Parasite-mediated reduction in fecundity of mountain hares

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Mountain hare populations in Scotland exhibit regular 10 year fluctuations in abundance. Simple models of host–parasite population dynamics suggest that parasite-mediated reductions in host fecundity can cause a transition from stable to cyclic host population dynamics. We tested the hypothesis that parasites reduce hare fecundity by experimentally reducing parasite burdens and recording female survival, body condition and fecundity. We captured 41 adult female hares in October 2002; 22 were treated with Ivermectin to remove parasites and 19 were left untreated as controls. The treated and untreated hares were culled in May 2003 together with a second control group of nine unhandled hares. Treatment with Ivermectin significantly reduced the abundance of *Trichostrongylus retortaeformis* and increased the fecundity of the hares, but had no measurable effect on body condition or over-winter survival. These results are consistent with the hypothesis that parasites may be a contributory cause of cycles in populations of mountain hares.

Keywords: parasites; mountain hares; population cycles

1. INTRODUCTION

There is increasing recognition that parasites can have a key role in population dynamics (Hudson *et al.* 2001). Simple analytic models of host–parasite dynamics predict three features that may lead to a destabilization of an otherwise stable equilibrium of host–parasite populations: (i) parasite-induced reduction in host fecundity; (ii) time delays in parasite recruitment; and (iii) a random or regular distribution of parasites in the host population (Anderson & May 1978; May & Anderson 1978). Experimental studies of Soay sheep, red grouse and Svalbard reindeer demonstrate that host–parasite interactions contribute to population instability (Gulland *et al.* 1993; Hudson *et al.* 1998; Albon *et al.* 2002).

Populations of mountain hares *Lepus timidus* (L.) exhibit regular changes in abundance throughout their circumpolar distribution. The amplitude and periodicity of

population fluctuations vary across their range. Populations of mountain hares in Scotland are characterized by regular 10 year cycles (Hewson 1976). Experiments on cyclic populations of snowshoe hares (*Lepus americanus* (Erxleben, 1777)) suggest that an interaction of predation, food, and in some cases parasites, can destabilize dynamics (Krebs *et al.* 1995; Murray *et al.* 1997). Mountain hares in Scotland typically occur on sporting estates where predators are killed and thus it is unlikely that predation plays a key role (Hewson 1976). Mountain hares are susceptible to infections by the nematodes *Trichostrongylus retortaeformis* and *Graphidium strigosum* (Iason & Boag 1988; Newey *et al.* 2004*a*), but their role in determining hare population dynamics has not been studied experimentally (Newey *et al.* 2004*b*).

In this study, we experimentally investigated the impact of nematode parasites on mountain hare demographic processes. We tested the hypothesis that reducing burdens of *T. retortaeformis* would increase mountain hare fecundity but have little effect on survival. *Trichostrongylus retortaeformis* is a direct life cycle helminth and therefore there is a time-delay in the recruitment of adult parasites. Newey *et al.* (2004*a*) have demonstrated that, while *G. strigosum* is highly aggregated within hare populations, *T. retortaeformis* is randomly distributed and therefore has the potential to act in a destabilizing manner.

2. METHODS

We used cage traps and long nets to captured 41 adult female mountain hares during October 2002 on 2 km^2 of moorland managed for red grouse shooting in the Highlands of Scotland. Yearling female hares were distinguished from adults by the imperforate state of the vagina and the presence of the apophyseal notch at the head of the tibia (Flux 1970). Morphometric data were collected from each hare prior to radio-collaring and release. Alternate hares were injected subcutaneously with 0.1 ml of Ivermectin, which has previously been shown to reduce parasite burdens (Newey *et al.* 2004*b*). Hares were located every two weeks to monitor survival. Treated hares, untreated hares and a second control group of unhandled hares were culled in May 2003. The stomach, intestine, ovaries and left kidney and associated fat were removed from each hare. We recorded the number of foetuses, body weight and left hind foot length. We estimated survival probability using the Kaplan–Meier method where females alive prior to culling were right-censored (SYSTAT v. 9).

Parasite burdens were assessed by separating the stomach and intestines and washing the contents of the duodenum and small intestine through 125 μm sieves. The residue was washed into 400 ml of water and the number of *T. retortaeformis* in four 10 ml sub-samples counted. The total number of *T. retortaeformis* was estimated from a regression equation that had been calibrated against total counts (Newey *et al.* 2004*b*).

The body condition of female hares in October was estimated from body weight including hind foot length as a covariate to allow for the effect of body size on body weight. Mountain hares undergo large changes in body weight associated with pregnancy and lactation, and therefore the use of any measure of body condition in May that included body weight is invalid (Iason 1990). We therefore used the kidney fat index derived as kidney weight/kidney fat as a measure of the body condition of culled hares (Iason & Boag 1988).

The fecundity of female hares was estimated by counting the number of corpora albicantia in the ovaries (Iason 1990). The ovaries from culled hares were frozen and sectioned by hand at *ca.* 1 mm intervals. The number of corpora albicantia from both ovaries was counted under a microscope with a ×10 magnification, and summed to use as a measure of fecundity.

Body weight, hind foot length and the number of corpora albicantia were normally distributed (Anderson–Darling test of normality, $p > 0.05$). Counts of *T. retortaeformis* showed a negative binomial distribution and were approximately normalized using a $\log_{10}$ transformation (Anderson–Darling test of normality, $p > 0.05$). Although the data from hares in October contain only one factor (treated or untreated), the data from hares in May contain two factors (treated or untreated and handled or not handled). We used analysis of variance to compare body weight, hind foot length, number of corpora albicantia and parasite intensity between groups. Examination of the

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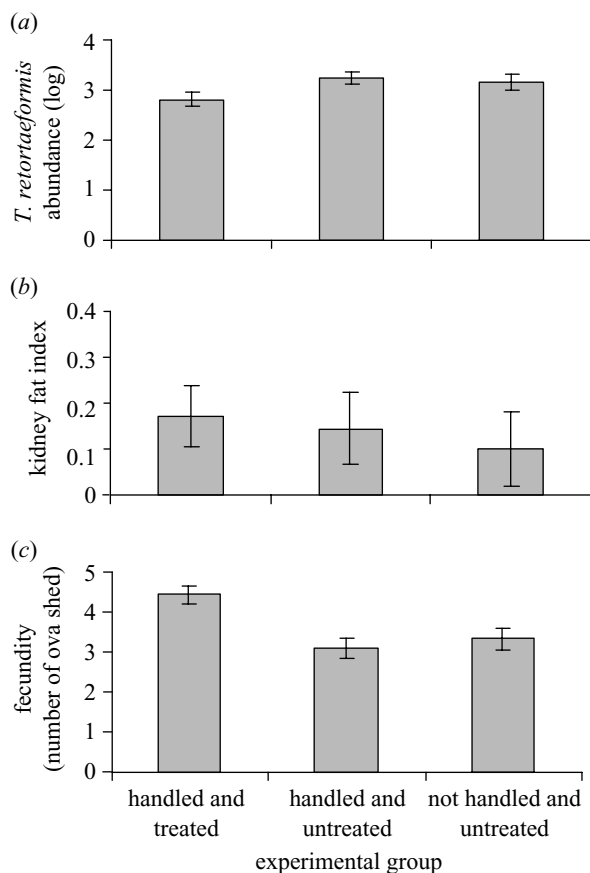
Figure 1. The effect of experimental treatment of female mountain hares with Ivermectin on (*a*) *Trichostrongylus retortaeformis* abundance (logged), (*b*) kidney fat index, and (*c*) fecundity. Figures are means ± s.e.m.

residuals showed that the distribution of the kidney fat index could not be normalized by transformation and we therefore used the Kruskal–Wallace test, a non-parametric technique that makes no assumptions regarding the data distribution. Analyses were carried out using SYSTAT (v. 9).

3. RESULTS

Forty-one female hares were captured in October. There was no significant difference in hind foot length ($F_{1,37} = 0.175$, $p > 0.05$) or body weight (after controlling for hind foot length, treatment: $F_{1,36} = 0.000$, $p > 0.05$) between hares assigned to the treated and untreated groups. Five treated and four untreated females died between December and May. There was no significant difference in survival probability of hares treated with Ivermectin (0.77 ± 0.10) and those that were untreated (0.76 ± 0.09) (Mantel-Haenszel log-rank test: $\chi^2_1 = 0.002$, $p > 0.05$). The intensity of *T. retortaeformis* infection in May was significantly lower in female hares that had been treated with Ivermectin than in hares that were either untreated or not handled, and treatment was the only significant factor (figure 1*a*; treatment: $F_{1,31} = 5.621$, $p < 0.05$; handling: $F_{1,31} = 0.172$, $p > 0.05$). There was no significant effect of treatment or handling on body condition as measured by the kidney fat index (figure 1*b*; treatment: $\chi^2_1 = 1.413$, $p > 0.05$; handling: $\chi^2_1 = 1.798$, $p > 0.05$). Female hares that had been treated with Ivermectin had significantly higher fecundity as measured by the counts of corpora albicantia than either of the control

groups, and treatment was the only significant factor (figure 1*c*; treatment: $F_{1,31} = 16.801$, $p < 0.01$; handling: $F_{1,31} = 0.443$, $p > 0.05$).

4. DISCUSSION

The key finding of this study was that the experimental reduction of parasites was associated with an increase in fecundity of female mountain hares. To our knowledge, this is the first direct evidence that macroparasites influence reproduction in hares. The significant effect of parasite infection on hare fecundity and the absence of a measurable effect of parasite infection on hare survival are two features of host–parasite dynamics known to contribute to the destabilization of the host–parasite equilibrium population point (Anderson & May 1978; May & Anderson 1978). These experimental results, in combination with the observed random distribution of *T. retortaeformis* across a sample of culled mountain hares (Newey *et al.* 2004*a*) and the time-delays in *T. retortaeformis* recruitment, are consistent with the hypothesis that parasites contribute to the unstable dynamics of mountain hare populations.

Experimental treatment with Ivermectin reduced burdens of *T. retortaeformis* in female hares. Anthelmentic treatment was applied in October and reduced parasite burdens were apparent when hares were culled in May. This was surprising as Ivermectin has no prophylactic effect and individual hares are reinfected either from the environment or from arrested larvae emerging in response to the removal of the gut fauna. Snowshoe hares treated with Ivermectin showed parasite burdens similar to untreated hares within six weeks (Murray *et al.* 1996). The infection rate of red grouse with *T. tenuis* on heather moorland is correlated with temperature and is highest in late summer and late winter (Hudson *et al.* 1992). The winter of 2003 was dry and cold and we speculate that the parasite infection rates were unusually low.

Natural mortality of mountain hares peaks in late winter and few animals die between June and October (Hewson 1976). Survival analysis suggested that parasite reduction had little effect on hare survival. This is contrary to the findings of Murray *et al.* (1997), who found that parasite reduction increased the survival of snowshoe hares; however, the main cause of death was predation through a strong interaction with nutrition. It was suggested by Murray *et al.* (1998) that snowshoe hares forage in a risk-prone manner when food stressed. Low predator density on our study site may explain why parasite reduction had no detectable effect on hare survival.

Mountain hares attain maximum body condition in January and February, which coincides with the onset of the breeding season, and body condition subsequently declines to reach a minimum in August (Flux 1970). If females invested energy benefits from reduced parasite burdens into reproduction we would not expect to find any difference in post-breeding body condition. Along with other correlative and experimental studies on mountain hares and snowshoe hares (Iason & Boag 1988; Murray *et al.* 1997; Newey *et al.* 2004*a*), we found no difference in body condition between parasite-reduced and parasite-normal hares.

Female mountain hares treated with Ivermectin had higher fecundity than untreated hares. Although

pregnancy rates, birth dates and litter size of mountain hares and snowshoe hares are closely related to nutritional status, previous experiments found that reducing the number of parasites did not influence reproduction in either species (Bloomer *et al.* 1995; Murray *et al.* 1997, 1998; Newey *et al.* 2004*b*). Mountain hares start to breed in January or February. A 50 day gestation and post-partum conception means that female hares typically produce three litters per year (Hewson 1976). Reproduction draws heavily on female body reserves and the number of young produced in the first and second litter has a negative effect on the number produced in the third litter (Flux 1970; Iason 1990). We suggest that nematode parasites suppress female fecundity by exerting additional energy demands. Female hares can improve their body condition when parasite burdens are reduced in winter, and invest this in reproduction.

The unstable population dynamics of vertebrates from the Northern Hemisphere have attracted the attention of ecologists for decades, but there is still no clear consensus on the factors causing instability (Turchin 2003). Studies on Soay sheep (Gulland *et al.* 1993), red grouse (Hudson *et al.* 1998) and Svalbard reindeer (Albon *et al.* 2002) have all shown that parasites affect the survival or fecundity of the host, however, to date, experimental evidence that parasites can regulate vertebrate populations and cause persistent instabilities is restricted to red grouse. The results of this study together with our earlier findings (Newey *et al.* 2004*a,b*) suggest that mountain hare populations in Scotland may also be regulated by parasites.

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