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Effects of sheep grazing on abundance and predators of field vole (*Microtus agrestis*) in upland Britain.

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Abstract

A technique using fresh feeding signs as an index of density was validated and used to survey the effects of sheep grazing on vole population densities in four upland habitats in the northern Peak District National Park, UK. In grazed areas *Molinia caerulea* grasslands supported most voles, *Nardus stricta* grasslands supported fewer and *Eriophorum vaginatum* and *Calluna vulgaris*-dominated areas supported least. There were highly significant negative relationships between vole sign density and sheep numbers in these habitats. Where sheep were excluded, these same habitats had between three and nine times higher sign densities, corresponding to between 1.5 and

2.5 times greater field vole densities. Population estimates of voles and predators such as short-eared owl approximately doubled under reduced grazing. Reducing sheep numbers in upland areas may therefore be critical in encouraging the recovery of predatory birds in the uplands.

Keywords: Microtus agrestis, grazing, moorland, field signs, vole predators.

1. Introduction

The field vole (*Microtus agrestis*) is thought to be Britain's most common mammal with a pre-breeding population estimated at 75 million individuals, most of them living in the uplands (Harris et al., 1995), though little is known of their ecology there. Both density and breeding success of several species of predators have been shown to be strongly related to field vole abundance (e.g. weasel *Mustela nivalis* (Tapper, 1979), hen harrier *Circus cyaneus* (Redpath et al., 2002), kestrel *Falco tinnunculus* (Thirgood et al., 2003; Village, 1982), tawny owl *Strix aluco* (Petty and Fawkes, 1997), short-eared owl *Asio flammeus* (Thirgood et al., 2003; Village, 1987), long-eared owl *Asio otus* (Sundell et al., 2004)). Recent changes in land use in Britain have resulted in an increase in the relative importance of field voles as a prey source for a number of predatory species (Love et al., 2000).

In British uplands, habitat preferences and effects of common land management strategies on vole populations are little known. Suitability of habitats for field voles is governed by two main factors – food availability and cover (Hansson, 1977); field voles show significant food preferences in British uplands (Wheeler, 2005) and sheep grazing limits food availability for field voles in Norwegian mountain pastures (Steen et al., 2005) while sheep and cattle grazing in Scottish upland grasslands decreases vole abundance (Evans et al., 2006). It has been shown previously that voles select some habitats based more on cover depth than food availability (Hansson, 1997; Lin and Batzli, 2001), though at low cover levels, food availability becomes the main selection factor. Grazing can affect plant composition and cover depth substantially, but the effects of this on field vole populations remain largely unstudied at wide scales despite being highly relevant to wider conservation efforts in upland areas.

Here I develop and validate a method for rapid assessment of field vole population density in uplands based on feeding signs. This is used to survey field voles across a wide area of British uplands in order to investigate the distribution of the species with relation to habitat and land management practices and understand the likely effects of extensifying sheep grazing on field voles and their predators.

2. Method

The study was carried out in the North Peak Environmentally Sensitive Area (ESA) of the Peak District National Park in Northern England in the years 2000 and 2001. The area consists of grasslands dominated by *Nardus stricta* and *Molinia caerulea*, (the former much more extensive than the latter) and by dwarf shrub heaths of *Calluna vulgaris* and a mixture of *Eriophorum vaginatum*, *Vaccinium myrtillus* and *Empetrum nigrum*.

Time and logistical constraints preclude the use of live trapping in wide-ranging studies of small mammals in inaccessible areas, and in such situations sign surveys are the only practical technique. Field voles leave grass clippings, piles of droppings and runways throughout their ranges. In order to assess the reliability of field signs as indicators of vole density in British uplands, signs were searched for in twenty sites, five in each of the four main North Peak ESA habitats (*Molinia* and *Nardus* grasslands, *Calluna* moorland and *Eriophorum* blanket bog). Here genus names of these dominant plants are used to describe habitat types, while full binomial names are used when referring to individual species. Signs were assessed by restricted random sampling of a 50m by 50m area (i.e. quarter ha) at each site. A one m² quadrat was searched for fresh or old droppings, grass clippings and runs in each 10m square of the sample area, giving twenty-five records at each site. The number of quadrats with each vole sign was multiplied by four to produce a per hectare vole sign index (VSI) for that sign. Each of the 20 sites surveyed for field signs was then trapped with snap traps for three nights. At each site 20 traps were set unbaited in field vole runs at 15m intervals across the site. Traps were checked and reset every 24h over three nights. Trapping was carried out in summer and autumn 2000 and 2001. The number of animals caught per 100 trap nights was used as a vole trapping index (VTI). Falsely triggered traps were discounted. VTI

was compared to VSI using General linear models (GLM) with numbers trapped square-root transformed for each of the field signs to assess relationships between the two.

Voles were also live-trapped at a single site in order to estimate density and correlate this with VSI. Forty nine Longworth small mammal traps (Chitty and Kempson, 1949) were placed at a grassland site within the wider study area at 10m intervals in a 60 x 60m grid. Traps were baited with wheat and blowfly pupae and lined with straw bedding to prevent mortality of rodents and shrews. The site was trapped for 5 nights every 6 weeks for 18 months. Traps were checked twice daily at 12h intervals or at dawn and dusk in winter months. Field voles were marked individually by fur clipping (Gurnell and Flowerdew, 1982). The first three nights were classified as the marking period and the final two nights the recapture period; a high proportion of marked individuals (60-80%) were recaptured. Live trapping index (LTI) was then calculated using the Lincoln-Petersen method divided by the trapping area (calculated as the total trapping grid area plus a border equivalent to the mean dispersal distance of recaptured individuals) in hectares. The Lincoln-Petersen method was deemed suitable for estimating population size in this study as population estimates were calculated over short time periods where major sex-biased dispersal was unlikely (Kendall, 1999). VSI and LTI were compared using linear regression.

Vole abundance was investigated at the landscape scale by searching 48 sites during late summer and autumn, twelve in each of the four habitats, for field vole signs and VSI was calculated as above. Cover of plant species in each quadrat was assessed and height of vegetation was measured using the drop-disc method (Stewart et al., 2001). Abundance in broad habitat types was assessed by comparing VSI for each of the four habitats. The percentage cover of the seven main plant species (*C. vulgaris*, *N.*

stricta, *V. myrtilus*, *E. nigrum*, *M. caerulea*, *E. vaginatum* and *Deschampsia flexuosa*)

was compared to VSI for each of the 48 sites using a GLM controlled for habitat.

Values of percentage cover for each plant species were arcsine-transformed before analysis to normalise them and allow analysis with standard parametric tests (Sokal and Rohlf, 1995). Sixteen sites, four in each habitat, were surveyed in the winter as well as summer to compare VSI between seasons. Individual sites were located at least half a km apart to ensure spatial independence.

2.1 Effect of sheep grazing

The effect of level of sheep grazing on field vole density was investigated by counting the number of sheep seen while walking a 500m transect at 27 sites surveyed in the summer and autumn of 2001 where field sign surveys were also carried out.

Simple stocking rates were not used as sheep tend to distribute themselves unequally across moorland, grazing the better sites and avoiding areas of poor vegetation (Clarke et al., 1995). Sheep numbers were then compared to the VSI at each site with a GLM controlled for habitat type.

Sign surveys were also carried out in sheep exclosures, which were either new plantations or areas of moorland fenced specifically to prevent sheep grazing under the ESA scheme (Anderson et al., 1997). Each exclosure was surveyed along with a patch of equivalent habitat outside the exclosure. Four exclosures of each of the four habitat types were surveyed. Differences were analysed using two-way ANOVA.

Differences in VSI were converted to pre-breeding vole population density using the relationship between VSI and LTI and the ratio between summer (breeding season, when most data were collected) and winter (pre-breeding season) VSI for each habitat. The area of each habitat was calculated from a Phase 1 habitat map of the North Peak ESA. Vole densities in each of the four habitats studied were calculated and used to

estimate vole population size in the North Peak area under scenarios of current grazing levels and under a major reduction in grazing.

Dyczkowski and Yalden (1998) estimated field vole consumption by a range of British predators and showed that likely productivity matched likely consumption. Their figures were used to estimate the field vole predator community that could be supported by the North Peak field vole population under current grazing levels and reduced grazing. Some of these predators, such as short-eared owls are rare in the ESA and nationally, so a local increase in their population would be a considerable conservation success. Annual vole consumption per individual predator and the proportion of voles consumed by each was calculated from Dyczkowski & Yalden (1998)'s estimates. Vole productivity was estimated by averaging typical productivity from southern lowland Britain and Sweden presented in Dyczkowski & Yalden (1998). The estimated number of predators in the region was then calculated by dividing the total voles consumed per predator by the annual vole consumption of each.

3. Results

VTI was significantly correlated with the number of survey quadrats with fresh clippings (GLM of square root no. caught against field signs controlled for Habitat, $n = 20$, $R^2 = 0.71$, $p < 0.01$), fresh droppings ($n = 20$, $R^2 = 0.29$, $p = 0.02$), old droppings ($n = 20$, $R^2 = 0.27$, $p = 0.02$) and runways ($n = 20$, $R^2 = 0.30$, $p = 0.01$) but not old clippings ($n = 20$, $R^2 = 0.01$, $p = 0.78$). Since the closest relationship was with fresh clippings, this was selected as the most reliable indicator of field vole density and was selected to calculate the VSI (Fig. 1). The relationship between VSI and VTI was described by the regression equation:

$$\text{VTI} = 0.32 \cdot \text{VSI} - 0.69$$

A test for the interaction effect between habitat and number of fresh clippings on voles caught was not significant (GLM $n = 20$, $F = 0.47$, $p = 0.74$), implying that the same relationship between fresh clippings counted and voles present holds for all four habitats, therefore validating this technique for estimating vole densities in all the upland habitats. VSI based on fresh grass clippings was also closely correlated with the live trapping index (LTI; $R^2 = 0.58$, $p = 0.01$) and the relationship described by the equation:

$$\text{LTI} = 0.37 \cdot \text{VSI} + 7.21$$

The relationship between VSI and both VTI and LTI had very similar slopes, differing mainly in the constant. Last-night capture success was low for snap-trapped sites (0.3 captures per trap night overall, corresponding to 12.3% of the total number of voles trapped) indicating that most of the population had been sampled. Given the practical difficulties of live trapping in remote upland areas, snap-trapping was therefore regarded as a suitable indicator of population density in these areas.

3.1 Vole abundance

There were significant differences in VSI between habitats (Fig. 2; ANOVA, $n = 48$, $p < 0.01$). *Molinia* sites had higher VSI than the other three habitats. Mean VSI in *Nardus* grasslands was two thirds that of *Molinia*, with *Eriophorum* and *Calluna* sites fewer again.

There was no significant relationship between the presence of any of the seven main plant species in a site and VSI (GLM controlled for habitat; *M. caerulea* $F = 0.09$, $p = 0.77$, *N. stricta* $F = 0.06$, $p = 0.81$, *D. flexuosa* $F = 0.15$, $p = 0.70$, *E. vaginatum*, $F = 0.92$, $p = 0.36$, *C. vulgaris* $F = 0.21$, $p = 0.66$, *V. myrtillus* $F = 1.15$, $p = 0.31$, *E.nigrum* $F = 1.63$, $p = 0.23$). Mean depth of cover at each site was compared to VSI, controlling for habitat and again no significant relationship was found (GLM, $n = 48$, $F = 0.94$, $p = 0.35$).

There were significantly more field signs in summer than in winter in all habitats (Fig. 2, ANOVA, $n = 16$, $F = 7.68$ $p < 0.01$), though the interaction term was not significant ($p = 0.53$). Thus, while winter VSI was significantly and substantially lower than in summer, the order of habitat preference was essentially the same.

3.2 Effect of sheep grazing

VSI showed a significant negative relationship with numbers of sheep seen when all habitats were combined (Fig. 3; GLM controlled for habitat, $n = 28$, $R^2 = 0.75$, $F = 20.150$, $p < 0.01$). The habitats individually did not show the same trends: *Molinia* sites had a significant negative relationship ($n = 9$, $F = 8.53$, $p = 0.02$), *Eriophorum* and *Nardus* approached significance at the 5% level ($n = 5$, $F = 9.70$, $p = 0.05$ and $n = 8$, $F = 4.60$, $p = 0.08$ respectively), but *Calluna* sites showed no significant relationship ($n = 6$, $F = 0.99$, $p = 0.38$).

Depth of cover was significantly greater in ungrazed than grazed areas (Table 1, two way ANOVA, $n = 16$, $F = 2.76$, $p = 0.04$) though there was no significant interaction

between grazing and habitat ($F = 0.40$, $p = 0.75$); i.e. grazing does not affect cover depth differently in different habitats.

There were highly significant differences between VSI in grazed and ungrazed sites for each habitat (Table 1; two way ANOVA controlled for Habitat, $F = 8.83$, $p = 0.01$). The most marked difference was in *Eriophorum* sites, where grazing reduced VSI by almost 90%. VSI decreased with grazing in *Molinia* sites by roughly 66%, in *Nardus* sites by 75% and in *Calluna* sites by over 70%.

There was no significant difference between the arcsine-transformed percentages cover of five of the seven common plant species inside and outside exclosures (Table 2). However *E. nigrum* was significantly more prevalent outside exclosures (paired sample t-test $n = 16$, $t = 2.11$, $p < 0.01$) and *D. flexuosa* ($n = 16$, $t = 3.50$, $p = 0.01$) was significantly more prevalent inside exclosures. There were increases in minor constituents of habitats between grazed and ungrazed sites. Those that are likely to be of importance to field voles are *Festuca ovina* and particularly *Agrostis spp.*, which have been shown to be favoured in the diet (Hansson, 1971; Wheeler, 2002, 2005). There was a significant overall increase in *Agrostis spp.* in ungrazed, compared to grazed, sites ($F = 6.62$, $p = 0.01$) but no significant increase in *F. ovina* ($F = 1.88$, $p = 0.18$).

3.3 Vole and vole predator population size

Differences in VSI were converted to vole population density using the equation relating LTI to VSI above. Pre-breeding population densities in each of the four habitats studied were calculated and used to estimate vole population size in the North Peak area under current grazing levels ('grazed') and a removal of grazing ('ungrazed'; Table 2). The estimated size of the field vole population of the North Peak ESA in the absence of grazing (412,300) is almost double the 216,000 voles estimated currently. The greatest contribution to this increase (43%) is from *Nardus*-dominated areas despite covering

only 20% of the North Peak while *Eriophorum*, *Calluna* and *Molinia*-dominated areas cover 37%, 35% and 8% of the land area respectively but contribute only 20%, 21% and 16% of the increase in field vole population.

The size of predator population that could be supported by this number of field voles was calculated (Table 3). The estimates of numbers of predators in the grazed North Peak ESA are remarkably close to the current population sizes for species for which estimates are available. There are regularly six or seven pairs of short-eared owls in the area (Brown and Shepherd, 1991; Sheffield Bird Study Group, 1985); the population of long-eared owls is about eight pairs (Sheffield Bird Study Group, 1985); populations of around 300 kestrels and 30 barn owls are estimated from maps in Gibbons *et al.* (1993).

4. Discussion

Sign indices have been used several times in the past to estimate field vole density, though techniques have varied substantially (Hansson, 1979; Redpath et al., 1995; Tapper, 1979; Village and Myhill, 1990). The most similar in technique and results to the method used here was the method of Lambin et al. (2000), also based solely on fresh grass clippings.

The two habitats (*Molinia* and *Nardus*) that supported the largest numbers of voles were those dominated by grasses, and the habitat (*Molinia*) that supported most voles had more of the grass species preferred in upland vole diet (Wheeler, 2005). However, no clear relationship was observed between the percentage cover of any of the main plant species and VSI. Vole habitat preference therefore, if based on food availability, appears to be at the broad habitat, not microhabitat, scale.

4.1 Effect of sheep grazing

Vole density in all habitats was much lower in the grazed majority of the North Peak, than in the exclosures studied. This is in broad agreement with the results of Evans et al. (2006) who demonstrate that increasing grazing levels in grasslands decreases field vole abundance. Moreover, this study demonstrates that grazing affects the four habitats studied differently and vole populations in grazed *Eriophorum* areas are considerably more depleted than in other habitats. *Nardus*-dominated grasslands in ungrazed sites have sign densities that are as high as in ungrazed *Molinia* sites. The effect of sheep grazing on habitat suitability for field voles must therefore be greater for *Nardus* and *Eriophorum* sites than *Molinia*. *Calluna* sites support few voles whether there are many or few sheep, implying either that they are inherently very poor field vole habitat, or that the presence of even a small number of sheep can degrade this habitat sufficiently to make it unsuitable for voles. Of the seven main plant species, the

only one that was significantly more prevalent inside exclosures was *D. flexuosa*, which has also been shown to be the preferred food of voles from British uplands in feeding trials and in the wild (Wheeler, 2005). However, there was no significant correlation between cover of *D. flexuosa* and VSI. An increase in *D. flexuosa* cover may be representative of a general increase in grass density and hence quality of cover as well as food.

There are major differences in abundances of field voles across the four habitat types studied here, but the magnitude of these differences is more than matched by that of differences between grazed and ungrazed sites. Sheep grazing in the North Peak therefore has as significant an effect on field vole distribution as differences in habitat types across the area. Consequently simple habitat improvement will be as effective as habitat modification in boosting vole numbers.

The key conservation implications of this study relate to field vole predators, particularly avian species, many of which are rare or threatened. Even if suitable nesting habitat for predators is present, it may support insufficient field voles to sustain a predator population. The habitat that contributes most to the increase in field vole numbers across the ESA (and hence to the potential for increase in predators) is *Nardus*-dominated grassland since this habitat supports large numbers of voles when not grazed and has a relatively high ratio of winter to summer vole density. Extensifying grazing on *Nardus* grasslands in the North Peak ESA therefore would appear to be key to boosting field vole numbers.

Estimates of predator populations in the North Peak ESA show that reducing grazing would double population sizes of key species such as the short-eared and long-eared owls (*Asio flammeus* and *A. otus*). There would also be significant increases in more common bird species such as kestrels and mammals such as stoats and weasels

that have undergone declines over recent decades (Gibbons et al., 1993; Harris et al., 1995). Low vole densities in the North Peak may explain why there is only one recent breeding record of the hen harrier, *Circus cyaneus* a species that selects moorland nesting sites in areas of high field vole density (Redpath et al., 2002), despite the presence of over 135 km² of apparently suitable heather moorland. Removing sheep from moorland is beneficial to much biodiversity (Anderson and Yalden, 1981; Dennis, 2003; Fuller and Gough, 1999; Hewson, 1982; Hill et al., 1992) and so promoting suitable vole habitat by reducing grazing ought to satisfy a range of conservation concerns. However, an increase in predator numbers would potentially cause declines in other species, particularly ground-nesting birds.

If upland habitats are to be managed to promote the conservation of vole predators, the effects of sheep grazing on field voles must be taken into account. Certainly removing sheep from moorland or reducing their numbers will increase vole densities and boost predator numbers.

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References

- Anderson, P., Tallis, J.H., Yalden, D.W., 1997. Restoring Moorlands. The Moorland Management Project Phase 3 Report, Bakewell, Derbyshire.
- Anderson, P., Yalden, D.W., 1981. Increased sheep numbers and the loss of heather moorland in the Peak District, England. *Biological Conservation*. 30, 195-213.
- Brown, A.F., Shepherd, K.B., 1991. Breeding Birds of the South Pennine Moors. Rep. No. 7. Joint Nature Conservancy Committee, Peterborough.
- Chitty, D., Kempson, D.A., 1949. Prebaiting small mammals and a new design of live trap. *Ecology*. 30, 536-542.
- Clarke, J.L., Welch, D., Gordon, I.J., 1995. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. *Journal of Applied Ecology*. 32, 166-176.
- Dennis, P., 2003. Sensitivity of upland arthropod diversity to livestock grazing, vegetation structure and landform. *Food, Agriculture and Environment*. 1, 301-307.
- Dyczkowski, J., Yalden, D.W., 1998. An estimate of the impact of predators on the British Field Vole (*Microtus agrestis*) population. *Mammal Review*. 28, 165-184.
- Evans, D.M., Redpath, S.M., Elston, D.A., Evans, S.A., Mitchell, R.J., Dennis, P., 2006. To graze or not to graze? Sheep, voles, forestry and nature conservation in the British uplands. *Journal of Animal Ecology*. 43, 499-505.
- Fuller, R.J., Gough, S.J., 1999. Changes in sheep numbers in Britain: implications for bird populations. *Biological Conservation*. 91, 73-89.
- Gibbons, D.W., Reid, J.B., Chapman, R.A., 1993. The New Atlas of Breeding Birds in Britain and Ireland: 1988-91. T&AD Poyser, London.

- Gurnell, J., Flowerdew, J.R., 1982. Live Trapping Small Mammals The Mammal Society, Reading.
- Hansson, L., 1971. Habitat, food and population dynamics of the field vole *Microtus agrestis* in south Sweden. *Viltrevy*. 8, 267-378.
- Hansson, L., 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. *Oikos*. 29, 539-544.
- Hansson, L., 1979. Field signs as indicators of vole abundance. *Journal of Applied Ecology*. 16, 339-347.
- Hansson, L., 1997. Population growth and habitat distribution in cyclic small rodents: to expand or to change? *Oecologia*. 112, 345-350.
- Harris, S., Morris, P., Wray, S., Yalden, D., 1995. A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans. JNCC, Peterborough.
- Hewson, R., 1982. The effect upon field vole (*Microtus agrestis*) habitat of removing sheep from moorland in west Scotland. *Journal of Zoology*. London. 197, 304-307.
- Hill, M.O., Evans, D.F., Bell, S.A., 1992. Long-term effects of excluding sheep from hill pastures in north Wales. *Journal of Ecology*. 80, 1-13.
- Kendall, W.L., 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology*. 80, 2517-2525.
- Lin, Y.-T.K., Batzli, G.O., 2001. The influence of habitat quality on dispersal, demography and population dynamics of voles. *Ecological Monographs*. 71, 245-275.
- Love, R.A., Webbon, C., Glue, D.E., Harris, S., 2000. Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997. *Mammal Review*. 30, 107-129.

- Petty, S.J., Fawkes, W.L., 1997. Clutch size variation in tawny owls (*Strix aluco*) from adjacent valley systems: can this be used as a surrogate to investigate temporal and spatial variations in vole density. In *Biology and Conservation of Owls of the Northern Hemisphere* (eds J.R. Duncan, D.H. Johnson, T.H. Nicholls), pp. 315-324. USDA Forest Service, North Central Forest Research Station.
- Redpath, C.J., Thirgood, S.J., Redpath, S.M., 1995. Evaluation of methods to estimate field vole *Microtus agrestis* abundance in upland habitats. *Journal of Zoology*. London. 237, 49-55.
- Redpath, S.M., Thirgood, S.J., Clarke, R., 2002. Field Vole *Microtus agrestis* abundance and Hen Harrier *Circus cyaneus* diet and breeding in Scotland. *Ibis*. 144, E33-E38.
- Sheffield Bird Study Group, 1985. *Birds of the Sheffield Area Including the North-East Peak District Sheffield City Libraries*, Sheffield.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry : The Principles and Practice of Statistics in Biological Research*. 3 edn. W.H. Freeman, New York.
- Steen, H., Mysterud, A., Austrheim, G., 2005. Sheep grazing and rodent populations: evidence of negative interactions from a landscape scale experiment. *Oecologia*. 143, 347-364.
- Stewart, K.E.J., Bourn, N.A.D., Thomas, J.A., 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology*. 38, 1148-1154.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P., Hanski, I., 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*. 73, 167-178.

- Tapper, S., 1979. The effect of fluctuating vole numbers on a population of weasels on farmland. *Journal of Animal Ecology*. 48, 603-617.
- Thirgood, S.J., Redpath, S.M., Graham, I.M., 2003. What determines the foraging distribution of raptors on heather moorland? *Oikos*. 100, 15-24.
- Village, A., 1982. The home range and density of kestrels in relation to vole abundance. *Journal of Animal Ecology*. 51, 413-428.
- Village, A., 1987. Numbers, territory size and turnover of short-eared owls *Asio flammeus* in relation to vole abundance. *Ornis Scandinavica*. 18, 198-204.
- Village, A., Myhill, D., 1990. Estimating small mammal abundance for predator studies: snap-trapping versus sign indices. *Journal of Zoology, London*. 222, 681-689.
- Wheeler, P.M., 2002. *The Distribution of Mammals Across the Upland Landscape*. PhD, University of Manchester, Manchester.
- Wheeler, P.M., 2005. The diet of field voles at low population density in upland Britain. *Acta Theriologica*. 50, 483-492.

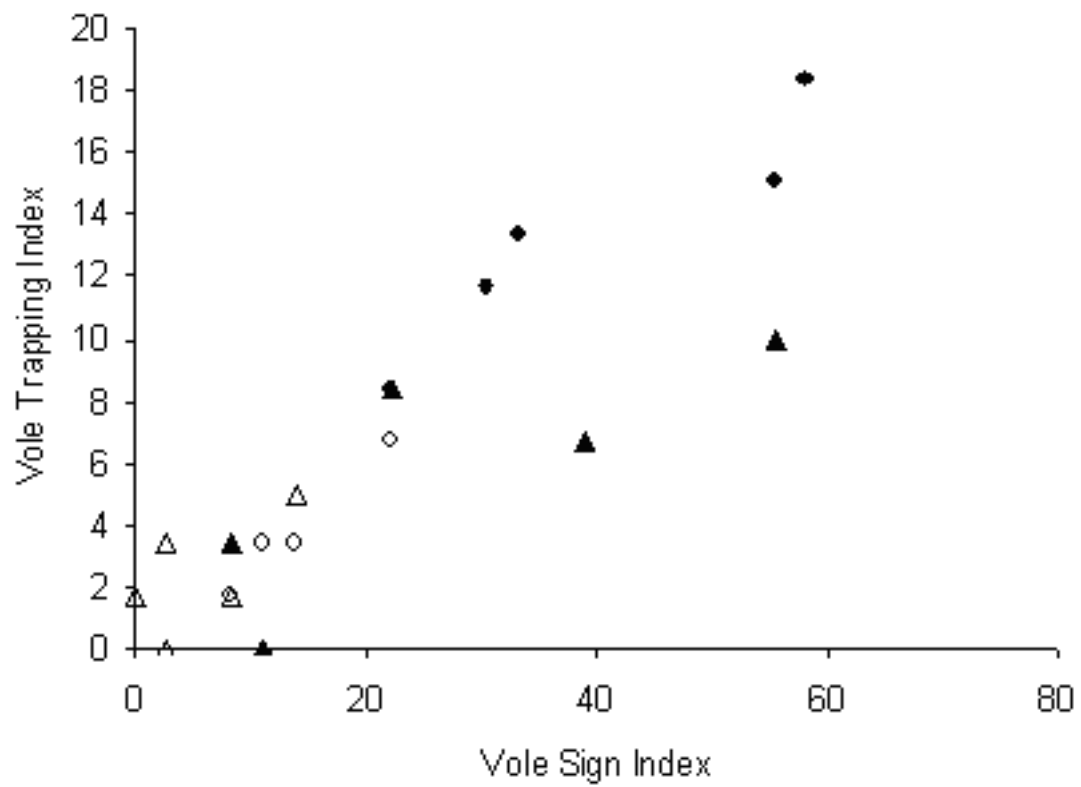


Figure 1. Relationship between Vole Sign Index (VSI) based on fresh clippings and Vole Trapping Index across four habitats, $R^2 = 0.71$, $p < 0.001$. *Molinia* closed circles, *Eriophorum* open circles, *Nardus* closed triangles, *Calluna* open triangles.

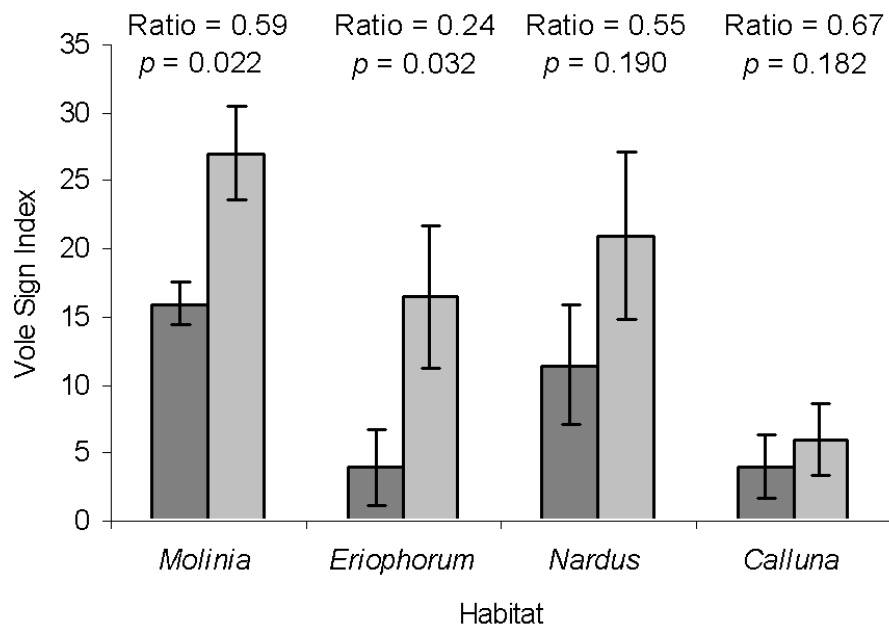


Figure 2. Mean vole sign index (\pm SE) and ratio of winter : summer VSI at sites surveyed in winter (dark grey) and summer (light grey). P values are paired sample t -test $n = 4$ pairs in each habitat.

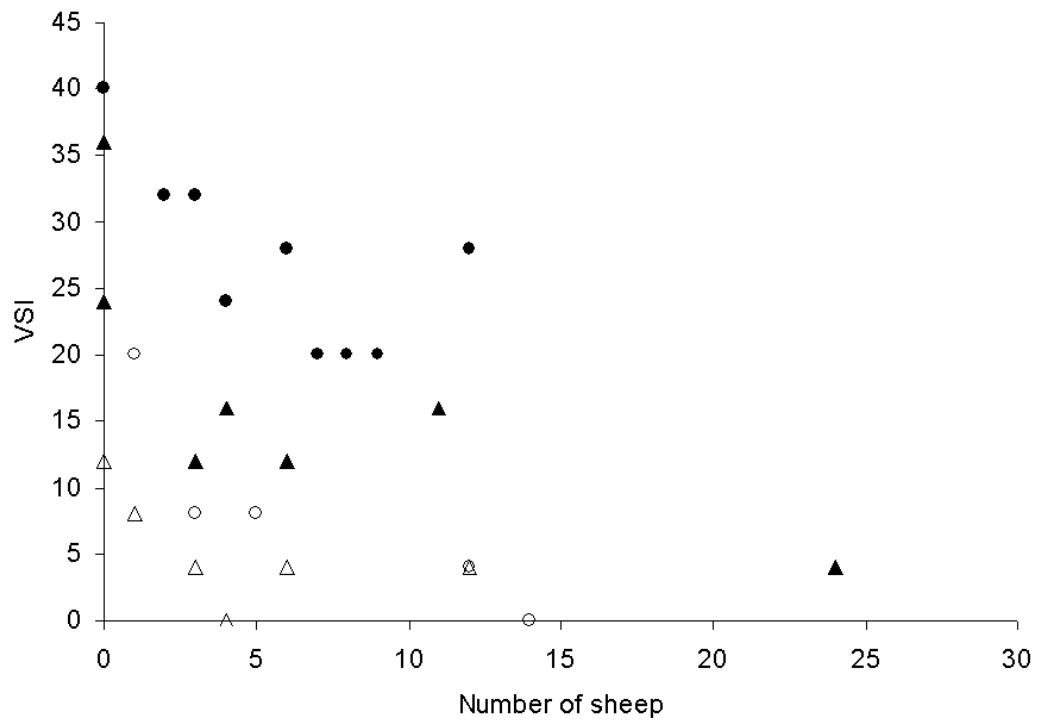


Figure 3. Decline in vole sign index (VSI) with increasing numbers of sheep seen on a 500m transect adjacent to the survey site. Symbols as in Fig. 1.

Table 1. Mean (SE) depth of cover and vole sign index (VSI) inside (ungrazed) and outside (grazed) exclosures in four main habitats in the North Peak ESA. Percentage change shows the decrease in each measure with grazing. Based on 20 pairs of sites in each habitat type.

Habitat	Cover Depth(cm)			VSI		
	Ungrazed	Grazed	% Change	Ungrazed	Grazed	% Change
<i>Molinia</i>	28 (3.6)	27 (2.6)	3.6	71 (2.5)	23 (1.9)	67.6
<i>Eriophorum</i>	23 (1.6)	18 (3.5)	21.7	42 (3.5)	5 (1.9)	88.1
<i>Nardus</i>	26 (3.5)	18 (1.9)	30.8	71 (2.5)	18 (6.6)	74.6
<i>Calluna</i>	31 (5.8)	26 (1.9)	16.1	18 (2.0)	5 (1.9)	72.2

Table 2. Extent of habitats in the North Peak ESA and associated field vole pre-breeding population densities (\pm standard error) and sizes under scenarios of widespread sheep grazing ('Grazed') and the removal of sheep grazing ('Ungrazed').

Habitat	Extent (ha)	Vole density ha ⁻¹		Vole population size (1000s of voles)		
		Ungrazed	Grazed	Ungrazed	Grazed	Change
<i>Molinia</i>	3220	19.8 (\pm 2.5)	10.2 (\pm 1.9)	63.9	32.8	31.1
<i>Eriophorum</i>	14309	5.5 (\pm 3.4)	2.7 (\pm 2.4)	78.8	38.9	39.9
<i>Nardus</i>	7869	18.3 (\pm 2.5)	7.7 (\pm 2.9)	144.2	60.3	83.9
<i>Calluna</i>	13561	9.2 (\pm 2.0)	6.2 (\pm 1.2)	125.3	84.0	41.3
TOTAL		13.3 (\pm 2.6)	6.6 (\pm 2.1)	412.3	216.0	196.3

Table 3. Estimated predator population (\pm 95% confidence interval) of North Peak ESA (total area = 390 km²) based on estimated field vole consumption. Annual consumption calculated from Dyczkowski & Yalden (1998).

Species	Annual vole consumption per individual	Number of predators	
		Grazed	Ungrazed
Fox	599	737 (\pm 235)	1407 (\pm 306)
Stoat	94	1561 (\pm 498)	2980 (\pm 648)
Weasel	476	1510 (\pm 482)	2882 (\pm 626)
Kestrel	2389	335 (\pm 107)	640 (\pm 139)
Barn owl	728	34 (\pm 11)	65 (\pm 14)
Little owl	871	60 (\pm 19)	115 (\pm 25)
Tawny owl	147	407 (\pm 130)	777 (\pm 169)
Long-eared owl	714	17 (\pm 6)	33 (\pm 7)
Short-eared owl	934	16 (\pm 5)	31 (\pm 7)