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Patterns of parasite prevalence and individual infection in yellow-bellied marmots

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Abstract

Patterns of infection and prevalence result from complex interactions between hosts and parasites, the effects of which are likely to vary by species. We investigated the effects of age, sex and season on the likelihood of individual infection, and the effects of host population size, sex ratio and age structure on parasite prevalence. We capitalized on data from a long-term study of yellow-bellied marmots *Marmota flaviventris* potentially infected with fecal–orally transmitted intestinal parasites (*Ascaris* sp., *Eimeria* spp. and *Entamoeba* sp.), ectoparasitic fleas *Thrassis stanfordi*, and a flea- and louse-transmitted blood parasite *Trypanosoma lewisi*. Patterns of individual- and group-level infection varied widely by parasite. Yearlings were more likely to be infected with *Tr. lewisi* and *Ascaris*. Yearlings were also slightly more likely than adults to have *Eimeria*, but female yearlings had higher infection levels than female adults, while male yearlings had lower infection levels than male adults. *Entamoeba* infection decreased as the season progressed. Adults and males were more likely to be infected with *Th. stanfordi*. *Ascaris* prevalence increased with colony size. There were no significant relationships between colony size and prevalence of *Entamoeba*, *Tr. lewisi*, *Eimeria* or *Thrassis*. There was a small, but significant positive correlation between male-biased sex ratio and prevalence of fleas. The host population's age structure affected the prevalence of infection of *Ascaris* and *Eimeria*. Overall intestinal parasite diversity increased with colony size. Taken together, our results show a great deal of variation in the likelihood of individual infection and patterns of parasite prevalence in marmots.

Introduction

Parasitism is an important factor affecting host population-level processes and individual animal behavior (Dobson, 1988; Crawley, 1992; Moore, 2002). The nature of the relationship between host population size and parasitism is important for social species where the adaptive value of sociality depends on the costs and benefits of living in groups of various sizes (Altizer *et al*., 2003; Blumstein, 2012). Studying this relationship can enhance our understanding of host responses to parasite pressures between individuals, populations and across varied ecological conditions – important conceptual questions. The relationship between host population size and parasite prevalence is also important for practical reasons. Populations become smaller because of habitat loss and fragmentation. If parasite prevalence changes with host population size, this should be considered when estimating the risks posed by parasites (Saunders, Hobbs & Margules, 1991; Holmes, 1996) and making management decisions.

Three important factors that can influence parasite prevalence are host population size, sex ratio and the age structure of the host population. Relationships between parasitism and host population size have been found (Grosholz, 1993; Burdon, Ericson & Muller, 1995; Ericson, Burdon & Muller, 1999; Smith, Ericson & Burdon, 2003; Lopez, Gallinot & Wade, 2005), but vary in strength from one system to another (Rifkin, Nunn & Garamszegi, 2012), and various factors are likely to affect observed patterns. For example, a recent meta-analysis found an overall positive relationship between host population size and parasite prevalence that varied with mode of parasite transmission (Rifkin *et al*., 2012). In many natural systems, both host and parasite characteristics change with host abundance. Fecundity, for example, is density dependent in many systems, in both hosts and parasites (see references in Dobson, Hudson & Lyles, 1992). Similarly, individual behavior changes in response to crowding. These individual-level changes are likely to be reflected at the population level and may modify the relationship between host population size and prevalence. Previous studies had also found sex bias in parasite infection (Poulin, 1996; Zuk & McKean, 1996; Letitia *et al*., 2000; Ferrari *et al*., 2004). In these cases, sex ratio differences could account for different levels of parasite prevalence. The age of hosts also affects their susceptibility to parasites, and the age structure of the host population can influence the dynamics of host parasite interactions (Kistler, 1985; Minchella & Scott, 1991; Murray & Cade, 1995; Bonsall & Eber, 2001).

Prevalence is a population-level trait that emerges from the aggregation of infections at the individual level. At the individual level, the likelihood of infection is affected by many factors, including the encounter rates between hosts and parasites, and host characteristics like age, size and sex (Zuk & McKean, 1996; Letitia *et al*., 2000; Ferrari *et al*., 2004). Overall patterns of infection and prevalence result from complex interactions between host and parasites biology, and the effects of these factors are likely to vary from one parasite species to another. Furthermore, it is often difficult to collect comprehensive data on multiple host groups in natural populations. Thus, despite the broad importance of parasites, factors affecting the likelihood of individual infection and parasite impact on host populations remain largely unknown in many systems.

We capitalize on long-term data from a field study of yellow-bellied marmots *Marmota flaviventris* to examine factors influencing the likelihood of infection in individuals, and to investigate the relationship between host population size, host sex ratio and host age structure, and the prevalence of multiple parasites. For up to 8 years, we measured the presence and abundance of a number of endoparasites and ectoparasites with different modes of transmission, and we have accurate census of host colony sizes in all years. Yellow-bellied marmots are hosts to fleas *Thrassis stanfordi* (Van Vuren, 1996), a flea- and louse-transmitted (MacNeal, 1904) blood parasite, *Trypanosoma lewisi* (Dias, 1937), as well as various intestinal parasites, including *Ascaris* sp. (a nematode), *Entamoeba* sp. (a protozoan) and *Eimeria* spp. (a coccidian) (Stark, 2006). Marmots live in colony sites (Blumstein *et al*., 2006) in which there is subdivision into social groups (Olson & Blumstein, 2010). The detailed data on infection at the individual level allowed us to analyze the role of an individual's age and sex on the likelihood of individual infection. The variation in colony sizes provides an outstanding opportunity to look for relationships between colony size, and (1) parasite prevalence and (2) parasite diversity. Large populations should be exposed to and be able to sustain a greater diversity of parasites, so we expected a positive relationship between population size and diversity of intestinal parasites (Rifkin *et al*., 2012). Detailed demographic data allowed us to investigate the role of host sex ratio and age structure on parasite prevalence. Thus, we were able to look at patterns of parasitism from two different perspectives: one looking at likelihood of individual infection and one looking at the colony-level prevalence. Additionally, we asked if any parasite represented a cost of sociality. Because parasitism may prevent host weight gain, which is critical for overwinter survival in marmots (Armitage, Blumstein & Woods, 2003), for any parasite whose prevalence was correlated with group size, we looked for a negative effect on overwinter survival. A positive relationship would indicate a cost of sociality.

Materials and methods

Yellow-bellied marmots are facultatively social, 3–5 kg, sciurid rodents (Armitage, 2003*a*) and populations have been studied at the Rocky Mountain Biological Laboratory in Gunnison County, CO, since 1962 (Armitage, 2010). In this area, marmots are seasonally active between mid- to late April, and late September to early October and hibernate the remainder of the year. Marmots at our study site live in geographically separate colonies. Exchange among colonies is rare (Armitage, 2003*b*), so we treated each colony as a separate population for these analyses. We focused on 11 colonies that varied substantially in size (from 6 to 106 individuals, mean = 31.8, standard deviation = 23.3).

We attempted to trap each individually marked animal every 2 weeks, and we regularly observed colony sites from mid-April to early September annually. Details of trapping and marking animals are presented elsewhere (e.g. Blumstein, Wey & Tang, 2009), but regular trapping and observation provided an accurate census of each colony's size each year. For these analyses, we used the maximum number of adults, yearlings and juveniles seen or trapped in a colony in a given year, even if they were present for only a portion of the year because each additional individual increases the risk of transmitting or importing a parasite, and because the maximum number of individuals detected is an accurate measurement while other measures rely on some degree of sampling.

From 2003 to 2008, we systematically collected data on the presence and abundance of blood parasites, intestinal parasites and fleas during the marmots' summer active seasons. To study blood parasites, we collected blood samples and made a thin film blood smear from each sample (detailed methods in Stark, 2006). Slides were stained using the Hema 3 Stat Pack (Thermo Fisher Scientific, Inc., Waltham, MA, USA) and systematically examined for the presence of *Tr. lewisi*, for up to 30 min. If no trypanosomes were detected after 30 min, we scored the parasite as absent for that sample.

To study intestinal parasites, fecal samples were collected from subjects who defecated in traps (see Wey & Blumstein, 2012), stored in formalin while fresh and analyzed within 6 months of collection by performing fecal floats using Ova Float™ Zn 118 (zinc sulfate heptahydrate; Butler Animal Health Supply, Dublin, OH, USA) on up to one sample per individual per month. We scored wet slides for the presence of three fecal–orally transmitted intestinal parasites: *Ascaris*, *Eimeria* and *Entamoeba*.

To study fleas *Th. stanfordi*, in 2007 and 2008, we combed marmots during trapping and counted fleas displaced onto a white cloth using a standardized procedure (details in Wey & Blumstein, 2012).

Statistical analyses

To analyze the likelihood of individual infection as a function of host age and sex, we used data on multiple samples per individual per year, if available, up to one sample per individual per month for blood and intestinal parasites, and up to one sample per 2 weeks for fleas. For each parasite, we fitted generalized linear mixed-effects models in R (R Development Core Team, 2012) with the lme4 package (Bates, Maechler & Bolker, 2012). We included fixed effects for age class, sex and Julian date, and random intercepts for individual, year and colony to account for repeated sampling within and between years. Parasites were scored as present or absent (1/0) in each sample, and outcomes were modeled with binomial family distributions. Initial models included an age by sex interaction, but only significant interactions terms were included in final models.

For all analyses involving colony prevalence or diversity, we computed colony statistics, and an individual that was infected in at least one sample per year was considered infected for that year. To test for the effect of population size on parasite prevalence, we fitted linear mixed-effects models with a random intercept for colony that accounted for the repeated sampling of colonies from 1 year to another. All population analyses were conducted in the Statistical Package for the Social Sciences version 20 (IBM, New York, NY, USA). Results with $P < 0.05$ were considered significant. Prevalence was $\log_{10}$ transformed in all analyses to meet model assumptions. The prevalence of *Tr. lewisi*, *Ascaris*, *Eimeria*, *Entamoeba* and *Th. stanfordi* infection was calculated for each colony each year by dividing the number of infected marmots by the number of marmots sampled in each colony. Between 2003 and 2010, we annually sampled an average of 35% of the individuals at our study site for the various parasites (Table 1). Our data spanned 2–8 years, depending on the parasite.

Other factors that may affect parasite prevalence are the male-to-female sex ratio and the ratio of subadults to adults (subsequently called age ratio) of the host population. In our system, males are larger and disperse further increasing their exposure to parasites, and there is male-biased parasitism by fleas (Wey & Blumstein, 2012). We also observed differences in the likelihood of infection of yearlings (subadults) and adult marmots. Therefore, populations with male-biased sex ratios would be expected to have higher overall parasite prevalence. Similarly, population prevalence would vary with the age ratio. We fitted linear mixed-effects models, again with a random intercept for colony, to look for relationships between the host population sex ratio and parasite prevalence, and between age ratio and prevalence, after accounting for year effects, and the effect of repeated sampling of colonies.

We also looked for a relationship between colony size and the total number of intestinal parasite species present (i.e. parasite diversity) in the colony. We fitted linear mixed-effects models, again with a random intercept for colony, to look for relationships between the host population size and intestinal parasite diversity after accounting for year effects and the effect of sampling colony sites repeatedly.

For any parasite whose prevalence was significantly correlated with group size, we also tested for an association with overwinter survival to determine if parasitism represented a cost of sociality. We compared the overwinter survival of infected and uninfected marmots fitting a logistic regression that also accounted for year and group effects because of repeated sampling.

Results

When we looked at the likelihood of individual infection as a function of age, sex and time of season, we found that results varied depending on parasite species (Tables 2 and 3). For *Tr. lewisi*, yearlings were more likely to be infected (Tables 2 and 3). For *Ascaris*, age class had the only significant effect with yearlings showing higher infection levels (Tables 2 and 3). For *Eimeria*, age class had a significant effect with yearlings having higher infection levels (Tables 2 and 3), but there was a significant interaction between age class and sex (Tables 2 and 3; adults and females as reference age class and sex, respectively), indicating that female yearlings had higher infection levels than female adults, while male yearlings had lower infection levels than male adults. For *Entamoeba*, we found significant seasonal effects (Tables 2 and 3); levels of infection decreased as the season progressed. For *Th. stanfordi*, likelihood of infection decreased with season (Tables 2 and 3), adults were more likely to be infected (Tables 2 and 3), and males were more likely to be infected (Tables 2 and 3).

We found that the relationship between colony size and prevalence differed by parasite (Fig. 1; Table 3). The prevalence of the blood parasite *Tr. lewisi* was highly variable and not related to host population size. Prevalence was low in most colonies, but high levels of prevalence were observed in both small and large colonies. There were strong annual effects ($F_{6,247} = 115.33$, $P < 0.0001$); in many years, few animals were infected.

The prevalence of *Ascaris*, on the other hand, increased linearly and significantly with colony size (Fig. 1b; Table 3). Small colonies tended to be free of *Ascaris*. In larger colonies, prevalence increased, but never reached more than 60%. The effect of year-to-year variation, controlled for in the analysis, was also significant (Table 3). *Ascaris* infection was not associated with overall overwinter survival ($\chi^2_1 = 0.137$, $P = 0.71$), although a logistic regression demonstrated that there were year effects ($\chi^2_1 = 5.12$, $P = 0.024$) and group effects ($\chi^2_8 = 18.35$, $P = 0.019$).

Eimeria was much more prevalent than *Ascaris*, with most colonies having 100% or nearly 100% infection. Only small colonies of fewer than 30 individuals had lower levels of prevalence (Fig. 1c). However, because there was little variation in prevalence among colonies of different size, we found no linear relationship between prevalence and colony size (Table 3).

The relationship between colony size and prevalence for *Entamoeba* was intermediate between the relationships in *Ascaris* and *Eimeria* (Fig. 1d). While prevalence reached 100% in both large and small colonies, there was a broader range of prevalence with lower prevalence corresponding to smaller colonies and higher prevalence to larger ones. However, the relationship was not statistically significant (Table 3).

Table 1 Sample sizes and overall prevalence of four yellow-bellied marmot parasites: one vector-transmitted blood parasite (*Trypanosoma*), three fecal–orally transmitted intestinal parasites (*Ascaris*, *Eimeria* and *Entamoeba*) and a flea *Thrassis stanfordi*

	Trypanosoma					*Ascaris*				
Year	Marmots sampled	Population size	% Sampled	Overall prevalence (%)	Range (%)	Marmots sampled	Population size	% Sampled	Overall prevalence (%)	Range (%)
2003	68	171	40	46	17–78	29	171	17	3	0–8
2004	72	265	27	7	0–100	80	272	29	28	0–57
2005	102	247	41	18	0–83	87	250	35	3	0–8
2006	124	329	38	2	0–20	126	329	38	3	0–43
2007	140	323	43	6	0–50	157	323	49	20	0–33
2008	72	308	23	4	0–20	106	308	34	16	0–44
2009	79	262	30	0	n/a					
2010	105	259	41	0	n/a					
Total	762	2164	35	9		585	1653	35	18	
	Eimeria					*Entamoeba*				
Year	Marmots sampled	Population size	% Sampled	Overall prevalence (%)	Range (%)	Marmots sampled	Population size	% Sampled	Overall prevalence (%)	Range (%)
2003	29	171	17	97	75–100	29	171	17	48	0–100
2004	80	272	29	93	0–100	80	272	29	76	0–100
2005	87	250	35	100	n/a	87	250	35	98	88–100
2006	126	329	38	99	97–100	126	329	38	94	71–100
2007	157	323	49	98	83–100	157	323	49	99	83–100
2008	106	308	34	96	88–100	106	308	34	99	94–100
Total	585	1653	35	97		585	1653	35	92	
	Th. stanfordi									
Year	Marmots sampled	Population size	% Sampled	Overall prevalence (%)	Range (%)					
2007	139	323	43	44	0–100					
2008	93	276	34	50	0–74					
Total	232	599	39	50						

Table 2 Likelihood of individual infection and 95% CI by four yellow-bellied marmot parasites: one vector-transmitted blood parasite (*Trypanosoma*), three fecal–orally transmitted intestinal parasites (*Ascaris*, *Eimeria* and *Entamoeba*) and a flea *Thrassis stanfordi*

Parasite sp.	Age class	Sex	Likelihood of infection	95% CI	*N*
Trypanosoma	Adult	F	0.02	0.01	576
		M	0.03	0.02	192
	Yearling	F	0.14	0.04	345
		M	0.06	0.02	359
Ascaris	Adult	F	0.10	0.03	402
		M	0.11	0.06	131
	Yearling	F	0.15	0.05	182
		M	0.17	0.05	190
Eimeria	Adult	F	0.93	0.03	402
		M	0.96	0.03	131
	Yearling	F	0.97	0.02	182
		M	0.94	0.03	190
Entamoeba	Adult	F	0.90	0.03	402
		M	0.89	0.05	131
	Yearling	F	0.87	0.05	182
		M	0.91	0.04	190
Th. stanfordi	Adult	F	1.28	0.35	245
		M	2.35	0.82	94
	Yearling	F	0.40	0.12	232
		M	0.55	0.16	304

N refers to the samples examined; statistical analyses accounted for repeated measures on individuals.
CI, confidence interval.

Levels of *Th. stanfordi* infection were generally high, and there was a positive trend between population size and flea prevalence (Fig. 1e), but the relationship was not significant (Table 3).

When we looked at the relationship between colony size and intestinal parasite diversity, we found a strong positive relationship ($F_{1,2.73}$ = 5 976 464.3, $P < 0.0001$; Fig. 1f). Marmots in large colonies were infected by more types of parasites than those in small colonies.

Variation in population size was also correlated with variation in adult male-to-female sex ratio ($r = -0.61$, $P < 0.001$), and this effect remained after controlling for both year studied and colony studied in a mixed-effects model. This correlation prevented us from studying the simultaneous effect of population size and adult sex ratio on prevalence. When adult male-to-female sex ratio, but not colony size, was entered into the mixed-effects model, we found that the prevalence of fleas was higher in populations with higher male bias in the sex ratio (Table 3). Sex ratio did not have a significant effect on the prevalence of any of the other parasites.

Because we found differences in the likelihood of infection between yearlings and adults, we tested whether parasite prevalence would be affected by the ratio of yearlings to adults (age ratio). We found that the age ratio affected the prevalence

Table 3 Summary of statistical results for four analyses: (1) likelihood of individual infection; (2) colony size versus prevalence; (3) sex ratio versus prevalence; (4) age ratio versus prevalence

		Trypanosoma		*Ascaris*		*Eimeria*		*Entamoeba*		*Thrassis stanfordi*	
Analysis	Factors	Statistic	*P*-value	Statistic	*P*-value	Statistic	*P*-value	Statistic	*P*-value	Statistic	*P*-value
1. Likelihood of individual infection	Season	$z = 0.43$	0.665	$z = -0.78$	0.437	$z = -0.32$	0.750	$z = -3.52$	0.0004***	$z = -3.22$	0.00129**
	Age class	$z = 5.16$	2.42E-07***	$z = 2.28$	0.022*	$z = 2.12$	0.034*	$z = -0.024$	0.981	$z = -5.08$	3.79E-07***
	Sex	$z = 0.79$	0.427	$z = 0.52$	0.605	$z = 1.34$	0.180	$z = -0.50$	0.882	$z = 1.96$	0.0505
	Age class × Sex	$z = -1.90$	0.058	n/a	n/a	$z = -2.12$	0.034*	n/a	n/a	n/a	n/a
2. Colony size	Colony size	$t = 12.5$	>0.1	$t = 786.9$	<0.001***	$t = -29.6$	0.329	$t = -1.1$	0.418	$t = 0.631$	0.548
	Year	$F = 115.3$	<0.001***	$F = 29.9$	<0.001***	$F = 2.8$	0.163	$F = 6.9$	>0.1	$F = 0.235$	0.645
3. Sex ratio	Sex ratio	$t = -2.9$	NS	$F = 181.9$	0.53	$t = 261.6$	NS	$F = 148.2$	0.148	$F = 7.5$	0.024*
	Year	$F = 89.0$	<0.001***	$F = 33.7$	Variable	$F = 482163.8$	Variable	$F = 24.2$	<0.001***	$F = 0.7$	0.433
4. Age ratio	Age ratio	$t = -1.97$	0.257	$F = 19.5$	0.013*	$F = 31.6$	0.001***	$F = 0.65$	0.665	$F = 0.9$	0.366
	Year	$F = 35.7$	0.009**	$F = 20.0$	0.001***	$F = 2.9$	0.143	$F = 5.3$	0.056	$F = 0.1$	0.763

All models controlled for repeated sampling of individuals and colonies within and between years, but only the test statistic and *P*-value for the factors of interest are shown.
*Significant at the 0.05 level.
**Significant at the 0.01 level.
***Significant at the 0.001 level.
Variable = significant effects some years but not others.
n/a, not applicable; NS, not significant.

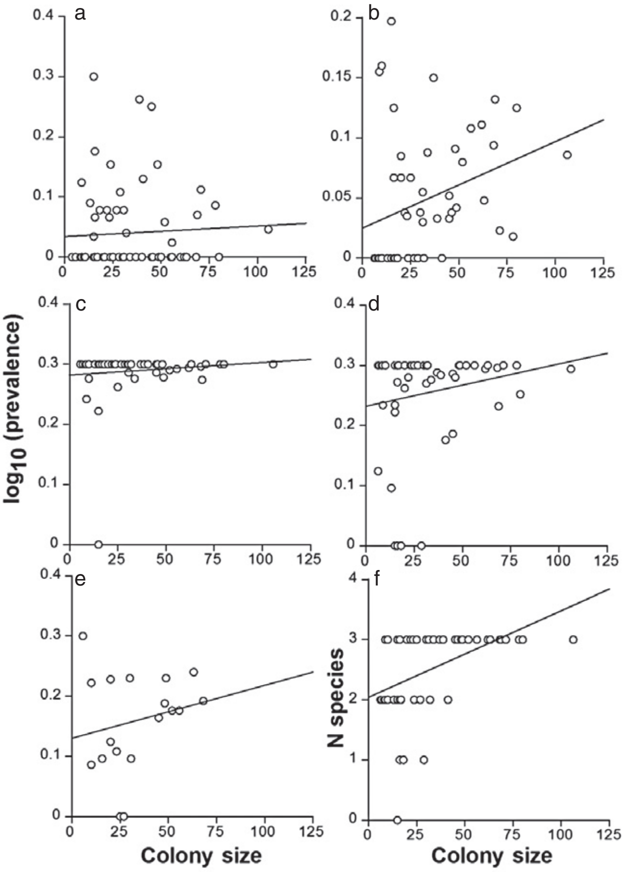

Figure 1 Relationship between colony size and parasitism. (a–e) show the relationship between colony size and prevalence of (a) a vector-transmitted parasite *Trypanosoma lewisi*, three fecal–orally transmitted parasites [(b) *Ascaris* sp., (c) *Eimeria* spp. and (d) *Entamoeba* sp.], (e) fleas *Thrassis stanfordi* and (f) the relationship between colony size and the number of endoparasites.

of *Ascaris* and *Eimeria* only (Table 3). For both of these parasites, the proportion of yearlings was positively correlated with prevalence.

Discussion

Our results show that the likelihood of individual infection can be affected by seasonal changes, age of the host and sex of the host. However, the exact nature of this effect is parasite species specific. Marmot age played a significant role in the likelihood of infection by *Ascaris*, *Eimeria* and *Tr. lewisi*, but the nature of the relationship varied by species. In *Eimeria* and *Tr. lewisi*, there was a significant interaction of age with sex. Marmot age had no significant effect on infection by *Entamoeba*; instead, there were significant seasonal effects. The differences in the likelihood of infection did not seem to vary predictably with the mode of transmission of these parasites, and other aspects of the life cycles of the host and parasites are likely to be important. These results might lead to the prediction of significant sex ratio effects on the prevalence of *Eimeria*, but this prediction was not supported by the prevalence analyses.

The relationships between parasite prevalence and host population size in marmots were diverse and complex. We found a significant positive relationship for the fecal–orally transmitted intestinal endoparasite *Ascaris*. This result is consistent with patterns of increasing parasite infection with group size seen in many systems (Côté & Poulin, 1995). The strong covariation between population size and sex ratio, however, allows for an alternative explanation: sex ratio rather than population size may account for this relationship. Despite the lack of an effect of sex on the likelihood of individual infection, we found a significant sex ratio effect; male-biased colonies had lower prevalence of *Ascaris*. We found no relationship between *Ascaris* infection and overwinter survival, suggesting that *Ascaris* infection does not pose a cost of sociality in this respect. The prevalence of *Ascaris* was also significantly affected by age ratio, a finding that suggests that yearlings play a significant role in the dynamics of this parasite. Wey & Blumstein (2010) previously demonstrated the importance of yearlings in maintaining social cohesion in this population, and this social cohesion may be associated with *Ascaris* prevalence.

For our other two fecal–orally transmitted parasites (*Eimeria* and *Entamoeba*), there was no significant relationship between population size and prevalence. With the intestinal parasite *Eimeria*, most individuals were infected and prevalence was at or near its 100% maximum. For *Entamoeba*, while there was no significant relationship either, there was an interesting trend: while small populations were observed with both low and high prevalence, large colonies were never observed with low prevalence. While colony sex ratio did not affect the prevalence of either *Eimeria* or *Entamoeba*, the age ratio of the population significantly affected the prevalence of *Eimeria*, suggesting that yearlings play a significant role in the transmission of *Eimeria*.

We also found no relationship between population size and prevalence for the vector-transmitted blood parasite *Tr. lewisi*. Many populations had very low levels of infection or were not infected (had zero prevalence). It appears that *Tr. lewisi* is not endemic in our study population. Our study may have coincided with a *Tr. lewisi* epidemic because this parasite has not been detected in marmots in subsequent years. The sex ratio and age ratio of host populations had no effect on the prevalence of this parasite either.

The relationship between population size and prevalence observed in *Entamoeba*, which has a wide range of prevalence in small populations, but only high prevalence in large populations, although not significant, is noteworthy because this relationship is not predicted by any host–parasite model, but this sort of transmission has been observed in a laboratory study (Lopez, 2005). In contrast with the other fecal–orally transmitted parasites in this study, the prevalence of *Entamoeba* was not influenced by any of the factors we tested: population size, sex ratio and age ratio. The different patterns seen among parasites with similar modes of transmission could be due to host immunity that varies for different parasites, to upper limits on colony sizes or to species-specific factors that affect parasite transmission and reproduction.

We also found a strong positive relationship between colony size and parasite diversity; larger colonies have more species of parasites in them. This pattern is reminiscent of the species–area relationships long established in ecological studies (MacArthur & Wilson, 1967). Just as larger habitats can sustain more species, larger host populations can sustain more species of parasites (Mooring & Hart, 1992). This positive relationship is also consistent with the overall pattern in Rifkin *et al.*'s (2012) meta-analysis: large populations suffer higher levels of parasitism. The variation in parasite diversity with population size should be relevant in a wide variety of studies, such as studies of behavior, population dynamics and/or community relationships: individuals in populations of different sizes may behave differently or vary in their roles in their communities in part because of the differences in the parasite communities they sustain. While there are costs and benefits to living in groups, the costs may vary depending on the size of the group because of the presence of different parasite communities.

In conclusion, this study allowed us to test, in the field, factors that might influence the likelihood of individual infection and factors that might affect parasite prevalence (at the population level). We were also able to look at the role of seasonal changes, host age and host sex on the likelihood of individual infection. We found that host age (yearling vs. adult) played a significant role in four of the five parasites we studied; however, the nature of the relationship varied from species to species. At the population level, we found that population size, sex ratio and age ratio influence parasite prevalence, although the nature of the effects is highly variable from one species to another. We also found a positive correlation between population size and parasite diversity. While this latter pattern is consistent with a cost of sociality, studies to date in this system (Van Vuren, 1996; Wey & Blumstein, 2012) have not found strong support for these costs. This could be due to the fact that most of our parasite data came from a series of good years when the marmot population increased dramatically (Ozgul *et al.*, 2010); in bad years, costs of parasitism may be enhanced. Additionally, animals may be able to counter the costs of increased parasitism in larger groups by behavioral means (e.g. Bordes, Blumstein & Morand, 2007), or as a result of the encounter dilution effect (Mooring & Hart, 1992). Future studies would profit from studying the putative behavioral and immune responses by which marmots have adapted to the potential costs of parasite infection.

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References

Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Pedersen, A.B., Poss, M. & Pulliam, J.R.C. (2003). Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu. Rev. Ecol. Syst.* **34**, 517–547.

Armitage, K.B. (2003*a*). Marmots (*Marmota monax*) and allies. In *Wild mammals of North America: biology, management, and conservation*, 2nd edn: 188–210. Feldhamer, G.A., Thompson, B.C. & Chapman, J.A. (Eds). Baltimore: Johns Hopkins University Press.

Armitage, K.B. (2003*b*). Dynamics of immigration into yellow-bellied marmot colonies. *Oecol. Mont.* **12**, 21–24.

Armitage, K.B. (2010). Individual fitness, social behavior, and population dynamics of yellow-bellied marmots. In *The ecology of place: contributions of place-based researcher to ecological understanding*: 134–154. Billick, I. & Price, M.V. (Eds). Chicago: University of Chicago Press.

Armitage, K.B., Blumstein, D.T. & Woods, B.C. (2003). Energetics of hibernating yellow-bellied marmots (*Marmota flaviventris*). *Comp. Biochem. Physiol. A* **134**, 101–114.

Bates, D., Maechler, M. & Bolker, B. (2012). lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4

Blumstein, D.T. (2012). Social behaviour. In *Behavioural responses to a changing world*: 119–128. Wong, B. & Candolin, U. (Eds). Oxford: Oxford University Press.

Blumstein, D.T., Ozgul, A., Yovovitch, V., Van Vuren, D.H. & Armitage, K.B. (2006). Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *J. Zool. (Lond.)* **270**, 132–138.

Blumstein, D.T., Wey, T.W. & Tang, K. (2009). A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. Biol. Soc.* **276**, 3007–3012.

Bonsall, M.B. & Eber, S. (2001). The role of age-structure on the persistence and the dynamics of insect herbivore–parasitoid interactions. *Oikos* **93**, 59–68.

Bordes, F., Blumstein, D.T. & Morand, S. (2007). Rodent sociality and parasite diversity. *Biol. Lett.* **3**, 692–694.

Burdon, J.J., Ericson, L. & Muller, W.J. (1995). Temporal and spatial changes in a metapopulation of the rust pathogen *Triphragmium ulmariae* and its host, *Filipendula ulmaria*. *J. Ecol.* **83**, 979–989.

Côté, I.M. & Poulin, R. (1995). Parasitism and group size in social animals: a meta-analysis. *Behav. Ecol.* **6**, 159–165.

Crawley, M.J. (Ed.) (1992). *Natural enemies: the population biology of predators, parasites and diseases*: Oxford: Blackwell Scientific Publications.

Dias, E. (1937). Trypanosomes in bat and marmot. *Trans. R. Soc. Trop. Med. Hyg.* **31**, 260.

Dobson, A.P. (1988). The population biology of parasite-induced changes in host behavior. *Q. Rev. Biol.* **63**, 139–165.

Dobson, A.P., Hudson, P.J. & Lyles, A.M. (1992). Macroparasites: worms and others. In *Natural enemies: the population biology of predators, parasites and diseases*: 329–348. Crawley, M.J. (Ed.). Oxford: Blackwell Scientific Publications.

Ericson, L., Burdon, J.J. & Muller, W.J. (1999). Spatial and temporal dynamics of epidemics of the rust fungus *Uromyces valerianae* on populations of its host *Valeriana salina*. *J. Ecol.* **87**, 649–658.

Ferrari, N., Cattadori, I.M., Nespereira, J., Rizzoli, A. & Hudson, P.J. (2004). The role of sex in parasite dynamics: field experiments on the yellow-necked mouse *Apodemus flavicollis*. *Ecol. Lett.* **7**, 88–94.

Grosholz, E.D. (1993). The influence of habitat heterogeneity on host-pathogen population dynamics. *Oecologia* **96**, 347–353.

Holmes, J.C. (1996). Parasites as threats to biodiversity in shrinking ecosystems. *Biodivers. Conserv.* **5**, 975–983.

Kistler, R.A. (1985). Host-age structure and parasitism in a laboratory system of two hymenopterous parasitoids and larvae of *Zabrotes subfasciatus* (Coleoptera: Bruchidae). *Environ. Entomol.* **14**, 507–511.

Letitia, A.D., Poulin, R., Ward, D.F. & Zuk, M. (2000). Sex differences in parasitic infections among arthropod hosts: is there a male bias? *Oikos* **88**, 327–334.

Lopez, J.L. (2005). Parasite prevalence and the size of host populations: an experimental test. *J. Parasitol.* **91**, 32–37.

Lopez, J.L., Gallinot, L.P. & Wade, M.J. (2005). Spread of parasites in metapopulations: an experimental study of the effects of host migration rate and local host population size. *Parasitology* **130**, 323–332.

MacArthur, R. & Wilson, E.O. (1967). *The theory of island biogeography*: Princeton: Princeton University Press.

MacNeal, W.J. (1904). The life-history of *Trypanosoma lewisi* and *Trypanosoma brucei*. *J. Infect. Dis.* **1**, 517–543.

Minchella, D.J. & Scott, M.E. (1991). Parasitism: a cryptic determinant of animal community structure. *Trends Ecol. Evol.* **6**, 250–254.

Moore, J. (2002). *Parasites and the behavior of animals*: New York: Oxford University Press.

Mooring, M.S. & Hart, B.L. (1992). Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. *Behaviour* **123**, 173–193.

Murray, A. & Cade, W.H. (1995). Differences in age structure among field cricket populations (Orthoptera; Gryllidae): possible influence of a sex-biased parasitoid. *Can. J. Zool.* **73**, 1207–1213.

Olson, L.E. & Blumstein, D.T. (2010). Applying the coalitionary-traits metric: sociality without complex cooperation in male yellow-bellied marmots. *Behav. Ecol.* **21**, 957–965.

Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S. & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482–485.

Poulin, R. (1996). Sexual inequalities in helminth infections: a cost of being a male? *Am. Nat.* **147**, 287–295.

R Development Core Team (2012). *R: a language and environment for statistical computing*: ISBN 3–900051-07-0, (http://www.R-project.org/); R Foundation for Statistical Computing, Vienna, Austria.

Rifkin, J.L., Nunn, C.L. & Garamszegi, L.Z. (2012). Do animals living in larger groups experience greater parasitism? A meta-analysis. *Am. Nat.* **180**, 70–82.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991). Biological consequences of ecosystem fragmentation. *Conserv. Biol.* **5**, 18–32.

Smith, D.L., Ericson, L. & Burdon, J.J. (2003). Epidemiological patterns at multiple spatial scales: an 11-year study of a *Triphragmium ulmariae – Filipendula ulmaria* metapopulation. *J. Ecol.* **91**, 890–903.

Stark, T. (2006). Parasite transmission, condition, and immune function in yellow-bellied marmots (*Marmota flaviventris*): what are the costs of sociality? MS thesis, University of California Los Angeles.

Van Vuren, D. (1996). Ectoparasites, fitness, and social behaviour of yellow-bellied marmots. *Ethology* **102**, 686–694.

Wey, T.W. & Blumstein, D.T. (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim. Behav.* **79**, 1343–1352.

Wey, T.W. & Blumstein, D.T. (2012). Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behav. Ecol. Sociobiol.* **66**, 1075–1085.

Zuk, M. & McKean, K.A. (1996). Sex differences in parasite infections: patterns and processes. *Int. J. Parasitol.* **26**, 1009–1024.