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The possible effects of landscape change on diet composition and body weight of mountain hares *Lepus timidus*

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In the UK and elsewhere in Europe, high densities of mountain hares *Lepus timidus* are associated with heather moorland, the area of which has been diminished by large-scale afforestation. The consequences of this landscape change for the diet composition and body weight of mountain hares were investigated by comparing mountain hare carcasses collected in November 1990 simultaneously from a large hare-fenced, young forestry plantation and from the adjacent heather moorland. The sex, age, diet composition and body weight of individual hares were recorded. There were readily identifiable differences in the diet composition and body weight of hares that occupied the two different habitats, the segregation of which had been rigorously maintained for the previous nine months and included the period of births of leverets. Adult females and leverets in the young forestry plantation had a higher proportion of grasses and a lower proportion of heather in their stomachs than the same age/sex classes on the open moorland, and leverets occupying the forestry plantation were significantly heavier than those inhabiting the moorland habitat. Large-scale afforestation results in an improvement in diet quality and body weights in young mountain hares during the early plantation stages, and in those early years following planting, commercial afforestation is probably not detrimental to mountain hare populations. Persistence of mountain hare populations in afforested landscapes could be facilitated by the incorporation of appropriate young age classes of forest.

Key words: body weight, diet composition, landscape change, mountain hares

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Landscape change is often considered in the context of habitat fragmentation where there is a gradual loss of habitat, reduced habitat patch size and increased distance between patches whilst the area of new habitat increases (Franklin & Foreman 1987, Andrén 1994). However, where rapid large-scale habitat change has taken place as in the afforestation of upland Britain, fragmentation and isolation of the remaining habitat fragments may be less important to the retention of existing species than the ability of individuals to meet their requirements within the new habitat. Over the last century in Britain there has been a considerable reduction in the extent of heather *Calluna vulgaris* L. Hull moorland in upland areas (Andersen & Yalden 1981, Usher & Thompson 1988) and in the north-east of Scotland nearly 60% of the moorland area lost became forestry plantations or woodland (Countryside Commission for Scotland & Nature Conservancy Council 1988). It may be predicted that this large-scale change in land use would adversely affect those bird and mammal species with specific requirements for moorland habitat characteristics (Thompson et al. 1988, Sykes et al. 1989).

In the uplands of Scotland, heather moorland is considered the typical habitat of mountain hares *Lepus timidus* L. (Hewson 1991). However, in a recent study of habitat selection by adult female mountain hares in a landscape composed of upland pasture, young forestry plantation and heather moorland, all three habitats were utilised but the young forestry plantation and upland pasture habitats were selected preferentially and the heather moorland was avoided (Hulbert et al. 1996). In this paper we investigate the diet composition and body weight of mountain hares occupying two of those habitats; a young forestry plantation and the adjacent heather moorland, and consider the implications of any observed differences in the context of landscape change.

Study area and methods

In November 1990, 32 mountain hares were shot from within the young forestry plantation and 28 hares from the adjacent heather moorland at Glenkirk at 550 m a.s.l. (OS Ref NJ 835318) in northern Scotland. Two-metre high Sitka spruce *Picea sitchensis* (Bong.) Carr. and lodgepole pine *Pinus contorta* Dougl. var. *latifolia* Wats. grew in the plantation and ericaceous dwarf shrubs dominated the ground flora in both habitats. The young plantation was enclosed by a 10-km long, 1-m high hare-proof fence. In November 1989 the fence was checked and 65 holes were closed, but in January and February 1990 snow covered the fence and in winter there was free movement of adult hares between the two habitats which was unavoidable. However, between March and November 1990 inclusive, fewer than three holes per month were found in the fence and repaired, and movement of hares of all ages between the two habitats during this period was considered negligible. Both habitats were intensively keepered and there were few predators.

Carcasses were weighed and their sex noted. As body weight may be associated to the intensity of infection by intestinal helminths (Yuill 1964) the alimentary tract was removed and examined, and the number (log (n+1)) of helminths present included as a covariate in the statistical analysis of body weight (Hulbert 1993). The results of the helminth counts will be presented and discussed elsewhere. Diet composition, which reflects what is actually eaten, was analysed using the plant epidermal fragments found in the stomach contents of each hare (Wallage-Drees et al. 1986, Homolka 1986) and the plant fragments were identified to species. The analysis was conducted as described in Iason & Waterman (1988).

Both eyes were removed from each hare, fixed in formalin and the lenses subsequently dissected and oven dried at 80°C for 48 hours. A mean eye lens weight was obtained for each hare and a frequency distribution of eye lens weight was plotted to establish which individuals were young of the year, i.e. leverets (Myers & Gilbert 1968, Flux 1970).

In general adult female mountain hares are more than 10% heavier than adult males (Flux 1970) and, therefore, the analysis of diet composition and body weight proceeded with three sex/age classes - adult males, adult females and leverets. Dietary composition was analysed on the logratio of *Calluna* to grasses and mean percentages quoted in the text are back transformed from these. The use of logratios avoids statistical problems associated with percentages of dietary components summing to 100% (Aitchison 1986). As the number of hares of each sex/age class was 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

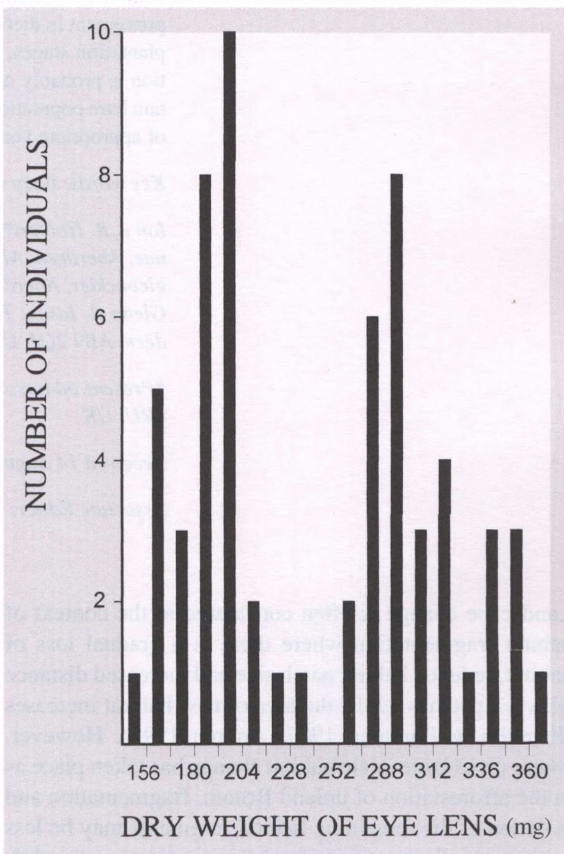

Figure 1. Frequency distribution of eye lens weight of mountain hares collected in November 1990 (N = 62).

habitat on diet composition and body weight of adults and leverets. Tests for differences between categories of hares were made by an analogue of the least significant difference method (Snedecor & Cochran 1980). All procedures were calculated on Genstat (Genstat 5 Committee 1993).

Results

The frequency distribution for eye lens weight is essentially bimodal with the lens weights of the leverets forming the first peak in the distribution and those of the adults forming the second peak (Fig. 1). Leverets were considered to be those hares that had a mean eye lens weight of less than 240 mg. The observed pattern is most unlikely to be due to sex as there was no significant sex difference in the mean eye lens weight for either adults or leverets (Adults: $F_{1,29} = 0.0$, $P > 0.05$; leverets: $F_{1,29} = 0.1$, $P > 0.05$). There was no significant difference between the frequency distribution for eye lens weight of leverets oc-

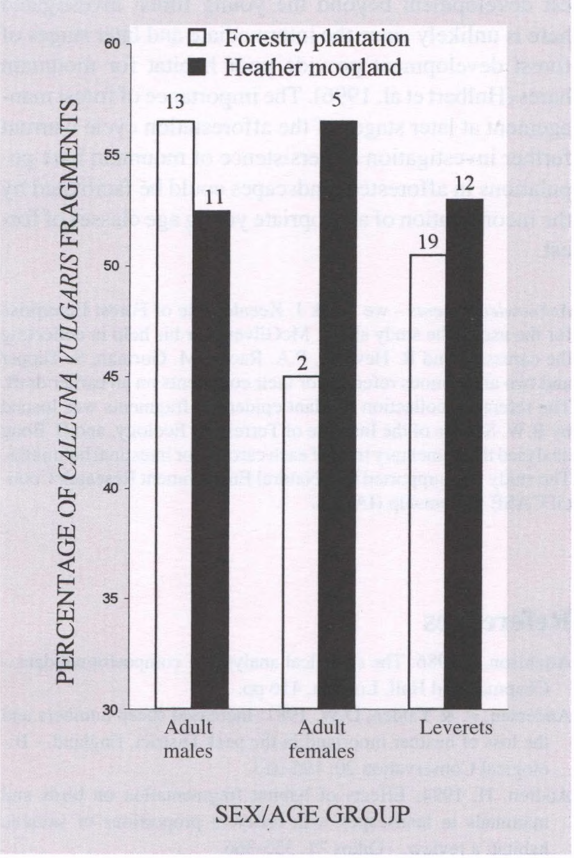

Figure 2. Percentage of *Calluna vulgaris* epidermal fragments found in the stomachs of adult mountain hares of both sexes and of leverets in the forestry plantation and the open moor. Sample sizes are given above each bar.

Table 1. Mean body weight (kg) of adult male, adult female and leveret mountain hares in the forestry plantation and on the heather *Calluna vulgaris* moorland. Sample sizes are given in parentheses. Unlike letters are significantly different (P < 0.05, L.S.D. test) for between-habitat comparisons.

	Habitat		
Sex/age	Forestry plantation	Heather moorland	s.e.d.
Adult ♂♂	2.71[a] (N = 13)	2.74[a] (N = 11)	0.099
Adult ♀♀	2.53[a] (N = 2)	2.79[a] (N = 5)	0.168
Leverets	2.65[a] (N = 19)	2.22[b] (N = 12)	0.078

cupying the two habitats (Kolmogorov-Smirnov test: $D_{19,12} = 0.4025$, $P > 0.05$) which implies that the seasonal pattern of births was not different between the two habitats.

Hare stomach samples from each habitat contained both *Calluna* and grasses which together accounted for 99.2% of the fragments identified. The two way interaction of sex/age and habitat on dietary composition revealed a significant effect ($F_{2,55} = 4.65$, $P < 0.05$). Adult female hares and leverets in the forestry plantation had a lower proportion of dietary *Calluna* than those on the moor, and this difference was opposite to that witnessed for adult males (Fig. 2). Indeed, the proportion of *Calluna* fragments in the stomachs of adult females obtained from the forestry plantation was significantly lower than that in the stomachs of adult females obtained from the moorland (P < 0.05).

For each sex of adult, there was no significant difference in the body weight of hares occupying the two different habitats ($F_{1,26} = 0.3$, $P > 0.05$) (Table 1). However, there was significant variation between habitats in the body weight of leverets, with those individuals occupying the forestry plantation being heavier than those inhabiting the open moorland ($F_{1,28} = 43.6$, $P < 0.001$) (see Table 1).

Discussion

ANOVA cannot be used to reliably analyse data sets that are unbalanced or where sample sizes are low. REML, however, is able to circumvent both problems by estimating the components of variation over all sources of information and then assign appropriate weight to comparisons depending on their respective sample sizes to obtain information on treatment effects (Genstat 5 Committee 1993). REML analysis demonstrated that there were differences in the diet composition of hares occupying the two different habitats. Adult females and leverets occupying the forestry plantation had a higher proportion of grasses and a lower proportion of *Calluna* in their stomachs than the corresponding age/sex class occupying the moorland and for the adult females this difference was significant. Previous work has established that the diet composition of mountain hares varies seasonally (Flux 1970, Iason & Waterman 1988), but in the present study we have shown that within a particular season, diet composition also varies according to the habitat occupied, further illustrating the plasticity of their foraging strategy. Similar results have been obtained for Irish hares *L. t. hibernicus* whose diet composition depended upon the habitat occupied (Tangney et al. 1995).

The greater proportion of dietary *Calluna* of the adult females and leverets occupying the moorland as compared to the plantation probably resulted in a higher diet quality for those individuals in the plantation since the digestibility of *Calluna* by hares is low (Pehrson 1983). No single study has examined the digestibility of both grasses and *Calluna* by hares, but other nutritional studies of herbivores have shown that grasses provide a greater proportion of easily digestible dry matter and a much greater fraction of available protein than *Calluna* (Milne et al. 1978, Kay & Staines 1981, van Soest 1982). Furthermore, the lower proportion of *Calluna* in the diet of forest hares means that they probably ingested lower amounts of plant secondary compounds which are present in *Calluna* in high concentrations (Jalal et al. 1982, Iason et al. 1993). These plant constituents may act as digestion inhibitors or are toxic to many mammalian herbivores (McArthur et al. 1991) including hares (Iason & Palo 1991, Sinclair et al. 1988). Adult females and leverets are the age/sex classes which would be expected to have higher nutrient and energy requirements due to reproduction and growth (Robbins 1983) and hence, to be more sensitive to the detrimental effects of a poor quality diet. They have been shown to ingest less *Calluna* than males when alternatives are available (Iason & Waterman 1988). However, during the non-reproductive period of this study, the difference between requirements of adult males and adult females are unlikely to be great; hence, it is difficult to explain why adult males ingest inferior diets in the forestry plantation compared to the other two age/sex classes. Dominance and access to food appear to be positively related to size in brown hares *Lepus europaeus* (Lindlöf 1978), and possibly in mountain hares (Hewson 1990). The potential role of greater female body weight in ranging behaviour and procurement of food resource during the non-reproductive period requires investigation.

There is evidence to suggest that both survival and reproductive performance are positively related to body size in many vertebrates (Sadleir 1969) including mountain hares (Iason 1989, Iason 1990) and that lactation performance, growth rate, body weight and birth weights of herbivores, including lagomorphs, are positively related to diet quality (Keith & Windberg 1978, Robbins 1983, Pehrson & Lindlöf 1984). Leverets occupying the forestry plantation had higher body weights than leverets on the moor. This difference may be due to increased pre- and/or post-weaning growth rates of forest leverets, the former being facilitated by improved lactation performance by adult females and the latter by the improved diet quality of the leverets. The autumn body weight of the adults did not differ between the two habitats, but this was to be expected as the adult population possibly mixed freely during periods when snow covered the fences. Longer term segregation which would effectively mimic large-scale afforestation, would probably result in longer term effects on nutritional ecology and more marked effects on body weights, including in the adult age class.

The likely demographic consequences of these dietary and body weight effects acting on reproduction and survival suggest that commercial afforestation of moorland at least in the early years following planting may not be wholly detrimental to hare populations. However, the persistence of these effects into subsequent stages of forest development beyond the young forest investigated here is unlikely since the intermediate and later stages of forest development provide poor habitat for mountain hares (Hulbert et al. 1996). The importance of forest management at later stages of the afforestation cycle warrant further investigation as persistence of mountain hare populations in afforested landscapes could be facilitated by the incorporation of appropriate young age classes of forest.

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