Parasite removal and its impact on litter size and body condition in Columbian ground squirrels (*Spermophilus columbianus*)

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The current interest in studies of parasite–host relationships is focusing on the impact of parasites on mate choice, sexual selection and individual fitness. While most studies have been done on birds and fishes, little is known about the interactions between parasites and reproductive success in mammals. In this study, I experimentally removed ectoparasites (mainly fleas) from some female Columbian ground squirrels using a commercially available powder, whereas other squirrels were left untreated as controls. The anti-parasite treatment led to an increase in female body condition during lactation and at weaning and an increase in litter size. The increase of body mass in treated females between birth of the young and weaning is also different from observations done over 8 years in the same population, where untreated females usually lost mass. In close to 400 litters from untreated females in the same area, only 2% had litter sizes as big as the treated females. I conclude that ectoparasites can have a profound impact not only on individuals but probably on the dynamics of the whole population.

Keywords: body mass; parasite removal; reproductive success; *Spermophilus columbianus*

1. INTRODUCTION

Parasites are thought to play a major role in the evolution of mating systems, mate choice and reproductive success (Hamilton & Zuk 1982; Hamilton *et al.* 1990; Møller *et al.* 1999). There is now a good understanding that animals are confronted with trade-offs between reproductive effort and immune defence (Nordling *et al.* 1998) and that there are strong effects of reproductive effort and parasite prevalence (Norris *et al.* 1994; Oppliger & Richner 1996; Ilmonen *et al.* 2000). The focus of studies on parasites in birds, fishes and amphibians has mainly been on sexual selection through mate choice (Hamilton & Zuk 1982; Westneat & Birkhead 1998) and on the costs of both immune responses to reproduction (Sheldon & Verhulst 1996; Møller *et al.* 1999) and of reproductive effort and immune defence (Nordling *et al.* 1998). The few experi-

mental studies that have been undertaken so far have concentrated on increasing parasite loads to look at the resulting effects on survival, recruitment, sexual behaviour and expression of secondary sexual characters (Møller *et al.* 1999). In some studies on birds and sheep, parasites or bacteria were experimentally removed to look at the underlying impact that parasites have on reproductive success, survival and even on population dynamics (Oppliger *et al.* 1994; Hudson *et al.* 1998; Coltman *et al.* 1999; Merino *et al.* 2000; Potti *et al.* 2002). In this study, I removed ectoparasites from female Columbian ground squirrels to investigate how this influences her body condition, the number of young produced and the viability of her offspring. While I expected that parasite removal would have a positive effect on the animal's energy budget, I investigated whether females would invest the extra energy into their offspring, into their own body condition, or both. The prevalence of fleas is high in the study population and all individuals carry some fleas. To my knowledge, this is the first experimental attempt to look at the impact of ectoparasites on reproductive success and body condition in a wild mammal.

2. METHODS

This study was conducted in the Sheep River Wildlife Sanctuary, Alberta, Canada (110° W, 50° N) in the foothills of the Rocky Mountains. Although the experimental data were collected in 2000, additional data on the reproductive success and mass development of females were collected from 1994 to 2001. All of these additional data and the experimental data come from three colonies of ground squirrels living within 2 km of each other.

The Columbian ground squirrel is a social rodent living in colonies on open meadows in northwestern America. About 4 days after emerging from hibernation, in late April, females breed. The mating behaviour, average number of young born per female and survival of the young from birth to weaning were known from previous studies on the same population (Neuhaus 2000a,b). Gestation length is *ca.* 24 days, and the young stay in the natal burrow for 27 days after birth (Murie & Harris 1982). By mid to late August all animals are hibernating.

To evaluate the number of juveniles emerging from the natal den, I watched and trapped the young as they emerged for the first time. To obtain masses, all animals were caught with live traps baited with peanut butter on a weekly basis. Masses were measured with a spring balance and rounded to the next 5 g. For the analyses, I used the masses at emergence from hibernation, at mating, birth and at emergence of the young.

For the experimental removal of ectoparasites in 2000, half of the females in one colony, randomly chosen (the first by a toss of a coin, then alternating), were treated with the commercially available Flea and Tick powder (Hagen). All experimental females were from the same colony as the control females and they were caught at the same frequency. The tick powder was applied by rubbing it into the fur of the females, while control females were rubbed the same way without powder being added. Care was taken that the treatment of experimental females did not take more time than the weighing and rubbing of control females (usually 2–3 min). Although I do not have quantitative data of parasite infestation, fleas were regularly seen on untreated females, whereas I noted fleas on treated females only on two occasions. The treatment against ectoparasites was done before mating and repeated weekly until the end of lactation by rubbing some powder into the fur of the females. Control females were caught at the same rate as experimental females. Because total litter loss is caused by infanticide or predation and is unrelated to body condition in my study animals (Neuhaus 2000b), I excluded all data from females suffering total litter loss. I therefore had a sample size of four females treated against ectoparasites and five control females that weaned young during the experiments. In addition, I also had data on mass differences from one neighbouring colony for the years 1994, 1995, 1997 and from the experimental colony from 1999 to 2001. Also, I had average litter sizes from two neighbouring groups (1994–2000) and from the experimental group (1994–1997, 1999 and 2001).

Figure 1. Body mass development in female Columbian ground squirrels from emergence in spring to the first emergence of their offspring 55 days later. Compared are mean masses of females treated with an anti-ectoparasite powder (circles and solid line) and of untreated females (squares and broken line). Time was set at zero for emergence of females from hibernation.

3. RESULTS

Body mass did not differ between experimental (458 g, standard deviation (s.d.) = 25) and control females (474 g, s.d. = 36) when emerging from hibernation in spring (U -test: $z = -0.735$, $p = 0.5$), or after the first anti-parasite treatment, when mating took place (controls: 487 g, s.d. = 48; experimental females: 485 g, s.d. = 35; U -test: $z = 0$, $p = 1$; figure 1). The body mass of treated (541 g, s.d. = 36) compared with untreated females (557 g, s.d. = 36) also did not differ if measured just after parturition (U -test: $z = -1.23$, $p = 0.2$). The body mass of females treated against ectoparasites (560 g, s.d. = 15) was significantly higher at the time of weaning compared with untreated females (518 g, s.d. = 28; U -test: $z = -1.968$, $p < 0.05$; figure 1). Accordingly, mass differences of the two types of females between birth and emergence of the young, and mass difference between spring mass and emergence mass differed significantly (mass change from birth to emergence of the young, U -test: $z = -2.205$, $p = 0.027$; mass change from spring to emergence of the young, U -test: $z = -2.449$, $p = 0.014$; figure 2a). Data from 85 females including the years 1994–2001 and a neighbouring colony showed untreated females losing on average 40 g (s.d. = 37, confidence interval (CI) = -48 to -32) between birth and juvenile emergence, whereas females treated against ectoparasites gained 19 g (s.d. = 28, CI = -26–64; U -test: $z = -2.76$, $p = 0.006$). There was no difference between untreated females in the experimental colony ($n = 12$) and those in the neighbouring colony ($n = 73$) (U -test: $z = 0$, $p = 1$).

All females mated with three to five males and there was no difference in the number of matings between treated and untreated females (U -test: $z = -0.13$, $p = 0.9$). The number of young weaned differed between litters: untreated females weaned on average 3.6 young (s.d. = 0.54), whereas treated females averaged 5.25 young per litter (s.d. = 0.5; U -test: $z = -2.547$, $p = 0.01$).

Figure 2. Comparisons of mass gain or mass loss between female Columbian ground squirrels treated against ectoparasites (filled bars) and untreated (open bars). (a) Average female mass change between birth and emergence of young, mass change of females from emergence in spring to the emergence of their young and total mass produced from adult emergence in spring to the emergence of the young, including litter mass. (b) Comparison of average litter masses, average mass per young and of the female mass and litter mass combined, from left to right.

To my knowledge, the average number of young per litter at emergence was higher for treated females than ever previously observed in this area: control females of the experimental colony and two neighbouring colonies weaned on average 2.8 (CI = 2.7–2.9) juveniles per litter in the years 1994–2001 (384 litters), the experimental colony had the highest average litter size over this time of 3.1 (CI = 2.9–3.3) juveniles per litter, while the two other colonies averaged, respectively, 2.6 (CI = 2.4–2.8) and 2.9 (CI = 2.8–3.2) young per litter. Treated females also had a higher total litter mass compared with litters of untreated females (U -test: $z = -2.449$, $p = 0.014$; figure 2b). The number of young surviving to yearling age was also higher in treated compared with untreated females: 3.5 young per litter survived to yearling age when the mother had been treated against parasites, whereas two young per litter survived in control litters (U -test: $z = -1.93$, $p = 0.05$). However, there was no difference in the proportional survival of young depending on the treatment (Fisher's exact test: $\chi^2 = 0.25$, $p = 0.44$). There was no significant difference between the average mass per young at first emergence in litters of treated females versus untreated females (U -test: $z = -1.47$, $p = 0.14$; figure 2b).

4. DISCUSSION

Female Columbian ground squirrels treated against ectoparasites did not only gain more mass during lactation, but also had significantly more emergent offspring than untreated females. This is an exceptional effect of

parasites on litter size because litter sizes at birth of five to six young are extremely rare in this area (less than 2%), with a usual average of between 2.8 and 3.6 young born per litter (Murie *et al.* 1980, 1998; Neuhaus 2000b). Because the number of matings did not differ owing to the treatment between females, the observed difference in litter size has to be attributed to differences in either the number of eggs ovulated, partial abortion or to partial litter loss during lactation rather than to sperm competition or to the number of sperm received (Birkhead 2000). Partial litter loss from birth to emergence has been calculated to be *ca.* 15% (Murie *et al.* 1980) and can therefore not account for this big difference between litter size in treated and untreated females. There was no difference of quality between territories chosen by treated compared with untreated females: only one out of the nine females had a different territory in the previous year. The observed difference in litter size, therefore, must be due to either increased ovulation, lower post-implantation loss, lower partial litter loss during lactation, or a combination of these.

The higher total litter mass at emergence from the natal burrow was due to the larger size of litters of females treated against parasites compared with those of untreated females (figure 2b). It is surprising that there was no difference between the average mass per young in larger litters of treated females versus smaller control litters (figure 2b) because body mass of young has been shown to decline with increasing litter sizes (Neuhaus 2000b).

From this experiment it seems obvious that ectoparasites in my study area have a profound negative effect on individual reproductive success and on body mass. Because I had a very small sample size, I was not able to look at female survival in relation to the experiment, but body mass has a strong influence on survival probability to the next year. If the increase of body condition in parasite-free females leads to a better survival, I predict that besides reproductive output, age structure of a colony could also change dramatically if the whole colony could be kept parasite free over an extended period of time.

My study shows that the constant presence of ectoparasites in these ground squirrels leads to a constantly lower reproductive success and survival of females and their offspring and probably affects the whole population, since all animals are infected to a certain degree. If parasites in this population could be removed permanently, I would expect higher population densities to result, leading to a change in population dynamics, as has been shown in the red grouse (Hudson *et al.* 1998). The impact of parasites on life-history traits and population dynamics in mammals is still poorly understood. My results suggest that parasites have a strong impact, in that I was able to detect fitness costs in reproductive output and body mass due to parasites despite a very low sample size.

This study presents evidence that the removal of omnipresent parasites can lead to changes in body condition and directly affects host fitness and life history. Therefore the coevolution of host and parasite has a profound impact on population dynamics and structure. Because ectoparas-

ites are found in many animal species, it is likely that they play a major part in determining individual life-history traits and population structure on a much larger scale than previously thought. The small sample size does however leave us with a relatively high level of uncertainty and the results therefore have to be interpreted with caution.

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