Patterns of ectoparasitism in North American red squirrels (*Tamiasciurus hudsonicus*): Sex-biases, seasonality, age, and effects on male body condition

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ABSTRACT

Within many species, males are often more heavily parasitised than females. Several hypotheses have been proposed to explain this phenomenon, including immunocompetence handicaps, sexual size dimorphism and behavioural differences. Here we set out to test the latter two hypotheses and make inferences about the former by assessing patterns of ectoparasitism across various life-history stages in a population of North American red squirrels (*Tamiasciurus hudsonicus*). We also conducted an ectoparasite removal experiment to investigate the effects of ectoparasites on male body condition. We found that males were more intensely parasitized than females, but only during the mating period. There was no difference in ectoparasite intensity between male and female juveniles at birth or at emergence, suggesting that ectoparasites do not exploit male red squirrels for longer-range natal dispersal. Male red squirrels in our population were slightly heavier than females, however we did not find any evidence that this dimorphism drives male-biased ectoparasitism. Finally, we could not detect an effect of ectoparasite removal on male body mass. Our results lend support to the hypothesis that ectoparasites exploit their male hosts for transmission and that male red squirrels are important for the transmission dynamics of ectoparasites in this population; however, the mechanisms (*i.e.*, immunocompetence, testosterone) are not known.

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1. Introduction

Parasites can affect the body condition, reproductive success, survival and physiology of their hosts (Booth et al., 1993; Brown and Brown, 2004; Hillegass et al., 2010; Khokhlova et al., 2004; Neuhaus, 2003; Scantlebury et al., 2007; Vaughan et al., 1989), often imposing significant energetic costs (Booth et al., 1993; Careau et al., 2010; Kam et al., 2010; Khokhlova et al., 2002; Scantlebury et al., 2007), which can result in parasite-induced evolutionary shifts in life-history traits (Chadwick and Little, 2005; Fredensborg and Poulin, 2006; Ohlberger et al., 2011; Richner, 1998; Richner and Tripet, 1999). Parasitism is often biased or structured by age, size, gregariousness, or sex of the host

(*e.g.*, Patterson and Ruckstuhl, 2013; Rifkin et al., 2012; Schalk and Forbes, 1997). Specifically, in many vertebrate species, males are commonly found to be the more intensely parasitized sex (Bacelar et al., 2011; Cowan et al., 2007; Gorrell and Schulte-Hostedde, 2008; Harrison et al., 2010; Moore and Wilson, 2002; Poulin, 1996; Schalk and Forbes, 1997; Waterman et al. 2014) and, thus, males may be accountable for much of the parasite transmission in many species and populations (Ferrari et al., 2004; Perkins et al., 2003, 2008; Skørping and Jensen, 2004). There have been many hypotheses offered to explain the phenomenon of male-biased parasitism. First, observed patterns of male-biased parasitism may be due to sexual dimorphisms in species where the male is the larger or more ornamented sex (*e.g.*, species with polygynous mating systems; Clutton-Brock et al., 1977). These individuals may offer more resources (*i.e.*, nutrients, space) to parasites ("well-fed host" hypothesis; Hawlena et al., 2005), may simply be larger targets for parasites (Moore and Wilson, 2002) and therefore easier to find, or, because of energetic constraints, larger/more ornate individuals may trade-off growth at the expense of immune function

(Rolff, 2002). Second, males are generally associated with a more risky lifestyle, particularly in polygynous species (Kraus et al., 2008), and these behaviours may increase the opportunities for males to acquire and transmit parasites (Moore and Wilson, 2002). Related to this, in mammals, males are the sex most likely to engage in natal dispersal and males often have larger home ranges than females (Cockburn et al., 1985; Dobson, 1982; Lane et al., 2009; Pusey, 1987; Wolff et al., 1988). As such, it has been hypothesized that male hosts offer their parasites better opportunities for dispersal and inbreeding avoidance, thereby improving the parasite's fitness. Third, levels of testosterone produced by males usually exceed those produced by females and testosterone has known immunosuppressive qualities (Zuk and McKean, 1996), which may reduce the ability of males to fend off parasite infections (immunocompetence handicap hypothesis), although support for this hypothesis is varied (Bilbo and Nelson, 2001; Roberts et al. 2007). Ultimately, trade-offs likely exist between combating an infection and the allocation of energy to growth, reproduction, and metabolism (Folstad and Karter, 1992; Owens, 2002).

Here we explore the patterns and consequences of ectoparasitism in a population of territorial rodents, North American red squirrels (*Tamiasciurus hudsonicus*), at various life-history stages. Male-biased parasitism has been observed previously in this species from a geographically distant population (Gorrell and Schulte-Hostedde, 2008). Male red squirrels do not possess secondary sexual characters (*i.e.*, antlers, bright colours) or sexual size dimorphisms that may affect parasitism and their parasite infection status can be tracked both from birth through to emergence and as adults. As such, red squirrels are a good species for exploring the topic of sex-biased parasitism, particularly since any observed male-bias in adult parasite infection intensity should result from differences in behaviour or physiology. We predicted that males would display higher ectoparasite intensities than females throughout the study period if body size dimorphism drives ectoparasite infection intensity; however, since any sexual size dimorphism is slight in this species (Boutin and Larsen, 1993; see Results) we did not expect to find any difference in ectoparasite intensity based on size alone. If ectoparasites preferentially select larger (heavier) hosts, then we expected heavier adult squirrels to host greater intensities of ectoparasites. Alternatively, larger animals may be larger because they have greater immunocompetence and, therefore, would be expected to have fewer parasites (within the same sex). Additionally, if males are preferred hosts due to their propensity to disperse and distribute contact-transmitted ectoparasites, then we predicted that males would be more heavily parasitized at the time of natal dispersal (emergence) or at the time of mating, when rates of host–host contact (*i.e.*, in the nest, between mating individuals) and off-territory ranging movements are greatest (Lane et al., 2009; Larsen and Boutin, 1994). Finally, we experimentally removed ectoparasites from male red squirrels to investigate the effects of ectoparasite infection on host body mass. If male hosts are the more heavily parasitized sex and there is an energetic cost associated with parasitism (Booth et al., 1993; Scantlebury et al., 2007), parasites should decrease the amount of energy available to support body maintenance (Speakman, 2008), with the prediction that ectoparasites would negatively affect the body mass of male red squirrels across time.

2. Materials and methods

This study was conducted in Sheep River Provincial Park, Alberta, Canada (110° W, 50° N; 1500 m) between April and October 2010 and 2011. Red squirrels were captured in coniferous-dominated forest by use of live-traps (XLF15, H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with peanut butter. One grid (10 × 4 trap pattern) was established at each site with forty traps spaced 50 m apart at three distinct sites (~6.75 ha per site) within a 5 km radius. Upon capture, each squirrel was ear tagged (Monel #1, National Band and Tag Co., Newport, Kentucky), weighed using a spring scale (±1 g; Pesola AG, Baar, Switzerland). For the dimorphism analysis, we also measured the zygomatic breadth (skull width) using a dial caliper to the nearest 0.1 mm (Scienceware #134160001, Bel-Art Products, Wayne, New Jersey). For consistency, all body masses used in the analyses were collected in the early morning (between 7h00 and 10h00) and masses collected on consecutive days were averaged. In both years, pregnant females were radiocollared (N = 12; SOM-2190, Wildlife Materials, Inc., Murphysboro, Illinois) and tracked to their nests at night following parturition to gain access to their offspring. Offspring were marked with unique ear notches shortly after birth and, where possible, the nest was revisited ~25 days later to mark the offspring with numbered ear tags (Monel #1, National Band and Tag Co., Newport, Kentucky).

At each capture all individuals were systematically searched for 2 min to count fleas (*Orchopeas caedens*, *Monopsyllus vison* [Mahrt and Chai, 1972]) using a flea comb and by visual inspection following the methods described by Patterson et al. (2013). Detailed flea counts from both adult males and females were collected in 2011, while counts from juveniles were taken in 2010 and 2011. In 2010, adult males were only inspected for the presence or absence of fleas using the aforementioned search technique at first capture to ensure that the removal experiment described below was not biased in any way. Fleas were counted, but never removed from untreated control animals. All juveniles were inspected for fleas at the time of first nest entry (birth) and at emergence from the nest (~40 days after parturition) when juvenile squirrels begin to explore, disperse, and settle away from the natal territory (Rusch and Reeder, 1978). While likely present, we did not quantify prevalence or intensity of lice, mites or ticks.

Data on flea intensities were divided into four groups based on life-history stage: mating adult, post-mating adult, juvenile birth and juvenile emergence. When mating, male red squirrels have scrotal testes, which become abdominal when mating ceases (Layne, 1954). Only reproductively mature males were included in this study. In 2011, mating was delayed compared to the two previous years, possibly due to a deep snow pack, late winter weather, poor food availability, and/or an impending spruce cone mast (J. Patterson, pers. obs.; Fletcher et al., 2013). For determining sexual dimorphism, we chose mass and zygomatic breadth of adults (>1 year) in spring 2011 (May) and fall 2011 (September–October). We only used individuals that we had trapped in previous years to ensure that yearlings were not included in the analysis. Although males were scrotal in May 2011, none of the females displayed signs of pregnancy via palpation or lactation in May 2011. In the September–October 2011 dimorphism analysis, we only included females who had ceased lactation.

For the parasite removal experiment, we captured reproductively active (*i.e.*, scrotal) adult males at the beginning of May 2010. Males were initially placed into treatment and control groups based on the flip of a coin and alternating thereafter. Males in the treatment group were each given 0.15 ml/kg of Bayer K9 Advantix (8.8% imidacloprid, 44.0% permethrin; Bayer HealthCare LLC, Animal Care Division, Shawnee Mission, Kansas) applied directly to the skin between the shoulder blades. Treatment was repeated every 30 days. At the dosage used, this combination of drugs has been shown to be highly effective at killing arthropod parasites with a low toxicity in mammals, including squirrels (Larsen et al., 2005; Metzger and Rust, 2002). Control and treated animals were both handled and trapped in the same manner and with equal effort; however, controls were not given the medication. We explored differences in average mass as well as mass gains and losses across time between treated and

control males at 30-day intervals: day 0 (when treatment started: first two weeks of May 2010), day 30 (30 days after initial treatment: first two weeks of June 2010) and day 90 (90 days after initial treatment: first two weeks of August 2010).

Where multiple flea counts or squirrel masses were obtained in the same period for the same individuals we took the average value for use in the analysis. All measures of median intensity of ectoparasites, as well as their associated 95% confidence intervals (CI), were determined using Quantitative Parasitology version 3.0 (Rózsa et al., 2000). All data were tested for normality and data that were normally distributed were analysed using a two-sample t-test or a generalized linear model (GLM). Non-normal data were difficult to properly transform, so in these cases Mann−Whitney tests and a full model GLM fitted with a quasi-Poisson distribution were used to compare the data. All means are reported ±1 standard deviation (SD) unless otherwise stated. All statistical analyses were conducted using R version 2.12.0 (R Development Core Team, 2010).

3. Results

3.1. Adult sexual dimorphism

Adult male red squirrels ($\overline{X} = 239.1 \pm 17.7$ g, n = 33) averaged 19.7 g heavier than adult females ($\overline{X} = 219.4 \pm 10.85$ g, n = 32) in May 2011 ($t_{58.7} = -5.12$, $p < 0.001$), resulting in a mass ratio of 1.09. The dimorphism in body mass persisted across time, as adult males ($\overline{X} = 237.5 \pm 20.9$ g, n = 16) were, on average, 22.6 g heavier than adult females ($\overline{X} = 214.9 \pm 16.3$ g, n = 17) in the fall season of 2011 ($t_{28.4} = 3.45$, $p = 0.002$), producing a mass ratio of 1.11. Average adult male zygomatic breadth ($\overline{X} = 27.4 \pm 1.0$ mm, n = 33) did not differ from that of adult females ($\overline{X} = 27.1 \pm 0.7$ mm, n = 32) in May 2011 ($t_{41.7} = -1.21$, $p = 0.232$).

3.2. Host body mass and ectoparasitism

Adult male red squirrel body mass during both the breeding period ($t = 0.071$, $p = 0.944$) and the post-mating period ($t = -1.173$, $p = 0.259$) did not predict the intensity of fleas during those time periods in 2011. Similarly, adult female red squirrel body mass during both the breeding period ($t = -0.840$, $p = 0.407$) and the post-mating period ($t = 0.950$, $p = 0.355$) in 2011 did not predict the intensity of fleas.

3.3. Temporal dynamics of ectoparasitism

Ectoparasitism in red squirrels was male-biased, however this bias was not observed during ontogeny but it was seasonally structured. No significant sex bias existed at either birth (Table 1; $U = 371$, $p = 0.119$) or emergence (Table 1; $U = 56.5$, $p = 0.934$). However, during the mating/pre-parturition period, adult males had significantly more fleas than adult females (Table 1; $U = 892$,

$p = 0.001$). Additionally, flea intensities were significantly female-biased during the lactation period (Table 1; $U = 198$, $p = 0.021$). Juveniles at birth were the most intensely parasitised host life-history stage for both sexes (Table 1). Males in the mating period had significantly higher flea intensities than males in the post-mating period ($U = 79$, $p < 0.0001$). There was no difference between flea intensities in adult females during and after their reproductive period ($U = 257.5$, $p = 0.768$). Life history stage was an important predictor ($t = -3.442$, $p = 0.0007$), but sex was not significant ($t = 1.158$, $p = 0.248$) and there were no interaction effects ($t = -1.151$, $p = 0.251$).

3.4. Ectoparasite removal

No effect of parasite removal on average body mass was observed in adult males between May (Day 0) and August (Day 90) 2010. Also, no effect was observed in body mass gains or losses of control (n = 12) and treated (n = 12) individual males across the treatment periods. Between Day 0 and Day 30 (June) control males lost an average of 4.29 g (SD = 13.12), while treated males lost an average of 5.93 g (SD = 7.56; $t_{11.4} = 0.309$, $p = 0.763$). Between Day 30 and Day 90 control males lost an average of 14.07 g (SD = 10.66), while treated males lost an average of 7.93 g (SD = 11.72; $t_{11.9} = -1.026$, $p = 0.325$). Over the course of the entire study (Day 0 to Day 90) control males lost an average of 14.75 g (SD = 9.75), while treated males lost an average of 13.06 g (SD = 8.36; $t_{11.7} = -0.349$, $p = 0.733$).

4. Discussion

We have shown that parasitism of red squirrels by fleas is seasonally sex-biased, with adult males facing increased infection intensities during the mating period and adult females incurring higher flea intensities than males during the lactation period. Ectoparasitism by fleas may be driven by the behaviour and life-history strategies of their hosts. For instance, fleas are transmitted through direct host−host contact, which in red squirrels typically only takes place between adults during the mating season (Steele, 1998) and in the natal nest. Females are in oestrous for only one day and during that time they may mate with an average of seven males (McFarlane et al., 2011). Males engage in a scramble competition for females and during coitus the male holds the female around the posterior abdomen while resting his head and anterior abdomen on her back (Steele, 1998). Copulations generally last for less than 60 s (Lane et al., 2009; McFarlane et al., 2011). Direct contact during mating increases the potential for transmission of contact-transmitted parasites and may be the only opportunity for ectoparasite transmission outside of the natal nest. Females, on the other hand, are exposed to higher intensities of fleas in the nest environment when rearing their young (Table 1) and, consequently, carry significantly more fleas during the

Table 1
Median number of fleas and median number of fleas per unit mass of the hosts across the four life-history stages for male and female red squirrels in Sheep River Provincial Park, Alberta. Number of individual hosts in the sample (n) and 95% confidence intervals (CI) are reported.

Life-history stage	n	No. of ectoparasites (median)	Range (min−max)	95% CI	No. of ectoparasites (median)/g*100
Juvenile male birth	28	5.0	0−18	3.0−7.0	11.09
Juvenile female birth	21	4.0	0−12	2.0−9.0	9.82
Juvenile male emergence	11	3.0	0−8	1.0−5.0	2.65
Juvenile female emergence	10	2.0	0−6	1.0−4.0	1.86
Adult male mating	36	3.5	0−17	2.0−4.0	1.48
Adult female pre-parturition	34	1.6	0−6	1.0−2.0	0.72
Adult male post-mating	17	1.0	0−2	1.0−2.0	0.43
Adult female lactation	19	2.5	1−6	2.0−3.0	1.07

lactation period than their adult male counterparts. Lactation and pregnancy are energetically demanding events for all female mammals (Speakman, 2008), during which maternal immunity is reduced (Jones et al., 2012; Lloyd et al., 1983) and increased susceptibility to parasite infection is common (e.g., Festa-Bianchet, 1989; Shubber et al., 1981). Flea intensities did not appear to differ based on female reproductive status in red squirrels, although we did not investigate flea intensities on pre-reproductive female hosts or host females well after lactation. There is no indication that adult females pay a personal cost to their body mass through ectoparasitism, although higher ectoparasite intensities in the nest appear to negatively affect the growth and survival of offspring (Patterson et al., 2013).

On their own, transmission dynamics may not fully explain the observed male-bias in flea abundance. During the reproductive period males of many species generally experience elevated levels of circulating testosterone (Boonstra et al., 2001; Brockman et al., 1998; Cavigelli and Pereira, 2000), with testosterone concentrations positively correlated with reproductive success in some species (Alatalo et al., 1996; Hutchison and Hutchison, 1983). Testosterone has been linked to lower immune function and higher parasite infection intensities in many species (Cox and John-Alder, 2007; Decristophoris et al., 2007; Folstad and Karter, 1992; Folstad et al., 1989; Mougeot et al., 2004, 2006; Saino et al., 1995). The link between testosterone and parasite infection is often cited as a key driver of male-biased parasitism as testosterone mediates sex differences in immune function and risky behaviour (Grear et al., 2009; Hughes and Randolph, 2001; Klein et al., 2004; Zuk and McKean, 1996). However, testosterone may also lead to elevated levels of circulating glucocorticoids and, as such, its effects may be correlated with stress-induced immunosuppression (Evans et al., 2000). Male red squirrels search extensively for receptive females during the mating period, while females generally stay on their territories during this time (Lane et al., 2009). Males may also spend less time grooming during the breeding period as they allocate energy and time to other functions, such as mate searching. Therefore, differences in ranging behaviour and activity budgets during the mating period could also explain the observed differences in flea intensities. Ultimately, male red squirrels during the reproductive period may experience elevated testosterone and stress hormone levels, lowered immune function, higher rates of intraspecific contact, increased ranging behaviour and reduced grooming, all of which may contribute to increasing their reproductive success (Gooderham and Schulte-Hostedde, 2011; Lane et al., 2009) and flea infection intensities concomitantly. Gooderham and Schulte-Hostedde (2011) found that male red squirrels with higher ectoparasite intensities had higher reproductive success, suggesting a trade-off between investment in reproduction and exposure to parasites. All of these factors may combine to produce the observed biases in male ectoparasitism during the reproductive period as fleas exploit host behaviour and physiology. Our findings seemingly contrast with those of Gorrell and Schulte-Hostedde (2008), who found that male red squirrels only had more fleas than females during the month of August; however, males in their population had become secondarily scrotal and reproductively active in August with subsequently higher testosterone levels than in July. As such, while our temporal patterns of ectoparasitism differ for adult males, the hypothesis that fleas favour their male hosts during the mating period is still supported across these two geographically distinct populations.

While we did not investigate the sex of the fleas, Gorrell and Schulte-Hostedde (2008) found that male red squirrels were more likely to be parasitised by male fleas. If dispersal and inbreeding avoidance are the objectives, then male fleas may prefer male red squirrels, but only during the breeding period and natal dispersal. Higher flea intensities on males during the reproductive period suggest that male red squirrels may be responsible for transmitting infective adult fleas between susceptible hosts. Male-driven parasite transmission has been observed in other rodent species (Ferrari et al., 2004; Perkins et al., 2003). But why might males be so important for the transmission of parasites? Perhaps, it may be due to sex-related differences in behaviour and home range size which are common amongst mammals (Greenwood, 1980). The potential roles of immunocompetence and androgen hormones also cannot be understated. Ultimately, the role of host sex in parasite transmission dynamics and the underlying mechanisms require further study.

Our finding that male-biased parasitism does not exist in juveniles at either birth or emergence from the nest suggests that fleas are not capitalizing on the ability of juvenile males to disperse in order to reduce possible effects of inbreeding. In red squirrels, dispersal is rather limited with most juveniles choosing to settle on or near their mother's territory (Larsen and Boutin, 1994), although long-range natal dispersal has been observed (Haughland and Larsen, 2004; Sun, 1997). Dispersal in red squirrels does not appear to be significantly sex-biased (Boutin and Larsen, 1993); however, pre-settlement ranging behaviour by dispersing males and females has not been adequately studied. Interestingly, in our population, red squirrels at birth experience, on average, the highest flea intensities than at any other life-history stage. This effect is even more pronounced when we take body mass into account (Table 1). While in the nest, fleas distribute themselves more or less equally amongst male and female neonates, yet the high infestation intensities experienced by neonates suggest that, in general, fleas are preferentially exploiting the relatively defenceless hosts for nutritional resources. This was corroborated by the GLM which showed life-history stage to be a more important predictor of flea intensity in host red squirrels than host sex. It is unclear why flea intensities decline from birth to emergence in juveniles, although we speculate that this decline may be the result of immune system development, which can take several weeks in rodents (Grindstaff et al., 2003; Hasselquist and Nilsson, 2009), juveniles learning to groom, and/or the life cycles of the ectoparasites. At northern latitudes, fleas parasitizing arboreal squirrels display annual cyclic population fluctuations, with each flea species possessing its own non-overlapping population peak (Day and Benton, 1980; Haukisalmi and Hanski, 2007). For flea species common during the host's reproductive period, a single annual population peak typically coincides with host lactation and the presence of host neonates in the nest (Day and Benton, 1980; Haukisalmi and Hanski, 2007). As such, a picture of flea development and transmission in red squirrel hosts begins to emerge coinciding with the life cycles of both host and parasite within which males appear to play an important role in the transmission of fleas, while juveniles of both sexes likely play an important role in the development and reproduction of fleas. Given the immunosuppressant and behavioural effects of reproduction in adult hosts, the time to acquire immunity and constant presence of neonates in the nest environment, and the annual lifecycles of fleas in arboreal squirrels at northern latitudes, the life-histories of both host and parasite may be driving the observe patterns of flea ectoparasitism in red squirrels.

Sexual dimorphism (observed here as heavier males) likely does not explain the male-bias in parasite infection intensity, as male-biased parasitism was only evident during the mating period, while the dimorphism persisted across time. The sexually-dimorphic mass ratios observed in this red squirrel population are consistent with those found in other, more northerly, geographic regions (Boutin and Larsen, 1993). Similarly, there was no apparent

effect of host mass on flea intensity, suggesting that fleas do not choose larger hosts. Alternatively, this finding could be taken to provide evidence that fleas do not affect the mass of their adult hosts. Taken as a whole, fleas of red squirrels do not appear to select for host size, regardless of host sexual dimorphism (Gorrell and Schulte-Hostedde, 2008), and, as such, these results do not support the "larger host" class of hypotheses (Moore and Wilson, 2002). This finding is generally supported by several other studies indicating that sex biases in ectoparasitism are not driven by body size sexual dimorphisms in small mammals (Krasnov et al., 2005; Morand et al., 2004; Scantlebury et al., 2010; Waterman et al., 2014).

The results of the parasite removal experiment did not support our hypothesis that ectoparasites affect the ability of adult males to maintain their body mass. Raveh et al. (2011) found no effect of ectoparasite removal on male body mass in Columbian ground squirrels (*Urocitellus columbianus*). A lack of any observable effect of ectoparasite removal on male body mass, however, does not mean that ectoparasites have no effect on males in this red squirrel population. In fact, quite the opposite may be true. Removal of energetically consumptive parasites may have freed energy and time for males to invest in other fitness-improving activities, such as territory defence, mate searching, food acquisition, sperm production, and vigilance. There may also have been effects on larder hoard depletion, which we did not assess. Furthermore, body mass measures may hide some of the underlying parasite-driven variation in the mass of certain organs (*e.g.*, spleen) and fat storage (Scantlebury et al., 2010), although body mass does appear to be a good predictor of body fat storage in red squirrels (Becker, 1992; Humphries & Boutin, 1999). Additionally, if parasites could be permanently removed, non-parasitized males may experience improved survival by not having to mount a costly immune response to ectoparasites (Hanssen et al., 2004) and, therefore, their possibility of improved lifetime reproductive success may be enhanced. As mate search tactics are under positive sexual selection pressure in male red squirrels (Lane et al., 2009), parasite removal prior to and during the mating period may allow males to invest more energy into mating effort, thereby leading to improved mating success. However, male red squirrels appear to trade-off reproductive investment and parasite infection (Gooderham and Schulte-Hostedde, 2011) and male Columbian ground squirrels did not experience increased reproductive success when ectoparasites were experimentally removed (Raveh et al., 2011). Variability in host and parasite genetics, parasite virulence, parasite co-infection, host demography, and environmental conditions may influence the effects of parasites on host reproductive success, body mass, and transmission dynamics, and these potential relationships require further study. Red squirrels represent an interesting system for further testing hypotheses about the effects of parasites on male reproductive success and sexual selection on male traits.

Acknowledgements

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