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The potential role of habitat on intestinal helminths of mountain hares, *Lepus timidus*

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Abstract

Over the last century in the uplands of Scotland, the extent of heather moorland which supports high densities of mountain hares *Lepus timidus* has diminished and has gradually been replaced by large-scale commercial forestry plantations or expanding natural woodlands. The potential impact of such a change in land use on host–parasite interactions was investigated by comparing the intensity and prevalence of infection of hares by parasites in two separate habitats: a large hare-fenced young forestry plantation and the adjacent open moorland. Carcasses were collected in November 1990 from within both habitats and after the woodland had been enclosed for nine months. Age, sex, fatness (kidney fat index) and degree of infection of hares were noted. Two parasites were recorded: the nematode *Trichostrongylus retortaeformis* and the cestode *Mosgovoyia pectinata.* Clear differences in the intensity of infection of adults occupying the different habitats had occurred in the nine months since woodland enclosure. Adult mountain hares in the woodland had levels of infections approaching four times that observed in hares occupying the open moorland and although not significant, the prevalence of infection was greater in hosts inhabiting the woodland than the open moorland. It is suggested that the parasite–host relationship differs between the two habitats and as heather-dominated moorland landscapes become more fragmented with the increasing establishment of woodlands, the impact of parasites on the life history strategies of mountain hares needs to be reconsidered.

Introduction

Host, parasite and landscape interactions are often overlooked when considering the impact of landscape change and habitat fragmentation on the ability of individuals to meet their requirements within the new or modified habitat (Teel *et al.*, 1996). While the host will utilize resources such as food, water and cover within a landscape, the parasite will additionally utilize the host for transportation. Furthermore, even a modest change (in landscape terms) in vegetation structure may have a profound impact on parasite life-histories, as some parasites require environmental conditions resulting from vegetation structure that supply a suitable environment for egg laying and the production of new larvae or moulting to subsequent stages (Crofton, 1948a,b). Consequently, the spatial and structural characteristics of a landscape, host movement and the transmission process itself should each determine the pattern and rates of parasite population dynamics, dispersal and re-infection of its host.

Throughout the last century in Britain, there has been a sharp decline and fragmentation in the extent of heather

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Calluna vulgaris moorland in upland areas and much has either been converted into commercial forestry plantations or has been replaced by the expansion of naturally regenerating woodlands (Anderson & Yalden, 1981; Countryside Commission for Scotland and Nature Conservancy Council, 1988; Usher & Thompson, 1988). Intuitively, such large scale structural and landscape changes will impact on the host–parasite relationship. Indeed, field experiments have indicated that the development of eggs and of free-living larval stages of gastrointestinal helminths is greater in cool, moist environments prevalent in woodland (Broekhuizen & Kemmers, 1976), and it may be predicted that this would lead to greater intensities of infection in hosts that inhabit such habitats.

In northern Europe, mountain hares are predominantly a species of mixed forest habitats although in Scotland and on the coastal islands of Sweden, mountain hares are traditionally associated with open heather moorlands (Flux, 1970; Angerbjörn, 1981). However, extensive populations of mountain hares do occur within young establishing woodlands in Scotland (Hulbert *et al.*, 1996a,b) and therefore in this paper, we investigate the prevalence and intensity of infection by helminths in mountain hares occupying a young forestry plantation and an open heather moorland and evaluate any observed differences in the framework of landscape change.

Materials and methods

Mountain hares carcasses were collected at 550 m above sea level in the foothills of the Cairngorm Mountains in northern Scotland in November 1990. Thirty-two mountain hares were shot from within a young 2–3 m high Sitka spruce *Picea sitchensis* and lodgepole pine *Picea contorta* var. *latifolia* woodland and 28 hares were shot from the adjacent heather moorland. Ericaceous dwarf shrubs and grasses dominated the ground flora in both habitats. The woodland was enclosed by a 10 km long, 1 m high hare-proof fence and movement of hares of all ages between the two habitats during the months of March and November 1990 inclusive was considered negligible (Hulbert & Iason, 1996). Movement between the two habitats prior to March 1990 was extensive and unhindered. Both habitats were intensively keepered and there were few predators.

Carcasses were weighed, their sex noted and the left kidney and associated fat removed and weighed separately. The ratio of fat weight to kidney weight (kidney fat index: KFI) was used as a measure of fatness (van der Merwe & Racey, 1991). Eye lens weight was used to establish which individuals were young of the year (i.e. leverets) (Hulbert & Iason, 1996). The contents of the stomach, small and large intestine were dissected and washed separately through a 125 μm sieve and examined in a dilution of up to 1:25 for intestinal helminths. Terminology describing the degree of infection of hosts by parasites is consistent with Margolis *et al.* (1982).

In general, adult female hares are more than 10% heavier than males (Flux, 1970) and therefore, the analysis proceeded with three sex/age classes for hares: adult males, adult females and leverets. Helminth counts and KFI were normalized by log $(n + 1)$ transformation for analysis and the mean values in the figure are back-transformed from these. As the number of animals of each sex and age were different in each habitat, a variance component model was fitted by residual maximum likelihood (REML) to calculate means and standard errors of difference (Robinson, 1987). The Wald test was used to test main effects and interactions of sex/age class and habitat on nematode infectivity of adults and leverets. Tests for differences between categories of hare were made by an analogue of the least significant difference method (Snedecor & Cochran, 1980). Transformed KFI and body masses were correlated with intensity of helminths using the Pearson product moment correlation coefficient. The prevalence of helminths in hosts inhabiting the contrasting habitats was compared using Fisher's exact probability test and χ^2 test (Siegel & Castellan, 1988). All analysis was conducted using Genstat 5.3.2–2 (Genstat 5 Committee, 1993).

Results

Prevalence and intensity of infection

Two species of gastrointestinal helminth were identified in the 62 mountain hares examined: the nematode *Trichostrongylus retortaeformis* and the cestode *Mosgovoyia pectinata*. All adult hares $(n = 31)$ were infected with *T. retortaeformis* and 70.9% $(n = 31)$ of the leverets were infected. Only one adult and five leverets were infected with *M. pectinata*, which were then excluded from further analysis. The mean intensity of infection with *T. retortaeformis* was 2045 (10–14,500). Ninety-one percent of the hares in the woodland were infected with *T. retortaeformis* and 78% of hares on the moorland were infected but this difference was not significant ($\chi^2 = 1.89$, $P > 0.05$).

Adult hares of both sexes had significantly greater intensities of infection with *T. retortaeformis* than that of leverets regardless of habitat ($F_{2,47} = 34.2$, $P < 0.001$) (fig. 1). As there was no significant difference in infection intensity between the two adult sexes, the analysis proceeded with data for both sexes combined and the leveret data removed. Adult hares inhabiting the woodland had significantly greater intensities of infection (up to four times) than that observed for moorland hares ($F_{1,29} = 14.3$, $P < 0.05$).

Body weight and fatness

For adult and leveret mountain hares, there were no significant correlations between either body weight or intensity of infection with *T. retortaeformis* or fatness and intensity of infection with *T. retortaeformis* regardless of habitat (table 1).

Discussion

Small and unbalanced sample sizes cannot be analysed reliably using ANOVA, but REML is able to circumvent both problems as in the present study (Hulbert & Iason, 1996). REML estimates the components of variation over all sources of information and then assigns appropriate

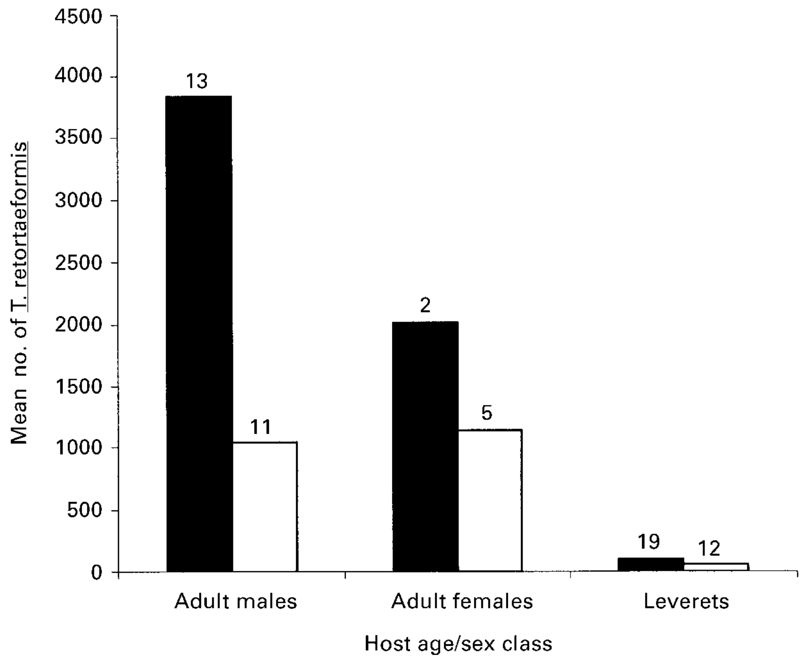

Fig. 1. The intensity of infection (=mean worn burden) in adult and leveret mountain hares with *Trichostrongylus retortaeformis* in the woodland ■ and on the moor □. Sample sizes are given above each bar.

weight to comparisons depending on their respective sample sizes to obtain information on treatment effects (Genstat 5 Committee, 1993). Following the removal of leverets from the data set, the analysis revealed that after only nine months of separation, the intensity of infection of adult mountain hares with trichostrongyle nematodes was almost four times greater in the woodland habitat than in those individuals occupying the more open moorland habitat. In the north-east of Scotland, nearly 60% of the moorland area lost over the last 30 years was to either forestry plantations or encroaching woodland and the remainder was predominantly to grassland habitats due to heavy grazing (Anderson & Yalden, 1981; Countryside Commission for Scotland and Nature Conservancy Council, 1988; Usher & Thompson, 1988). Such changes can occur rapidly and especially for new woodlands, can occur within a few years. Previous studies have indicated that the population and community dynamics of helminths may be associated with

Table 1. Pearson product moment correlation coefficient of body weight and kidney fat index (KFI) with intensity of infection of adult and leveret mountain hares with *Trichostrongylus retortaeformis* in the woodland and on the open moor.

Hare/habitat	Body weight	KFI
Adult/woodland	0.276 (15)	0.332 (14)
Adult/moor	0.086 (16)	−0.05 (16)
Leveret/woodland	0.023 (16)	−0.257 (15)
Leveret/moor	0.450 (6)	0.208 (6)

Sample size in parenthesis.

extrinsic habitat factors that change across geographic regions (Custer & Pence, 1981) but this study confirms that such differences can be extremely localized (Boggs *et al.*, 1978; Jacobsen *et al.*, 1978) and can develop very rapidly.

During autumn and early winter, the intensity of infection of mountain hares with *T. retortaeformis* is generally at its lowest level (Boag & Iason, 1986) but in this study, the level of infection in the woodland is very high and indeed the highest ever recorded for mountain hares (Boag & Iason, 1986). In part, such an increase could be related to an increasing transmission rate associated with higher host densities (Keith *et al.*, 1985) but, from a related study, there is no conclusive evidence that hare populations within young woodlands are any higher than on adjacent moorlands (Hulbert *et al.*, 1996a). Rather, moist, warm conditions are required before the eggs of *T. retortaeformis* hatch and develop into infective larvae (Crofton, 1948b; Prasad, 1959). Within sheltered habitats, such as woodlands, rates of turbulent transfer of air are reduced and consequently temperatures and relative humidity are generally higher than in more exposed habitats (Jones, 1983). Broekhuizen & Kemmers (1976) demonstrated that considerably more third stage infective larvae were present in shady conditions under trees than in open pastures and, as the rate of helminth intake is likely to be directly related to the availability of infective larvae, higher intensities of infection by the helminths should be observed within woodland habitats. The present paper confirmed this hypothesis.

A greater proportion of hares in the woodland was observed to be infected with *T. retortaeformis* than those in the open moorland habitat. Although not significant, perhaps a far clearer result would have emerged had the study been carried out over a number of years and at several sites and this is a major limitation of this work. Nevertheless, this study was a snapshot taken during one month after nine months of enforced separation between the two habitats. Longer term segregation, which would effectively mimic large-scale afforestation, may result in longer term effects on the population dynamics of helminths and the consequent impact on the host, the mountain hare. However, the persistence of these effects into the later stages of the forest rotation are unlikely because once the canopy closes and the ground vegetation dies back (Sykes *et al.*, 1989), the forest provides a poor habitat for hares (Hulbert *et al.*, 1996a). Nevertheless, from the present study and that of Hulbert & Iason (1996) it is evident that the parasite and host (mountain hare) population dynamics and their interactions are quite different within woodland compared to moorland habitats. As new woodlands are established and mature forests felled and/or restructured, a more fragmented mosaic of preferred and avoided habitats will be created and the impact on the life history strategies of hares requires further evaluation (Iason & Boag, 1988).

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