Austral ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2016) **41**, 512–518

Temporal fluctuation in shrub species preferences of two native rodents: The effect of infection status on habitat use

M. ISABEL DONOSO,[1] FRANCISCO E. FONTURBEL,[1]* ROCÍO A. CARES,[1] ESTEBAN ODA,[1] PATRICIA A. RAMIREZ[2] AND CAREZZA BOTTO-MAHAN[1]

[1]*Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile (Email: fonturbel@gmail.com) and* [2]*School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand*

Abstract Small mammals use plant species for gathering food resources and for shelter. Preferences for certain plant species are related to nutritional restrictions and behavioural patterns, which could be altered in the presence of an infectious disease. Several native small mammals are part of the wild cycle of the protozoan *Trypanosoma cruzi*, responsible for Chagas disease in humans. This is a vector-borne disease transmitted by insects of the subfamily Triatominae. We examined the effect of *T. cruzi* infection status on the use and preference patterns of shrub species by two native rodent species: *Octodon degus* and *Phyllotis darwini*. This study was conducted during four sampling years (2010–2013) in a hyper-endemic zone of Chagas disease located in a semiarid Mediterranean ecosystem. We captured individuals of 599 *O. degus* and 575 *P. darwini* (89% of the total captures), which were related to nine shrub species and examined for *T. cruzi* infection. In a community-level analysis, infected and non-infected *O. degus* used individual shrub species within the shrub community significantly non-randomly relative to their availability; the same pattern was detected for non-infected *P. darwini* individuals, whereas infected individuals used the shrub community according to the abundance of each shrub species. Examining individual preferences, both rodents showed a strong preference for *Flourensia thurifera* and *Colliguaja odorifera* regardless of their infection status. Preferences for specific shrub species were variable among years, showing a 'core' of preferred shrub species and variable levels of use of the remaining ones. Our results show that *T. cruzi* infection in wild small mammals can modify habitat use patterns and preferences for certain shrub species, probably affecting processes acting at community level.

Key words: infection-mediated plant-animal interaction, *Octodon degus*, *Phyllotis darwini*, *Trypanosoma cruzi*, wild cycle of Chagas disease.

INTRODUCTION

Plant–animal interactions play a key role in community structure, with mutualistic (e.g. seed dispersal) and antagonistic (e.g. herbivory and parasitism) processes acting simultaneously (Strauss & Irwin 2004). Animals often use plant resources to gather food (e.g. seeds, leaves, roots and floral rewards) and/or as shelter sites that provide appropriate microclimatic conditions and reduce predation pressure (Yunger *et al.* 2002; Milstead *et al.* 2007). These interactions may be structured by the spatial arrangement of resources (Milstead *et al.* 2007), as well as by inter-specific competition for a limiting resource (Yunger *et al.* 2002; Warren *et al.* 2014). However, little is known about the potential effect of an interacting third party (e.g., a parasite) on plant–animal interaction dynamics. While some studies have reported behavioural changes in parasitized animals (e.g. Day & Edman 1983; Vyas *et al.* 2007; Owen *et al.* 2010; Amman *et al.* 2013), their potential influence on interactions between infected animals and the plant community remains largely unknown.

The interaction between small mammals and the plant community has been studied extensively (for more than 20 years) in the semiarid-Mediterranean scrublands of Chile (Kelt *et al.* 2004a,b; Gutierrez *et al.* 2010). Rodent foraging plays a major role in plant community dynamics because of differential seed consumption (Kelt *et al.* 2004b; Andreo *et al.* 2009). This ecosystem is also a hyper-endemic zone of Chagas disease, which is produced by the flagellated parasite *T. cruzi* that causes tissue damage and organ enlargement in humans. *T. cruzi* is transmitted in the wild by the reduviid hemipteran vector *Mepraia spinolai* (Botto-Mahan *et al.* 2005b), which infects many native and introduced mammal species (Botto-Mahan *et al.* 2009, 2010, 2012). A previous study reported behavioural changes in infected wild rodents, altering their movement behaviour because of alterations in their body condition (Jiménez *et al.* 2015). To the best of our knowledge, no study has assessed the potential effect of *T. cruzi* infection on small mammal behaviour related to how they use the shrub species available in the environment. We

*Corresponding author.
Accepted for publication October 2015.

doi:10.1111/aec.12338

expected infected individuals to use sub-optimal habitats because of altered movement behaviour, even though some species have been described as asymptomatic reservoirs of *T. cruzi* (Botto-Mahan *et al.* 2012).

We examined the effect of *T. cruzi* infection on the preferences for shrub species of two abundant and highly infected native rodent species. Specifically, we studied the association among rodents and shrub species in four consecutive years, examining the effect of infection status on these preferences. To this purpose, we used two methodological approaches, a community-level test and a species-by-species differential use analysis.

METHODS

Study area

This study was carried out in a protected area in Chile, Las Chinchillas National Reserve, located approximately 60 km east of the Pacific coast (31°30'S, 71°06'W). This semiarid-Mediterranean area presents scarce rainfall concentrated between June and August. Mean annual precipitation is 185 mm, varying from 45 to 200 mm across the sampled years, alternating long droughts and unusual years of high rainfall seemingly associated with El Niño events (di Castri & Hajek 1976; Lima *et al.* 1999). Vegetation is thorny and mainly represented by *Flourensia thurifera*, *Bahia ambrosioides* and *Porlieria chilensis* as the most common shrub species (Medel *et al.* 2004).

This reserve is part of a hyper-endemic zone of Chagas disease in Chile (Schenone *et al.* 1995). Chagas disease or American trypanosomiasis is a vector-borne disease caused by the flagellated protozoan *T. cruzi* and transmitted by triatomine insects (Hemiptera: Reduviidae) to several mammal species (Coura & Vinas 2010), involving both domestic and wild transmission cycles (Xavier *et al.* 2012). The triatomine *M. spinolai* is the main wild vector of *T. cruzi* in Chile (Botto-Mahan *et al.* 2005b). Populations of this endemic vector can reach up to 46.2% *T. cruzi* infection (Botto-Mahan *et al.* 2005b); several mammal species serve as reservoir hosts of *T. cruzi* including native rodents, carnivores, marsupials and introduced lagomorphs (Schenone *et al.* 1995; Rozas *et al.* 2007; Botto-Mahan *et al.* 2009, 2010, 2012) with prevalence levels up to 71% (Jimenez & Lorca 1990; Rozas *et al.* 2007; Muñoz-Pedreros & Gil 2009; Botto-Mahan *et al.* 2010, 2012) and a large temporal variability across species (Botto-Mahan *et al.* 2010).

The sampling sites were stony slopes mainly inhabited by several native rodent species; the most abundant are the brush-tailed rat (*O. degus*, Octodontidae) and Darwin's leaf-eared mouse (*P. darwini*) (Botto-Mahan *et al.* 2005a). *T. cruzi* infection levels of these species range from 20% to 60% for *O. degus* and 10% to 58% for *P. darwini* (2000 *vs.* 2005) (Botto-Mahan *et al.* 2010). *O. degus* is a long-lived diurnal and social rodent, whereas *P. darwini* is a nocturnal and solitary species. Furthermore, *O. degus* is considered to be a feeding specialist, whereas *P. darwini* is considered a generalist species (Bozinovic 1997).

Small mammal trapping and blood sample collection

Small mammal trapping was performed using 300 wire mesh live animal traps (a collapsible box of 24 × 8 × 9 cm; FORMA Products and Services, Santiago, Chile), baited with oatmeal flakes and provided with cotton balls for bedding. Traps were arranged on three grids of 100 traps each (Appendix S1, available in online Supplementary Material), covering a total area of 3.39 ha. Each grid consisted of two lines of 50 traps separated by 10 m. Traps were set underneath the nearest shrub to the 10 m location to ensure shade and protection from extreme temperatures (very high during the day and very low during the night). Trap locations were kept constant during the four sampling years (marks were left in the field between years), with less than 5% variation among years because of shrub mortality. Although we have field evidence that rodents use the chosen shrub species, bait may be attracting some individuals to some shrub species otherwise ignored. Here, we faced a methodological trade-off, compromising some accuracy in order to have a large sample size. Small mammal collection was carried out for four to five nights from 19:00 to 09:00 h during the austral summer of 2010 to 2013 (first week of January). Capturing and handling procedures met the guidelines of the American Society of Mammalogists (Sikes *et al.* 2011). Plant nomenclature followed Hoffmann (1980).

Each *O. degus* and *P. darwini* captured was sexed, weighed and measured (total body length and tail length) under short-term isoflurane anaesthesia (Lee 2004; Jekl *et al.* 2011). From these individuals, 0.2 mL of blood was withdrawn by (i) saphenous vein puncture for *O. degus* with a 21G needle and (ii) masseteric vein puncture for *P. darwini* with a 21G needle (Morton *et al.* 1993; Johnson-Delaney 2006). Individuals were ear-tagged with a unique combination of numbers to avoid pseudo-replication (i.e. to exclude recaptures from the analyses) and released at the point of capture after complete recovery from anaesthesia. The blood extraction procedure was conducted following the international recommendations for mammalian blood extraction (Johnson-Delaney 2006) and authorized by the Ethics Committee of the Faculty of Science (University of Chile), Chilean Agriculture and Livestock Bureau permit resolutions N° 0048 and N° 7462 (SAG) and National Forest Corporation permit resolutions N° 32/2009 and N° 61/2010 (CONAF).

PCR detection of *Trypanosoma cruzi* in blood samples

Whole genomic DNA was isolated from blood samples and stored at −20 °C (AXYGEN, AxyPrep Blood Genomic DNA Miniprep Kit, Calfornia, USA). The Polymerase Chain Reaction (PCR) assay for *T. cruzi* was performed as previously reported using primers 121 (5′-AAA TAA TGT ACG GG(T/G) GAG ATG CAT GA-3′) and 122 (5′ GGG TTC GAT TGG GGT TGG TGT-3′) to amplify the variable region of minicircle DNA (Veas *et al.* 1991). Samples were tested in

 doi:10.1111/aec.12338

triplicate and considered positive if at least two out of the three assays gave amplifications. Samples with only one positive assay were considered doubtful and repeated three additional times. Each trial included positive and negative controls. The PCR products were analyzed by electrophoresis on 2% agarose gels and visualized by staining with ethidium bromide. A 330 base pair product indicated a positive result.

Vegetation sampling

Live traps were associated with 18 shrub species, but for comparative purposes, we considered only the nine plant species (*F. thurifera*, *Heliotropium stenophyllum*, *Baccharis salicifolia*, *P. chilensis*, *Bridgesia incisifolia*, *C. odorifera*, *Schinus polygamus*, *Adesmia arborea* and *Ophryosporus paradoxus*) present in the 4 years of sampling. All those shrub species are known to be used by native small mammals (Cortés *et al.* 1994 and personal observations of trails, faeces and urine). To determine their availability in the study area, we set ten 50 m line transects each year to estimate the relative abundance of each shrub species (following Cares *et al.* 2013). Transects were randomly placed all around the study site and not limited to the live trapping grids.

Data analysis

The associations of each rodent species (*P. darwini* and *O. degus*) with the shrub species at the community level were analyzed for each year by likelihood-ratio goodness-of-fit G-tests, using the number of captures of each rodent associated with each shrub species corrected for their relative availability in the field to estimate the expected values of association under a random process (Sokal & Rohlf 1995). G-tests were performed separately considering the *T. cruzi* infection status of each rodent species (i.e. four G-tests per each sampling year).

To assess rodent preferences for shrub species based on the differential use of each shrub species recorded, we estimated the actual use of each shrub species, calculated as the number of captures under a particular shrub divided by the total captures (recaptures were not considered). We also determined the availability of each plant species, calculated as the number of traps placed under a given plant species divided by the total traps set under plants. With this information, we estimated habitat selection patterns using the compositional analysis approach (originally proposed by Aebischer *et al.* 1993 for habitat use based on telemetry data), which corrects the use/availability ratio of each category (in this case, each shrub species) by the remaining categories available (i.e. the other shrub species available in the sampling area). Use patterns among plant species were assessed pairwise, using the following equation:

$$\mathrm{Use}_{i,j} = \ln\left(U_i / U_j\right) - \ln\left(A_i / A_j\right)$$

where U is the actual use of the plant species *i* and *j*, and A refers to the availability of those plant species in the environment. Positive values indicate preference for a given plant species (i.e. it is used more than expected by its availability in the environment), and negative values indicate avoidance. By adding the pairwise values of each plant species, we obtained an overall value, from which we ranked plant species from 0 (least used) to 8 (most used).

RESULTS

During the sampling period (2010–2013) 1326 individuals of six small mammal species were captured: *P. darwini*, *O. degus*, *Abrothrix olivaceus*, *Abrocoma bennetti*, *Thylamys elegans* and *Oligoryzomys longicaudatus* (Table 1). Considering that the rodents *O. degus* and *P. darwini* were the most abundant species (accounting for 89.4% of total captures), we focused our analyses on these two species. Inter-annual *T. cruzi* infection prevalence ranged between 14% and 73% in *O. degus* and 15% and 59% in *P. darwini*. Detailed information about these rodents (including abundance, gender, infection status, body size and weight) is available in supplementary Appendix S3.

The relative abundances (all years combined) of the shrub species assessed were as follows: *F. thurifera* (Fth, 36.9%), *H. stenophyllum* (Hst, 20.8%), *B. salicifolia* (Bsa, 16.2%), *P. chilensis* (Pch, 8.7%), *B. incisifolia* (Bin, 7.5%), *C. odorifera* (Cod, 3.7%), *S. polygamus* (Spo, 2.5%), *A. arborea* (Aar, 2.1%) and *O. paradoxus* (Opa, 1.5%) (see Appendix S2 and Appendix S4 for details of each plant species).

Table 1. Small mammal species captured in Las Chinchillas National Reserve, Chile

	Captures and abundances per sampling year			
Mammal species	2010	2011	2012	2013
Octodon degus	184 (275 ± 29.1)	126 (189 ± 23.2)	222 (357 ± 36.5)	67 (100 ± 35.8)
Phyllotis darwini	212 (352 ± 35.5)	161 (223 ± 26.9)	112 (169 ± 22.4)	90 (111 ± 12.0)
Other	61	35	29	27

Number of captures is shown by species and year. The abundance ± 1SE estimated by the MARK programme is indicated in parentheses (using a Jackknife estimator based on a closed population model as described in Botto-Mahan *et al.* 2012).

doi:10.1111/aec.12338

Associations among rodent species and shrub community

Non-infected *O. degus* individuals used individual shrub species within the shrub community significantly non-randomly relative to their availability in 2011, 2012 and 2013, while infected *O. degus* individuals showed the same pattern in 2010, 2011 and 2013 (Table 2). However, non-infected *P. darwini* individuals used the shrub community irrespective of availability in 2011, 2012 and 2013, but infected *P. darwini* individuals used the shrub community according to availability in the environment during the four sampling years (Table 2).

Individual shrub species preferences

Infected and non-infected individuals of *O. degus* and *P. darwini* showed strong preferences for *F. thurifera* and *C. odorifera* (Tables 3 and 4, respectively; detailed information is available in Appendix S5), which were used up to eight times more than the other species, whereas *A. arborea* and *O. paradoxus* were the shrub species least used by both rodents. These preferences were highly variable among sampling years, between species and between infected and non-infected individuals. Both rodent species show a 'core' of species (*F. thurifera*, *H. stenophyllum* and *P. chilensis*) consistently preferred over time, species and infection status, whereas the remaining species showed variable use levels (Fig. 1).

DISCUSSION

Trypanosoma cruzi infection is associated with behavioural changes in the two rodent species studied, related to how they used the shrub community. Both rodents used the shrub species available significantly non-randomly relative to their availability, except for infected *P. darwini* individuals. *O. degus* and *P. darwini* preferred

Table 2. Summary of G-tests conducted to examine the association between each rodent species and the overall shrub community during 2010–2013, using the number of captures associated with each shrub species and their relative availability in the field

		Non-infected		Infected	
Mammal species	Year	G	P	G	P
Octodon degus	2010	12.50	0.131	15.96	**0.043**
	2011	52.96	<**0.001**	30.25	<**0.001**
	2012	42.40	<**0.001**	15.19	0.056
	2013	21.75	**0.005**	30.09	<**0.001**
Phyllotis darwini	2010	7.66	0.467	5.61	0.691
	2011	33.30	<**0.001**	7.46	0.488
	2012	32.95	<**0.001**	14.49	0.070
	2013	46.53	<**0.001**	15.01	0.059

Analyses were performed separately for infected and non-infected individuals. Bold figures denote significant *P*-values, indicating that the shrub community is not used according to shrub species relative abundances.

Table 3. Compositional analysis summary for infected (I) and non-infected (NI) *Octodon degus* individuals for each sampling year

	Sampling years							
	2010		2011		2012		2013	
Shrub species	NI	I	NI	I	NI	I	NI	I
Adesmia arborea	8(+)	1(−)	3(−)	8(+)	6(+)	0(−)	6(+)	1(−)
Baccharis salicifolia	4(+)	3(+)	4(+)	2(−)	3(−)	3(+)	3(+)	3(−)
Bridgesia incisifolia	1(−)	7(+)	8(+)	6(+)	7(+)	6(+)	8(+)	0(−)
Colliguaja odorifera	6(+)	2(+)	1(−)	0(−)	1(−)	2(−)	0(−)	2(−)
Flourensia thurifera	3(+)	4(+)	5(+)	3(+)	5(+)	7(+)	2(+)	5(+)
Heliotropium stenophyllum	5(+)	8(+)	7(+)	7(+)	8(+)	5(+)	7(+)	6(+)
Ophryosporus paradoxus	0(−)	5(+)	2(−)	1(−)	0(−)	1(−)	1(−)	8(+)
Porlieria chilensis	2(−)	6(+)	6(+)	4(+)	4(+)	8(+)	4(+)	7(+)
Schinus polygamous	7(+)	0(−)	0(−)	5(+)	2(−)	4(+)	5(+)	4(+)

Ranked values are presented, ranging from the least (0 value) to the most (8 value) preferred shrub species. Use behaviour (positive values indicate preference and negative values indicate avoidance) is indicated in parentheses.

 doi:10.1111/aec.12338

Table 4. Compositional analysis summary for infected (I) and non-infected (NI) *Phyllotis darwini* individuals for each sampling year

	Sampling years							
	2010		2011		2012		2013	
Shrub species	NI	I	NI	I	NI	I	NI	I
Adesmia arborea	1(−)	8(+)	8(+)	2(−)	8(+)	2(−)	1(−)	0(−)
Baccharis salicifolia	7(+)	4(+)	5(+)	4(+)	1(−)	4(+)	3(−)	2(−)
Bridgesia incisifolia	3(+)	5(+)	6(+)	0(−)	2(+)	5(+)	6(+)	7(+)
Colliguaja odorifera	4(+)	3(+)	7(+)	1(−)	6(+)	8(+)	4(+)	6(+)
Flourensia thurifera	6(+)	2(−)	3(+)	6(+)	4(+)	6(+)	5(+)	5(+)
Heliotropium stenophyllum	5(+)	0(−)	4(+)	7(+)	7(+)	7(+)	8(+)	4(+)
Ophryosporus paradoxus	8(+)	1(−)	0(−)	3(−)	0(−)	3(−)	2(−)	1(−)
Porlieria chilensis	2(+)	7(+)	2(+)	5(+)	5(+)	0(−)	7(+)	8(+)
Schinus polygamus	0(−)	6(+)	1(+)	8(+)	3(+)	1(−)	0(−)	3(+)

Ranked values are presented, ranging from the least (0 value) to the most (8 value) preferred shrub species. Use behaviour (positive values indicate preference and negative values indicate avoidance) is indicated in parentheses.

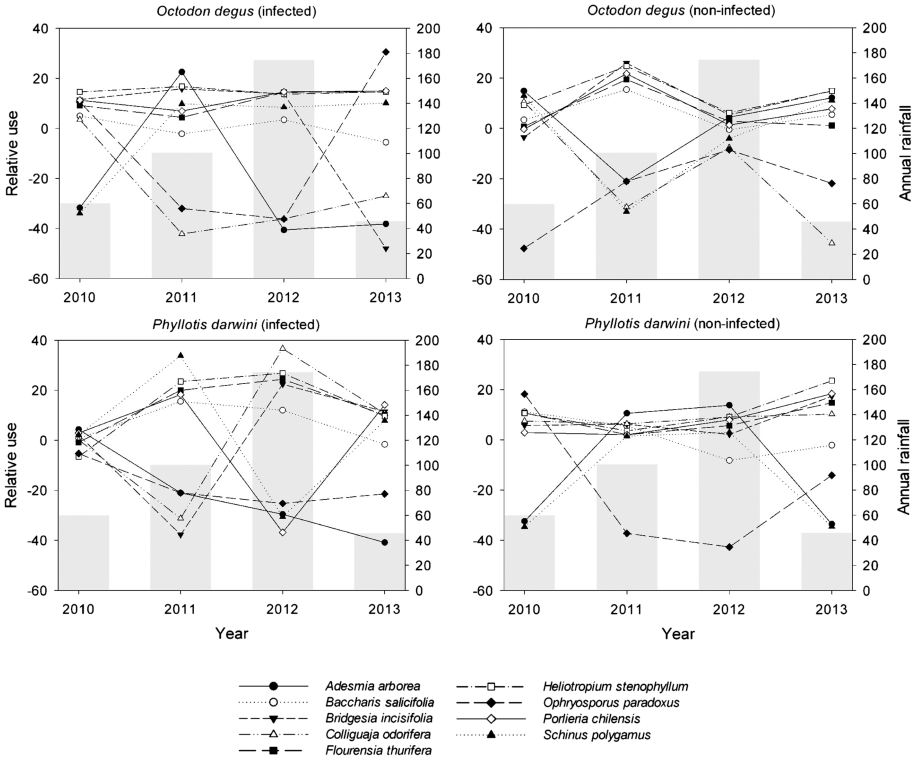

Fig. 1. Relative use of each plant shrub species available in each sampling year for infected and non-infected rodents; values > 0 indicate preference, and < 0 indicate avoidance. Grey bars in the background represent the cumulative rainfall of the past 12 months previous to the sampling events.

some plant species (particularly *F. thurifera* and *C. odorifera*), which were consistently used regardless of their relative abundance. Those shrub species might be providing shelter or food resources for *O. degus* and *P. darwini*, whereas other species do not. On the other hand, other shrub species such as *O. paradoxus* and *A. arborea* were largely ignored, irrespective of their abundance. Those preferences seem to be affected by the infection status, infected individuals being less selective than non-infected ones (especially *P. darwini*). Additionally, preference patterns of both rodent species varied from 1 year to another during the four sampling years. Notwithstanding, because of very low infection prevalence in some years, we cannot discount that some

doi:10.1111/aec.12338

of the non-significant results detected may emerge from low-sample sizes in the infected individual groups.

Previous studies have identified inter-specific competition as the most important mechanism responsible for determining the foraging behaviour of *O. degus* and *P. darwini* (Andreo *et al.* 2009); *O. degus* outcompeting *P. darwini* and displacing it to sub-optimal (i.e. open) areas (Yunger *et al.* 2002; Kelt *et al.* 2004c). A previous study in this area (Jiménez *et al.* 2015) showed behavioural changes related to *T. cruzi* infection status, where infected *O. degus* individuals decreased movement distances, while infected *P. darwini* increased theirs compared with non-infected individuals. Such changes might be related to impaired competitive capabilities in infected rodents, which would be displaced to sub-optimal areas by non-infected individuals.

Additionally, plant-animal interactions may be also modulated by abiotic factors. Rainfall has been acknowledged as the main driver of abundance and composition changes in the plant community, which alters the competition between *O. degus* and *P. darwini* (Andreo *et al.* 2009; Gutierrez *et al.* 2010). In our 4-year dataset, the variation in rodent and plant abundance might be related to variation in the cumulative precipitation of the previous year (cf. Table 1, Fig. 1 and Appendix S3). In those years with abundant precipitation, calculated as the cumulative 1-year rainfall previous to the sampling date, higher rodent abundances were detected, and their preference patterns intensified, whereas after a year with scarce precipitation, abundances decreased, and rodents were less selective on the available shrub species.

The temporal fluctuations in *O. degus* and *P. darwini* abundance may significantly alter the abundance of certain plant species as a result of seed predation pressure. Shrub preference patterns and their temporal variation could be also influenced by the prevalence of an infectious organism such as *T. cruzi*, which has very variable prevalence levels across years (Botto-Mahan *et al.* 2010, 2012, 2015). Our results show that *T. cruzi* infection in wild small mammals is able to modify habitat use and preference patterns for certain shrub species. To the best of our knowledge, this is the first study reporting the effects of infection status on the differential use of plant species, which may be related to the altered movement behaviour previously reported for these rodent species (Jiménez *et al.* 2015). In summary, both rodents exhibited preferences for shrub species, which were affected by infection status and were variable in time.

ACKNOWLEDGEMENTS

A. Bacigalupo, P. Correa, F. González, C. Jiménez, A. López, V. Manríquez, M. Martínez, L. Moreno, N. Peña, T. Poch, M. Puebla, G. Rojo and A. Yáñez-Meza assisted in the field, and F. Peña in the laboratory. V. Ardiles and J. Arriagada of the Herbarium of National Museum of Natural History (SGO) provided preserved plant material and advice. We especially thank R. Medel, M.A. Sepúlveda, C. González-Browne and two anonymous reviewers for important suggestions to improve the clarity of early versions of this manuscript. We are grateful to F. Osorio and the Flora Chilena online encyclopaedia for the *Schinus polygamus* photograph. We thank CONAF-Illapel for logistic support. Financial support for this study was provided by FONDECYT 11090086 & 1140521 (CBM). EO and RAC were supported by CONICYT Doctoral and Master Fellowships, respectively. A CONICYT-Becas Chile Doctoral Scholarship supported PAR.

REFERENCES

Aebischer N. J., Robertson P. A. & Kenward R. E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–25.

Amman B. R., Manangan A. P., Flietstra T. D., *et al.* (2013) Association between movement and Sin Nombre virus (Bunyaviridae: Hantavirus) infection in North American deermice (*Peromyscus maniculatus*) in Colorado. *J. Wildlife Dis.* **49**, 132–42.

Andreo V., Lima M., Provensal C., Priotto J. & Polop J. (2009) Population dynamics of two rodent species in agroecosystems of central Argentina: intra-specific competition, land-use, and climate effects. *Popul. Ecol.* **51**, 297–306.

Botto-Mahan C., Acuña-Retamar M., Campos R., Cattan P. E. & Solari A. (2009) European rabbits (*Oryctolagus cuniculus*) are naturally infected with different *Trypanosoma cruzi* genotypes. *Am. J. Trop. Med. Hyg.* **80**, 944–6.

Botto-Mahan C., Bacigalupo A., Correa J. P., Oda E. & Solari A. (2012) Field assessment of *Trypanosoma cruzi* infection and host survival in the native rodent *Octodon degus*. *Acta Trop.* **122**, 164–7.

Botto-Mahan C., Campos R., Acuña-Retamar M., Coronado X., Cattan P. E. & Solari A. (2010) Temporal variation of *Trypanosoma cruzi* infection in native mammals in Chile. *Vector-Borne Zoonot.* **10**, 317–9.

Botto-Mahan C., Cattan P. E., Canals M. & Acuña M. (2005a) Seasonal variation in the home range and host availability of the blood-sucking insect *Mepraia spinolai* in wild environment. *Acta Trop.* **95**, 160–3.

Botto-Mahan C., Ortiz S., Rozas M., Cattan P. E. & Solari A. (2005b) DNA evidence of *Trypanosoma cruzi* in the Chilean wild vector *Mepraia spinolai* (Hemiptera: Reduviidae). *Mem. I. Oswaldo Cruz* **100**, 237–9.

Botto-Mahan C., Rojo G., Sandoval-Rodríguez A., Peña F., Ortiz S. & Solari A. (2015) Temporal variation in *Trypanosoma cruzi* lineages from the native rodent *Octodon degus* in semiarid Chile. *Acta Trop.* **151**, 178–181.

Bozinovic F. (1997) Diet selection in rodents: an experimental test of the effect of dietary fiber and tannins on feeding behavior. *Rev. Chil. Hist. Nat.* **70**, 67–71.

Cares R. A., Muñoz P. A., Medel R. & Botto-Mahan C. (2013) Factors affecting cactus recruitment in semiarid Chile: a role for nurse effects? *Flora* **208**, 330–5.

Cortés A., Pino C. & Rosenmann M. (1994) Water balance of a small mammals assemblage from two localities of the arid

 doi:10.1111/aec.12338

mediterranean region of north-central Chile: a field study. *Rev. Chil. Hist. Nat.* **67**, 65–77.
Coura J. R. & Vinas P. A. (2010) Chagas disease: a new worldwide challenge. *Nature* **465**, S6–S7.
Day J. F. & Edman J. D. (1983) Malaria renders mice susceptible to mosquito feeding when gametocytes are most infective. *J. Parasitol.* **69**, 163–70.
di Castri F. & Hajek E. R. (1976) *Bioclimatología de Chile*. Ediciones de la Universidad Católica de Chile, Santiago de Chile.
Gutierrez J. R., Meserve P. L., Kelt D. A., *et al.* (2010) Long-term research in Bosque Fray Jorge National Park: twenty years studying the role of biotic and abiotic factors in a Chilean semiarid scrubland. *Rev. Chil. Hist. Nat.* **83**, 69–98.
Hoffmann A. (1980) *Flora silvestre de Chile, zona central: una guía para la identificación de las especies vegetales más frecuentes*. Ediciones Fundación C, Gay, Santiago de Chile.
Jekl V., Hauptman K. & Knotek Z. (2011) Diseases in pet degus: a retrospective study in 300 animals. *J. Small Anim. Pract.* **52**, 107–12.
Jiménez C., Fontúrbel F. E., Oda E., Ramírez P. A. & Botto-Mahan C. (2015) Parasitic infection alters rodent movement in a semiarid ecosystem. *Mamm. Biol.* **80**, 255–9.
Jimenez J. E. & Lorca M. (1990) American trypanosomiasis in wild vertebrates and its relation to the vector *Triatoma spinolai*. *Arch. Med. Vet.* **22**, 179–83.
Johnson-Delaney C. A. (2006) Common procedures in hedgehogs, prairie dogs, exotic rodents, and companion marsupials. *Vet. Clin. Exot. Anim.* **9**, 415–35.
Kelt D. A., Meserve P. L., Forister M. L., Nabors L. K. & Gutierrez J. R. (2004a) Seed predation by birds and small mammals in semiarid Chile. *Oikos* **104**, 133–41.
Kelt D. A., Meserve P. L. & Gutierrez J. R. (2004b) Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *J. Biogeogr.* **31**, 931–42.
Kelt D. A., Meserve P. L., Nabors L. K., Forister M. L. & Gutierrez J. R. (2004c) Foraging ecology of small mammals in semiarid Chile: the interplay of biotic and abiotic effects. *Ecology* **85**, 383–97.
Lee T. M. (2004) *Octodon degus*: a diurnal, social, and long-lived rodent. *Ilar J.* **45**, 14–24.
Lima M., Marquet P. A. & Jaksic F. M. (1999) El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. *Ecography* **22**, 213–8.
Medel R., Vergara E., Silva A. & Kalin-Arroyo M. (2004) Effects of vector behavior and host resistance on mistletoe aggregation. *Ecology* **85**, 120–6.
Milstead W. B., Meserve P. L., Campanella A., Previtali M. A., Kelt D. A. & Gutierrez J. R. (2007) Spatial ecology of small mammals in north-central Chile: role of precipitation and refuges. *J. Mammal.* **88**, 1532–8.
Morton D. B., Abbot D., Barclay R., *et al.* (1993) Removal of blood from laboratory mammals and birds. *Lab. Anim* **27**, 1–22.
Muñoz-Pedreros A. & Gil C. C. (2009) Orden Rodentia. In: *Mamíferos de Chile* (eds A. Muñoz-Pedreros & J. Yáñez) 93–157. CEA Ediciones, Valdivia, Chile.
Owen R. D., Goodin D. G., Koch D. E., Chu Y. K. & Jonsson C. B. (2010) Spatiotemporal variation in *Akodon montensis* (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in a subtropical forest ecosystem. *J. Mammal.* **91**, 467–81.
Rozas M., Botto-Mahan C., Coronado X., Ortiz S., Cattan P. E. & Solari A. (2007) Coexistence of *Trypanosoma cruzi* genotypes in wild and periodomestic mammals in Chile. *Am. J. Trop. Med. Hyg.* **77**, 647–53.
Schenone H., Contreras M. C., Salinas P., Sandoval L., Rojas A. & Villaroel F. (1995) Epidemiology of Chagas disease in Chile. Frequency of *Trypanosoma cruzi* human infection by age groups and regions. *Boletín Chileno de Parasitología* **50**, 84–6.
Sikes R. S., Gannon W. L. & Care and Use Committee (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**, 235–53.
Sokal R. R. & Rohlf F. J. (1995) *Biometry. The Principles and Practice of Statistics in Biological Research*. WH Freeman and Co., New York, USA.
Strauss S. Y. & Irwin R. E. (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Evol. S.* **35**, 435–66.
Veas F., Breniere S. F., Cuny G., Brengues C., Solari A. & Tibayrenc M. (1991) General procedure to construct highly specific kDNA probes for clones of *Trypanosoma cruzi* for sensitive detection by polymerase chain reaction. *Cell. Mol. Biol.* **37**, 73–84.
Vyas A., Kim S. K., Giacomini N., Boothroyd J. C. & Sapolsky R. M. (2007) Behavioral changes induced by *Toxoplasma infection* of rodents are highly specific to aversion of cat odors. *Proc. Natl. Acad. Sci. U. S. A.* **104**, 6442–7.
Warren R. J., Giladi I. & Bradford M. A. (2014) Competition as a mechanism structuring mutualisms. *J. Ecol.* **102**, 486–95.
Xavier S. C. D., Roque A. L. R., Lima V. D., *et al.* (2012) Lower richness of small wild mammal species and Chagas disease risk. *PLoS Neglect. Trop. D.* **6**, e1647.
Yunger J. A., Meserve P. L. & Gutierrez J. R. (2002) Small-mammal foraging behavior: mechanisms for coexistence and implication for population dynamics. *Ecol. Monogr.* **72**, 561–77.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Location of the three live-trapping grids in the study area.
Appendix S2. Images of plant species assessed in the study area.
Appendix S3. Descriptive data for *Octodon degus* and Phyllotis darwini for each sampling year.
Appendix S4. Description of the plant species included in the analyses.
Appendix S5. Compositional analysis of use patterns for infected and non-infected individuals by rodent species.

doi:10.1111/aec.12338