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Ectoparasites, Fitness, and Social Behaviour of Yellow-Bellied Marmots

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VAN VUREN, D. 1996: Ectoparasites, fitness, and social behaviour of yellow-bellied marmots. *Ethology* **102**, 686—694.

Abstract

Parasites can cause a loss of fitness for their hosts, potentially influencing social behaviour patterns of the host that promote or hinder parasite transmission. I studied yellow-bellied marmots (*Marmota flaviventris*) and their ectoparasites to determine if ectoparasites reduce the fitness of marmots and to test whether ectoparasite loads differ according to social behaviour. Three taxa of ectoparasites were identified, fleas (*Oropsylla stanfordi*), lice (*Linognathoides marmotae*), and mites (family Dermanyssidae). High ectoparasite loads were related to slower growth, lower overwinter survival, and reduced reproduction, suggesting that ectoparasites are a fitness cost for marmots. Ectoparasite loads were not higher in colonial than in noncolonial marmots, nor in polygynous than in monogamous adult males. There was a trend, however, toward higher ectoparasite loads in marmots that were dispersing rather than philopatric. Further, ectoparasite loads differed among groups of marmots that nested or hibernated communally, indicating that spatial scale is important in understanding the relationships between parasites and social behaviour.

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Introduction

Parasites may affect the fitness of their vertebrate hosts in several ways. In addition to being a direct cause of death (RAYOR 1985; BROWN & BROWN 1986; MOLLER 1987), parasites can negatively affect reproduction, growth, and physical condition (BROWN & BROWN 1986; SHIELDS & CROOK 1987; RUBENSTEIN & HOHMANN 1989; MOLLER 1991; RICHNER et al. 1993; OPPLIGER et al. 1994; MERINO & POTTI 1995). Vertebrates respond with a variety of behavioural adaptations to counter the threat of parasitism (HART 1990). For example, the presence of parasites influences behaviour such as grooming (HART et al. 1992), movement (ANDERSON 1975), and habitat selection (MERILÄ & ALLANDER 1995).

Because transmission of many parasites is affected by contact between individuals, parasites may also influence social behaviour (FREELAND 1976; RUBENSTEIN &

HOHMANN 1989; CÔTÉ & POULIN 1995; LOHLE 1995). Inter-individual spacing is closer and frequency of physical contact is greater within social groups than among solitary individuals; thus, an increased risk of parasitism is considered a cost of sociality (ALEXANDER 1974; HOOGLAND 1979; MÖLLER 1987; POULIN 1991). Similarly, parasites may play a role in mating systems, since monogamy should carry a lower likelihood of parasite transmission than polygamy (LOHLE 1995). Further, if parasite risk is sufficiently high, individuals might disperse, thereby severing social contact (HOLEKAMP 1986; BROWN & BROWN 1992). The social implications of parasite transmission, however, are poorly known (LOHLE 1995).

The yellow-bellied marmot (*Marmota flaviventris*) is a hibernating, ground-dwelling squirrel that inhabits high-elevation areas in western North America (FRASE & HOFFMANN 1980). Yellow-bellied marmots harbour a variety of ectoparasites (FRASE & HOFFMANN 1980), but effects on fitness are unknown. Social behaviour varies intraspecifically in ways that may influence ectoparasite transmission. Some yellow-bellied marmots are highly social and live in colonies, whereas others live alone (VAN VUREN & ARMITAGE 1994a). The mating system ranges from monogamy to polygyny (ARMITAGE 1991). Most marmots disperse, but some remain philopatric (ARMITAGE 1991). Additionally, marmots usually inhabit separate burrows, but sometimes marmots share the same burrow (ARMITAGE & GURRI-GLASS 1994; LENIHAN & VAN VUREN 1996a).

The purpose of this study was to determine if ectoparasites reduce the fitness of yellow-bellied marmots and to test whether ectoparasite loads differ according to sociality, mating system, and dispersal. I predicted that ectoparasite loads would be lower on noncolonial or monogamous marmots, and higher on dispersers.

Methods

Study Animal

The study was conducted in the East River Valley near Rocky Mountain Biological Laboratory (elevation 2900 m), Gunnison County, Colorado, USA. Yellow-bellied marmots have been studied here since 1962 (ARMITAGE 1991). Marmots hibernate from Sept. until May. Mating occurs shortly after emergence from hibernation, and young-of-the-year emerge above ground during late Jun. or early Jul. Because of the short active season and the energetic demands of a long hibernation, rapid growth is important for marmots, especially young; about one-half of young do not survive their first hibernation (VAN VUREN & ARMITAGE 1994a), in part because they did not gain sufficient weight (LENIHAN & VAN VUREN 1996a). Most dispersal occurs when marmots are yearlings. Almost all males and about one-half of females disperse, while the remaining females are recruited as residents of their natal locality (ARMITAGE 1991). Reproductive maturity is reached at age 2 yr.

Marmots live at discrete habitat patches, typically rock outcrops or talus near meadows. Larger patches support colonies consisting of one adult male and 2–12 adult females, along with young and yearlings. Smaller habitat patches support just one adult female, her offspring, and sometimes an adult male (VAN VUREN & ARMITAGE 1994a). The mating system in colonies is typically harem-polygynous, in which the one adult male is territorial and excludes all other adult males (ARMITAGE 1974). The mating system of noncolonial marmots varies; some males are polygynous and some are monogamous. Communal burrow use has been reported in two kinds of circumstances; littermate young almost always hibernate together during their first winter (LENIHAN & VAN VUREN 1996a), and pairs of closely related adult females occasionally share the same nest and may also nurse their young communally (ARMITAGE & GURRI-GLASS 1994).

Data Collection

Each year since 1962 all marmots in the study area have been trapped, ear-tagged, and weighed. Young have been ear-tagged shortly after emergence from the natal burrow, so age is known for most marmots. Since 1983, most yearlings and noncolonial adults have been implanted with radio transmitters (VAN VUREN 1989) from which data have been collected to describe dispersal and the mating system (VAN VUREN 1990).

Ectoparasites were collected during Jun. and Jul. 1993 from 43 marmots ≥ 1 yr old that lived in four colonies and 11 noncolonial localities; these marmots comprised 65% ($n = 66$) of all marmots ≥ 1 yr old resident in the study area. Each marmot was trapped, chemically restrained with an intramuscular injection of ketamine hydrochloride (FRASE & VAN VUREN 1989), then transferred to a plastic bag. Four cotton balls soaked in chloroform were inserted into the bag, which was enclosed tightly about the neck of the marmot. After 2 min the marmot was removed from the bag, and its fur was combed thoroughly and repeatedly until all anaesthetized ectoparasites had been collected and preserved in 70% ethanol. Ectoparasites were later identified; fleas were counted, whereas other taxa were scored as present or absent.

Each marmot was sampled only once, so temporal variation in ectoparasite loads within individuals was unknown. Because ectoparasite loads may vary seasonally (HOOGLAND 1979; ARNOLD & LICHTENSTEIN 1993), the duration of sampling was shortened as much as possible; 36 marmots (84%) were sampled within the first 33 d of data collection. Further, marmots were sampled in the order they were captured, with no discernable bias according to fitness measure or social environment.

Growth rates were measured for 10 yearling marmots that were trapped and weighed repeatedly during May and Jun. 1993. A least-squares regression was fitted to weights for each yearling; growth rate (g/d) was the slope of the regression equation. Marmots were considered to have died overwinter if they were known to have been alive late in the active season but were not recaptured after intensive trapping effort the following spring. Successful reproduction by adult females was suggested by swollen nipples during lactation and subsequently was confirmed when a litter appeared above ground at the female's burrow. Adult males were considered polygynous if their home range during 1993 included two or more adult females that they interacted with; males were monogamous if their home range and interactions included only one female. Dispersal occurred when a yearling emigrated from its natal home range and established a new, nonoverlapping home range.

Statistical Analyses

Numbers of fleas were compared among marmots using parametric tests; data were log-transformed to meet the requisite assumptions. Because some marmots carried no fleas, a value of one was added to all counts before transformation. Means are presented with associated standard deviations and represent back-transformed values. Prevalences of ectoparasites were compared using a G-test of independence whenever expected frequencies were ≥ 5 .

Results

Marmot Ectoparasites

Ectoparasites from three taxa were identified. A total of 1169 fleas (522 male, 647 female) was collected, all of them of one species, *Oropsylla [Thrassis] stanfordi*. All but four marmots (91%, $n = 43$) harboured fleas, with as many as 166 fleas per marmot (median = 11). Lice of one species, *Linognathoides marmotae* (Ferris), were collected from 24 marmots (56%). Mites of an unidentified species (family Dermanyssidae) were collected from one marmot (2%).

Number of fleas was not correlated with age in marmots ($r = -0.135$, $p > 0.40$), nor did mean number of fleas differ (t-test, $t = 1.11$, $p = 0.27$) between male ($\bar{X} = 16.3$, $SD = 2.60$, $n = 12$) and female ($\bar{X} = 9.2$, $SD = 4.61$, $n = 31$) marmots. Similarly, prevalence of lice among marmots did not differ according to marmot age ($G = 2.23$,

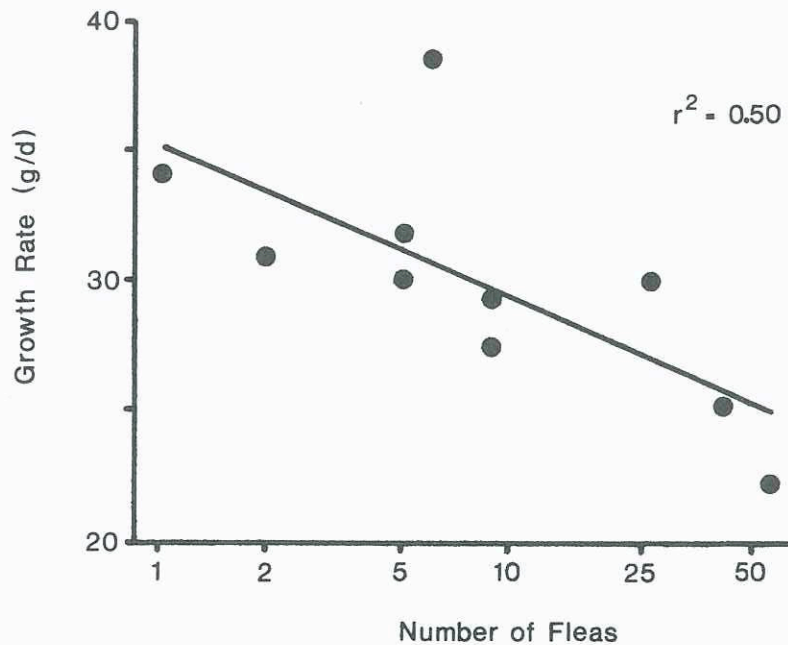


Fig. 1: Relationship between growth rate and a log transformation of flea load, calculated as $\log(x + 1)$, of yearling yellow-bellied marmots. A linear regression, $y = 35.2 - 5.71 \log(x + 1)$, explained 50% of the variation in growth rate ($p = 0.02$)

$p > 0.25$, $df = 2$; some ages combined to improve expected frequencies) or sex ($G = 0.227$, $p > 0.50$, $df = 1$). Thus, age and sex were not considered in further analyses.

Costs of Ectoparasites

Regression analysis indicated that number of fleas explained a significant portion of the variation in growth rate among yearling marmots ($F = 8.04$, $df = 1, 8$, $p = 0.02$); yearlings with greater flea infestations grew more slowly (Fig. 1). Of 32 marmots that entered hibernation during fall 1993, 28 survived overwinter and 4 died. Marmots that died overwinter harboured more fleas ($\bar{X} = 44.6$, $SD = 3.85$; $t = 2.17$, $p = 0.04$) than did marmots that survived ($\bar{X} = 8.1$, $SD = 4.04$). Nine of 19 adult females produced litters during 1993. Females that failed to reproduce harboured more fleas ($\bar{X} = 23.9$, $SD = 3.91$; $t = 2.51$, $p = 0.02$) than those that successfully reproduced ($\bar{X} = 3.4$, $SD = 5.27$).

Ectoparasites and Social Behaviour

The number of fleas on colonial marmots ($\bar{X} = 8.3$, $SD = 4.05$, $n = 14$) did not differ statistically ($t = 0.87$, $p = 0.39$) from the number of fleas on noncolonial marmots ($\bar{X} = 13.0$, $SD = 4.22$, $n = 27$). Similarly, prevalences of lice among colonial (36%) and noncolonial (63%) marmots were not statistically different, although there was a trend

toward a higher prevalence in noncolonial marmots ($G = 2.78$, $0.10 > p > 0.05$). Two marmots were excluded from these analyses because they had just emigrated into the study area from an unknown social environment.

The number of fleas on polygynous adult males ($\bar{X} = 13.1$, $SD = 2.15$, $n = 4$) did not differ statistically ($t = 0.18$, $p = 0.86$) from the number of fleas on monogamous males ($\bar{X} = 11.7$, $SD = 2.54$, $n = 5$). Six female yearlings dispersed during the summer of 1993, and four remained philopatric. There was a trend toward a higher number of fleas on dispersing ($\bar{X} = 14.8$, $SD = 3.77$) than on philopatric ($\bar{X} = 3.1$, $SD = 2.62$) marmots, although the difference was not significant ($t = 1.75$, $p = 0.12$).

Marmots sampled for ectoparasites included a pair of 4-year-old sisters that nested communally, a litter of yearlings that had hibernated communally with their mother, a litter of yearlings that had hibernated communally without their mother, and a litter of 2-year-olds that had remained together and hibernated communally as yearlings. An analysis of variance indicated that variation in number of fleas among these four groups ($\bar{X} = 3.8$ – 87.6) was almost statistically significant ($F = 3.41$, $df = 3,12$, $p = 0.053$).

Discussion

All three taxa of ectoparasites identified in this study have been found on yellow-bellied marmots previously (OLSEN 1938; ALLRED 1961; SENGER 1966). Similarly, previous information on prevalence and intensity, although sparse (ESKEY 1936; JELLISON 1945; ALLRED 1961), is similar to that reported here.

Ectoparasites may harm their hosts in several ways (HOOGLAND 1979). Ectoparasites remove blood, their bites may damage the skin and underlying tissues, and the host may expend valuable time grooming to remove ectoparasites. Further, ectoparasites may transmit debilitating or lethal diseases (HOOGLAND 1979). The mechanisms by which ectoparasites affect marmots are uncertain. The amount of blood removed from marmots is unknown, but ectoparasites can cause anaemia in other hosts (MARSHALL 1981). I saw no obvious evidence of wounds or infections due to ectoparasite bites. Marmots often groom, but devotion of time to a particular activity does not necessarily mean that the activity is costly (ARMITAGE 1988).

Nonetheless, my results suggest that ectoparasites, especially fleas, exert a fitness cost on marmots. Yearlings with high ectoparasite loads had slower growth rates, with probable fitness consequences; marmots with low body mass at entry into hibernation are less likely to survive overwinter (ARMITAGE 1994; LENIHAN & VAN VUREN 1996a). I did not weigh marmots at entry into hibernation, but high ectoparasite loads on marmots that failed to survive overwinter are consistent with the hypothesis that ectoparasites reduce the likelihood of survival by inhibiting growth. Similarly, high ectoparasite loads on alpine marmots (*M. marmota*) exacerbate weight loss during hibernation, thereby contributing to higher overwinter mortality (ARNOLD & LICHTENSTEIN 1993).

The proportion of females that produced litters (0.47) is close to the long-term average (0.48) for this population (ARMITAGE 1986). For female marmots, reproductive success in a given year is influenced by factors such as age, sufficient food resources, and social interactions that inhibit reproduction (ARMITAGE 1986, 1994; VAN VUREN &

ARMITAGE 1991). My results suggest that ectoparasites also affect reproduction; females that failed to produce litters had higher ectoparasite loads. In alpine marmots, females with high ectoparasite loads reproduced later in the season (ARNOLD & LICHTENSTEIN 1993).

Disease transmission is a potential cost of ectoparasites for yellow-bellied marmots. Fleas and lice that parasitize marmots, including *Oropsylla stanfordi* (ESKEY 1936; STARK 1957), are vectors for plague (*Yersinia [Pasteurella] pestis*). Marmots can become infected with plague (POLLITZER 1954), although blood samples collected from 35 of the 43 marmots in my study all tested negative for *Y. pestis* (C. SCOTT pers. comm.). Thus, in addition to depressing growth, survival, and reproduction of marmots, ectoparasites may be vectors for lethal diseases.

Previous research has shown that parasite load increases with social group size in a variety of host species (HOOGLAND & SHERMAN 1976; FREELAND 1979; HOOGLAND 1979; BROWN & BROWN 1986; SHIELDS & CROOK 1987; RUBENSTEIN & HOHMANN 1989), although ARNOLD & LICHTENSTEIN (1993) found no relationship between parasite load and group size in alpine marmots. In the case of highly mobile parasites (CÔTÉ & POULIN 1995), attack rate may actually decrease in larger host groups (DUNCAN & VIGNE 1979; RUTBERG 1987; RUBENSTEIN & HOHMANN 1989). Few studies, however, have compared parasite infestations between social and nonsocial individuals of the same species. Parasite prevalences or intensities were lower for solitary than for colonial barn swallows (*Hirundo rustica*) (MÖLLER 1987; SHIELDS & CROOK 1987) and male bats (*Plecotus townsendii*) (KUNZ 1976), but did not differ for female bats (KUNZ 1976). Taken together, however, the weight of evidence from previous studies is consistent with the prediction that increased sociality leads to an increased risk of parasitism.

Thus my results, indicating no significant difference in flea loads between colonial and noncolonial marmots, are surprising; indeed, prevalence of lice exhibited a trend in the opposite direction. Similarly, I found no significant difference in ectoparasite loads between polygynous and monogamous males, even though reproductive males frequently come into physical contact with, and enter the burrows of, females living in their home range.

HOLEKAMP (1986) hypothesized that the cost of high ectoparasite loads may cause individuals to disperse to another locality, but found no relation between ectoparasite load and dispersal in Belding's ground squirrels (*Spermophilus beldingi*). In contrast, BROWN & BROWN (1992) reported that dispersal in cliff swallows (*H. pyrrhonota*) was strongly associated with high levels of ectoparasitism. Because dispersal in marmots probably involves a cost-benefit assessment of prospects for success in the natal area (VAN VUREN & ARMITAGE 1994b), it seems likely that ectoparasites, which appear to have a fitness cost for marmots, would play a role in dispersal. My results are consistent with this expectation; dispersing marmots exhibited a trend toward higher ectoparasite loads, although the difference was not statistically significant.

Flea loads on marmots were relatively consistent within groups that hibernated or nested communally but varied substantially among groups. Similar relationships were reported for ectoparasites of alpine marmots (ARNOLD & LICHTENSTEIN 1993) and endoparasites of primates (FREELAND 1979). Most fleas require the nest of their host to

complete their life cycle (MARSHALL 1981); thus, although fleas readily jump between hosts that are in close proximity during social interactions (MARSHALL 1981), communal burrows may be the most important opportunity for flea movement between marmots. The cost of acquiring parasites in communal burrows probably is offset by the benefits. Littermate young almost always hibernate communally, perhaps because the energetic benefits of joint hibernation improve survival (LENIHAN & VAN VUREN 1996b), as is the case for alpine marmots (ARNOLD 1990). Communal nesting by adult females is uncommon and probably occurs because of both direct and indirect fitness benefits (ARMITAGE & GURRI-GLASS 1994).

In conclusion, I found that high ectoparasite loads in yellow-bellied marmots were related to slower growth, lower overwinter survival, and reduced reproduction, although I cannot conclude that ectoparasites caused these relationships. For example, another factor such as inadequate food intake may have caused marmots to suffer both heavy ectoparasite infestation and slow growth. Nonetheless, my results are consistent and suggest that high ectoparasite loads cause a loss of fitness in marmots. Contrary to predictions, however, ectoparasite loads were not higher in either colonial or polygynous marmots.

Spatial scale is important in understanding parasite transmission among hosts (LOYE & CARROLL 1995). At the scale of the social or mating system of marmots, ectoparasites are not a cost of sociality or polygyny. But at the smaller scale of the burrow system, parasites are a potential cost of nesting or hibernating communally and, probably, of philopatry.

Acknowledgements

I thank K. B. ARMITAGE, R. GRAY, and C. LENIHAN for assistance in data collection, and especially C. SCOTT for support and assistance throughout the study. I particularly thank R. KIMSEY for identifying and counting ectoparasites. Facilities were provided by Rocky Mountain Biological Laboratory, and funding was provided by the University of California Agricultural Experiment Station.

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Received: September 18, 1995

Accepted: February 14, 1996 (J. Brockmann)