Parasitism underground: determinants of helminth infections in two species of subterranean rodents (Octodontidae)

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SUMMARY

Patterns of infection among hosts in a population are often driven by intrinsic host features such as age or sex, as well as by positive or negative interactions between parasite species. We investigated helminth parasitism in 2 South American rodent species, *Ctenomys australis* and *C. talarum* (Octodontidae), to determine whether the unusual solitary and subterranean nature of these hosts would impact their patterns of infection. We applied generalized linear models to infection data on a total of 7 helminth species (1 in *C. australis* and 6 in *C. talarum*). Host age and season of capture influenced infection levels in some of the helminth species, but none were influenced by host body condition. In *C. talarum*, 4 pairs of helminth species showed significant associations, either asymmetrical or symmetrical, and with 3 of the 4 being positive; strong inter-specific facilitation appears likely in 1 case. Also, we found that female hosts, especially non-pregnant ones, harboured heavier infections of 2 nematode species than male hosts. This is in sharp contrast to the general male-bias reported for most studies of nematodes in wild mammals, and we develop explanations for these results based on the unusual ecology of these subterranean rodents.

Key words: *Ctenomys*, Argentina, fossorial rodents, sex-biased infection, species interactions, host reproductive status.

INTRODUCTION

Variability among host individuals in the number of parasite species they harbour, and in the severity of infection by these species, is a universal feature of any host population (Poulin, 2007). This variability is the outcome of several processes: heterogeneous distribution of infective stages and their chance encounter with hosts, differences among individual hosts in their exposure or susceptibility to infection, as well as direct and indirect interactions among parasites within the host that may have positive or negative effects on infections by certain species (Poulin, 2001, 2007).

Studies on rodent hosts have demonstrated the action of these processes. For instance, interactive associations between pairs of helminth species among host individuals have been observed repeatedly in both laboratory (Holland, 1984) and field studies (Haukisalmi and Henttonen, 1993; Behnke *et al.* 2005). Interactions between parasite species are not

always negative; there is evidence that infection by one species can facilitate infection by others via a decrease in host immune responses (Behnke *et al.* 2009). These processes, combined with chance exposure to patchily distributed infective stages, would be enough to generate much variation in parasite species richness and infection levels among individual hosts. In addition to these factors, however, there exist intrinsic differences in past exposure and susceptibility to parasites among individual hosts; for instance, older hosts have been exposed for longer and should harbour more parasites than young ones, and there may also be behavioural or physiological differences between host sexes influencing infection patterns (Behnke *et al.* 1999; Eira *et al.* 2006). In particular, host sex is considered to be important, because the immunosuppression induced by testosterone generally causes males to harbour more parasites than females (Poulin, 1996; Schalk and Forbes, 1997). In rodents, this often leads to males, especially older males, harbouring a substantial portion of the parasite population, and releasing disproportionately more infective stages into the environment than females (Ferrari *et al.* 2004; Luong *et al.* 2009). Females may also experience immunosuppression during breeding or lactation, at which

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times their infections may be higher than those of non-reproducing females (Vandegrift and Hudson, 2009).

In some host species, however, unusual ecological conditions may either exacerbate differences in parasite richness and infection levels among individual hosts, or homogenize infections such that inter-individual differences become very small. In subterranean herbivorous rodents of the South American genus *Ctenomys* (Octodontidae), for instance, individuals live singly in permanently sealed burrow systems and in low-density populations (Malizia *et al.* 1991; Malizia, 1998). They only emerge occasionally from their burrows for brief surface excursions to collect plant material, although they also feed on below-ground parts of plants and may engage in coprophagy (Busch *et al.* 1989; del Valle *et al.* 2001). Pregnant females and those with pups make even fewer surface visits than other members of the population, and young females remain with their mothers almost until maturity (Malizia, 1998). Individuals place fecal pellets outside the plugged entrance of their burrow to signal that it is occupied, and they will inspect fecal deposits from neighbouring burrows during their occasional surface excursions (Fanjul *et al.* 2003); this may provide opportunities for parasite transmission. The extremely sedentary nature of these fossorial rodents, with most of the time spent in the underground burrow and little contact with conspecifics, may affect their exposure to parasites and impact on inter-individual variation in infections.

There have only been a few previous parasitological studies of *Ctenomys* rodents (Rossin and Malizia, 2002, 2005; Rossin *et al.* 2004, 2005 *a*, *b*, 2006 *a*, *b*, 2009) or other fossorial rodents (e.g., Scharff *et al.* 1997). Here, we focus on the determinants of infection by separate helminth species in 2 species, *C. australis* and *C. talarum*. Specifically, we examined (i) whether a male bias is observed in infection levels in these 2 species characterized by sexual size dimorphism, with males being 30–50% heavier than females (Malizia *et al.* 1991), and (ii) what kinds of inter-specific associations exist among helminth species.

MATERIALS AND METHODS

Hosts were caught across seasons at 2 localities. Specimens of *C. talarum* were caught at Mar de Cobo, Buenos Aires Province (37°58′S, 57°34′W) during 2000–2001, whereas those of *C. australis* were caught at Necochea, Buenos Aires Province (38°33′S, 58°45′W) during 2003–2004. The distribution of both species is linked to micropatterns of soil and vegetation; *C. australis* inhabits areas with sparse vegetation and deep sandy soils, while *C. talarum* lives in areas with dense vegetation, and compact and shallow soils (Malizia *et al.* 1991; Comparatore *et al.*

1992). In the field, inhabited burrow systems were distinguished by the presence of conspicuous mounds of fresh soil brought to the surface during burrowing activities of the rodents. Live traps were placed in these burrows close to their entrance, and checked every hour throughout the day during each trapping session. Trapped rodents were killed by over-exposure to ether and returned to the laboratory for measurements and dissection for parasites.

For each host individual, the following information was recorded: (i) date of capture, with dates subsequently grouped into seasons; (ii) body length (cm), excluding the tail; (iii) body mass (g), including foetuses in the case of pregnant females; (iv) age in years, determined based on the extent of epiphyseal ossification of the humeri (Malizia and Busch, 1991); (v) reproductive condition, i.e. immature or mature; (vi) sex, with females separated into pregnant and non-pregnant; and (vii) the identity, number and location of each endohelminth.

Since variables like age, body length, body mass, sex and reproductive condition are correlated with each other and thus not statistically independent, we collapsed them into 3 predictor variables that were independent and still captured all the relevant biological information. They were: (i) age in years, (ii) sex, which included the 3 categories–males, non-pregnant females and pregnant females, and (iii) body condition, which corresponded to the residual value of body mass regressed against body length. These regressions were significant (*Ctenomys australis*: mass $= 26\cdot6$*length$- 420\cdot7$, $r^2 = 0\cdot64$, $F_{1,43} = 79\cdot1$, $P < 0\cdot0001$; *C. talarum*: mass $= 7\cdot3$*length$- 35\cdot4$, $r^2 = 0\cdot47$, $F_{1,79} = 72\cdot1$, $P < 0\cdot0001$), and positive residuals indicate animals heavier than average for their length, whereas negative values indicate animals with a lower mass than expected for their body length.

We used generalized linear models performed in the R environment (version 2.9.1; R Development Core Team, 2009) to evaluate the independent effect of multiple predictor variables on infection by each parasite species, separately for each host species. For common (prevalence $\geqslant 48\%$) parasite species, the response variable was abundance of infection, i.e. the number of individual parasites per host (with uninfected hosts included in the analysis), and we used a quasipoisson error structure with a log-link function. A quasipoisson error structure provided a better fit (based on deviance) between models and data than the negative binomial, although using the former or the latter generally yields the same results in a GLM (see Crawley, 2007, pp. 556–558). For relatively rare parasites (prevalence $< 30\%$), the response was a binary variable, i.e. presence or absence of the parasite, and we used a binomial error with complementary log-log link function (Crawley, 2007). In all GLMs, the predictor variables were season of capture (4 seasons), age (continuous variable,

Table 1. Summary of the parasite species and their infection parameters in the two rodent host species

| Host species	Parasite species	Site of infection	Prevalence (%)	Mean parasite abundance	Range of abundances
Ctenomys australis (N = 45)	*Trichuris pampeana*	Caecum	95·6	21·4	0–60
	Pudica ctenomydis	Small intestine	15·6	0·2	0–3
	Taenia talicei	Abdominal cavity	8·9	1·2	0–15
Ctenomys talarum (N = 81)	*Trichuris pampeana*	Caecum	48·1	2·1	0–19
	Pudica ctenomydis	Small intestine	29·6	2·9	0–114
	Graphidiodes subterraneus	Stomach	24·7	5·1	0–155
	Paraspidodera uncinata	Large intestine & caecum	93·8	48·1	0–183
	Strongyloides myopotami	Small intestine	14·8	1·1	0–30
	Trichostrongylus duretteae	Small intestine	3·7	0·1	0–7
	Taenia talicei	Abdominal cavity	64·2	9·8	0–95
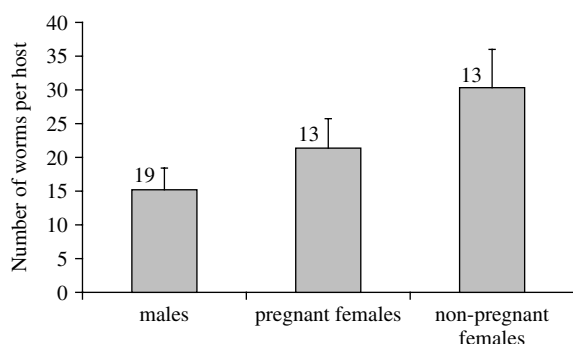
Fig. 1. Mean (±S.E.) number of the nematode *Trichuris pampeana* per host in the rodent *Ctenomys australis* as a function of the sex and reproductive status of the hosts. Numbers above bars are the number of hosts per category.

1–6 years), sex (males, non-pregnant females, pregnant females), body condition, and infection by other parasite species, treated either as a continuous variable (abundance) or as a binary one (presence or absence) for rare species. Exploratory analyses, if necessary with reduced models (i.e. fewer factors in order to avoid empty cells), indicated that second-order interactions were all non-significant, and therefore they were not included in the final models. Higher-order interactions (three-way and above) could not be evaluated because of limited sample sizes.

RESULTS

Overall, 45 *Ctenomys australis* (2–6 years of age, 78–530 g in body mass, 13 non-pregnant females, 13 pregnant females, and 19 males) and 81 *C. talarum* (1–6 years of age, 48–187 g in body mass, 25 non-pregnant females, 17 pregnant females, and 39 males) were included in the study. Except for cysts of the cestode *Taenia talicei* found in the body cavity of both rodent species, all other helminths recovered were nematodes associated with the digestive tract (Table 1). All parasites are acquired by ingestion,

except *Strongyloides myopotami* which has skin-penetrating infective stages.

In *C. australis*, both the cestode *T. talicei* and the nematode *Pudica ctenomydis* were not common (Table 1); they were included as predictor variables in the GLM summarized below, but not as response variables, i.e. their patterns of infection were not the subjects of separate GLMs. Only *Trichuris pampeana* was subject to an analysis, and of all predictors considered, only sex (sex [males]: change in coefficient estimate = −0·713, $t = -2·07$, $P = 0·0458$) had a significant effect on its abundance of infection in the GLM. Males tended to harbour fewer nematodes of this species than pregnant and non-pregnant females (Fig. 1).

In *C. talarum*, the nematode *Trichostrongylus duretteae* occurred at very low prevalence and abundance of infection (Table 1), and it was therefore excluded from all analyses. All other species were included as predictors of the presence or abundance of other species, and all were the response variable in their own dedicated GLM. Some significant effects emerged from those analyses (Table 2). There were seasonal effects in 2 parasite species, both of which were more likely to infect hosts during the warmer spring and summer months. Two parasite species were positively correlated with host age, although host body condition had no effect on the presence or abundance of any of the parasite species (Table 2). One species, *Strongyloides myopotami*, was less likely to occur in males than in females (Table 2; Fig. 2). Finally, there were some significant associations among pairs of parasite species. First, there was a negative association between *Pudica ctenomydis* and *Graphidiodes subterraneus*, although only significantly affecting the latter. Second, there was a positive association between *G. subterraneus* and *S. myopotami*, although again it was not symmetrical and only significant for the latter species (Table 2). Third, there was a significant positive association between the presence of *P. ctenomydis* and that of *S. myopotami*. Finally, there was a strong positive association between the

Table 2. *Results of GLMs evaluating the effects of several factors on either the abundance or presence of six parasite species in the rodent host Ctenomys talarum*

(Data shown are changes in coefficient estimates (compared to intercept; significant ones in bold) when that factor alone is excluded from the model; significance is based on a *t*-test.)

Factor	*Trichuris pampeana* (abundance)	*Pudica ctenomydis* (presence)	*Graphidiodes subterraneus* (presence)	*Paraspidodera uncinata* (abundance)	*Strongyloides myopotami* (presence)	*Taenia talicei* (abundance)
(Intercept)	2·143	−1·896	−3·437	2·236	−13·588	0·654
Season (spring)	−0·705	1·682	−0·211	0·201	**5·945***	−0·813
Season (summer)	0·233	**2·438***	−1·007	−0·053	**4·524***	−0·362
Season (winter)	−0·419	−1·413	−2·218	0·365	5·767	0·084
Age	−0·433	−0·494	−0·012	**0·316****	**1·970***	0·273
Sex (pregnant females)	−0·306	1·542	1·027	0·222	−3·376	0·162
Sex (males)	0·644	1·061	1·540	0·282	**−7·097****	0·068
Body condition	−0·006	−0·009	−0·038	−0·002	0·014	0·002
T. pampeana (abundance)	—	−0·089	0·052	0·006	0·330	0·023
P. ctenomydis (presence)	−0·741	—	**−2·552***	0·128	**4·555***	0·475
G. subterraneus (presence)	0·150	−1·577	—	−0·152	**3·188***	**1·299****
P. uncinata (abundance)	0·001	0·009	0·001	—	−0·005	0·001
S. myopotami (presence)	0·261	**1·355***	1·472	0·228	—	−0·264
T. talicei (abundance)	0·007	0·029	**0·196****	0·001	−0·041	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
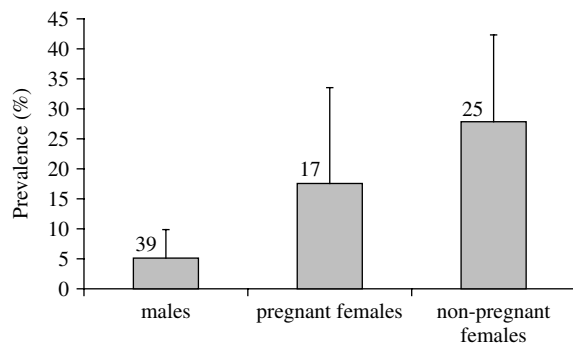
Fig. 2. Prevalence (± 95 % confidence interval), i.e. percentage of individuals infected, of the nematode *Strongyloides myopotami* per host in the rodent *Ctenomys talarum* as a function of the sex and reproductive status of the hosts. Numbers above bars are the number of hosts per category.
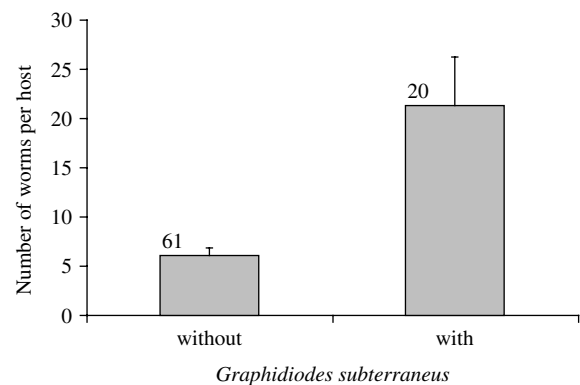
Fig. 3. Mean (± S.E.) number of the cestode *Taenia talicei* per host in the rodent *Ctenomys talarum* as a function of whether or not the host harboured the nematode *Graphidiodes subterraneus*. Numbers above bars are the number of hosts per category.

presence of *G. subterraneus* and the abundance of *Taenia talicei* across hosts (Fig. 3); hosts infected by *G. subterraneus* harboured over 3 times more *T. talicei*, on average, than those not infected by *G. subterraneus*.

DISCUSSION

The unusual solitary and subterranean lifestyle of *Ctenomys* rodents may create patterns of infections among individual hosts that could depart from those observed in other rodents living above ground and with greater likelihood of interactions with conspecifics. We specifically looked at possible sex-biases in infection patterns, and at statistical associations among parasite species, to determine to what extent host characteristics and/or interspecific

interactions among parasites might structure the helminth communities in *Ctenomys australis* and *C. talarum*.

Of the 7 tests of sex bias we performed (1 helminth species in *C. australis* and 6 in *C. talarum*), 2 showed a significant pattern. Unlike the widely reported male-bias that is particularly common in nematode infections of mammals (Poulin, 1996; Schalk and Forbes, 1997) and generally attributed to testosterone-induced immunosuppression (Zuk and McKean, 1996), we observed a clear female bias in both cases. This arose despite the sexual size dimorphism in these species, where males are significantly larger than females (Malizia *et al.* 1991). In the case of the nematode *Strongyloides myopotami* in *C. talarum*, the bias could be attributed in part to the

behaviour of females, which spend more time in their burrows than males, both while pregnant and after giving birth. Since this nematode has free-living infective stages that penetrate host skin, the virtual immobility of females for prolonged periods could facilitate re-infection as well as mother-to-daughter transmission, since the latter have high phylopatric tendencies, staying in their mother's burrow for long periods (Malizia *et al.* 1995). These behaviours specific to females should enhance the probability of infection. The same behaviours may also predispose *C. australis* females to higher infections by the nematode *Trichuris pampeana*, although if this is the case we might expect the other parasites acquired by ingestion to show female-biased infections, and they do not. Breeding, from pregnancy to the end of lactation, may also cause immunosuppression in females (Zuk and McKean, 1996), which can lead to increased infections (e.g. Vandegrift and Hudson, 2009). Our results for both cases show that non-pregnant females had higher infections than pregnant ones. Because of our method of capture, it was not possible to determine whether or not non-pregnant females were lactating pups at the time of sampling. Although some non-pregnant females had well-developed mammary glands surrounded by areas where the fur has been lost, this is not a sure sign of lactation, and the entire burrow could not be excavated to search for pups. Nevertheless, the 2 sex biases we observed join a short list of exceptions (Dick *et al.* 2003; Zahn and Rupp, 2004; Krasnov *et al.* 2005) that go against the general pattern in which males are more frequently or heavily infected than females; the reversed pattern observed in subterranean *Ctenomys* rodents may be a consequence of their unusual lifestyle.

Our generalized linear models also revealed other effects on infections. Indeed, host age and season of capture both influenced infection levels of some helminth species, as seen in other rodent-parasite systems (Behnke *et al.* 1999; Eira *et al.* 2006; Vandegrift and Hudson, 2009). These effects are neither unusual nor surprising. Older hosts have had longer to acquire and accumulate parasites, and we found a positive effect of host age on infection in 2 species. Warmer parts of the year are often associated with higher rates of infection because hosts are more active and feed more than during cold periods. Summer peaks in nematode infections have been reported in geomyid pocket gophers from North America, another taxon of subterranean rodents (Gardner, 1991). In the case of the nematode *Strongyloides myopotami* in *C. talarum*, it is also likely that the skin-penetrating infective larvae are more active during spring and summer months, and thus more likely to contact host bodies. The one factor that did not affect infections in our study systems was host body condition, measured here as observed body weight relative to that expected for a given body

length. This suggests that hosts that fed more did not automatically acquire more ingestion-transmitted parasites, and that heavily-infected hosts did not incur reductions in body condition as a consequence of infection.

We also uncovered statistically significant associations between parasite species among the helminths infecting *C. talarum*. Our generalized linear models, because they take into account other species as well as other confounding factors, should yield more robust tests of pairwise associations between parasite species than many earlier correlation tests (see Haukisalmi and Henttonen, 1998; Poulin, 2005). Of the 4 pairwise associations we found 2 were asymmetric, i.e. one species affected the presence or abundance of another, but not vice versa. This is actually a common phenomenon in helminth communities (see Poulin, 2007, for review). Also, pairs of significantly associated species consisted, in 3 of the 4 cases, of species living in different microhabitats within the host, suggesting that immune-mediated effects are more likely explanations than active resource competition. Recent studies have emphasized that positive interactions are as frequent, if not more frequent, than negative ones in helminth communities of rodents and other mammals (Behnke *et al.* 2005, 2009; Lello *et al.* 2004). For instance, Behnke *et al.* (2009) have provided data suggesting that the nematode *Heligmosomoides polygyrus* facilitates infection of its rodent host, *Apodemus sylvaticus*, by other helminths by suppressing parts of its immune response. In our study, 3 of 4 significant associations were positive, suggesting either some form of facilitation as in the preceding example, or that both species are acquired together in a way that generates a statistical association. However, in the case of the positive association between the nematodes *Pudica ctenomydis* and *Strongyloides myopotami*, some form of active facilitation seems likely, since the two species have different modes of infection: the former species in the pair is acquired by ingestion, whereas the latter penetrates host skin. Interestingly, a relative of *S. myopotami*, the well-studied *S. ratti*, is very sensitive to host immune status, and any helminth that could suppress host responses should concomitantly facilitate *S. ratti* infections (Wilkes *et al.* 2004).

Overall, a range of factors combines to determine the presence or abundance of infection of the various helminths found in the 2 *Ctenomys* species. These range from the season of capture to interactions among parasite species. In particular, we found that when differences in infections exist between host sexes, they go against the general trend for nematodes in mammals, and show a female bias that may be a direct consequence of the solitary and subterranean life of these rodents compared to most other host species studied to date. These results argue for a strong role of ecology in determining infection

patterns, even to the extent of overshadowing physio-logical differences between hosts.

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