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Factors influencing molehill distribution in grassland: implications for controlling the damage caused by molehills

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Summary

1. Moles are perceived as pests of farms, gardens, sports fields and nature reserves, mainly because they form molehills. The danger and inhumaneness of current methods of mole control (e.g. poisoning with strychnine or the use of mole traps) means that non-lethal methods are sought. We examined the possibility of controlling molehill distribution by using management procedures that alter the availability of earthworms, the principal food of moles.
2. The abundance of molehills and earthworms was monitored over 2 years in an acid grassland where pesticide (with and without insecticides and molluscicides), grazing (continuous grazing by rabbits vs. hay meadow), soil pH (with and without lime), herbicide (with and without herb- and grass-specific herbicides) and fertilizer (N, P, K, Mg) treatments were imposed.
3. In the experimental area of 4608 m^2, a total of 1062 molehills formed, each with an average area of 0·14 m^2; a disturbance rate equivalent to 3·2% of the soil surface over 2 years. Peak molehill production occurred in spring and autumn, with few molehills formed at other times of the year.
4. Molehill production in grazed areas was one-third that of hay meadows. Half as many molehills formed in unlimed as limed plots. Significantly fewer molehills formed in areas where grass species were removed (herb-rich) than areas where no species were removed. Insecticide, molluscicide and fertilizer application had no significant effect on molehill production.
5. The treatments that had fewer molehills also had less earthworms, indicating that molehill production was decreased, indirectly, through the treatments reducing food availability.
6. Reducing the number of molehills through management procedures that decrease earthworm availability offers an alternative to lethal control of moles. This could be achieved by allowing (or encouraging) soil pH to fall (e.g. withholding lime application; through the use of acidifying nitrogen-fertilizers), by creating herb-rich swards or by preventing plant biomass from accumulating for long periods. These methods will be more applicable to gardens, sports fields and nature reserves than to farms, where conflicts with normal farming practices would make them difficult to implement.

Key-words: earthworm, grazing, mole, plant removal, soil pH.

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Introduction

European moles *Talpa europaea* L. are perceived as pests of farms, gardens, sports fields and nature reserves mainly due to them forming molehills during the development of a network of tunnels in which they feed, breed and live (Stone 1989; Atkinson, Macdonald & Johnson 1994). Molehills are viewed as aesthetically unattractive, act as sites for weed invasions (e.g. *Cirsium* sp., Davies 1966; Jalloq 1975; Goszczynska & Goszczynski 1977), cause soil contamination of hay and silage crops (Thomas 1966;

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Atkinson, Macdonald & Johnson 1994) and damage farm machinery. As an indication of the perceived pest status of moles, a recent survey of farmers reported that almost half of the respondents undertook some form of mole control (Atkinson, Macdonald & Johnson 1994).

Most mole control in Britain involves poisoning them with strychnine or killing them in mole traps. However, these lethal methods are viewed as environmentally dangerous and inhumane (discussed in Atkinson, Macdonald & Johnson 1994), and non-lethal methods are sought. One possible non-lethal method is to use repellents to exclude moles from particular areas (Gorman & Stone 1989; Atkinson & Macdonald 1994). A further possibility is to control the distribution of moles, and the extent to which they form molehills, via habitat manipulation. Some researchers have suggested that this may be possible by manipulating the abundance of the principal food source of moles, earthworms (Shilova *et al.* 1971; Schaefer 1981). However, it is not clear how the distribution of molehills will respond to differences in food supply. For example, Atkinson, Macdonald & Johnson (1994) point out that moles in areas of high food availability may be inconspicuous as a stable tunnel system would give rise to adequate food. Molehills might be a greater problem where food is scarce, as moles need to produce new tunnels continually to gain access to adequate food.

In this paper, we examine how molehill distribution might be manipulated by grassland management procedures that alter the distribution and abundance of earthworms. Molehill distribution and earthworm abundance were measured in acid grassland where pesticide (with and without insecticides and molluscicides), grazing management (continuous grazing vs. hay meadow), soil pH (with and without lime), herbicide (with and without herb- and grass-specific herbicides) and fertilizer (N, P, K, Mg) treatments were imposed. Previous studies have shown that these treatments can impact on earthworm populations (Edwards & Lofty 1972) but in few cases do we know whether they also affect mole activity (Ennik 1967; Schaefer 1981). We use our results to point out that many of the current management procedures of grasslands may in fact be encouraging molehill production, and discuss whether and where habitat manipulation is a feasible method of controlling the distribution of molehills.

Methods

STUDY SITE

The study of molehill disturbance was carried out in a long-term field experiment in Nash's Field, Silwood Park, Berkshire, UK (National Grid reference 41/944691). Nash's Field is 6-ha species-poor grassland on acid sandy soil, with a long history of rabbit *Oryctolagus cuniculus* L. grazing (National Vegetation Classification: acidic variant of MG6; Rodwell 1992). The grassland was dominated by the grasses *Agrostis capillaris*, *Anthoxanthum odouratum*, *Festuca rubra* and *Holcus mollis* and the herbs *Galium saxatile* and *Rumex acetosella* (nomenclature follows Stace 1997). The field was surrounded by oak *Quercus robur* and birch *Betula pendula* woodlands and a bracken *Pteridium aquilinum* stand. Nash's Field experiences an average annual rainfall of 653 mm, with little seasonal pattern. Soil tests taken from Nash's Field at the start of the experiment showed soil pH in $H_2O = 4{\cdot}9$, bicarbonate phosphorus (P) $= 5{\cdot}6\ \text{mg kg}^{-1}$, potassium (K) $= 88\ \text{mg kg}^{-1}$, calcium (Ca) $= 638\ \text{mg kg}^{-1}$, magnesium (Mg) $= 37{\cdot}5\ \text{mg kg}^{-1}$ and sodium (Na) $= 8{\cdot}6\ \text{mg kg}^{-1}$.

TREATMENTS

The experiment, which began in 1991, was a six-factor factorial replicated in two blocks using a split-plot design. The experimental treatments were insect and mollusc herbivory (whole plots), vertebrate herbivory (subplots), lime application (sub-subplots), interspecific plant competition (sub-sub-subplots) and fertilizer application (sub-sub-sub-subplots). One block was laid out in what was judged to be a moist area of the field (downslope) and one in a slightly drier (upslope) area. Each block contained four whole plots, each 22×44 m, which were separated from each other by at least 10 m (Fig. 1).

Invertebrate herbivory was manipulated by a factorial combination of chemical pesticides (with and without insecticide sprays, with and without molluscicide pellets, $2 \times 2 = 4$ treatments) applied to the four whole plots in each block. Insects were suppressed by applying a combination of knockdown (Ambush, Zeneca, Haslemere, Surrey, GU27 3JE, UK, cypermethrin synthetic pyrethroid at 150 g active ingredient ha^{-1}) and systemic (Dimethoate 40, Atlas Interlades, Low Moor, Bradford, BD12 0JZ, UK; dimethoate at 336 g active ingredient ha^{-1}) insecticides as foliar sprays. Molluscs were suppressed by applying pellets of metaldehyde (Mifaslug, Farmers Crop Chemicals Ltd, Inkberrow, Worcs., WR7 4LJ, UK) at 960 g active ingredient ha^{-1}. In each year from 1991 to 1997, all pesticides were applied three times during the spring–summer period in April, May and June.

Vertebrate herbivory was manipulated by erecting fences around one half (plot size 22×22 m) of each invertebrate herbivory whole plot in June 1991, giving eight fenced and eight grazed plots. The fences were 1 m high and were constructed of 3-cm square wire-mesh supported by posts every 4 m. The wire was buried 5 cm deep with the bottom 15 cm turned outwards. The fences excluded rabbits but not larger vertebrates like roe deer *Capreolus capreolus* L., which could easily jump the fences. The fenced plots were treated as a hay meadow with a single hay cut being

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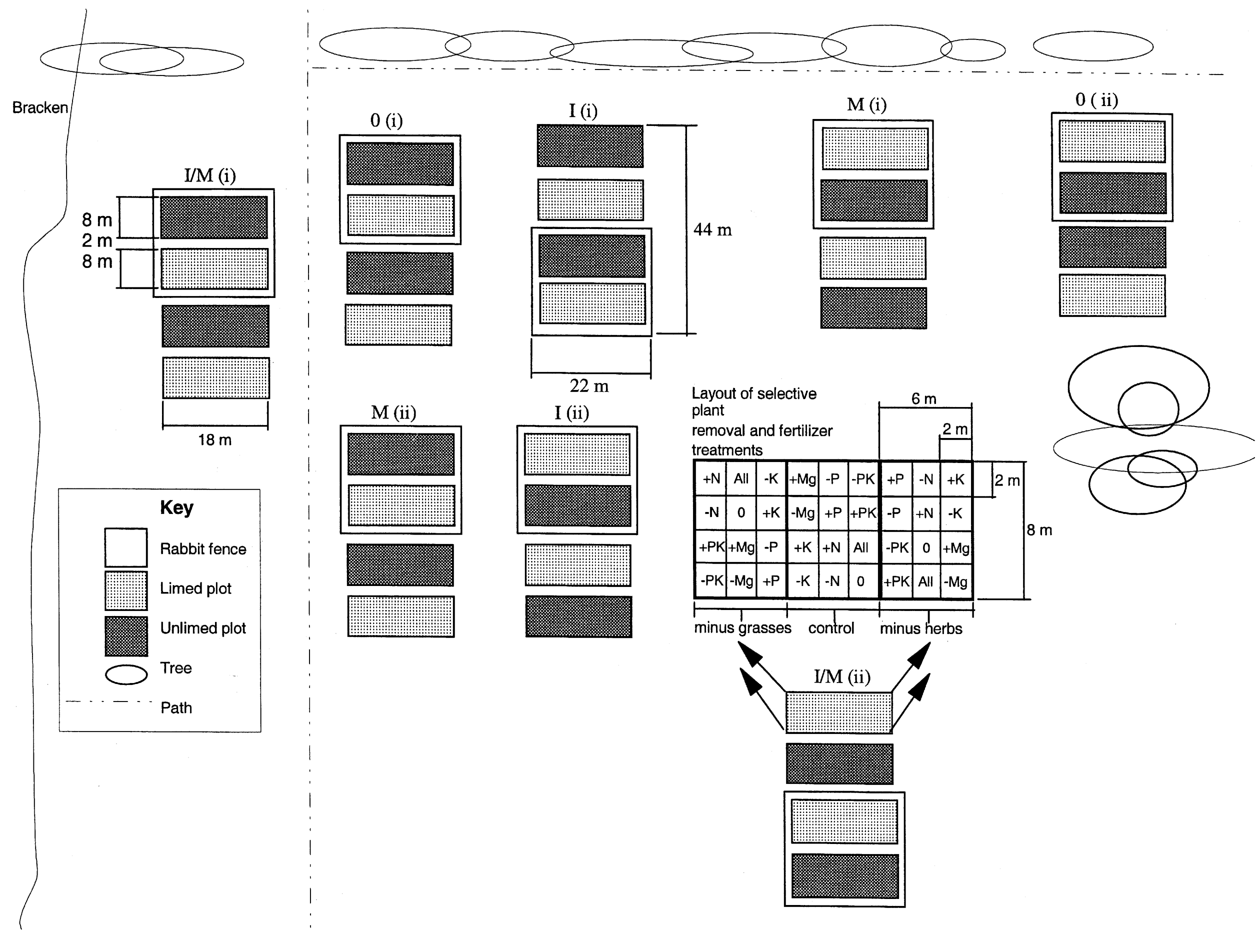

Fig. 1. Plan of the experimental layout in Nash's Field. Two blocks (i = upslope; ii = downslope) were laid out in summer 1991. Each block contained four large plots (44 × 22 m) to which insect-exclusion and mollusc-exclusion treatments were allocated at random in a two-factor factorial design (I = insecticide applied, M = molluscicide applied, 0 = neither insecticide or molluscicide applied). Half of each large plot was fenced against rabbits, the other half was grazed. Within each rabbit treatment, the plots were split and half (18 × 8 m) were limed. The lime plots were each split into three herbicide treatment plots (8 × 6 m) and treated with selective herbicides (minus-grass or minus-herb) or left as a control. Each herbicide plot was divided into 12 nutrient addition plots (2 × 2 m) in three columns of four plots. The total experimental area was 4608 m^2.

taken at a height of 10 cm above the soil surface in late August each year. The cut herbage was raked and removed to prevent dead matter accumulating. The only management of the grazed plots was the removal of tree saplings (mainly *B. pendula* and *Q. robur*) in April each year as necessary. This meant that fluctuations in rabbit numbers and grass production led to variation in the carryover of standing live and dead organic matter at the end of winter on the grazed unfenced plots, but not on the mown fenced plots. In general, standing biomass in summer was substantially higher on fenced plots (g dry matter m^{-2} 1995: grazed = 128, fenced = 380; 1996: grazed = 291, fenced = 463). In the remainder of the paper, plots grazed by rabbits will be termed 'grazed' and those fenced against rabbits termed 'fenced'.

Soil pH was manipulated by applying lime (CaO) at 20 t ha^{-1} to one 8 × 18-m plot in each fenced and each grazed plot in autumn 1991 and again in autumn 1994. One further 8 × 18-m plot was left unlimed in each grazed and fenced plot. There was a 2-m guard strip around the outside of each plot and a 2-m gap between the limed and unlimed plots. Soil pH in summer 1997, 3 years after lime application, was 7·0 on limed plots and 4·4 on unlimed plots.

Three plant competition treatments were assigned to three contiguous 6 × 8-m plots within each limed and unlimed plot: (i)'control' = intact grassland; (ii) 'minus-herb herbicided' = herbs removed with selective herbicide (dicamba + MCPA + mecoprop, 260, 2080, 4160 g active ingredient ha^{-1}, respectively; Pasturol, Inkberrow, Worcs., WR7 4LJ, UK); (iii) 'minus-grass herbicided' = grasses removed with selective herbicide (sethoxydim, 870 g active ingredient ha^{-1}; Checkmate, Rhone Poulenc Agriculture Ltd, Essex, CM5 0HW, UK).

The herbicides were applied in late April each year from 1992 to 1994 inclusive. These treatments created marked differences in the proportion of grasses and herbs. In summer 1994, a year after the herbicides were applied, the proportion of the above-ground biomass comprised of grasses was 85%, 98% and 61% for the control, minus-herb and minus-grass plots, respectively (the remainder was herbs). The minus-grass plots still contained significant quantities of grass as *Festuca rubra* appeared to be resistant to the herbicide.

Soil fertility was manipulated by applying nitrogen (N), phosphorus (P), potassium (K) and magnesium (Mg) fertilizers to 12 2 × 2-m subplots arranged in a 3 × 4 grid in each plant competition plot. These fertilizer plots were made up of four plots where each nutrient was applied singly (+N, +K, +P, +Mg), four plots where all but one nutrient were applied (+PKMg [−N], +NKMg [−P], +PNMg [−K], +PNK [−Mg]), one plot where P and K were applied together (+PK), one plot where all but P and K were applied (+NMg [−PK]), one plot where all nutrients were applied (+PKNMg) and one plot where no nutrients were applied. N was applied as ammonium nitrate, P as triple super phosphate, K as potassium muriate and Mg as magnesium sulphate during the first week in April of each year. The rates of application were: N at 150 kg ha^{-1}, P at 35 kg ha^{-1}, K at 225 kg ha^{-1} and Mg at 11 kg ha^{-1}. Fertilizer treatments were applied in pairs to adjacent plots, with each pair allocated at random, independently for each competition plot. The pairs of nutrient treatments were applied as follows: +N and +PKMg, +K and +NPMg, +P and +NKMg, +Mg and +NPK, +PK and +NMg, all and none. The rationale for applying the nutrients in pairs, rather than in a fully randomized design, was twofold: to minimize the risk of applying nutrients to the wrong plot, and to give an immediate visual impression of the role of each nutrient in adjacent plots.

This experimental design gave 1152 plots in all: eight invertebrate herbivory plots, 16 rabbit grazing plots, 32 lime plots and 96 competition plots, each containing 12 2 × 2-m fertilizer plots. The total area covered by the 2 × 2-m fertilizer plots was 4608 m^2.

SURVEY OF MOLEHILLS

Molehills were counted as a measure of mole activity and no attempt was made to census mole populations. We considered that it was important to count the molehills, rather than the moles themselves, as the formation of molehills is the primary reason why moles are considered to be pests of grasslands. Molehills were counted every 3 months over a 2-year period from early spring 1995 to early spring 1997. Molehill counts were done in March, June, September and December of 1995 and 1996, and in March of 1997, with the counts being carried out at the end of each month. For the purposes of this paper, we consider that January–March is winter, April–June is spring, July–September is summer and October–December is autumn. On every occasion, molehills were counted in all (1152) of the 2 × 2-m fertilizer plots and the position of each molehill was marked on a map of the quadrat. By overlaying maps from successive dates we were able to determine the creation of new molehills. When recording, particular care was taken in observing whether there were any surface runs (i.e. shallow mole tunnels just below the soil surface that fail to push up any spoil; Mellanby 1971). None was observed during the experiment.

The area of soil disturbed by individual molehills was estimated in late December 1995 and 1996. A 1 × 1-m quadrat was placed over the top of an individual molehill and an outline of the molehill was drawn on paper using a 10 × 10 grid of 0·1-m square cells as a guide. The area of each molehill was then determined by planimetry. Measurements were made for all of the molehills that had formed since the last census (226 molehills for December 1995 and 306 for December 1996).

SURVEY OF EARTHWORM CASTS

We estimated earthworm abundance in order to relate the distribution of molehills to the food supply of moles. Previous studies have shown that earthworms are the major constituent of the diet (Mellanby 1971; Sims & Gerard 1985), although insects (larvae and adults) and vegetable matter are sometimes eaten (vegetable matter perhaps by accident; Mellanby 1971). We used the area of earthworm casts as an indirect measure of earthworm abundance. The area of earthworm casts was assessed in the +Mg and +NPK (i.e. all but Mg) fertilizer plots in late September 1996, the time of peak earthworm cast activity in Nash's Field (G.R. Edwards, unpublished data); earthworm casts were not recorded in the remaining 10 fertilizer plots. A 25 × 25-cm quadrat was placed in the centre of each plot and the area covered by earthworm casts was traced onto a sheet of paper using a 5 × 5 grid of 5-cm square cells as a guide. The area of earthworm casts was then determined by planimetry.

To assess whether or not the area of earthworm casts was a reliable estimate of earthworm abundance, we examined the relationship between earthworm cast area and earthworm mass in September 1996. In the grassland surrounding the experimental plots, the area of earthworm casts was recorded in 45 randomly placed 25 × 25-cm quadrats. The soil in each quadrat was excavated with a spade to a depth of 30 cm and any earthworms present were collected (mainly *Allolobophora longa* Ude and *Lumbricus terrestris* L.), washed, dried on filter paper and weighed. We found a significant positive correlation between the earthworm cast area (m^2 per m^2 ground area) and earthworm mass (g dry weight m^{-2} to depth of 30 cm) [$r = 0{\cdot}8$, $P < 0{\cdot}001$; earthworm mass = $-2{\cdot}4 + 462{\cdot}5$ (area)]. Thus, we were confident that the area of earthworm casts was a reliable estimate of earthworm abundance in Nash's Field, and so a reliable estimate of the food available to moles.

STATISTICAL ANALYSIS

The total number of molehills that formed over the 2-year census period was used as the response variable

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for analysing the effect of treatments on molehill disturbance. The total number of molehills was analysed in the statistical package GLIM (NAG 1985) using log-linear models with Poisson errors and an empirical scale parameter (Crawley 1993). An entirely separate analysis was conducted at each level of the split-plot design using total counts of molehills calculated at the appropriate plot size (e.g. at the insecticide-molluscicide level, analysis was based on eight plots where the number of molehills was summed across the 144 fertilizer plots in each plot: 576 m^2 per plot; see Fig. 2 for plot sizes). There were too few molehills in any one fertilizer plot to allow significance testing, but apparent patterns were noted. The area of earthworm casts was analysed by analysis of variance (ANOVA) of a split-plot design. Following this, analysis of covariance was carried out on the number of molehills, using the average area of earthworm casts for each plot as the covariate.

Results

NUMBER, AREA AND SEASONAL PATTERN OF MOLEHILLS

A total of 1062 molehills formed in the whole experimental area (4608 m^2) during the 2-year census period. Molehills were found in all eight of the whole plots (i.e. insecticide and molluscicide plots) at each census. The mean area covered by individual molehills in December 1995 and 1996 was 0·14 m^2. This is equivalent to 3·2% of the grassland being disturbed by moles over 2 years if a constant area of molehills throughout the year is assumed. The molehills were formed primarily in two periods, one in autumn (October–December) and one in spring (April to June); far fewer molehills formed at other times of the year (Fig. 2).

EFFECTS OF EXPERIMENTAL TREATMENTS ON MOLEHILL PRODUCTION

Fewer molehills formed on grazed than fenced plots ($P < 0{\cdot}01$), on unlimed than limed plots ($P < 0{\cdot}05$) and on plots where grass species were removed compared to plots where herb species were removed or to control plots where no species were removed ($P < 0{\cdot}05$, GLIM with Poisson errors; Fig. 3a). Insecticide and molluscicide application had no significant effects on the number of molehills and no interactions between any treatments were significant ($P > 0{\cdot}1$, GLIM with Poisson errors; Fig. 3a). There was no obvious effect of the N, P, K or Mg fertilizers on the number of molehills that formed, although the small plot size (2 × 2 m) would make detection of any effect difficult (mean number of molehills per 2 × 2-m plot formed over the 2-year period: +N = 0·82, no N = 1·0; +P = 0·87, no P = 0·97; +K = 0·89, no K = 0·94; +Mg = 0·97, no Mg = 0·87).

A clear feature of the grassland surrounding the experimental plots was the rows of molehills that formed immediately adjacent to soil paths used by walkers and occasionally vehicles. In most cases rows of molehills formed alongside one edge of the soil path, and it was rare to find molehills on both sides of the path.

EFFECTS OF TREATMENTS ON EARTHWORM CASTS

The area of earthworm casts in September 1996 was lower on grazed than fenced plots ($F_{1,4} = 12{\cdot}2$, $P < 0{\cdot}05$), on unlimed than limed plots ($F_{1,8} = 10{\cdot}05$, $P < 0{\cdot}01$) and on plots where the grass species were removed compared to plots where herb species were removed or to control plots where no species were removed ($F_{2,32} = 9{\cdot}86$, $P < 0{\cdot}01$; Fig. 3b). Insecticide ($F_{1,3} = 0{\cdot}62$, $P > 0{\cdot}1$), molluscicide ($F_{1,3} = 1{\cdot}16$, $P > 0{\cdot}1$) and fertilizer ($F_{1,48} = 0{\cdot}44$, $P > 0{\cdot}5$) application had no significant effects on the area of earthworm casts (Fig. 3b) and no interactions between any of the treatments were significant.

At each level of the split-plot design there was a significant, positive effect of earthworm cast area on the number of molehills ($P < 0{\cdot}01$, GLIM with Poisson errors; Fig. 4). Analysis of covariance showed that the significant effects of lime application and grass

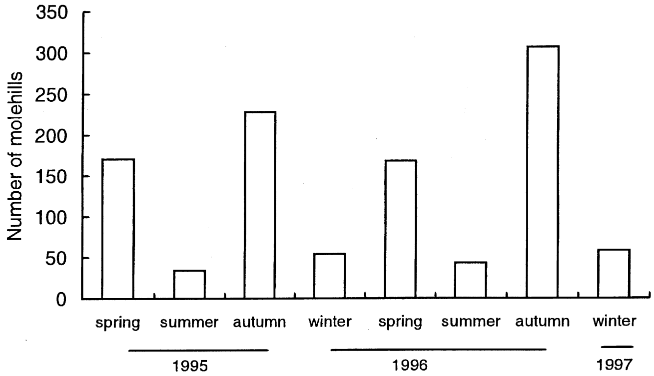

Fig. 2. Seasonal pattern of molehill formation in Nash's Field over 2 years from March 1995 to March 1997. Bars are the total number of molehills formed in 3-month periods in the 4608-m^2 experimental area.

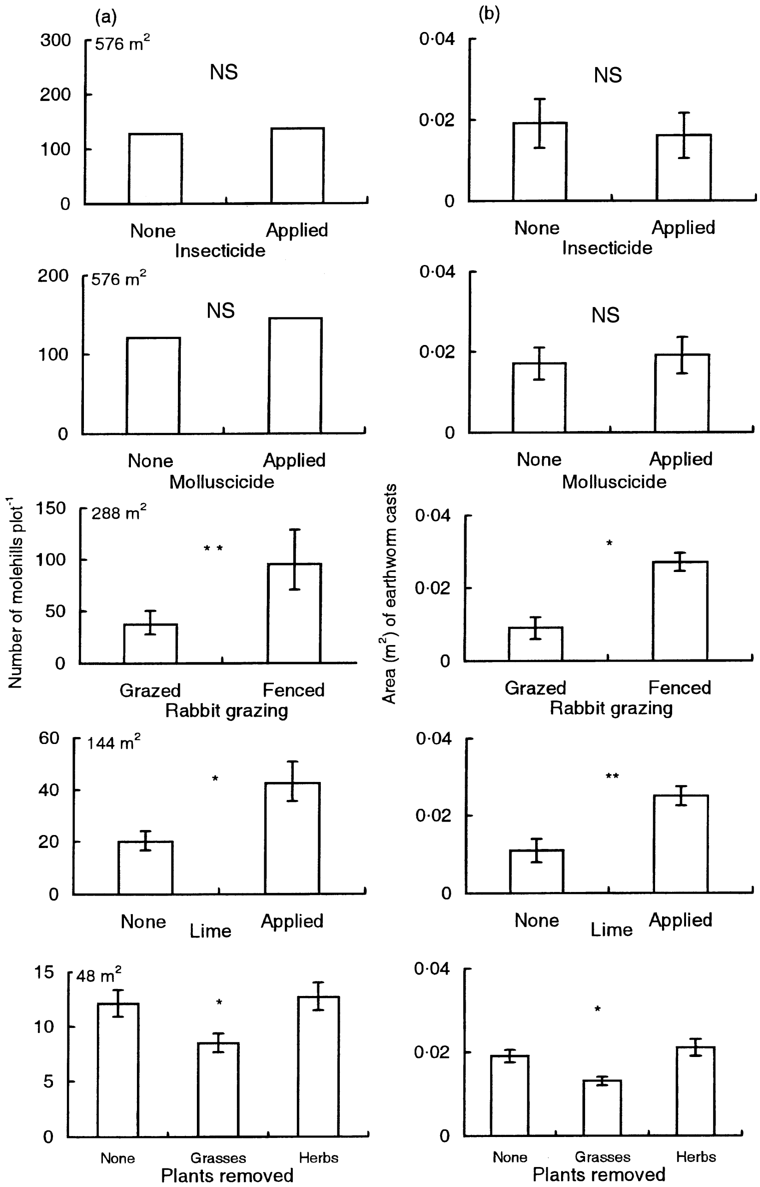

Fig. 3. The main effects of insecticide spray, molluscicide pellets, fencing, lime application and plant species removal on (a) the mean number of molehills formed per plot over 2 years from March 1995 to March 1997 (± SEM, back-transformed from logs) and (b) the mean area (m^2) of earthworm casts per m^2 ground area in September 1996 (± SEM). Note the change in scale of the *y*-axis between treatments for the molehill data; data are presented at the plot sizes at which the statistical analyses were done (shown in the top left of each figure). $*P < 0{\cdot}05$, $**P < 0{\cdot}0$, NS = no significant difference.

removal on the number of molehills became non-significant when earthworm cast area was used as a covariate. The effect of fencing on the number of molehills was still significant when earthworm cast area was used as a covariate ($P < 0{\cdot}05$, GLIM with Poisson errors).

Discussion

SEASONAL PATTERN OF MOLEHILL PRODUCTION

The formation of molehills showed a distinct seasonal pattern, with most damage to the soil surface occurring in autumn and spring. This is consistent with previous reports of the seasonal pattern of molehill formation (Goszczynska & Goszczynski 1977; Stone 1989). The autumn peak probably reflects the need for moles to build new, deeper tunnels, or to re-dig old tunnels, in order to find earthworms that have moved deeper into the soil at the onset of cold weather. The spring peak may reflect the construction of radiating tunnels by males prior to the breeding season in an effort to find females, although these are often surface tunnels (Mellanby 1971; Gorman & Stone 1989) which were not noted in this study.

TREATMENT EFFECTS ON MOLEHILLS

Our study showed that common management procedures of grasslands could markedly affect molehill

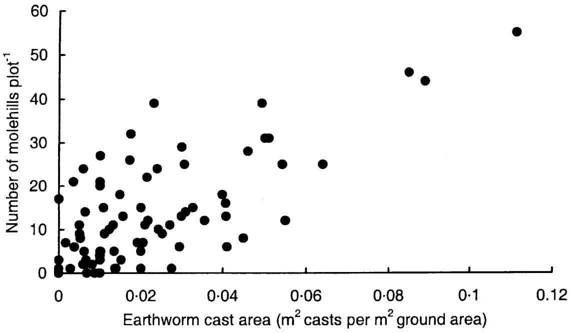

Fig. 4. Relationship between the area of earthworm casts (m^2 per m^2 ground area) and molehill production (molehills formed over 2 years per 48 m^2) at the selective plant-removal level of the split-plot design ($r = 0{\cdot}68$, $P < 0{\cdot}01$, $n = 96$). The area of earthworm casts is averaged across the +Mg and +NPK fertilizer plots in each plant-removal plot. Using the relationship derived between earthworm cast area and earthworm mass, 0·1 m^2 would correspond to an earthworm mass of 2·2 g dry weight m^{-2} and 0·12 m^2–53·1 g dry weight m^{-2} (see text for details).

distribution patterns. There were fewer molehills on unlimed than limed plots, on grazed than fenced plots and on plots where grass species (herb-rich) had been removed than plots where herb species had been removed or there was no species removal. The effect of lime is consistent with previous observational studies that have found significant positive correlations between the number of molehills and soil pH (Funmilayo 1977; Schaefer 1979; Schaefer & Sadleir 1981). The effect of rabbit fencing is in keeping with the observation of more molehills in grassland cut for hay and silage than continuously grazed by cattle (Ennik 1967). It is plausible, however, that the result of Ennik (1967) reflects the preference of moles for cut plots because they have fewer soil vibrations (e.g. no cattle moving) rather than differences in food supply or ease of maintenance of tunnel systems. To our knowledge, no study has previously documented a reduced number of molehills in areas where the species composition is dominated by herb species.

There was evidence from this study to suggest that the reduced number of molehills on unlimed, grazed and minus-grass herbicided plots was due to the indirect effects of these treatments on earthworm abundance. Consistent with previous studies (Funmilayo 1977; Schaefer & Sadleir 1981) we found significant positive correlations between earthworm abundance and molehill number. Moreover, the treatments where earthworms were least abundant also had the fewest molehills (Fig. 3) and the significant effects of liming and herbicide on the number of molehills became non-significant when the area of earthworm casts was used as a covariate. Thus, it appears that molehill production may have been reduced on plots that were grazed, unlimed and treated with grass-specific herbicides because these treatments had reduced earthworm abundance.

It is unclear from this study whether there were more molehills in areas of high earthworm abundance because the density of moles was higher there or because the moles that occupied these areas dug more tunnels. While it has been argued that moles living in areas of high earthworm abundance may dig more because they have more available energy (Schaefer & Sadleir 1981), it has also been argued that moles living in areas of high earthworm abundance may need to dig little, and hence create few molehills, because a stable tunnel system would give rise to adequate food (Atkinson, Macdonald & Johnson 1994). Regardless of the reason, the clear picture that emerged from this study was that the damage caused by molehills was greatest where earthworm abundance was the highest. Thus, there was no evidence from this study to support the idea that molehill damage might be greater on soils having a poorer food supply because more tunnelling is required to find food.

The significant effect of rabbit fencing on the number of molehills remained even when the area of earthworm casts was fitted as a covariate. This suggests that there was an effect causing an increased number of molehills on fenced plots extra to that associated with the increased number of earthworms on fenced plots. The exact nature of this effect is not clear, but it may be due to subtle differences in soil structure between the grazing treatments, which meant that tunnels in the closely grazed areas stayed open longer and required less maintenance than those in fenced areas. Alternatively, it could have been that tunnels were damaged during hay cutting (with a sickle bar mower) and this resulted in moles re-excavating tunnels, thereby producing new molehills.

In contrast to a previous study (Shilova *et al.* 1971), we detected no significant effects of the chemical pesticides (insecticides: dimethoate and pyrethroid; molluscicide: metaldehyde) on the number of molehills. The differing result between the two studies may reflect the effect of the chemicals applied on earthworm abundance. Whereas the insecticides used by Shilova *et al.* (1971) (aldrin, dieldren, chlordane and sevin) killed earthworms, we failed to detect any effect of our pesticides on earthworm abundance. We also did not detect any apparent effect of the different fertilizers on molehill production, although the small fertilizer plot size (2 × 2 m) relative to mole foraging areas would make detecting any effect difficult. Previous studies (Ennik 1967; Schaefer 1981) have pointed out that nitrogen fertilizers could potentially reduce mole digging by causing a reduction in soil pH, and hence earthworm abundance. However, in this study the ammonium nitrate fertilizer did not affect soil pH (mean no fertilizer plots = 5·7, mean +N plots = 5·6), and hence there was little chance for this mechanism to operate.

Our study showed that molehill distribution within the 6-ha area of Nash's Field (experimental area = 4608 m^2) was sensitive to differences in habitat created by experimental treatments down to the fine spatial scale of 48 m^2 (e.g. 6 × 8-m minus-grass herbicided plots). It is likely that these distribution patterns will represent the digging behaviour of a small number of individuals. Mole trapping data show that 10 moles ha^{-1} would be considered a high density in grassland, although figures as high as 45 moles ha^{-1} have been reported (Mellanby 1971). We must therefore be cautious in scaling the results to larger areas and, in particular, to situations where one experimental treatment (e.g. grazed area of low food supply) encompasses the territories of many moles and no alternative areas are available. The question at what spatial scale differences in food supply become important, and how highly territorial animals like moles might compete for different sized areas of high food supply, warrants further investigation.

MOLEHILLS AND SOIL PATHS

A feature of the distribution of molehills in Nash's Field was the rows of molehills that formed along one side of soil paths that were used by walkers and occasionally by vehicles. The reason for this is not clear, but it might reflect an avoidance by the moles of tunnelling under the paths, perhaps because the soil there was compacted and difficult to dig in or because there were too many soil vibrations (Ennik 1967). Alternatively, the observed pattern might reflect the fact that the moles dug deeper tunnels beneath the paths (with spoil heaps pushed to one side) which were perhaps used by many moles (e.g. communal tunnels; Mellanby 1971; Stone 1986). This later point, and the observation that moles do leave their tunnels and travel above-ground from site to site (Mellanby 1971; Stone 1986), questions whether localized soil compaction could be used as a means of restricting moles to some areas.

IMPLICATIONS FOR CONTROL OF MOLEHILLS

1. By recognizing that the potential damage caused by moles is restricted to brief periods in autumn and spring, and by directing control measures at this time, it may be possible to minimize the conflict between moles and humans. For example, where there are few molehills, or where the area is small, the soil heaps could simply be removed as they are formed, so minimizing any long-term effects (e.g. weed invasion). This may be particularly useful for isolated cases on farms, for individual householders (e.g. lawns), for sports fields or for small nature reserves, and would reduce the necessity for poisons or traps in such situations.

2. By adopting management procedures that reduce the abundance of earthworms, the number of molehills could be reduced. This could be achieved by preventing biomass from accumulating for long periods, by allowing (or encouraging) soil pH to fall (e.g. withholding lime, or through the use of acidifying N fertilizers; Schaefer 1981) or by creating herb-rich swards (e.g. grass-selective herbicides). Again, these options may be more appropriate in the management of nature reserves, gardens or sports fields. Indeed, as molehills can act as sites for colonization in grasslands (sometimes of rare species; Watt 1974) options that increase the abundance of earthworms, and so molehills, might be encouraged on nature reserves if the aim is to restore plant species richness. On farms, however, management options that aim to minimize the problem of molehills by reducing earthworm abundance appear less suitable as they conflict with traditional management procedures (e.g. hay and silage making; the beneficial effects of earthworms on soil fertility; Edwards & Lofty 1972), and lethal methods like strychnine poisoning and mole traps may continue to be used. However, the danger and inhumaneness of these lethal methods lend some urgency to the need for further study of different methods of control. These investigations should assess alternative, indirect methods of control, including those examined here and the use of repellents (Atkinson & Macdonald 1994), as well as investigations of the economic benefits of different methods of control (Stone 1989; Atkinson, Macdonald & Johnson 1994).

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