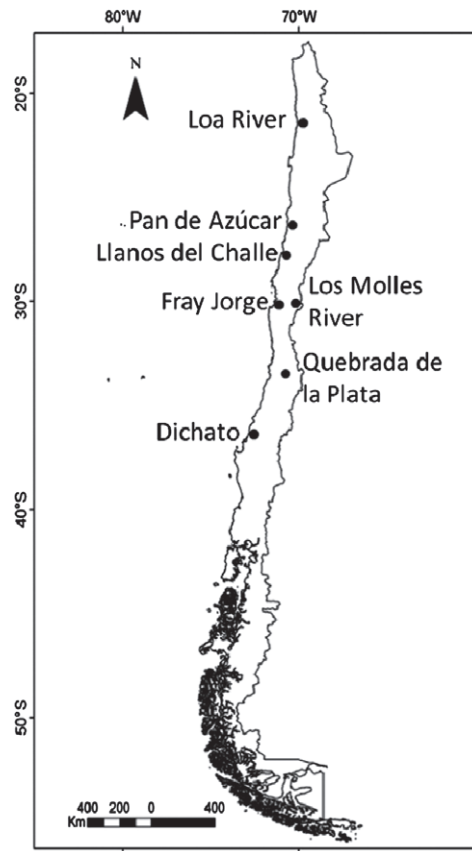
### Study areas

Seven sites were sampled in order to assess the small mammal communities, between December 2008 and March 2009 in northern and central Chile (Table 1, Fig. 1): (a) Loa River (Region II of Antofagasta), located in northern Chile comprises the desert vegetation type and it is characterized by being the only estuary in the region with the presence of some small wetlands surrounding the river's mouth and a few patches of shrubby vegetation in nearby areas (Dirección General de Aguas, 2004; Luebert & Plissock, 2006); (b) Pan de Azúcar National Park (located on the border of the Region II of Antofagasta and III of Atacama) belongs to the desert scrub vegetation type. In this area there are two different vegetative zones, one of them more extended and dominated by cactuses, and another zone located near the coast, where there is greater diversity of shrubs vegetation, owing to the presence of coastal fog (Corporación Nacional Forestal – CONAF, 2002; Luebert & Plissock, 2006); (c) Llanos del Challe National Park (Region III of Atacama), is characterized by a climate typical of coastal desert with abundant cloudiness, causing a vegetation cover mainly composed of xerophytic plants (CONAF, 1997; Luebert & Plissock, 2006); (d) Los Molles River (Region IV of Coquimbo), a high altitude site. Although this site is located within the desert scrub vegetation type, it is characterized by a rocky semiarid high altitude valley, located at 2500 m above sea level (a.s.l.) (Luebert & Plissock, 2006); (e) Fray Jorge National Park (Region IV of Coquimbo) is located within the desert scrub vegetation type, and it presents a vegetation characteristic of coastal scrub, plus a small particular area characterized by Valdivian humid relict rainforest species (CONAF, 1998; Luebert & Plissock, 2006); (f) Quebrada de la Plata (Santiago Metropolitan Region) is located within the sclerophyll scrub vegetation type of central Chile, which corresponds to the sclerophyllous scrubland tree zone (Luebert & Plissock, 2006); and (g) Dichato is located in the VIII Region of Bío-Bío, south-central Chile. Although this locality is within the sclerophyll deciduous forest vegetation type, the intense

**Table 1.** Sites along north and central Chile where field captures were carried out.

Locality	S	W	Altitude (m)
Loa River	21°25'	70°2'	28
Pan de Azúcar National Park	26°9'	70°40'	11
Llanos del Challe National Park	28°11'	71°9'	56
Fray Jorge National Park	30°39'	71°39'	187
Los Molles River	30°44'	70°25'	2518
Quebrada de La Plata	33°29'	70°53'	585
Dichato	36°31'	72°54'	71

Latitude, longitude and altitude are given (from north to south) for each site.



**Fig. 1.** Map of Chile with the localities studied. See Table 1 for exact location of each study site.

deforestation of native forest shows a landscape almost covered with pine (*Pinus* spp.) plantations (Luebert & Plissock, 2006).

### Sampling and flea identification

In each locality, seven transects were built, located at 50–100 m away between each other. Each transect had 25 trap stations at 10-m intervals. A modified mesh version of the Sherman type live trap was installed on the floor in each station. A total of 175 traps were activated per night.

**Table 2.** Geographical distribution and hosts of fleas in Chile.

Distribution	Host species	n <sub>H</sub>	Flea species	n <sub>F</sub>
Pan de Azúcar NP (Region III)	<i>P. darwini</i>	11	<i>Delostichus phyllotis</i> *	2
			<i>Hectopsylla (Hectopsylla) cypha</i> *	10
Llanos del Challe NP (Region III)	<i>T. elegans</i>	9	<i>Neotyphloceras chilensis</i>	1
			<i>P. darwini</i>	1
Los Molles River (Region IV)	<i>A. bennetti</i>	1	<i>Tetrapsyllus (Tetrapsyllus) tantillus</i> †	3
			<i>A. olivacea</i>	12
	<i>P. xathopygus</i>	7	<i>Ectinorus (Ichyonus) angularis</i> †	1
			<i>Neotyphloceras chilensis</i> *	23
	<i>P. xathopygus</i>	7	<i>Tetrapsyllus (Tetrapsyllus) tantillus</i> *	7
			<i>Hectopsylla (Hectopsylla) cypha</i> †	10
Fray Jorge NP (Region IV)	<i>T. elegans</i>	17	<i>Neotyphloceras chilensis</i>	11
			<i>Tetrapsyllus (Tetrapsyllus) tantillus</i> *	2
	<i>A. longipilis</i>	16	<i>Neotyphloceras chilensis</i>	16
			<i>Hectopsylla (Hectopsylla) cypha</i> †	20
	<i>A. olivacea</i>	11	<i>Neotyphloceras chilensis</i>	74
			<i>Neotyphloceras crassispina crassispina</i> †	63
	<i>O. degus</i>	1	<i>Plocopsylla wolffsohni</i>	1
			<i>Sphinctopsylla ares</i>	7
	<i>O. longicaudatus</i>	13	<i>Tetrapsyllus (Tetrapsyllus) tantillus</i>	10
			<i>Tetrapsyllus (Tetrapsyllus) simulans</i>	13
	<i>P. darwini</i>	7	<i>Hectopsylla (Hectopsylla) cypha</i> *	20
			<i>Neotyphloceras chilensis</i>	22
	<i>O. degus</i>	1	<i>Neotyphloceras crassispina crassispina</i> *	13
			<i>Tetrapsyllus (Tetrapsyllus) corfidii</i> †	1
	<i>O. longicaudatus</i>	13	<i>Tetrapsyllus (Tetrapsyllus) tantillus</i>	5
			<i>Delostichus smiti</i>	5
	<i>P. darwini</i>	7	<i>Neotyphloceras chilensis</i>	1
			<i>Hectopsylla (Hectopsylla) cypha</i> †	2
Quebrada de La Plata (Santiago Metropolitan Region)	<i>T. elegans</i>	31	<i>Neotyphloceras chilensis</i>	13
			<i>Neotyphloceras crassispina crassispina</i>	7
	<i>A. longipilis</i>	1	<i>Hectopsylla (Hectopsylla) cypha</i> *	36
			<i>Neotyphloceras chilensis</i>	8
	<i>O. degus</i>	8	<i>Neotyphloceras chilensis</i>	3
			<i>Polygenis (Polygenis) platensis</i> †	1
	<i>P. darwini</i>	13	<i>Tetrapsyllus (Tetrapsyllus) sp.‡</i>	2
			<i>Neotyphloceras chilensis</i>	2
	<i>P. darwini</i>	13	<i>Neotyphloceras crassispina crassispina</i>	1
			<i>Neotyphloceras crassispina crassispina</i>	1
	<i>P. darwini</i>	13	<i>Plocopsylla wolffsohni</i>	1
			<i>Sphinctopsylla ares</i> *	1

The traps were baited with a mix of oatmeal, tuna fish and banana. The captured specimens were brushed during 5 min with 70% ethanol in order to collect fleas. The collected fleas were preserved in 70% ethanol. After processing each specimen, they were released at the same location where they were previously captured. The small mammals were identified using descriptions given in Wilson and Reeder (2005), Muñoz-Pedreros and Yáñez (2000, 2009) and Iriarte (2008). In the laboratory, fleas were cleared in potassium hydroxide, and mounted in Canada balsam for taxonomic identification using descriptions published by Hopkins and Rothschild (1966), Johnson (1957) and Smit (1987). We follow the classification proposed by Whiting *et al.* (2008) for the higher taxa. Voucher specimens were deposited in the collections of the Ecología Terrestre laboratory at the Universidad de Chile, Chile, and in the Departamento de Entomología at the Museo de La Plata, Argentina.

#### Data analysis

Flea diversity and abundance were estimated using the following variables: flea specific richness ( $S$  = number of species), Shannon specific diversity index ( $H = -\sum [p_i \ln p_i]$ , where  $p_i$  is the proportion of species  $i$  in the flea assemblage), mean abundance ( $MA$  = total number of specimens of a particular parasite species in a sample of a particular host species or locality divided by the total number of hosts of that species or locality, including both infested and non-infested hosts), and prevalence ( $P$  = number of hosts infested with one or more specimens of a particular parasite species divided by the number of hosts examined for that parasite species  $\times 100$ ) (Begon *et al.*, 1988; Bush *et al.*, 1997). In addition, we used the most captured host species ( $n > 10$ ) in order to calculate the dependent variables of the flea community, considering all localities in a single analysis ( $P$  = ratio of infested specimens

Table 2. Continued

Distribution	Host species	n <sub>H</sub>	Flea species	n <sub>F</sub>
Dichato location (Region VIII)	<i>A. longipilis</i>	29	<i>Ctenoparia inopinata</i>	19
			<i>Ectinorus (Ectinorus) sp.</i> ‡	1
			<i>Neotyphloceras crassispina crassispina</i>	56
			<i>Sphinctopsylla ares</i>	18
			<i>Tetrapsyllus (Tetrapsyllus) rhombus</i>	56
	<i>A. olivacea</i>	38	<i>Ctenoparia inopinata</i>	8
			<i>Neotyphloceras crassispina crassispina</i>	35
			<i>Sphinctopsylla ares</i>	9
			<i>Tetrapsyllus (Tetrapsyllus) rhombus</i>	19
			<i>Tetrapsyllus (Tetrapsyllus) comis</i> §	1
	<i>O. bridgesi</i>	1	<i>Ctenoparia inopinata</i>	1
	<i>O. longicaudatus</i>	10	<i>Ctenoparia inopinata</i>	10
			<i>Neotyphloceras crassispina crassispina</i>	5
			<i>Sphinctopsylla ares</i>	2
			<i>Tetrapsyllus (Tetrapsyllus) rhombus</i> ¶	1
<i>Tetrapsyllus (Tetrapsyllus) rhombus</i> ¶			12	
<i>P. darwini</i>	14	<i>Ctenoparia inopinata</i> ¶	1	
		<i>Neotyphloceras crassispina crassispina</i>	1	
		<i>Sphinctopsylla ares</i>	1	
		<i>Tetrapsyllus (Tetrapsyllus) rhombus</i> ¶	1	

\*New locality.

†New host and locality.

‡Unidentified species.

§New Chilean record.

¶New host.

n<sub>H</sub>, number of individual hosts captured; n<sub>F</sub>, number of individual fleas collected. This table only includes host species and localities where fleas were found.

by species of flea per host species) (Begon *et al.*, 1988; Bush *et al.*, 1997).

## Results

Three hundred fifty-two small mammals belonging to 12 species, 5 families and 2 orders, were captured during the study period, encompassing the following (Order, family, species): Order Didelphimorphia, Family Didelphidae, *Thylamys elegans* (*n* = 57) (Waterhouse, 1839); Order Rodentia, Family Cricetidae, *Abrothrix longipilis* (*n* = 46) (Waterhouse, 1837), *Abrothrix olivacea* (*n* = 127) (Waterhouse, 1837), *Phyllotis darwini* (*n* = 55) (Waterhouse, 1837), *Phyllotis limatus* (*n* = 4) (Thomas, 1912), *Phyllotis magister* (*n* = 21) (Thomas, 1912), *Phyllotis xanthopygus* (*n* = 7) (Waterhouse, 1837), *Oligoryzomys longicaudatus* (*n* = 23) (Bennett, 1832); Family Octodontidae, *Octodon bridgesi* (*n* = 1) (Waterhouse, 1844), *Octodon degus* (*n* = 9) (Molina, 1782); Family Abrocomidae, *Abrocoma bennetti* (*n* = 1) (Waterhouse, 1837); and Family Muridae, *Mus musculus* (*n* = 1) (Linné, 1758). The most frequently captured species was *A. olivacea* (*n* = 127), and the less common were *A. bennetti*, *M. musculus* and *O. bridgesi* (*n* = 1, for each species).

A total of 675 fleas from 17 species and subspecies were collected from the small mammals (see Table 3), which belong to the following families, subfamilies, genus, (subgenus), species and subspecies: Ctenophthalmidae, Ctenophthalmiinae: *Neotyphloceras crassispina crassispina* (Rothschild),

*Neotyphloceras chilensis* (Jordan, stat. nov.); Hystrichopsyllidae, Hystrichopsyllinae: *Ctenoparia inopinata* (Rothschild); Pulicidae, Tungidae: *Hectopsylla (Hectopsylla) cypha* (Jordan); Stephanocircidae, Craneopsyllinae: *Plocopsylla wolffsohni* (Rothschild) and *Sphinctopsylla ares* (Rothschild); Rhopalopsyllidae, Rhopalopsyllinae: *Polygenis (Polygenis) platensis* (Jordan & Rothschild); Parapsyllinae: *Delostichus phyllotis* (Johnson), *Delostichus smiti* (Jameson & Fulk), *Ectinorus (Ichyonus) angularis* (Smit & Rosicky), *Tetrapsyllus comis* (Jordan), *Tetrapsyllus (Tetrapsyllus) corfidii* (Rothschild), *Tetrapsyllus (Tetrapsyllus) rhombus* (Smit), *Tetrapsyllus (Tetrapsyllus) simulans* (Jameson & Fulk), and *Tetrapsyllus (Tetrapsyllus) tantillus* (Jordan & Rothschild). The specimens, *Ectinorus (Ectinorus) sp.* and *Tetrapsyllus (Tetrapsyllus) sp.* could not be identified taxonomically by the poor condition of the samples, and they were not included in the analysis.

A total of three new host records, nine new localities and nine new host and locality records are documented in this study (Table 2). Moreover, *Tetrapsyllus (Tetrapsyllus) comis* is reported for the first time in Chile (Table 2).

The most frequently captured species were *Neotyphloceras crassispina crassispina* (*n* = 198) and *Neotyphloceras chilensis* (*n* = 175), followed by *Hectopsylla (Hectopsylla) cypha* (*n* = 98), whereas the least common species were *Delostichus phyllotis* and *Plocopsylla wolffsohni* (*n* = 2, each species) and *Ectinorus (Ichyonus) angularis*, *Ectinorus (Ectinorus) sp.*, *Polygenis (Polygenis) platensis*, *Tetrapsyllus (Tetrapsyllus) comis*, *Tetrapsyllus (Tetrapsyllus) corfidii* and *Tetrapsyllus (Tetrapsyllus) sp.* (*n* = 1, each species) (Table 3).

**Table 3.** Number of specimens (N), mean abundance (MA) and prevalence (P%) of captured fleas species by each assessed locality.

Fleas	Pan de Azúcar NP n = 15			Llanos del Challe NP n = 18			Los Molles river n = 20			Fray Jorge NP n = 66			Q. de la Plata n = 54			Dichato n = 92			Total
	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	
<i>C. inopinata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	29	0.32 ± 0.09	17.39	29
<i>D. phyllotis</i>	2	0.13 ± 0.09	13.33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
<i>D. smiti</i>	—	—	—	—	—	—	5	0.08	1.51	—	—	—	—	—	—	—	—	—	5
<i>E. angularis</i>	—	—	—	—	—	—	1	0.05 ± 0.06	5.00	—	—	—	—	—	—	—	—	—	1
<i>H. cypha</i>	10	0.67 ± 0.41	26.67	—	—	—	10	0.50 ± 0.4	10.00	78	1.18 ± 0.5	34.85	—	—	—	—	—	—	98
<i>N. chilensis</i>	—	—	—	2	0.11 ± 0.08	11.11	34	1.70 ± 0.38	75.00	134	2.03 ± 0.29	46.97	5	0.92	7.41	—	—	—	175
<i>N. c. crassispina</i>	—	—	—	—	—	—	83	1.26 ± 0.51	28.79	2	0.04 ± 0	3.71	—	—	—	113	1.23 ± 0.16	61.95	198
<i>P. wolffsohni</i>	—	—	—	—	—	—	1	0.01	1.51	1	0.02	1.85	—	—	—	—	—	—	2
<i>P. platensis</i>	—	—	—	—	—	—	—	—	—	1	0.02	1.85	—	—	—	—	—	—	1
<i>S. ares</i>	—	—	—	—	—	—	7	0.11 ± 0.07	4.55	1	0.02	1.85	—	—	—	33	0.36 ± 0.06	27.17	41
<i>T. comis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0.01 ± 0.01	0.01	1
<i>T. corfidii</i>	—	—	—	—	—	—	—	—	—	1	0.01	1.51	—	—	—	—	—	—	1
<i>T. rhombus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	78	0.84 ± 0.23	31.52	78
<i>T. simulans</i>	—	—	—	—	—	—	—	—	—	13	0.19 ± 0.35	4.54	—	—	—	—	—	—	13
<i>T. tantillus</i>	—	—	—	—	—	—	12	0.60 ± 0.24	40.00	15	0.23 ± 0.17	15.15	—	—	—	—	—	—	27
Total	12	0.80 ± 0.4	40.00	2	0.11 ± 0.08	11.11	57	2.85 ± 0.4	85.00	337	5.06 ± 0.71	81.17	10	0.18 ± 0	20.03	254	2.76 ± 0.40	67.39	672
Species richness (S)	2	—	—	4	—	—	9	—	—	5	—	—	5	—	—	5	—	—	16
Species diversity (H)	0.45	—	—	1.01	—	—	1.49	—	—	1.36	—	—	1.26	—	—	—	—	—	—

n, number of captured hosts specimens by locality; (localities are arranged from north to south). (MA shows means ± 1 SE).

**Table 4.** Number of specimens (N), mean abundance (MA) and prevalence (P%) of captured fleas species from six representative host species.

Fleas	<i>A. longipilis</i> n = 46			<i>A. olivacea</i> n = 127			<i>O. longicaudatus</i> n = 23			<i>P. darwini</i> n = 55			<i>P. xanthopygus</i> n = 7			<i>T. elegans</i> n = 57			Total		
	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)	N	MA	P(%)			
<i>C. inopinata</i>	19	0.41 ± 0.22	19.57	8	0.06 ± 0.06	4.72	1	0.04	4.35	1	0.02	1.82	—	—	—	—	—	—	29		
<i>D. phyllotis</i>	—	—	—	—	—	—	—	—	—	2	0.04 ± 0	3.64	—	—	—	—	—	—	2		
<i>E. angularis</i>	—	—	—	1	0.01	0.79	—	—	—	—	—	—	—	—	—	—	—	—	1		
<i>H. cypha</i>	20	0.43 ± 0.21	19.58	20	0.16 ± 0.18	5.51	2	0.09 ± 0	8.69	46	0.84 ± 0.68	16.36	10	1.43 ± 0.53	28.57	—	—	—	98		
<i>N. chilensis</i>	76	1.65 ± 0.53	23.91	22	0.17 ± 0.29	3.94	13	0.56 ± 0.32	21.74	9	0.16 ± 0.17	9.09	11	1.57 ± 0.28	85.71	20	0.35 ± 0.17	17.50	151		
<i>N. c. crassispina</i>	119	2.59 ± 0.50	65.21	48	0.38 ± 0.21	18.89	18	0.78 ± 0.13	56.52	13	0.24 ± 0.07	16.36	—	—	—	—	—	—	198		
<i>P. wolfsobni</i>	1	0.02	2.17	—	—	—	—	—	—	1	0.02	1.82	—	—	—	—	—	—	2		
<i>P. platensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0.02 ± 0.02	1.75	1		
<i>S. ares</i>	25	0.54 ± 0.15	34.78	9	0.07 ± 0	5.51	5	0.22 ± 0	21.74	2	0.04 ± 0	3.64	—	—	—	—	—	—	41		
<i>T. corfitati</i>	—	—	—	1	0.01	0.79	—	—	—	—	—	—	—	—	—	—	—	—	1		
<i>T. rhombus</i>	66	1.43 ± 0.63	36.96	19	0.15 ± 0.17	7.87	2	0.09 ± 0	8.69	1	0.02	1.82	—	—	—	—	—	—	88		
<i>T. simulans</i>	13	0.28 ± 0.37	13.04	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13		
<i>T. tantillus</i>	12	0.26 ±	17.39	12	0.09 ± 0.18	5.51	—	—	—	—	—	—	—	—	—	—	—	—	26		
Total	351	7.63 ± 1.05	93.48	140	1.10 ± 0.24	38.58	41	1.78 ± 0.26	86.96	75	1.40 ± 0.39	45.45	23	3.29 ± 0.75	100	21	0.37 ± 0.11	17.29	651		
Species richness(S)	9			9			6			8			3			2			14		
Species diversity (H)	1.77			1.83			1.37			1.22			0.93			0.19			—		

n, number of captured host specimens. See text for details. MA shows means ± 1 SE.

High values of flea species richness and diversity were found at Fray Jorge National Park (hereafter NP), whereas Los Molles River, Fray Jorge NP and Dichato presented the highest values of MA and prevalence. The number of individuals of each flea species by site is shown in Table 3. Although, 83 small mammals belonging to 3 species [*A. olivacea* ( $n=59$ ), *P. magister* ( $n=20$ ) and *P. limatus* ( $n=4$ )] were captured in Loa River, no fleas were found on those animals at this site. From a host perspective, when analysing all sites together, we observed high values of flea richness and diversity in *A. olivacea*, *A. longipilis* and *P. darwini*, and high values of MA and prevalence in *O. longicaudatus*, *A. longipilis* and *P. xanthopygus* (Table 4).

Six representative small mammal species that showed high values of flea richness and diversity were selected (Table 4). These host species, *A. olivacea*, *A. longipilis*, *P. darwini*, *O. longicaudatus* and *T. elegans*, were captured in many sites and showed a broad distribution, and showed high number of captures (Table 2). Furthermore, we also included in this analysis an additional rodent species, *P. xanthopygus* that, although it was captured in smaller quantities, it was only captured in the high altitude site, and, before this study, there were no known records of fleas captures at high altitude in southern South America (see Table 2). When the parameters and community indices of these mammals were analysed, we observed that more than 70% of the fleas collected come from only two species of the genus *Abrothrix*. Moreover, these species had higher values of richness and diversity of parasites (see Table 4), with one exception, *P. darwini*, which showed high values of richness ( $S=8$ ), diversity ( $H=1.22$ ) and number of fleas collected ( $n=75$ ; see Table 4). The number of specimens for each flea species for six representative host species is detailed in Table 4.

## Discussion

### *New hosts and localities records*

The majority of species and subspecies of fleas recorded in this study were previously collected in Chile, with the exception of *T. (T.) comis*, previously reported in Ecuador in 1942 (Johnson, 1957). The present study contributes to extend the distributional range of several flea species. On the one hand, *D. phyllotis*, previously recorded in Santiago and in a site located at 50 km E from Vallenar, in the Region III (Jameson & Fulk, 1977), has been now captured in Pan de Azúcar NP, between regions II and III, whereas *H. (H.) cypha*, previously recorded in Argentina as well as in Limarí and Valparaíso, in the regions IV and V of Chile, respectively (Alarcón, 2000), has now extended its distribution to Fray Jorge NP and Pan de Azúcar NP in the region IV and III, respectively. Similarly, *N. crassispina crassispina*, previously recorded from Concepción in the region VIII to Valparaíso in the V region (Alarcón, 2000, 2003) and *T. (T.) corfidii*, recorded from Concepción in the VIII region to Valparaíso in the V region (Alarcón, 2000, 2003), extends its distributional range considerably to the north, to Fray Jorge NP in the region IV. Furthermore, two subspecies of *P. (P.) platensis*, namely

*P. (P.) p. platensis* and *P. (P.) p. cisandinus*, were recorded in Iquique and Antofagasta (regions XV and II) in Chile (Alarcón, 2000). Moreover, Lareschi and Linardi (2009) suggest the absence of subspecies within *P. (P.) platensis*; therefore, the distribution of this species is extended to Central Chile in the Santiago metropolitan region.

*Neotyphloceras chilensis* was recently elevated to species status based on characteristics of its modified abdominal segments in both sexes (Sanchez *et al.*, 2012). The geographical distribution of this species shows a higher occurrence in southwestern South America (Hastriter, 2001). This last author also mentioned the occurrence of *N. chilensis* in sympatry with *N. crassispina crassispina*, in Peñuelas Lake National Park, Valparaíso Province, central Chile, and previously, Beaucournu and Alcover (1990), recorded it in sympatry with *N. crassispina hemisus* in Lake Curruhue, Neuquén Province, Argentina. In the present study, we report that *N. chilensis* lives in sympatry with *N. c. crassispina* in Fray Jorge NP and Quebrada de la Plata. According to Alarcón (2000), the distribution of *N. chilensis* in Chile extends from General Carrera, in the region XI, to Antofagasta, in the region II. In the present study, we expand its altitudinal distribution from sea level to 2500 m a.s.l. in Los Molles River (region IV).

On the other hand, *T. (T.) tantillus* (previously reported from Ultima Esperanza in the region XII to Elqui in the region IV), *E. (I.) angularis* (reported in Magallanes in the region XII) and *H. (H.) cypha* were recorded in places below 900 m a.s.l (Alarcón, 2000). In the present study, we report those fleas being captured over 2500 m a.s.l in Los Molles River (region IV). As far as we know, this is the first record of fleas being sampled at 2000 m a.s.l. in Chile (see Alarcón, 2000, 2003; Hastriter *et al.*, 2001; Beaucournu *et al.*, 2006).

Thirteen host-flea associations are mentioned for the first time for 10 species and 2 subspecies of fleas (see Table 2). Some of these fleas, such as *T. (T.) corfidii*, *T. (T.) tantillus*, *T. (T.) rhombus*, *N. chilensis*, *N. c. crassispina* and *C. inopinata*, have been previously reported for several species of rodents in South America (see Alarcón, 2000, 2003; Hastriter, 2001; Hastriter *et al.*, 2001). However, the host-flea associations shown in this study expand significantly the range of hosts used by four species of fleas in Chile. We founded *Hectopsylla (H.) cypha* on *A. longipilis*, *P. xanthopygus* and *O. longicaudatus*, and previously it was reported only on *A. olivacea* and *P. darwini* (see Alarcón, 2000). Similarly, *A. olivacea* (captured in Los Molles River) is reported as new host record for *E. (I.) angularis*, which had been previously reported for an unidentified species of *Abrothrix* in Magallanes region XII (Alarcón, 2000), where *A. olivacea* is not present (see Muñoz-Pedreros & Yáñez, 2009). On the other hand, *P. (P.) platensis* was previously recorded on *Ctenomys fulvus* and *C. robustus* in Chile (Alarcón, 2000), and we now report for the first time this flea on the endemic marsupial from Chile, *Thylamys elegans* (Meynard *et al.*, 2002). Moreover, *P. xanthopygus* (captured in Los Molles River) is reported as new host record of *N. chilensis*. Finally, *T. (T.) comis*, previously reported in Ecuador in 1942 on *Sigmodon* sp. (Johnson, 1957), and to the best of our knowledge, not reported since discovery, has been found on the endemic rodent of central Chile, *O. bridgesi*, in Dichato

in the region VIII, revealing a new record for this flea species in Chile.

#### Flea-small mammal community analysis

All small mammal species captured in the present study have been previously reported from Chile (see Iriarte, 2008; Muñoz-Pedrerros & Yáñez, 2009). In agreement with Cofré and Marquet (1999) and Iriarte (2008), we found that *A. olivacea* has a wide distribution and it is abundant in Chile, whereas *A. bennetti* and *O. bridgesi*, endemic species in Chile (Iriarte, 2008; Muñoz-Pedrerros & Yáñez, 2009), are rare.

The prevalences and MAs of fleas varied considerably by location, where Llanos del Challe NP and Quebrada de La Plata showed the lowest abundances and prevalences, whereas Los Molles River, Fray Jorge NP and Dichato showed the highest abundances and prevalences (Table 3). In contrast, total prevalences tend to be lower in other localities situated in other South American countries compared with the studied Chilean sites. For example, small mammal-flea associations in localities along the La Plata and Paraná Rivers, Argentina (Pampa biome) showed prevalences of 25% or less (Lareschi, 1996; Lareschi *et al.*, 2003, 2007; Lareschi & Krasnov, 2010). In two sites in Brazil, the total prevalence of fleas was 37.6% in Belo Horizonte (Cerrado biome) (Linardi *et al.*, 1984) and 26.5% in Santa Catalina (Paranense rainforest) (Linardi *et al.*, 1991). By contrast, a study carried out in Ñacuñan Biosphere Reserve, Argentina (Monte Desert biome), showed total prevalences greater than 90% (Lareschi *et al.*, 2004), providing evidence of one of the areas with the highest prevalence of fleas on small mammals recorded in South America, in Argentina's Patagonia, where ectoparasites of small mammals are represented mainly by fleas (Sanchez & Lareschi, personal observation). Because fleas are parasites only as adults and the habitat of the fleas are the hosts in particular habitats (Marshall, 1981; Krasnov, 2008), the differences between community variables assessed between the localities may be associated to a host-parasite co-evolutionary process and/or to environmental conditions. Therefore, population and community composition of fleas is determined not only by the composition of the host but also by the properties of their habitat (Morand *et al.*, 2008; Mize *et al.*, 2011). Although there are several previous studies showing that environmental conditions such as temperature (e.g. Nunn *et al.*, 2005; Lindenfors *et al.*, 2007), humidity (e.g. Moreno, 2010) and soil type (e.g., Guerra *et al.*, 2002; Manangan *et al.*, 2007) affect the distribution and structure of parasite communities, a recent study by Bazán-León (2011), focused on the two most abundant host species of the present study, did not find any relationship between environmental conditions (temperature, humidity and aridity index) and geographical position (latitude and altitude) with several parasite community variables (species richness and diversity, abundance and prevalence).

By contrast, there is no convincing explanation for the absence of fleas in host individuals caught at the Loa River, northern Chile, whereas other haematophagous insects, such as lice and flies, were collected during the study. Future

studies should focus on assessing which factors would limit flea abundance in this locality.

#### Acknowledgements

We are grateful to R. Pozo, I. Cotorás, C. Quilodrán, D. Medina, and R. Zúñiga for field and lab assistance. Research was funded by FONDECYT-Chile 1090794, CONICYT-CSIC 2009-137, Fundación BBVA BIOCON06/109, and the Institute of Ecology and Biodiversity (ICM-P05-002-Chile, and PFB-23-CONICYT-Chile). The identification of fleas was carried out during the visit of E. A. Bazán-León to the Centro de Estudios Parasitológicos y de Vectores (CEPAVE), working in the laboratory was supported by grants PICT2010-338 and 11N618 (ANCyT and UNLP, Argentina).

#### References

- Alarcón, M.E. (2000) Present state of the knowledge of Siphonaptera in Chile (Insect: Siphonaptera). *Gayana*, **64**, 1–17.
- Alarcón, M.E. (2003) Fleas (Insecta: Siphonaptera) on three species of rodent at Concepción, VIII Region-Chile. *Gayana*, **67**, 16–24.
- Anderson, R. & May, R. (1991) *Infectious Diseases of Humans: Dynamics and Control*. Oxford University Press, Oxford.
- Bazán-León, E.A. (2011) Ecología parasitaria de dos especies de pequeños mamíferos de Chile, *Abrothrix olivacea* (Rodentia: Cricetidae) y *Thylamys elegans* (Didelphimorphia: Didelphidae). MSc Dissertation. Facultad de Ciencias, Universidad de Chile.
- Beaucournu, J.C. & Alcover, J.A. (1990) Puce récoltées dans la province de Neuquén (Argentine); description de 4 nouveaux taxa (Insecta Siphonaptera). *Annales de Parasitologie Humaine et Comparee*, **64**, 489–505.
- Beaucournu, J.C. & Gallardo, M.H. (1978) Quelques nouvelles puces du Chili (Siphonaptera) parasites de *Ctenomys* (Rod. Octodontidae). *Bulletin de la Societe de Pathologie Exotique*, **70**, 438–450.
- Beaucournu, J.C. & Gallardo, M.H. (1989) Contribution a la faune du Chili; puces nouvelles de la moitié nord (Insecta, Siphonaptera). *Revue Suisse de Zoologie*, **94**, 181–188.
- Beaucournu, J.C. & Gallardo, M.H. (1991) Siphonaptères du Chili; description de 4 espèces nouvelles (Siphonaptera). *Bulletin de la Societe Entomologique de France*, **96**, 185–203.
- Beaucournu, J.C. & Gallardo, M.H. (1992) Catalogue provisoire des Puces du Chili. 2<sup>e</sup> partie (Insecta: Siphonaptera). *Bulletin de la Societe Francaise de Parasitologie*, **10**, 93–130.
- Beaucournu, J.C., Gallardo, M.H. & Launay, H. (1986) Puces (Siphonaptera) nouvelles ou peu connues du Chili: description de *Plocopsylla diana* n. sp. (Stephanocircidae). *Annales de Parasitologie Humaine et Comparee*, **61**, 359–366.
- Beaucournu, J.C. & Kelt, D.A. (1990) Contribution à la faune du Chili: puces nouvelles ou peu connues de la partie sud (Insecta, Siphonaptera). *Revue Suisse de Zoologie*, **97**, 67–668.
- Beaucournu, J.C. & Torres-Mura, J.C. (1986) Un *Tetrapsyllus* nouveau du Chili (Siphonaptera, Rhopalopsyllidae). *Revue Française d'Entomologie*, **8**, 9–12.
- Beaucournu, J.C., Torres-Mura, J.C. & Gallardo, M.H. (1988) Description de la femelle de *Ctenoparia topali* Smit, 1963 et clef dichotomique du genre *Ctenoparia* Rothschild, 1909 (Siphonaptera, Hystri-chopsyllidae). *Annales de Parasitologie Humaine et Comparee*, **63**, 380–383.



- Beaucournu, J.C., Vergara, P., Balboa, L. & Gonzalez-Acuña, D.A. (2006) Description d'une nouvelle puce d'oiseau provenant du Chili (Siphonaptera: Ceratophyllidae). *Parasite*, **13**, 227–230.
- Begon, M., Harper, J.L. & Townsend, C.R. (1988) *Ecología: individuos, poblaciones y comunidades*. Omega, Barcelona.
- Blanchard, E. (1852) Pulicidas. *Historia física y política de Chile*, Vol. 7 (ed. by C. Gay) Vol., pp. 325–327. Museo de Historia Natural de Santiago, Maulde & Renou, Paris.
- Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology*, **83**, 575–583.
- Cofré, H. & Marquet, P.A. (1999) Conservation status, rarity, and geographic priorities for conservation of Chilean mammals: an assessment. *Biological Conservation*, **88**, 53–68.
- Combes, C. (2001) *Parasitism: The Ecology and Evolution of Intimate Interactions*. University of Chicago Press, Chicago, IL.
- CONAF (1997) Plan de Manejo: Parque Nacional Llanos del Challe. Documento de trabajo N° 250.
- CONAF (1998) Plan de Manejo: Parque Nacional Fray Jorge. Documento de trabajo N° 297.
- CONAF (2002) Plan de Manejo: Parque Nacional Pan de Azúcar. Documento de trabajo N° 373.
- Degen, A. (2008) Effect of macroparasites on the energy budget of small mammals. *Micromammals and Microparasites: From Evolutionary Ecology to Management* (ed. by S. Morand, B. Krasnov & R. Poulin), pp. 371–399. Springer, Tokyo.
- Dirección General de Aguas (2004) *Cuenca Río Loa. Diagnóstico y clasificación de los cursos y cuerpos de agua según objetivos de calidad*. Ministerio de Obras Públicas, Santiago, Chile.
- Fitze, P., Tschirren, B. & Richner, H. (2004) Life history and fitness consequences of ectoparasites. *Journal of Animal Ecology*, **73**, 216–226.
- Fredes, F. (2008) Pulgas. *Zoología Médica II* (ed. by M. Canals & P. Catán), pp. 255–269. Editorial Universitaria, Universidad de Chile, Santiago.
- Guerra, M., Walker, E., Jones, C., *et al.* (2002) Predicting the risk of Lyme disease: habitat suitability for *Ixodes scapularis* in the North Central United States. *Emerging Infectious Diseases*, **8**, 289–297.
- Hastriter, M.W. (2001) Fleas (Siphonaptera: Ctenophthalmidae and Rhopalopsyllidae) from Argentina and Chile with two new species from the Rock Rat, *Aconaemys fuscus*, in Chile. *Annals of Carnegie Museum*, **70**, 169–178.
- Hastriter, M.W., Alarcón, M.E. & Whiting, M.F. (2001) A collection of fleas (Siphonaptera) from the San Martín Reserve, Valdivia Province, Chile. *Proceeding of the Entomological Society of Washington*, **103**, 437–443.
- Hopkins, G.H. & Rothschild, M. (1966) *An Illustrated Catalogue of Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History)*. Vol. II. *Cotoposyllidae, Vermipsyllidae, Stephanocircidae, Ischnopsyllidae, Hysophthalmidae, and Xiphopsyllidae*. British Museum (Natural History), London.
- Iriarte, A. (2008) *Mamíferos de Chile*. Lynx Edicions, Barcelona.
- Jameson, E.W. & Fulk, G.W. (1977) Notes on some fleas (Siphonaptera) from Chile. *Journal of Medical Entomology*, **14**, 401–406.
- Johnson, P.T. (1957) A classification of the Siphonaptera of South America with descriptions of new species. *Memoirs of the Entomological Society of Washington*, **5**, 1–298.
- Koella, J.C. & Turner, P. (2008) Evolution of parasites. *Evolution in Health and Disease*, 2nd edn (ed. by S. C. Stearns & J. C. Koella), pp. 229–237. Oxford University Press, Oxford.
- Krasnov, B.R. (2008) *Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology*. Cambridge University Press, Cambridge.
- Krasnov, B.R., Poulin, R. & Morand, S. (2008) Patterns of macroparasite diversity of small mammals. *Micromammals and Microparasites: From Evolutionary Ecology to Management* (ed. by S. Morand, B. Krasnov & R. Poulin), pp. 197–232. Springer, Tokyo.
- Krasnov, B.R., Matthee, S., Lareschi, M., Korralo-Vinarskaya, N.P. & Vinarski, M.V. (2010) Co-occurrence of ectoparasites on rodent hosts: null model analyses of data from three continents. *Oikos*, **119**, 120–128.
- Lareschi, M. (1996) Estudio preliminar de la comunidad de roedores (Rodentia: Muridae) y sus ectoparásitos (Acari, Phthiraptera y Siphonaptera) en Punta Lara (Buenos Aires). *Revista de la Sociedad Entomológica Argentina*, **55**, 113–120.
- Lareschi, M. & Krasnov, B.R. (2010) Determinants of ectoparasites assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. *Medical and Veterinary Entomology*, **24**, 284–292.
- Lareschi, M. & Linardi, P.M. (2009) Morphological variability in *Polygenis (Polygenis) platensis* (Jordan & Rothschild) (Siphonaptera: Rhopalopsyllidae: Rhopalopsyllinae) and taxonomic consequences. *Zootaxa*, **2310**, 35–42.
- Lareschi, M., Notarnicola, J., Navone, G. & Linardi, P.M. (2003) Arthropod and filarioid parasites associated with wild rodents in the northeast marshes of Buenos Aires, Argentina. *Mémoires do Instituto Oswaldo Cruz*, **98**, 673–677.
- Lareschi, M., Ojeda, R. & Linardi, P.M. (2004) Flea parasites of small mammals in the Monte Desert biome in Argentina with new host and locality records. *Acta Parasitologica*, **49**, 63–66.
- Lareschi, M., Notarnicola, J., Nava, S. & Navone, G. (2007) Parasite community (Arthropods and Filarioids) associated with wild rodents from the marshes of La Plata River, Argentina. *Comparative Parasitology*, **74**, 141–147.
- Linardi, P.M., Botelho, J.R., Pereira-Neves, D. & Cunha, H.C. (1984) Sobre algunos ectoparasitos de roedores silvestres de Belo Horizonte, MG. *Revista Brasileira de Biologia*, **44**, 215–219.
- Linardi, P.M., Botelho, J.R., Ximenez, A. & Padovani, C.R. (1991) Notes on ectoparasites of some small mammals from Santa Catarina State, Brazil. *Journal of Medical Entomology*, **28**, 183–185.
- Lindenfors, P., Nunn, C., Jones, K., Cunningham, A., Sechrest, W. & Gittleman, J. (2007) Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography*, **16**, 496–509.
- Luebert, F. & Plissock, P. (2006) *Sinópsis bioclimática y vegetal de Chile*. Editorial Universitaria, Santiago, Chile.
- Macchiavello, A. (1948) Siphonaptera de la Costa Sur-Occidental de América (Primera Lista y Distribución Zoo-geográfica). *Boletín de la Oficina Sanitaria Panamericana*, **27**, 412–460.
- Macchiavello, A. (1954) Reservoirs and vectors of plague. *Journal of Tropical Medicine and Hygiene*, **57**, 1–68.
- Manangan, J.S., Schiweitaer, S.H., Nibbelink, N., Yabsley, M.J., Gibbs, S.E.J. & Wimberly, M.C. (2007) Habitat factors influencing distributions of *Anaplasma phagocytophilum* and *Ehrlichia chaffeensis* in the Mississippi alluvial valley. *Vector-Borne and Zoonotic Diseases*, **7**, 563–573.
- Marshall, A.G. (1981) *The Ecology of Ectoparasitic Insects*. Academic Press, New York, NY.
- Meynard, A., Palma, R. & Rivera-Milla, E. (2002) Filogeografía de las llacas del género *Thylamys* (Marsupialia, Didelphidae) en base

- a secuencias del gen mitocondrial citocromo b. *Revista Chilena de Historia Natural*, **75**, 299–306.
- Mize, E.L., Tsao, J.I. & Maurer, B.A. (2011) Habitat correlates with the spatial distribution of ectoparasites on *Peromyscus leucopus* in southern Michigan. *Journal of Vector Ecology*, **36**, 308–320.
- Møller, A.P. (1997) Evidence of larger impact of parasites on hosts in the tropics: investment in immune function within and outside the tropics. *Oikos*, **82**, 265–270.
- Morand, S., Krasnov, B.R., Poulin, R. & Degen, A.A. (2008) Micromammals and macroparasites: who is who and how do they interact? *Micromammals and Microparasites: From Evolutionary Ecology to Management* (ed. by S. Morand, B. Krasnov & R. Poulin), pp. 3–12. Springer, Tokyo.
- Moreno, L. (2010) Patrones de estructuración de las comunidades de ectoparasitos en Milvago chimango (Falconidae, Caracarinae) en Chile. PhD Dissertation. Facultad de Ciencias, Universidad de Chile, Santiago, Chile.
- Muñoz-Pedreros, A. & Yáñez, J. (2000) *Mamíferos de Chile*. CEA Ediciones, Valdivia, Chile.
- Muñoz-Pedreros, A. & Yáñez, J. (2009) *Mamíferos de Chile*, 2nd edn. CEA Ediciones, Valdivia, Chile.
- Nunn, C., Altizer, S., Sechrest, W. & Cunningham, A. (2005) Latitudinal gradients of parasite species richness in primates. *Diversity and Distributions*, **11**, 249–256.
- Poulin, R. (2007) *Evolutionary Ecology of Parasites*, 2nd edn. Princeton University Press, Princeton, NJ.
- Rothschild, N.C. (1904) Description of a new species of Siphonaptera from South America. *Revista Chilena de Historia Natural*, **8**, 147–148.
- Rothschild, N.C. (1906) New species of Chilean Siphonaptera. *Revista Chilena de Historia Natural*, **10**, 35–39.
- Rothschild, N.C. (1909a) A new flea from Chile. *Revista Chilena de Historia Natural*, **13**, 104–106.
- Rothschild, N.C. (1909b) A new species of *Stephanocircus* from Chile. *Revista Chilena de Historia Natural*, **13**, 181–183.
- Rothschild, N.C. (1910) New Chilean Siphonaptera. *Revista Chilena de Historia Natural*, **14**, 25–28.
- Sanchez, J., Amor, V., Bazán-León, E.A., Vásquez, R.A. & Lareschi, M. (2012) Redescription of *Neotyphloceras chilensis* Jordan, new status (Siphonaptera: Ctenophthalmidae: Neotyphloceratini). *Zootaxa*, **3259**, 51–57.
- Smit, F.G.A.M. (1987) *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History)*. Vol. 7. *Malacopsylloidea (Malacopsyllidae and Rhopalopsyllidae)*. Oxford University, Oxford.
- Smit, F.G.A.M. & Rosicky, B. (1972) Some Siphonaptera from Chile. *Folia Parasitologica*, **19**, 365–368.
- Whiting, M.F., Whiting, A.S., Hastriter, M.W. & Dittmar, K. (2008) A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. *Cladistics*, **24**, 1–31.
- Wilson, D.E. & Reeder, D.M. (2005) *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd edn. John Hopkins University Press, Baltimore, MD.

Accepted 7 November 2012

First published online 18 March 2013