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DO INTESTINAL HELMINTHS AFFECT CONDITION AND FECUNDITY OF ADULT MOUNTAIN HARES?

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ABSTRACT: The abundance of the intestinal helminth *Trichostrongylus retortaeformis* in adult mountain hares (*Lepus timidus*) from a moor in northeastern Scotland was assessed monthly. Weight and fatness of each hare was measured and the reproductive output of females was estimated by sectioning ovaries. Abundance of the parasite was lower in December and January than at other times of year, and there was no difference in abundance between male and female hares. There was no correlation between intensity of infection with *T. retortaeformis* and weight or fatness of hares either at the onset of the reproductive period (February and March) or at its termination (August and September). We found no relationship between fecundity of female hares and parasite abundance.
Key words: Mountain hares, *Lepus timidus*, *Trichostrongylus retortaeformis*, condition, fecundity, host–parasite relationship.

INTRODUCTION

Mountain hares (*Lepus timidus*) in populations from Scotland have shown changes in numbers similar to those occurring in the cyclic oscillations of the snowshoe hare (*Lepus americanus*) in North America (Hewson, 1976, 1985; Keith, 1983). Parasitic disease has not been causally implicated in the snowshoe hare cycle (Erickson, 1944; Windberg and Keith, 1976) and recent studies have concluded that helminths are unlikely to be an important factor (Keith et al., 1985; Keith et al., 1986). Rather, the snowshoe hare cycle has been hypothesised to be due to a predator–prey oscillation (Elton and Nicholson, 1942; Keith et al., 1984). However, in Scotland predators are controlled by game-keepers and there is no evidence of a relationship between numbers of predators and hares (Hewson, 1985). Conversely, there is experimental evidence that a high mean intensity of infection with the helminth (*Trichostrongylus tenuis*) in female red grouse (*Lagopus lagopus*) in upland Britain, reduces their breeding success by decreasing clutch size and chick survival (Hudson, 1986). A mathematical model incorporating this effect has been used to simulate the cyclic fluctuations in numbers of grouse shot (Potts et al., 1984). Therefore, it is pertinent to examine whether parasites might have a role in the population dynamics of mountain hares in Scotland.

The nematode *Trichostrongylus retortaeformis* has a direct life cycle, the eggs from female worms being voided in the feces of the host lagomorph, where they hatch and moult into infective larvae (Lapage, 1955). The infective larvae migrate onto the herbage (Crofton, 1948a, b) where they are ingested. They become embedded in the mucosa of the small intestine where they develop into adult male and female worms whose feeding results in damage to the intestinal lining (Barker and Ford, 1975).

Dunsmore (1980) has shown a reduction in birth weight and numbers of offspring weaned by captive rabbits (*Oryctolagus cuniculus*) infected with *T. retortaeformis*. It has been demonstrated also that infections with trichostrongyle nematodes may cause lower body weights and possibly increased mortality of other lagomorphs (Yuill, 1964; Barth and Brull, 1975; Broekhuizen and Kemmers, 1976). The incidence and prevalence of intestinal helminths in the mountain hares in this sample has been described by Boag and Iason (1986). The purpose of this study was to examine the effects on adult hares of the most prevalent helminth species, the nematode *T. retortaeformis*. In particular, we investigated the annual changes in the abundance of the helminth and whether there are negative correlations with (1) weight and fatness of adult hares and (2) fecundity of female hares. These measures are of significance to the adult mortality and reproductive output components of population performance. Any negative effects of helminths on these parameters may or may not be causal but they could identify potential population regulatory mechanisms which require experimental investigation.

MATERIALS AND METHODS

Between April 1984 and March 1985, 193 mountain hares were collected from an area of managed grouse moor at Corgarff, Aberdeenshire, Scotland (57°09'N, 3°12'E). Hares were live-trapped in stopped snares (Young's, Misterton, Somerset, England) from April to December 1984 after which they were shot on the study area as part of control operations. The study area was about 700 ha of heathland, mainly ling (*Calluna vulgaris*), rising to 750 m from improved pasture at 350 m above sea level. Carcasses were weighed and their sex noted. One hundred and nineteen adults were distinguished from leverets on the basis of the complete fusion of the apophyseal notch at the head of the tibia which takes place at 8 to 10 mo of age (Walhovd, 1965). For each carcass the left kidney and the fat associated with it was dissected and weighed separately. The ratio of fat weight to kidney weight expressed as a percentage (KFI) was used as a measure of fatness (Flux, 1971). The ovaries of each female were sectioned free-hand at approximately 1 mm after being deep-frozen. These sections were then counted for corpora lutea and corpora albicantia, the appearance of which is described by Newson (1964). The corpora albicantia of mountain hares persist for the duration of the breeding season as shown for many mammals with small litter sizes (Rowlands and Weir, 1984), and hence the sum of corpora lutea and corpora albicantia approximated to the number of young produced or in utero in that year. We used this as our estimate of fecundity of females.

The alimentary tracts were removed and the contents of the stomach, small intestine and large intestine were separately washed through a 125-μm sieve. A maximum dilution of 1:25 of the residues were counted for nematodes. Helminth counts were normalized by the $\log(x + 1)$ transformation before statistical analysis (Snedecor and Cochran, 1980). Although the sensitivity of this method was not tested, it is similar to that recommended for the assessment of helminths in domestic animals (Anonymous, 1977), the statistical analysis of aliquot size having been investigated by Gill et al. (1986). Terminology describing the degree of infection of hosts by parasites is consistent with Margolis et al. (1982).

During the year, body weight and fatness of hares fluctuate (Table 1), but do so especially rapidly in females during the reproductive period due to gestation and parturition. However, examination of the association between these parameters and helminth burdens is possible outside of the breeding season. Within sexes and seasons, body weight and fatness are only weakly correlated (Flux, 1970) and we used these as indices of different facets of condition. Females which are largest at the onset of reproduction produce more total offspring across the whole season (Iason, 1987), whereas the presence of fat at any time represents a short-term energy store (Whittaker and Thomas, 1983). Analyses of variance were used to compare between months for female fecundity and mean intensity of infection in the summer period. Comparisons of the variation in intensity of infection between males and females throughout the year were made on samples combined into bimonthly periods to increase sample sizes. Correlations between helminth abundance and condition measures were made within February to March and August to September, the onset and termination of reproductive activity, respectively. Statistical methods were used according to Snedecor and Cochran (1980). A probability of ≤ 0.05 associated with a statistic was assumed to be significant.

RESULTS

Helminth abundance

In the 119 adult hares the abundance of *T. retortaeformis* differed significantly between bimonthly periods ($F = 17.86$, df $= 5,107$, $P < 0.001$). There was a marked increase from December through March and the high level persisted through the period October to November in males but declined slightly in these months in females (Fig. 1). There was no difference in abundance of *T. retortaeformis* between the sexes ($F = 1.68$, df $= 1,107$, $P > 0.05$) and the two-way analysis of variance re-

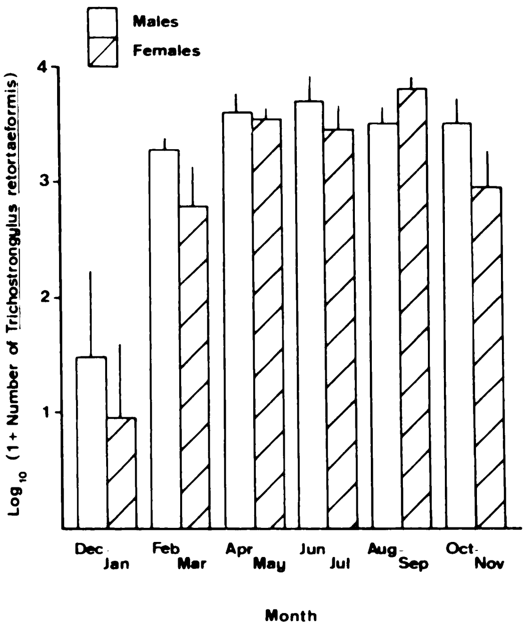

FIGURE 1. Means and standard deviations of transformed numbers of parasites in adult male and female mountain hares from Corgarff, Scotland, in each bimonthly period from April 1984 to March 1985. Sample sizes given in Table 1.

vealed no interactive effect of month and sex on abundance of the helminth (Fig. 1). Only 6% of adult hares were infected with the cestode *Mosgovoyia pectinata* (Boag and Iason, 1986) and there was no significant correlation between intensity of infection with *T. retortaeformis* and *M. pectinata* in any bimonthly period.

Body weight and fatness

The mean kidney fat index in August to September was much lower than the February to March value for both sexes, although body weights were similar and generally far less variable (Table 1). In August to September there were negative correlations between body weight and KFI, and intensity of infection with *T. retortaeformis* (Table 2) although they were not statistically significant for either sex or the sexes combined. In February there were no significant correlations between body weight or fatness and intensity of infection with *T. retortaeformis* (Table 2).

TABLE 1. Mean kidney fat index (KFI) and body weight of adult male and female mountain hares from Corgarff, Scotland, from April 1984 to March 1985.

	Males			Females		
Period	KFI (%)	Body weight (kg)	*n*	KFI (%)	Body weight (kg)	*n*
Apr–May	12	2.5	10	25	2.9	18
Jun–July	19	2.8	4	16	3.0	20
Aug–Sept	26	2.8	8[a]	6	2.8	13[a]
Oct–Nov	13	2.7	4	5	2.7	6
Dec–Jan	7	2.5	3	3	2.6	5
Feb–Mar	99	2.7	16	41	2.8	12

[a] Body weight was not recorded for one male and one female in September 1984.

Fecundity of female hares

To examine the effect of *T. retortaeformis* on the fecundity of individual female hares it is desirable to make comparisons within one reproductive season because there are probably differences in reproductive performance between years (Flux, 1970). There were significant differences in fecundity between the months April to October 1984 ($F = 3.86$, df = 6,45, $P < 0.01$) (Table 3). This result is due to hares which were sampled later in the breeding season having had more litters. To correct for this effect the fecundity of females was expressed as a deviation from the mean number of corpora lutea and corpora albicantia of females sampled in that month. From April to October, there was no difference between months in mean intensities of *T. retortaeformis* in adult females ($F = 1.79$, df = 6,49, $P > 0.05$). There was no correlation between fecundity of females corrected for monthly differences and intensity of infection with *T. retortaeformis* ($r = 0.16$, df = 51, $P > 0.05$).

DISCUSSION

There is a marked seasonal pattern of abundance of *T. retortaeformis* in adult mountain hares in this study. In rabbits and some other mammals the development of trichostrongyles may be inhibited in the host usually as fourth stage larvae

TABLE 2. Pearson product moment correlation coefficients of body weight and kidney fat index (KFI) with intensity of infection with *T. retortaeformis* in August to September 1984 and February to March 1985.

	Body weight	KFI
August–September		
Males	−0.22 (12)[a]	−0.21 (13)
Females	−0.54 (7)	0.07 (8)
Both sexes	−0.29 (19)	−0.35 (21)
February–March		
Males	−0.06 (12)	0.11 (12)
Females	−0.11 (16)	0.14 (16)
Both sexes	−0.12 (28)	0.20 (28)

[a] Sample size in parentheses.

TABLE 3. Fecundity of female mountain hares (mean numbers of corpora lutea and corpora albicantia) in the months April to October 1984.

Fecundity of females	Apr	May	Jun	Jul	Aug	Sep	Oct
Mean	2.6	3.2	3.6	4.0	4.9	6.2	3.0
n	8	9	14	6	8	5	3

but sometimes at the third stage (Michel, 1952; Eysker, 1978; Gibbs, 1986). If this phenomenon also occurred in mountain hares it might contribute to the apparent reduction in the numbers of nematodes during early winter that we observed (Fig. 1); arrested larvae present within the intestinal wall would not have been detected by our method of counting. The rise in worm abundance in February coincides with the onset of the hare's reproductive period and may be due to the development of arrested larvae within the host, stimulated by changes in the host's reproductive hormones (Blitz and Gibbs, 1972). An alternative explanation for the increase in mean intensity of infection with *T. retortaeformis* in February is that the ingestion of infective larvae from the vegetation is increased. Free-living stages of trichostrongyles may survive over winter and this survival may be enhanced by persistent snow cover which ameliorates soil temperature (Gibson and Everett, 1967). However, in northeastern Scotland February is the coldest month and, although larval survival may be possible, the successful development of over-wintering free-living stages of trichostrongyles sufficient to cause the observed increase is unlikely.

If the suggestion that the endocrine status of the host affects the relationship between lagomorphs and *T. retortaeformis* was correct (Dunsmore, 1971), the absence of a sex difference in seasonal pattern of parasite abundance is somewhat surprising. In female Scottish mountain hares, lactation often continues until October whereas in the males the testes have usually regressed by August (Flux, 1970). This study concords with others on the European rabbit which have found no association between host sex and intensity of infection with *T. retortaeformis* (Dudzinski and Mykytowycz, 1963; Boag, 1985). However, with larger samples of rabbits, Dunsmore and Dudzinski (1968) found significant differences between the sexes, but generally there are conflicting reports on the variation in prevalence and intensity of helminth infection with host sex (Keith et al., 1986).

In contrast to studies on the cyclic red grouse populations of Britain (Hudson, 1986), we found no depression of fecundity of female mountain hares with increased intensity of infection with trichostrongyles. Although we only collected samples within one breeding season (1984), there was much variability in fecundity between females with estimates of fetal number ranging from one to eight. Prenatal losses were low in this particular year (Iason, 1987) and hence the numbers of corpora lutea counted probably reflects the number of young born.

Keith et al. (1984) found that snowshoe hares that have been preyed upon are in poorer condition than survivors, hence a slight negative effect of parasites on condition may increase mortality due to predators. This is unlikely to occur in mountain hares in Scotland since predators are of less significance than in North America. Moreover, although some of the intensities of infection with *T. retortaeformis* were very large (Boag and Iason, 1986), there was no significant association between intensity of infection and either body weight or fatness of adult hares. This result persisted in both August to September and February to March, when the annual cycle of fatness is low and high, respectively (Table 1). We might expect *a priori,* that a negative association between parasite intensity and condition would be more likely to result in mortality at the time of year when fatness is lowest. However, the main period of adult mortality in mountain hares is not in the autumn but is from February to May (Flux, 1970), when the correlation between intensity of infection and condition is very weak (Table 2).

Any possible effects revealed by correlational studies such as this must be supported experimentally before causality can be assigned (Yuill, 1964; Hudson, 1986). Even then, the effects need not be regulatory to the host population. *Trichostrongylus retortaeformis* is the most common helminth of adult mountain hares; very few were infected with other intestinal helminths, and lungworms were not found (Boag and Iason, 1986). In this very simple host–parasite interaction we found no significant negative correlations between intensity of infection and adult condition or female fecundity. This independent study supports the conclusions of recent work which also failed to find a strong role of helminth infections in the population dynamics of snowshoe hares (Keith et al., 1985; Keith et al., 1986). However, trichostrongyles are known to impair growth in other species of grazing mammals (Reveron et al., 1974; Sykes and Coop, 1976), including lagomorphs (Yuill, 1964; Dunsmore, 1980). Any possible role of *T. retortaeformis* in cyclic changes in mountain hare populations is more likely to be due to a decrease in recruitment through a reduction in growth and survival of young rather than through a reduction of adult condition or fecundity.

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BOOK REVIEW . . .

Bacterial Protein Toxins, P. Falmagne, J. E. Alouf, F. J. Fehrenbach, J. Jeljaszewics, and M. Thelestam (eds.). Gustav Fischer Verlag, Stuttgart, Germany (U.S. Edition, VCH Publishers Inc., Dearfield Beach, Florida 33442, USA). 1986. 398 pp. $83.75 U.S.

This volume is a compilation of abstracts and complete short papers presented at the second European workshop on bacterial protein toxins held in Wepion, Belgium, 30 June to 4 July 1985. Topics covering the major aspects of bacterial protein toxins included structure, mode of action, interaction with cell receptors and membranes, synthesis, regulation, secretion, internalization and pathogenicity. Also included are aspects of applied toxinology in medicine and agriculture through the use of either wild-type or chemically or genetically modified toxins.

The symposium primarily dealt with human pathogens such as *Escherichia coli*, *Cornybacterium diptheriae*, *Salmonella* spp., *Pseudomonas aeruginosa*, and *Staphylococcus aureus*. Only a few pathogens of animals are included (e.g., *Bacillus anthracis*), only because they also are important to humans. Most of the papers are highly technical and deal with the subject matter on a cellular and subcellular level. One chapter by J. E. Alouf provides a good overview of the effects of bacterial protein toxins on host immunologic defense mechanisms. Another paper by Luthy et al. contains an excellent summary of the pathogenic action of *Bacillus thuringiensis* toxin in arthropods. The last section of the book deals with techniques of cloning bacterial toxins for possible vaccine development.

In general, this book probably is concerned too much with human pathogens and the cellular and subcellular mechanisms of action of their toxins to be useful to most wildlife disease biologists. Additionally, the book already is out of date since the conference was held 3 yr ago and the third workshop already has taken place (28 June to 2 July 1987, Oberlingen, Federal Republic of Germany); presumably, the proceedings from this conference also will be published.

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