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# Do parasite burdens in spring influence condition and fecundity of female mountain hares *Lepus timidus*?

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Mountain hare *Lepus timidus* populations show unstable dynamics with regular 7-10 year fluctuations in abundance. We tested the hypothesis that parasites destabilise hare dynamics by experimentally reducing parasite burdens and recording female body condition and fecundity. We trapped and radio tagged 42 female hares in April 2000 and 2001 in the Central Highlands of Scotland. Of these, 23 were treated with Ivermectin to remove intestinal parasites and 19 were left untreated as controls. The treated and untreated hares were killed in October together with a second control group of 19 unhandled hares. Treatment with Ivermectin reduced the abundance of the parasite *Trichostrongylus retortaeformis* and increased the body condition of hares. There was a trend for increased fecundity in treated hares, but this was not statistically significant. Our study demonstrates that parasites can reduce mountain hare condition and may affect their fecundity. We conclude that a host-parasite interaction is a possible mechanism for destabilising mountain hare dynamics.

*Key words: body condition, fecundity, Ivermectin, Lepus timidus, mountain hares, parasites, population cycles*

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Studies of the cyclic fluctuations of northern vertebrate species have played a central role in the development and understanding of population dynamics (Royama 1992). They have allowed examination of the nature of density dependence, the mechanisms and scale of synchrony and the role of stochastic factors in maintaining instability (Stenseth 1999, Lindström, Ranta, Kokko, Lundberg & Kaitala 2001). However, even though it is 75 years since Elton (1927) first described cycles in lynx fur returns, there is still no clear consensus on what causes cycles (Berryman 2002, Turchin 2003). The difficulty of conducting experiments at suitably large spatial scales is one factor contributing to the lack of progress in this field (May 1999).

Populations of mountain hare *Lepus timidus* in Scotland show unstable dynamics with regular 7-10 year fluctuations in abundance (Watson & Hewson 1973, Hewson 1976). The ecological mechanisms causing these fluctuations are currently unknown. Large-scale experiments on cyclic populations of snowshoe hares *L. canadensis* suggest that predation and food availability interact to destabilise hare dynamics (Krebs, Boutin, Boonstra, Sinclair, Smith, Dale, Martin & Turkington 1995). However, mountain hares in Scotland typically occur on sporting estates where predators are rigorously controlled, and thus it is unlikely that predation causes mountain hare cycles. Large-scale experiments on cyclic populations of red grouse *Lagopus lagopus scoticus* have demonstrated that parasite induced reduction in host fecundity caused by the nematode *Trichostrongylus tenuis* in conjunction with a low degree of parasite aggregation is the principal factor generating cycles (Hudson, Dobson & Newborn 1998). Research on Soay sheep *Ovis aries* (Gulland, Albon, Pemberton, Moorcroft & Clutton-Brock 1993) and Svalbard reindeer *Rangifer tarandus plathyrynchus* (Albon, Stien, Irvine, Langvatn, Ropstad & Halvorsen 2002) have also indicated that parasites can have an important role in destabilising host dynamics. High burdens of the intestinal parasites *T. retortaeformis* and *Graphidium strigosum* have been documented in mountain hares raising questions about the role of parasites in mountain hare dynamics (Iason & Boag 1988).

Theoretical models (Anderson & May 1978, May & Anderson 1978) suggest that four features of host-parasite dynamics can lead to population instability: 1) parasite-induced reduction in host fecundity should be large enough to cause population declines; 2) parasite-induced reduction in host survival should be small enough to allow the host and parasite to co-exist; 3) there should be time delays in recruitment to the adult parasite population; and 4) parasites should be randomly distributed within the host population; otherwise the deaths of a few hosts might reduce the parasites to levels insufficient to cause declines. In this paper, we examine the first of these features in the mountain hare-*T. retortaeformis* system. We experimentally investigate the hypothesis that parasites destabilise mountain hare populations by reducing female body condition and fecundity.

## Methods

We studied the impact of parasites on mountain hare population dynamics on two areas of heather moorland near Newtonmore in the Central Highlands of Scotland during 2000-2001. Both areas were managed for red grouse and consisted of a mosaic of different-aged stands of heather giving way to lichens and grasses at higher altitudes. Avian and mammalian predators were killed by gamekeepers, but were present at low density on both sites in both years.

We captured a total of 42 female mountain hares in April 2000 and April 2001 using baited cage traps and fitted them with 25 g necklace radio tags (Biotrack Ltd., UK). We used body weight as a measure of condition, and as weight incorporates skeletal size, we used hind foot length as a covariate to control for size. Alternate hares were injected subcutaneously with 0.1 ml Ivermectin. Ivermectin has been used to reduce intestinal parasites in snowshoe hares in a number of previous studies (Bloomer, Willebrand, Keith & Keith 1995, Murray, Keith & Cary 1996, Sovell & Holmes 1996). Treated and untreated hares were shot in October each year together with a control group of 19 unhandled hares, and body condition was assessed as described above. Trapping, anthelmentic treatment and euthanasia were conducted under license from Scottish Natural Heritage and the UK Home Office.

Parasite burdens were assessed by removing the stomach, duodenum and small intestine of killed hares and subsequently washing the contents through sieves. We searched the stomach residue by eye and recorded the total number of *G. strigosum*. The contents of the small intestine and duodenum were washed into 400 ml of water, and four 10 ml subsamples removed. We searched the subsamples by eye and estimated the total number of *T. retortaeformis* using the regression equation: total count ~ 0.82 (sum of four sample counts from duodenum) + 0.57 (sum of four sample counts from small intestine; $F_{3,2} = 277.3$, $P < 0.001$, adjusted $r^2 = 0.993$). The sampling regime and regression equation were derived from a pilot study comprising a series of sample and total counts from the small intestine, duodenum, appendix and large intestine. The four subsamples counted for each section of the intestine were summed and entered into a multiple regression against the total count. The model, presented above, was derived by backward elimination of the least significant variable until the best model was found.

Fecundity was estimated by counting the number of *corpora lutea* and *corpora albicantia* in ovary cross-sections after killing. Ovaries were removed and frozen to -20°C before being sectioned by hand into 1-mm sections. Sections were examined under a 10x stereomicroscope and the number of *corpora lutea* and *corpora albicantia* were summed to give a measure of fecundity. In the analysis of fecundity we include hind foot length as a covariate to control the effects of age and size on reproductive performance.

Body weight, hind foot length, parasite counts and *corpora* counts were normalised by a log x+1 transformation before analysis. We used a two-way ANOVA to test for difference in body weight between hares assigned to treated and untreated groups at capture in April and to test for differences in April body weight between years. The effect of year, treatment and handling on parasite burden, body weight and fecundity were investigated using a three-way ANOVA which included interaction terms for year and treatment and year and handling. Our study design did not allow us to test for a treatment and handling interaction. We used backwards stepwise elimination to remove non-significant ($P > 0.05$) factors and interactions from the initial model to generate a minimum acceptable model (MAM). To minimise bias introduced by young of the year being included in the unhandled control group, only females positively identified by cross-sectioning of ovaries as having bred were included in the analysis. All statistical analyses were conducted in SYSTAT v.9.

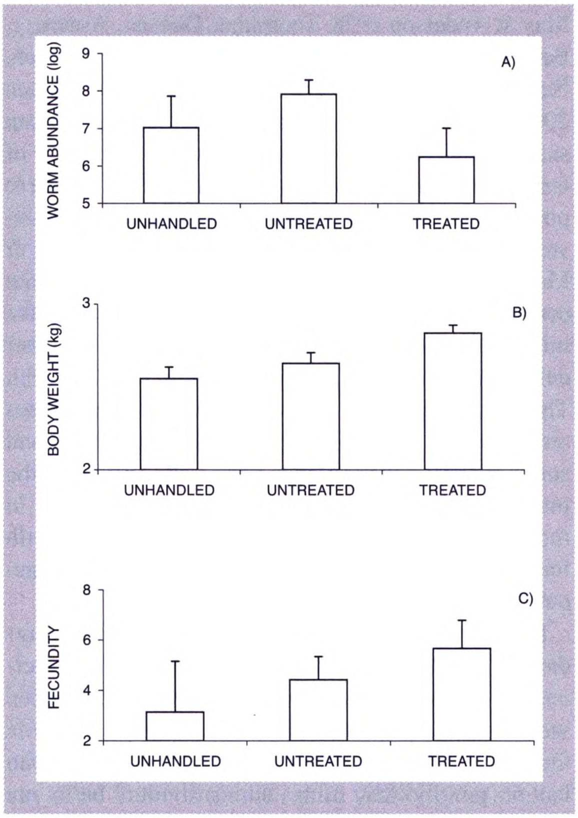

Figure 1. Effect of anthelmentic treatment on: A) abundance of *T. retortaefirnus* (logarithmic), B) body weight (in kg); and C) fecundity of female mountain hares. Values shown are means with 1 SE. Unhandled hares were neither trapped nor treated, untreated hares were trapped but not treated, and treated hares were both trapped and treated.

## Results

There was no significant difference in body condition between hares assigned to treated and untreated groups at time of capture in April ($F_{1,30} = 0.57$, $P = 0.46$). Hares caught in April 2000 tended to be in better condition than animals caught in April 2001, but these differences, along with the year-treatment interaction, were not significant (Year: $F_{1,30} = 3.66$, $P = 0.07$, Year* Treatment: $F_{1,30} = 0.60$, $P = 0.44$). Hares treated with Ivermectin had significantly lower intensities of *T. retortaeformis* than untreated hares when killed in October, and treatment was the most significant explanatory variable ($F_{1,34} = 24.85$, $P < 0.001$; Fig. 1A). Burdens of *T. retortaeformis* were significantly higher in 2001 than in 2000 ($F_{1,34} = 4.73$, $P = 0.037$). We did not find any *G. strigosum* in gut samples from the two study sites. Treated hares were in significantly better condition when killed in October than either untreated hares or unhandled hares, and treatment was the most significant explanatory factor ($F_{1,34} = 5.89$, $P = 0.021$; Fig. 1B) along with hind foot length which was used as a co-variate ($F_{1,34} = 4.12$, $P = 0.05$). Unhandled hares weighed less when killed in October than handled hares but not significantly so ($F_{1,35} = 0.96$, $P = 0.33$). There were no significant differences in body size, as measured by hind foot length, between handled and unhandled hares ($F_{1,35} = 0.131$, $P = 0.719$). Although hares treated with Ivermectin tended to have more *corpora* bodies than untreated or unhandled hares the differences were not statistically significant ($F_{1,34} = 2.861$, $P = 0.10$; Fig. 1C). The lack of statistical significance was most likely due to small sample size and associated low statistical power (power = 0.48 (S-Plus v.6.)).

## Discussion

Epidemiological theory suggests that unstable host population dynamics may be caused by high levels of parasite-induced reduction in host fecundity in conjunction with low levels of parasite-induced host mortality, time delays in parasite recruitment and randomly distributed parasite populations (Anderson & May 1978, May & Anderson 1978, Tompkins, Dobson, Arneberg, Begon, Cattadori, Greenman, Heesterbeek, Hudson, Newborn, Pugliese, Rizzoli, Rosa, Rosso, & Wilson 2001). The results of our study suggest that parasites can suppress body condition and, possibly, fecundity of female mountain hares and therefore may contribute to population instability. Our data do not allow us to investigate the remaining features of the Anderson & May (1978) model. However, time delays occur between production of nematode eggs and recruitment of the infective larvae into the host, and there will be a further delay if larvae enter a period of arrested development. The effects of parasites on the survival of mountain hares are currently unknown. Concurrent with the present study, we are undertaking a large-scale survey of the prevalence and intensity of infection of parasites in mountain hare populations that will address the fourth feature of the Anderson & May model (S. Newey, unpubl. data).

Experimental treatment with Ivermectin reduced burdens of intestinal parasites in mountain hares. Anthelmentic treatment was applied in April, and reduced worm burdens were still apparent six months later in October. This was somewhat 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. Parasite reinfection in snowshoe hares may lead to levels of infection similar to background levels within six weeks of anthelmentic treatment, although there is considerable variation among different species of parasites (Murray et al. 1996, Sovell & Holmes 1996). To our knowledge there are no comparable data on reinfection rates for mountain hares. The experimental reduction of parasite burden in the current study was associated with a significant increase in body condition of the treated hares measured in October. This was again somewhat surprising as previous experimental reductions of parasite burdens in snowshoe hares did not directly affect hare body mass or fat storage (Murray, Cary & Keith 1997, Murray, Keith & Cary 1998). Furthermore, Iason & Boag (1988) found no correlation between the intensity of infection with *T. retortaeformis* and weight and fatness of mountain hares at the onset of reproduction in February or at its completion in September.

There was a strong suggestion that mountain hares treated with Ivermectin had higher fecundity than untreated or unhandled hares, however, due to small sample sizes and associated low power this relationship was not statistically significant. The lack of a significant effect of anthelmentic treatment on fecundity may also have been influenced by the timing of the treatment. Female mountain hares become pregnant with their first litter in March, and experimental parasite removal in April may have a limited effect on fecundity. Previous research has shown that pregnancy rates, birth dates and litter size in both mountain hares and snowshoe hares are closely related to nutritional status in winter (Vaughan & Keith 1981, Angerbjörn 1986). We are currently experimentally reducing parasite burdens in female hares during the autumn and winter and will assess fecundity during the following summer.

Parasites could reduce the reproductive output of mountain hares either by reducing female body condition and subsequent ability to reproduce or by reducing the quality and survival of the young hares. Here we only investigated the effect of parasites on female body condition and fecundity. However, female hares in better condition are likely to breed earlier in the season and produce heavier young (Iason 1989). Leverets born early tend to go into the winter with a larger body mass (Hewson 1968, Keith & Windberg 1978, Iason 1989) and heavier individuals are less susceptible to overwinter mortality (Keith & Windberg 1978, Boutin 1984, Iason 1990). Future studies could profitably investigate the likelihood of recruitment of leverets into the breeding population in relation to the parasite burden and body condition of their mothers.

There is increasing recognition that parasites can have important effects on the dynamics of vertebrate populations (Hudson, Rizzoli, Grenfell, Heesterbeek & Dobson 2001). To date, however, experimental evidence that parasites can regulate vertebrate populations is limited to the red grouse-*T. tenius* system (Hudson et al. 1998). The role of parasites in lagomorph population dynamics remains contentious due to the lack of conclusive experimental evidence. Although temporal changes in the prevalence and intensity of helminth infections have been reported in cyclic populations of snowshoe hares (Keith, Cary, Yuill & Keith 1985, Keith, Keith & Cary 1986), experimental reduction of parasites have produced no detectable effects on snowshoe hare body condition, fat deposits, male sexual development or female fecundity (Bloomer et al. 1995, Murray et al. 1997, 1998). However, these studies have demonstrated that parasite reduction increased the survival rates of snowshoe hares principally due to reduced predation on individuals with low parasite burdens (Murray et al. 1997, Murray 2002). Models of hare, predator and parasite dynamics demonstrate that parasite-induced vulnerability to predation acts in a destabilising manner and makes population cycles more likely (Ives & Murray 1997). The small sample size and low power obtained in the current study means that we must attach considerable caution to our main findings that parasite reduction improved body condition and possibly fecundity of female mountain hares. We have, however, shown that the mountain hare-*T. retortaeformis* system is amiable to manipulation in the field and holds great potential for the large-scale experiments necessary to understand the dynamics of cyclic populations of vertebrates.

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