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Source: *Behavioral Ecology and Sociobiology*, Vol. 66, No. 1 (January 2012), pp. 57-66

Published by: Springer

Stable URL: <http://www.jstor.org/stable/41414711>

Accessed: 06-05-2016 20:32 UTC

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Sociality, exotic ectoparasites, and fitness in the plural breeding rodent *Octodon degus*

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Received: 10 January 2011 / Revised: 21 June 2011 / Accepted: 24 August 2011 / Published online: 2 September 2011
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Abstract Social animals are susceptible to high infection levels by contact-transmitted parasites due to increased conspecific interaction. Exotic parasites are known to have adverse consequences on native hosts. We examined the relationship between social group size and exotic ectoparasite loads, and adult infection levels with per capita fitness and offspring survival in the plural breeding rodent *Octodon degus* in central Chile. Degus at our site were almost entirely infected by two exotic ectoparasites: the fleas *Leptopsylla segnis* and *Xenopsylla cheopis*. Neither group size nor number of females per group predicted the abundance of either exotic flea species. The per capita number of pups (per capita fitness) that emerged from burrow systems used by

known social groups was negatively correlated with abundance of *L. segnis* but not *X. cheopis*. On adults, *X. cheopis* abundance was three times greater than *L. segnis* but was not significantly correlated with per capita fitness. In females, *L. segnis* abundance was negatively correlated with peak body mass during pregnancy. Adult ectoparasite load was not correlated with offspring survival. Based on these results, we hypothesize that high infection levels of *L. segnis* result in decreased reproductive fitness of adult female degus but are not a cost of sociality because parasite loads are not predicted by social group size. Further work is needed to experimentally test this hypothesis and to determine if *L. segnis* serves as a vector for a deleterious pathogen. Lastly, the lack of native ectoparasites may explain why a previous study at our site determined that behavioral adaptations needed to cope with high ectoparasite burdens (e.g., grooming) are not extensive in degus; they simply have not had the coevolutionary time needed for selection of these behaviors.

Communicated by C. Brown

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Keywords Coevolution · Ectoparasites · Fitness · Fleas ·
Invasive parasite · Sociality

The arms-race paradigm typically prevails when host and parasite coevolve (Anderson and May 1982). Host behavioral and physiological adaptations that minimize transmissibility and reduce pathogenicity are favored by selection, resulting in negligible impacts of parasites on host fitness and survival (Freeland 1976, 1979; Møller et al. 1993; Altizer et al. 2003). Native hosts, however, are often susceptible to exotic parasites given that little evolutionary time has passed in order for hosts to develop defense mechanisms against foreign infectious agents (Dobson and Foufopoulos 2001). Indeed, introduced parasites have contributed to the population decline of several mammals including black-footed

ferrets (*Mustela nigripes*; Thorne and Williams 1988), prairie dogs (*Cynomys* sp.; Stapp et al. 2004), Serengeti lions (*Panthera leo*; Roelke-Parker et al. 1996), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) (Leroy et al. 2004). In colonial prairie dogs (*Cynomys* sp.), exotic plague (*Yersinia pestis*) has led to epizootics, causing near 100% mortality of infected colonies and severe population crashes (Cully and Williams 2001). Studies that investigate the interplay between introduced parasites and native host behavior provide novel opportunities to gain insight into host–parasite coevolution and increase our understanding of invasive disease biology.

Highly social animals may be at greater risk of infection by contagious parasites relative to solitary living species due to high rates of conspecific interaction (Alexander 1974; Møller et al. 1993; Altizer et al. 2003). For example, parasite abundance is greater in the highly social black-tailed prairie dogs, (*Cynomys ludovicianus*) compared to the loosely colonial white-tailed prairie dogs (*Cynomys leucurus*) (Hoogland 1979). In birds, social passerines incur greater risk of contact-transmitted parasites relative to sympatric, solitary species (Poulin 1991). Additional empirical studies conducted on mammals and birds have demonstrated a positive relationship between host social group size and contact-transmitted parasite loads within species (Hoogland and Sherman 1976; Freeland 1979; Brown and Brown 1986; Côté and Poulin 1995; Whiteman and Parker 2004). Thus, increased infection by contagious parasites is hypothesized to be a widely occurring burden of group living (Alexander 1974; Møller et al. 1993; Altizer et al. 2003).

Studies addressing the links between sociality, parasitism, and fitness have largely focused on animals that form nonbreeding aggregations (Blanco et al. 1997) or colonial breeding hosts (Brown and Brown 1986; Roelke-Parker et al. 1996). In colonial swallows, high ectoparasite loads (i.e., swallow bugs, *Oeciacus vicarius*) are correlated with decreased nestling body mass, resulting in increased juvenile mortality (Brown and Brown 1986). Additional research has focused primarily on social species in which one female breeds and nonbreeders provide alloparental care (i.e., singular breeders, Silk 2007). For example, several studies have demonstrated a positive link between ectoparasite loads and decreased over winter survival in singular breeding marmots (Arnold and Lichtenstein 1993, Van Vuren 1996). Together these studies suggest that contagious parasites may pose a fitness cost to colonial animals and singular breeders, yet the fitness consequences of ectoparasitism in social species in which most group members rear their offspring (i.e., plural breeders, Silk 2007) are poorly known.

Fitness consequences of sociality vary considerably across taxa with different breeding systems (Silk 2007); what is the role of parasitism in explaining this variation? In

particular, fitness costs of parasitism in species with multiple breeding females that exhibit communal care to young have been given little attention. In plural breeders with communal care, the risk of vertical transmission of parasites from adults to offspring is high due to extensive care of young. In mammals, the risk of parasite transmission increases during communal nursing, i.e., where offspring suckle milk from nonmaternal females (Roulin and Heeb 1996). Ectoparasite loads are greater in plural breeding and communally nursing black-tailed prairie dogs (*C. ludovicianus*), relative to sympatric yet loosely colonial white-tailed prairie dogs (*C. leucurus*). However, the fitness costs of ectoparasitism in *Cynomys* sp. remain unclear (Hoogland 1979). Given the potential for multiple modes of transmission (e.g., horizontally: adults-to-adults; vertically: mothers and nonkin nursing females to offspring), research into the fitness consequences of parasitism in communal breeders with extensive parental care may provide insight into the primary drivers of variation in fitness across social systems and taxa (Hayes et al. 2011; Silk 2007).

Degus (*Octodon degus*) are highly social caviomorph rodents that live in groups consisting of kin and unrelated individuals including several males and reproductive females, which frequently use the same burrow systems (Ebensperger et al. 2004; Hayes et al. 2009). Burrow systems are extensive, involving numerous burrow openings (Hayes et al. 2007). Females breed plurally and engage in a number of social activities that inevitably increase contact between mothers and pups including indiscriminately accepting nondescendent young (Ebensperger et al. 2007) as well as nursing own and nondescendent offspring (Ebensperger et al. 2006; Becker et al. 2007). These intimate behaviors likely facilitate opportunities for vertical transmission of contact-transmitted ectoparasites to both descendent and nondescendent young. Degus at our site produce one litter per year consisting of five to six offspring (Meserve et al. 1984; Ebensperger et al. 2007).

We previously determined that social group size in degus is not correlated with food availability, distance to cover, or burrow density of burrow systems (Hayes et al. 2009). We also determined a weak but significant relationship between the per capita number of weaned offspring and the number of females per group, but not with total group size. Food availability at burrow systems, distance to cover, and density of burrow openings were not correlated with per capita fitness or pup survival. Postweaning survivorship of pups was not correlated with either social group size or number of females per group (Hayes et al. 2009). So, it is likely that other factors explain variation in fitness in degus.

Herein, we investigate the sociality–parasite–fitness nexus in a wild population of degus in central Chile. We test the hypothesis that ectoparasite loads are influenced by social group size. If increased ectoparasitism is a cost of

sociality, we expect to see a positive relationship between ectoparasite loads and both total group size as well as the number of females per group. We also examine the fitness consequences of infection. We predict that greater abundance of exotic ectoparasites is negatively correlated with the per capita number of pups that emerge from burrow systems used by known social groups (hereafter referred to as per capita fitness). In order to determine if ectoparasite loads explain our previous observation that increasing female group size is negatively correlated with per capita fitness (Hayes et al. 2009), we test for differences in ectoparasite loads between males and females and the relationship between per capita fitness, and the ectoparasite loads of all adults and adult females, separately. Additionally, we predict that the abundance of ectoparasite loads by social group is negatively correlated with the proportion of offspring that survive up to 2 months post weaning. We quantify ectoparasite loads of adult degus during the period of female pregnancy to lactation, per capita fitness, and pup survival up to 2 months. Given that parasites may act synergistically or competitively in their impact on hosts (Pedersen and Fenton 2007), we also test correlations between ectoparasite species to determine the influence of their interactions on host fitness.

Materials and methods

Study site

We monitored degu social groups at the Universidad de Chile's experimental field station, Rinconada de Maipú (33° 23' S, 70°31' W, elevation ~495 m) in central Chile, during the austral winter to spring transition in 2006 and 2007. The climate is Mediterranean type, featuring cool wet winters and warm dry summers. The habitat, known as Chilean matorral, consists of an open landscape with scattered shrubs. In June 2006 and 2007, we conducted five consecutive days of grid trapping using large Sherman live traps (30×10×9.5 cm) (H.B. Sherman Traps Inc., Tallahassee, FL, USA) and locally produced metal live traps baited with dry oats on previously established trapping grids (grid 1=0.18 ha [30×60 m] and grid 2=0.25 ha [50×50 m]) (Burger et al. 2009). Grid trapping allowed us to determine the density of degus and to assign radio collars for tracking individuals to burrow systems with radio telemetry (see below). During grid trapping, we set traps at fixed stations spaced at 5-m intervals (91 traps on grid 1 and 121 traps on grid 2) in the morning prior to animal emergence. After 2 h, we determined the location of all captures and closed the traps. We recorded the sex, body mass, and reproductive status of all animals. We marked animals at first capture by clipping no more than one toe per foot and released them at their

point of capture. Marking techniques are described elsewhere (Hayes et al. 2009) and are in accordance with the standard animal care and use protocol established by the American Society of Mammalogist (2007). We also recorded recaptured animals and fitted some adult females with radio transmitters (RI-2D, Holohil Systems Limited, Ontario, Canada and SOM-2190A, Wildlife Materials Incorporated, Murphysboro, IL) weighing no more than 5% of animals body mass.

Nighttime telemetry and burrow trapping

Subsequent to establishing active burrow systems, we conducted nighttime telemetry and burrow trapping during late Sep–Nov in 2006 and late Aug–Nov 2007. These periods correspond with late pregnancy through lactation in females. We defined a burrow system as a group of burrow openings spanning 2–3 m in diameter (Ebensperger et al. 2004; Hayes et al. 2007). Therefore, we used a combination of nighttime telemetry and burrow trapping to determine overnight association of individuals at burrow systems to identify social groups (Ebensperger et al. 2004; Hayes et al. 2009). To verify which burrow systems individuals used, we tracked radio-collared animals once per night ca. 1 h after sunset with a handheld, 3-element Yagi antenna and an LA 12-Q receiver (AVM Instrument Co., CA) or FM-100 receiver (Advanced Telemetry Systems, MN) from mid June to September. We trapped active burrow systems during the austral winter to spring transition (Sep–Nov) of both years by placing 10–12 traps at each active burrow system (Burger et al. 2009). As with grid trapping, we set traps baited with dry oats in the morning prior to animal emergence (0700–0800 h) at burrow openings, along runways, or at nearby dustbathing sites. At ca 1.5 h after degu emergence from burrows, we determined the identity and location of all captured individuals and closed traps until the next trapping event. Animals were processed similarly to grid trapping and then released at the same burrow system of their capture.

Sixteen and thirty-four radio-collared individuals had sufficient data (> six nighttime fixes) to be assigned group membership in 2006 and 2007, respectively. Using nighttime telemetry, we located animals in burrow systems 34.0±3.2 times in 2006 and 18.3±4.2 times in 2007 (Hayes et al. 2009). Previous studies of degu sociality indicate that this telemetry effort, in conjunction with burrow trapping, is sufficient to accurately quantify degu social groups (Ebensperger et al. 2004; Ebensperger et al. 2009; Hayes et al. 2009).

Determining social groups

To determine social group size and composition, we compiled a symmetric similarity matrix of pairwise tempo-

ral associations by burrow use locations from trapping and telemetry data for all adult degus (Whitehead 2009). We calculated a proportion of nightly overlap per individual with all other adult degus from these pairwise comparisons based on the number of times that two individuals were located or captured in the same burrow system divided by the number of times that the same two individuals were located or captured. We conducted hierarchical cluster analysis (average linkage method) of the association matrix using SOCPROG (Whitehead 2009) to demarcate social groups. This technique clusters individuals by both preferred as well as least preferred partnerships. In other words, two individuals can be members of a group because they are documented together frequently, or because they both do not associate with individuals outside of their groups. In order to assign groups, we only used individuals with at least i) three captures at burrow systems or ii) six nighttime telemetry fixes in burrow systems. We confirmed the fit of data using cophenetic correlation coefficient to determine the actual association indices and the levels of clustering in the diagram. We chose maximum modularity criteria (Newman 2004) to cut off the dendrogram and define social groups (Whitehead 2009).

Measures of fitness

Burrow trapping sessions corresponded with female lactation and pup emergence from burrow systems (Hayes et al. 2009), which enabled us to evaluate the per capita fitness correlates of ectoparasitism. Degus produce precocial young with relatively short lactation periods and begin eating solid foods early in ontogeny (Veloso and Kenagy 2005). Thus, it is unlikely that trapping pups during postparturition impacts pup survivorship or fitness of the mothers. Degus are plural breeders and rear their offspring communally, so we could not use burrow trapping to determine maternity of pups within social groups. Our estimate of fitness is, therefore, based on the number of offspring, per female, per social group that emerge from burrow systems used by known social groups. We also determined pup survival up to 2 months post burrow emergence following Hayes et al. (2009). Both measures are based on the assumptions that all pregnant females produced litters of equal size and successfully reared offspring to emergence. Because all females in our study displayed physical signs of pregnancy and lactation and probably contributed to the production of pups for each social unit, we feel our assumption is valid. Previous studies used similar indices to estimate fitness and juvenile survival for plural breeding caviomorph rodents (Lacey 2004) including degus (Hayes et al. 2009).

In order to determine if adult parasite loads affect offspring survival, we calculated an index of pup survivorship based on

the proportion of offspring caught during the first 2 months of life (up to 70 g; Ebensperger et al. 2007; Hayes et al. 2009) that were recaptured as juveniles (>70 g) when individuals become more active aboveground (Ebensperger and Hurtado 2005; Ebensperger et al. 2007). We limited survivorship analysis to 2 months because juvenile mortality in degus is high (>65%) in the wild (Meserve et al. 1984; Ebensperger et al. 2009). In this analysis, we included offspring that weighed <70 g at first capture and weighed >70 g at a future recapture during the austral winter–spring. We continued trapping until >95% of pups captured in a single trapping effort (i.e., 1 day) were recaptures. We recaptured most individuals at least 1–2 weeks after initial capture. We also included individuals that were not recaptured during the austral winter–spring but were captured during subsequent spring, summer, or autumn trapping. We failed to capture offspring weighing less than 70 g at first capture for one social group in 2006; therefore, we excluded this group from our analysis of offspring survival. We also excluded two social groups in 2006 found in the area of grid 2 in our offspring survival analysis that were included in the analysis of ectoparasite loads and group size because this grid was not monitored for social groups in 2007 due to low population density. Male degus have a high rate of migration or disappearance (Ebensperger et al. 2009) and females rarely survive to produce a second litter (Hayes et al. 2009). Therefore, we could not determine the effects of current ectoparasitic infection on future reproductive success.

Quantifying ectoparasite loads

To test the parasite–fitness burden hypothesis, each adult degu was sampled for ectoparasitic fleas during the period of female lactation. We sampled for ectoparasites by brushing adults with a flea comb over a 19-L bucket containing a few milliliters of 95% ethanol (to euthanize ectoparasites). We combed each degu 15 times from anterior to posterior, and five times posterior to anterior on the dorsal side of the body, five times anterior to posterior and posterior to anterior on each flank, and five times on the top of the head from the posterior attachment of the ears to above the eyes (Perez-Orella and Shulte-Holstedde 2005). We stored ectoparasites in 95% ethanol for identification and count in the lab with a dissecting microscope.

Statistical analyses

We quantified ectoparasite loads following Bush et al. (1997) with some modification: (1) *Abundance*—mean number of individuals of a particular parasite and (2) *Prevalence*—proportion of host individuals infected by particular parasite taxa. Since we had no a priori knowledge

of social group members, values reflect sampled individuals only.

We performed statistical tests using SPSS 16.0 (Chicago, IL, USA). We used Mann–Whitney U test to compare parasite loads between adult females and males. We ran analysis of covariance (ANCOVA) with group size estimates (total group size and number of females) as covariates and year as the fixed factor to test the prediction that increasing ectoparasite abundance is a cost of sociality. We ran ANCOVAs to test year as a fixed factor and flea abundances as covariates to test the predictions that per capita fitness decreased with increasing ectoparasite loads. We do not report main effects in analyses in which statistically significant interactions were detected. We used a Spearman rank correlation to test the relationship between ectoparasite loads of natal group adults (total and females only) and pup survival up to 2 months. For all analyses, we tested normality assumptions using Shapiro–Wilk's test; Levene's test determined if variances in the data were homogenous. We analyzed data that were not normalized or homogenized using nonparametric statistics. All tests were two-tailed. Data are reported as means \pm SE. The alpha level was set at 0.05.

Results

Over the course of 2 years, we determined group sizes, parasite loads, and fitness measures for 20 degu social groups. We monitored 65 adult degus belonging to 11 social groups in 2006 and 60 adult degus belonging to nine social groups in 2007. No individuals were present in both years. Descriptive statistics of social group composition are reported elsewhere (Hayes et al. 2009). Across years, total group size (adult males and females) ranged from 2 to 11 adults; female group size ranged from one to eight. We sampled ectoparasites from 59 and 49 adult degus that belonged to social groups in 2006 and 2007, respectively. In both years, we sampled >75% of individuals per social group for ectoparasites. A total of 687 fleas were collected in 2006, of which 587 (85%) were *Xenopsylla cheopis* and 98 (14%) were *Leptopsylla segnis*. In 2007, we collected 432 total fleas. Of these, 270 (62.5%) were *X. cheopis* and 162 (37.5%) were *L. segnis*. The overall flea abundance (both flea species) of adult degus in 2006 was 11.64 ± 6.66 and 8.82 ± 9.03 in 2007. In 2006, *X. cheopis* abundance on adult degus was 9.95 ± 6.13 ; *L. segnis* of adult degu abundance was 1.66 ± 1.93 . In 2007, *X. cheopis* abundance on adult degus was 5.51 ± 6.27 and *L. segnis* abundance 3.31 ± 4.63 . Across years, all degus sampled were infected with *X. cheopis*. Prevalence of *L. segnis* was 67.8% (40/59) in 2006 and 81.6% (40/49) in 2007 (Table 1). Only two adults (one male and one female) (3.3% prevalence) were

Table 1 The prevalence and origin of ectoparasites found on adult degus by year. Exotic species are in bold

Year	Ectoparasite	Prevalence	Origin
2006	<i>Xenopsylla cheopis</i>	100.0%	Old World^a
	<i>Leptopsylla segnis</i>	67.8%	Old World^a
	<i>Abrocomophaga hellenthali</i>	3.3%	New World ^b
	<i>Ornithonyssus bacoti</i>	1.7%	Unknown
2007	<i>Xenopsylla cheopis</i>	100.0%	Old World^a
	<i>Leptopsylla segnis</i>	81.6%	Old World^a

^a From Krasnov (2008)

^b From Price and Timm (2000)

infected with the native chewing louse, *Abrocomophaga hellenthali* in 2006; no degus were infected with *A. hellenthali* in 2007. One adult male was infected with the tropical fowl mite, *Ornithonyssus bacoti* in 2006; zero adults were infected with *O. bacoti* in 2007. The abundance of *X. cheopis* did not differ between sexes (Table 2) in 2006 ($U=337.5$, males $N_1=21$, females $N_2=38$, $P=0.33$) or 2007 ($U=157$, males $N_1=13$, females $N_2=36$, $P=0.08$). Similarly, the abundance of *L. segnis* on adult males did not differ from adult females (Table 2) in 2006 (Mann–Whitney U test: $U=390.0$, males $N_1=21$, females $N_2=38$, $P=0.88$) or 2007 ($U=169$, males $N_1=13$, females $N_2=36$, $P=0.14$).

Group size and parasite loads

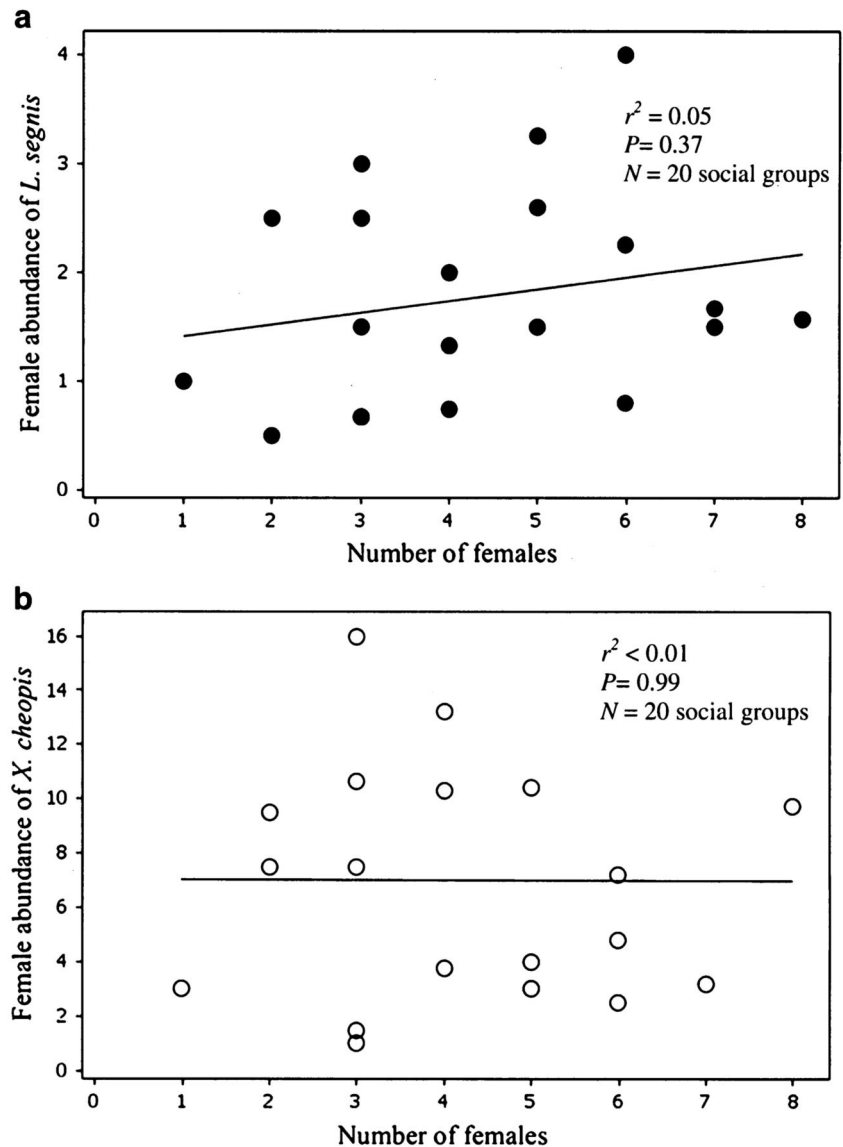
Across years, abundance of *L. segnis* was not predicted by total group size (ANCOVA: model $F_{1,15}=0.949$, $P=0.345$). Likewise, the number of adult females per group did not predict the abundance of *L. segnis* on adult females (ANCOVA: model $F_{1,16}=0.168$, $P=0.688$; Fig. 1a). There was not a year \times group size interaction in either analysis (total group size: $F_{1,15}=1.296$, $P=0.273$; female group size: $F_{1,15}=0.018$, $P=0.895$).

A year \times group size interaction was detected ($F_{1,15}=5.072$, $P=0.039$) in the analysis of *X. cheopis* abundance and total group size. However, subsequent regressions for each year did not reveal statistically significant relationships between the abundance of *X. cheopis* and total group size in 2006 ($r^2=0.33$, $P=0.104$) or 2007 ($r^2=0.09$, $P=$

Table 2 Exotic ectoparasite loads (mean \pm SE) of adult degus by sex and year. Sample sizes are in parentheses

Year	Ectoparasite	Males	Females
2006	<i>Xenopsylla cheopis</i>	8.76 ± 1.28 (21)	10.61 ± 1.01 (38)
	<i>Leptopsylla segnis</i>	1.76 ± 0.49 (21)	1.61 ± 0.28 (38)
2007	<i>Xenopsylla cheopis</i>	9.92 ± 2.89 (13)	3.92 ± 0.44 (36)
	<i>Leptopsylla segnis</i>	5.23 ± 1.5 (13)	2.61 ± 0.70 (36)

Fig. 1 The relationship between abundance of ectoparasites (**a** *L. segnis*, **b** *X. cheopis*) of adult females and number of adult females and number of adult females per social group



0.370). The abundance of *X. cheopis* on adult females did not differ between years (year * group size interaction, $F_{1,16}=0.066$, $P=0.801$) and was not predicted by the number of females per group (ANCOVA: model $F_{1,16}=2.854$, $P=0.111$; Fig. 1b).

Fitness consequences of parasitism

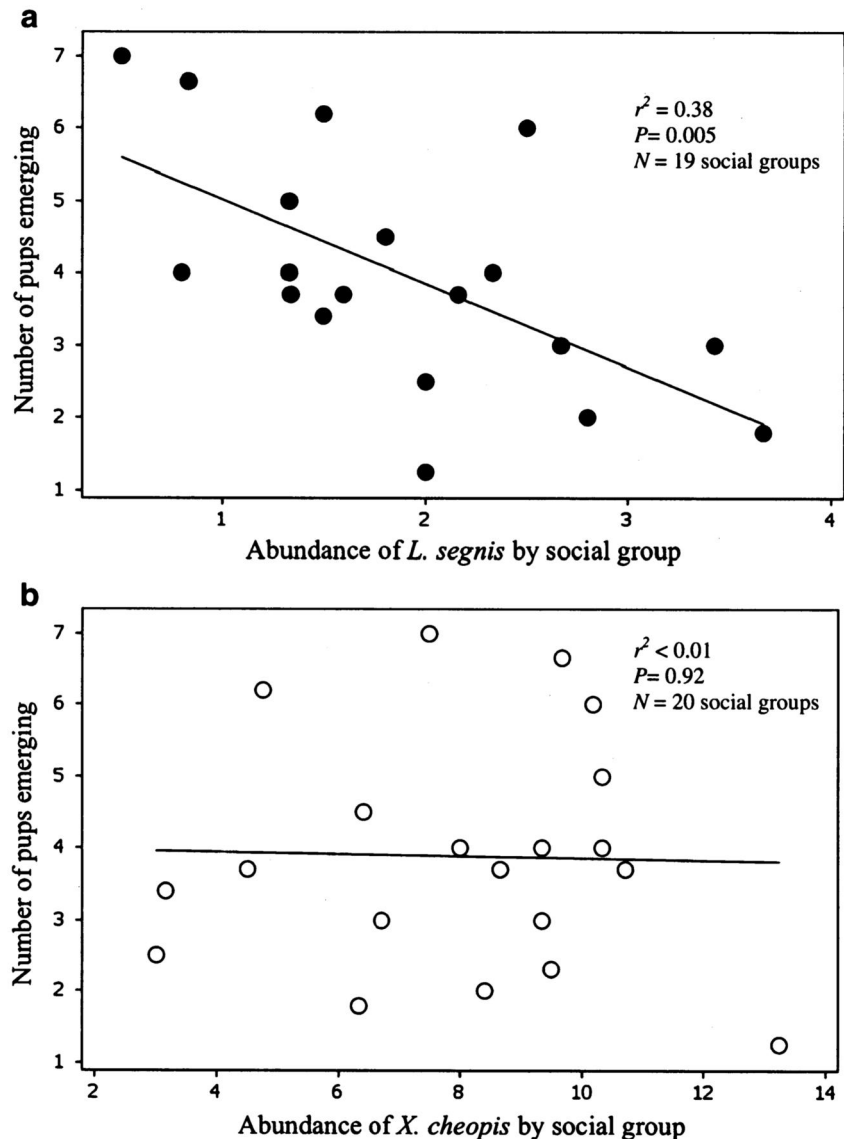
The number of pups emerging from burrow systems used by known social groups was negatively correlated with abundance of *L. segnis* on all adult group members ($F_{1,15}=7.957$, $P=0.013$; Fig. 2a) and adult female group members ($F_{1,16}=4.885$, $P=0.042$). Neither analysis revealed a year * *L. segnis* abundance interaction detected (total group abundance: $F_{1,15}=0.217$, $P=0.648$; abundance on females: $F_{1,16}=0.004$, $P=0.951$). Per capita fitness was not predicted by the abundance of *X. cheopis* of total group size ($F_{1,16}=$

2.304, $P=0.149$; Fig. 2b) or female group size ($F_{1,16}=0.148$, $P=0.705$). Neither analysis revealed a year * *X. cheopis* abundance interaction (total group abundance: $F_{1,16}=0.927$, $P=0.350$; abundance of females: $F_{1,16}=0.253$, $P=0.622$).

The proportion of pups in a group that survived up to 2 months after initial capture was not correlated with total adult ectoparasite abundance of the group for the flea *L. segnis* (Spearman correlation: $r_s=-0.006$, $N=16$, $P=0.982$) or *X. cheopis* (Spearman correlation: $r_s=-0.092$, $N=16$, $P=0.734$). Similarly, pup survival up to 2 months did not correlate with adult female abundance of *L. segnis* (Spearman correlation: $r_s=-0.298$, $N=17$, $P=0.245$) or *X. cheopis* (Spearman correlation: $r_s=-0.010$, $N=17$, $P=0.969$).

Our trapping effort in 2007 encompassed peak pregnancy (Aug); therefore, we regressed individual peak female

Fig. 2 The relationship between per capita number of pups that emerge from burrow systems used by known social groups and ectoparasite abundance (**a** *L. segnis* and **b** *X. cheopis*) of adult degus per social group



mass during pregnancy against individual female ectoparasite loads. In this analysis, peak female mass was negatively correlated with the abundance of *L. segnis* (Spearman correlation: $r_s = -0.49$, $N = 36$, $P = 0.002$). There was no relationship between peak female mass and the abundance of *X. cheopis* (Spearman correlation: $r_s = -0.095$, $N = 36$, $P = 0.583$). Finally, there was no correlation between the abundance of *L. segnis* and *X. cheopis* at the total group ($r^2 = 0.0094$, $P = 0.69$) or female group levels ($r^2 = 0.037$, $P = 0.42$).

Discussion

Contrary to our predictions that parasitism is a cost of sociality, the abundance of exotic ectoparasitic fleas was neither correlated with the total number of adults per group

nor number of females per group. However, the abundance of the exotic flea *L. segnis* was negatively correlated with per capita fitness at the social group level, as well as adult females per group, across both years of our study. Ectoparasite loads of adult degus were not correlated with pup survival. *L. segnis* abundance was negatively correlated with peak female body mass during pregnancy. The more abundant and prevalent *X. cheopis* was not correlated with either per capita fitness or peak female body mass during pregnancy.

Our finding that social group size and ectoparasite loads are not correlated in degus contradicts previous reports of increased parasite loads as a function of group size in a wide range of hosts (Côté and Poulin 1995), including birds (Brown and Brown 1986; Hoi et al. 1998; Whiteman and Parker 2004) and mammals (Hoogland 1979; Freeland 1979; Rubenstein and Hohmann 1989; Davies et al. 1991).

However, a few studies on rodents also failed to find a significant relationship between social group size and ectoparasite load (Arnold and Lichtenstein 1993; Van Vuren 1996; Hillegass et al. 2008). Fitness decreased with increasing mite abundance in Alpine marmots (*Marmota marmota*), but group size had no effect on ectoparasite load (Arnold and Lichtenstein 1993). Cape ground squirrels (*X. inauris*) in large and small groups showed no difference in tick abundance (Waterman 2002). In yellow-bellied marmots (*Marmota flaviventris*), ectoparasite load (fleas, lice, and mites) was no different between colonial and noncolonial groups (Van Vuren 1996). Future studies are needed to determine other factors (e.g., population density) that may predict parasite loads in degus.

The impact of parasites on host fitness and survival ranges from relatively benign to highly virulent. Naïve hosts in their native geographic range have had little evolutionary time to develop defense mechanisms against foreign parasites. The potential for population declines as a result of infection by exotic pathogens is therefore high (Dobson and Foufopoulos 2001). Our findings that the abundance of *L. segnis* was negatively correlated with per capita fitness and peak female mass during pregnancy, lead us to hypothesize that this exotic ectoparasite is negatively impacting fitness of degus in their native range. This is consistent with previous reports of social mammals burdened by exotic infectious agents (Thorne and Williams 1988; Roelke-Parker et al. 1996; Cully and Williams 2001; Leroy et al. 2004; Stapp et al. 2004). Further monitoring is needed to determine the long-term consequences of *L. segnis* on the life history and population dynamics of *O. degus*.

It is possible yet unlikely that *L. segnis* preferentially chooses individuals in poor body condition. Similar to other organisms, ectoparasites are expected to fit an ideal free distribution (Johnson et al. 2004), allocating themselves among their hosts such that individual fitness is maximized. This would result in ectoparasites being more abundant on larger rather than smaller individuals (Davies et al. 1991), a pattern not supported by our results. Instead, two of our findings suggest that *L. segnis* poses a negative impact on *O. degus* fitness during their relatively long gestation period (~3 months). First, the abundance of *L. segnis* was negatively correlated with peak body mass of females during pregnancy (i.e., maternal condition) and per capita fitness at the social group level as well as females per group. Second, there was no relationship between ectoparasite loads of adults in natal groups and pup survival up to 2 months. We therefore hypothesize that adult females in groups burdened with high infection levels gain less body mass during gestation and produce fewer pups per capita than females in social groups with fewer *L. segnis*. Additional work is needed, however, to test this hypothesis. The development of ectoparasite removal techniques (e.g.,

Hillegass et al. 2010) may allow in situ experimental manipulation of parasite loads, allowing further evaluation of the causal relationship between per capita fitness and *L. segnis* abundance in degus.

To our knowledge, this is the first documentation of the exotic fleas, *X. cheopis* and *L. segnis*, on degus in Chile. In their native range, *X. cheopis* and *L. segnis* appear to *only* have deleterious effects on their native hosts during zoonotic outbreaks (Azad 1990). Both fleas are now widely distributed if not cosmopolitan due to the introduction of *Rattus* and *Mus* (Krasnov 2008), and field collections have found both species infected with the bacterium, murine typhus (*Rickettsia typhi*; Azad 1990). Future studies are needed to determine if *L. segnis* serves as a vector for a deleterious pathogen (e.g., bacterium or virus) explaining our negative correlation between abundance of this flea and fitness in degus. Why there is a differential effect of the two exotic parasites on fitness is also yet to be determined. Perhaps *L. segnis* is a competent vector for a specific infectious agent that *X. cheopis* is not. Moreover, our analysis is restricted to per capita fitness measures. The development of microsatellite primers (Quan et al. 2009) coupled with ectoparasite manipulation (Hillegass et al. 2010) will enable future studies to elucidate the direct fitness consequences of infection by *L. segnis* in degus.

Host behavioral adaptations for the resistance or avoidance of parasites are selected when coevolution occurs between host and parasites, resulting in reduced parasite transmission (Hamilton and Zuk 1982; Altizer et al. 2003). These behaviors may include allogrooming (Hart 1992; Johnson et al. 2004; Hillegass et al. 2008; Mooring et al. 2006), dispersal from groups with high infection levels (Brown and Brown 1986; Mooring and Hart 1992; Johnson et al. 2004), and prevention of unfamiliar individuals from entering social groups (Freeland 1976, 1979), mitigating high susceptibility to infection by ectoparasites. Allogrooming has specifically been demonstrated to be more effective at ectoparasite removal than self-grooming (O'Brien 1993; Stopka and Graciasova 2001), suggesting that this social behavior may in fact reduce ectoparasite burdens. Allogrooming may only be adaptive, however, when host and parasites coevolve. Degus at our site spend a rather small percentage of their time above ground engaged in either self-grooming or in direct social interactions (6%), including allogrooming (Ebensperger and Hurtado 2005). Our sampling only found one confirmed native ectoparasite (*A. hellenthali*) on degus in very low prevalence (Table 1). Previous reports suggest that native ectoparasites on degus are rare (Price and Timm 2000; Castro and Cicchino 2002). Based on these observations, we hypothesize that *O. degus* has simply not had the evolutionary time needed to develop behavioral adaptations (e.g., allogrooming, self-grooming) needed to cope with the current high burdens of exotic

ectoparasitism. Future studies of parasitism, host behavior, and fitness should consider the origin of parasites and their coevolutionary histories with their hosts.

Acknowledgements We thank Universidad de Chile, in particular, former field station administrator J.D. Garcia, for help in facilitating fieldwork, V. Quirici, C. León, R. Castro, L. Ortiz Tolhuysen, M. Pardue, N. Schaferkotter, and J. Childers for field assistance, and A. Edelman and R. Fiorillo for helpful comments on this manuscript. This work was funded by the National Science Foundation EPSCoR (#0553910), the Louisiana Board of Regents Research Competitiveness Program (#LEQSF 2007–2009-RD-A-39), The University of Louisiana at Monroe HHMI Program and the ULM Office of Academic Affairs, the Sigma Xi Scientific Society, the American Society of Mammalogists, FONDECYT grants 1020861 and 1060499 and by Centro de Estudios Avanzados en Ecología y Biodiversidad (FONDAP 1501-001). The authors declare no conflict of interest. Field procedures followed guidelines established by the American Society of Mammalogists Animal Care and Use Committee, were approved by the ULM Institutional Animal Care and Use Committee, and are in accordance with U.S. and Chilean laws (permit no. 1-58.205 [2711] by Servicio Agrícola y Ganadero).

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