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NAME OF SUPERVISOR / *NOM DU DIRECTEUR DE THÈSE* R.M.F.S. Sadleir, Professor

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ASPECTS OF HABITAT SELECTION IN THE COAST MOLE (*Scapanus orarius*) IN BRITISH COLUMBIA

by

Valentin H. Schaefer

B.Sc., McGill University, 1972
M.Sc., University of Toronto, 1974

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
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Name: Valentin Henry Schaefer

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Examining Committee:

Chairman: Dr. A. L. Turnbull

Dr. R.M.F.S. Sadleir, Senior Supervisor

Dr. P. Belton

Dr. N.A.M. Verbeek

Dr. R.W. Mathewes, Non-Supervisory Committee Examiner

Dr. H.R. MacCarthy, External Examiner

Date approved 20d Oct. 1978.

Title of Thesis/Project/Extended Essay

Aspects of habitat selection in the coast mole (*Scapanus orarius*)

in British Columbia

Author:

(signature)

Valentin Henry Schaefer

(name)

20 October, 1978

(date)

ABSTRACT

The relationship between the density of molehills (number of molehills/100 m^2), and the habitat of the coast mole were determined for 10 fields in the Lower Mainland of British Columbia. Some properties of the soil at depths of 10 and 20 cm, and the abundance of earthworms in the moles' habitat were considered.

Study plots containing molehills had significantly ($p \leq .05$) higher soil moisture, higher water content at 10 cm, lower bulk density at 10 cm, less air space at 20 cm, and an almost significantly ($p = .06$) heavier mean weight of worms than plots without molehills. The number of molehills was significantly and positively correlated with the mean and total weights of earthworms in the plots, negatively with soil bulk density, positively with soil moisture at 10 cm, positively with soil water content at 20 cm, and positively with soil pH at 10 cm.

The relationship between the density of molehills and the physical characteristics of the soil was examined for seasonal variation in three fields. The number of molehills in the study plots was significantly and negatively correlated with the bulk density of the soil in summer, autumn, and spring, and with soil air space at 20 cm in spring. In winter, possibly because of the higher soil moisture at that time, there was no significant correlation between the bulk density of the soil and molehill density. The distribution of molehill numbers also changed seasonally. Moles dug over a greater

number of areas in autumn or winter than in the summer, possibly because of increases in soil moisture.

The recruitment (immigration plus reproduction) in a coast mole population, and the movements of a single coast mole, were also studied. Moles did not push up hills in certain plots because the habitat was unsuitable, and not because of a lack of individuals to fill, or inadequate dispersal abilities to enter, the plots of the size used to determine habitat preferences.

A field experiment demonstrated that Ennik's (1967) conclusion that nitrogen fertilizer reduces the number of molehills in a given area requires qualification. A laboratory experiment demonstrated that nitrogen fertilizer does reduce soil pH and hence the weights of earthworms. Thus it may, under certain field conditions, indirectly reduce molehill numbers.

The number of molehills pushed up within three mole territories was significantly and positively correlated with soil moisture and pH over time within one summer's observations. No correlation was found between molehill densities and the concentrations of O_2 and CO_2 in the tunnels. The highest level of CO_2 found in a tunnel was 5.5%, and the lowest level of O_2 was 14.3%. The concentrations of both gases in the tunnels followed those in the air spaces in the adjacent soil. Concentrations of O_2 were significantly negatively correlated with soil moisture, CO_2 positively.

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Chapter 1. Introduction

Habitat selection has been defined as "the repertoire of behavioural responses to environmental stimuli by means of which an animal locates its preferred habitat" (Meadows and Campbell 1972). The concept of habitat selection is simple: An animal lives in an environment which best suits its needs. The biological conditions however, are complex. Animals live in environments consisting of three main components - chemical (e.g. oxygen, salinity, macromolecules), physical (e.g. light, gravity, pressure, temperature, substrate characteristics), and biological (e.g. intraspecific and interspecific factors) - and are affected by many of the interactions occurring between these components.

Habitat selection also depends on the ability of an animal to assess and respond to different environmental factors. For example, an animal may be able to detect changes in pH as small as 0.1, yet may not respond to differences less than 1.0. An animal choosing between habitats differing in pH will thus not prefer one to the other unless it is able to detect the difference and, furthermore, does not tolerate its present circumstances. Two additional aspects of habitat selection theory must be considered. First, the animal may be exposed to only a limited number of habitats. Its choice does not necessarily represent the optimum habitat for the species. The animal presumably chooses the best among those available.

Secondly, it is necessary to consider the differences between preference limits for a species, environments where individuals of a species undergo physiological change, and lethal limits for a species. Preference limits can be regarded as the range of habitats within which most individuals of a species may be found. Outside these limits are extreme environments where some individuals can still survive but undergo a degree of physiological change. Finally, there are environments in which the habitat characteristics (e.g. pH, oxygen, temperature) are lethal to all members of the species.

In the literature, studies of habitat selection are more common for invertebrates than for vertebrates. The number of factors involved in habitat selection for most vertebrates is considerable and their effects are most easily determined under controlled laboratory conditions. The natural habitat of a mammal, for example, is generally difficult to reproduce experimentally. Even if most of the conditions could be simulated, the normal home range sizes cannot be duplicated in captivity. Such restrictions have confined studies of lethal limits of mammals to simple laboratory experiments (e.g. Harris 1952) or to work in field enclosures (e.g. Wecker 1963). In situ studies, while more comprehensive, are not as rigorous (e.g. Hardy 1945, Pruitt 1953).

Habitat selection studies in birds have concerned themselves mainly with nesting, availability of food, and lethal climatic conditions (Klopfer and Hailman 1965). As Lack (1933) pointed out, such studies fail to acknowledge the instinctive nature of habitat selection. He mentions several examples in which a species is not found in a habitat with acceptable food supply, nesting conditions, and climate. Lack suggests that the reason for their absence is that individuals of the species instinctively recognize the habitat as unsuitable because it is occupied by another species better adapted to it. It is, therefore, other species of birds, and not an unsuitable physical environment, which is important in such cases (Lack 1933).

No comprehensive study of habitat selection in moles has been published. Most accounts of their habitats are based on casual observation (Mellanby 1971). Two papers, however, report their preferred habitats for moles from more detailed studies. Milner and Ball (1970) studied the general habitat of the European or common mole (<u>Talpa europaea L.</u>) in Snowdonia (North Wales). They concluded that moles were less numerous in rocky or stony soils, and preferred freely drained areas with a pH greater than 4.0. Arlton (1936) described the optimal habitat of the eastern mole (<u>Scalopus aquaticus L.</u>) as soft soil with humus, moisture, and food. He mentions that moist soft soils permit tunnelling. A mole leaves an area if the soil becomes dry and hard and worms are found at some depth. In experiments, moles showed no preferences when presented with soils varying in moisture content (Arlton 1936).

Moles (Talpidae) are found throughout most of the world (Walker 1964). The common mole of Europe and Asia has the widest distribution and probably causes the most agricultural damage. All moles are fossorial i.e. they spend most of their lives underground. Their diets consist mainly of soil invertebrates. Vegetable matter, usually in the form of plant roots, is sometimes eaten by some species.

There are two species of moles (Subfamily Scalopacinae) found in the Lower Mainland of British Columbia. These are the Townsend mole (Scapanus townsendii Bachman), and the coast mole (S. orarius True). The Townsend mole is the larger of the two, adult males reaching an average length of 20 cm (Cowan & Guiguet 1956). It eats mainly soil invertebrates but its diet can commonly include 40% vegetable matter (Moore 1933). It is considered to be an agricultural pest in the northwestern United States, the damage in 1 Oregon county being estimated at $100,000 annually (Wick 1961). In B.C. it is found only locally in a 5-square mile (13 km^2) area around Huntingdon (Cowan and Guiguet 1956) and it is therefore of little economic importance in Canada.

In B.C., the coast mole occurs as far east as Hope and north to the Coastal Mountains. It is not found on any of the Gulf Islands or on Vancouver Island (Cowan and Guiguet 1956). Its habitat is restricted to agricultural areas and it is generally not found above an altitude of 1,000 feet. Within the species' range in B.C. it is found in almost all types of soils - glacial till, alluvial clay, sands, gravels, and river deposits. It ranges in numbers from about 4/ac (9.88/ha) to 1/35 ac (1/14.17 ha). The biology of this species has been studied by Glendenning (1959) and his findings will be briefly summarized below.

The coast mole is territorial throughout most of the year. Around October moles which have been living in cultivated fields move into heavily sodded grasslands which are their favourite habitat. Digging is most frequent from October-March during which time one mole may push up from 200-400 hills. Tunnels are constructed at three different levels. Surface tunnels are made just below the surface of the earth and are usually used only once while the male is hunting, during dispersal, or while finding a mate. Most of the regular hunting tunnels used daily are built at a depth of 15-20 cm. They serve as an extensive pit trap (Mellanby 1967) into which earthworms (Lumbricidae) and other invertebrates enter and are caught. A deeper system of tunnels is constructed during dry weather while moles are searching for food, usually at a depth of 1-2 m.

Each territory of the coast mole is occupied by only one mole. When this mole is removed no new hills appear. The tunnels excavated by the occupant are circular or slightly vertically flattened, about 5 cm in diameter, and contain small chambers about 10 cm in diameter approximately every m. Moles dig with their forepaws which have strong claws. Soil is pushed to the surface of the ground at various intervals along the tunnels. Dirt from the deeper tunnels is voided through other tunnels. A detailed description of how the coast mole probably digs is found in Skoczen (1958).

The coast mole mates from early January to early March. Males construct long tunnels (marked by large, widely-separated hills) to nearby territories in search of females. Females may expand their territories at this time as is the case for the eastern mole (Harvey 1976). Females construct a nest out of dried grass in a chamber about 15 cm below the surface. The nest of the coast mole is not marked by large mounds of dirt as are found for the European (Godfrey and Crowfoot 1960) and Townsend (Kuhn et al. 1966) moles. About 2-4 young are born from the end of February to the end of April. They remain in the nest for about 3 weeks, forage in the female's territory for another few weeks, and are then forced to disperse.

The principal prey of coast moles are earthworms which comprise 93% of their diet. Arthropods, molluscs, and other soil invertebrates are also eaten. Caged adults may eat nearly twice their weight in earthworms daily i.e. 100-150 gm wet weight, which represents upwards of 100 worms. In addition to nourishment earthworms also provide the mole with water.

Moles live up to 3 years in the wild. About 45% of a natural population studied by Glendenning (1959) consisted of adults over 1 year old. Adult male coast moles are about 16 cm long and weigh about 74 gm; adult females average 15.7 cm and 70 gm.

Moles were once thought to be beneficial to agriculture by improving the aeration and drainage of the soil, destroying harmful soil insects, and circulating soil minerals (Abaturov 1972, Demela 1950). These benefits have been supplanted by modern agricultural practices and moles are now considered to be pests. They still undoubtedly consume cutworms, weevils, larvae, root maggots, wireworms, and white grubs, but do not reduce the populations to an appreciable extent.

Some of the types of damage caused by moles is listed below (after Kuhn 1970):

1) while tunnelling they uproot seedlings killing them directly, and expose their roots to frost and drought,
2) tunnels are occupied by meadow voles (<u>Microtus</u> spp.) which eat exposed roots and bulbs,
3) molehills can cover and thus kill up to 10% of a sward in a territory.
4) molehills ruin farm machinery,
5) molehills sometimes cause soil erosion,
6) molehills are breeding grounds for weedy plant species which invade the pasture and dilute the sward,
7) hay and silage may be contaminated with dirt and curing retarded, and,
8) lawns may be damaged and the turf undermined.

Moles have no natural enemies which consistently prey upon them except for owls and cats which capture the dispersing young in spring (Giger 1965, Cowan 1942, Southern 1954). Otherwise moles seem to be limited only by their food supply and the area of suitable habitat. Severe frost does not appear to reduce mole numbers. Flooding from exceptionally heavy rain and spring run-off causes some mortality but this is insignificant (moles are good swimmers (Reed and Riney 1943), and only die under these situations because of earthworm mortality and not because of drowning).

A few species of fleas and mites have been found on moles (Fain 1969, Fuller 1942, Jurik 1968) and several species of nematodes have been found in their stomachs (Cameron and Parnell 1933, Frankland 1959, Furmaga 1958; 1959). Neither the internal nor the external parasites appear to harm their host. Therefore it seems unlikely that a means of biological control for the mole will be found.

Poisoned baits, poison gases, soil fumigants, pesticides, and land husbandry techniques have been largely unsuccessful in controlling the coast mole, although land husbandry may have some effect (Glendenning 1959). Kuhn (1970) has successfully used dry pelleted baits containing 1% thallium sulfate to control the Townsend mole. Insecticides such as aldrin, dieldrin, chlordane, and sevin (Shilova _et_ _al_. 1971) control mole activity by killing their principal food source, the earthworm. Killing the earthworms is not, however, desirable because of their beneficial effects on soil fertility (Evans 1948, Evans and Build 1948).

The only effective means of mole control known at present is to trap them. There are several traps commercially available but the English scissor trap is the best (Rudge 1963). This method of control is, unfortunately, uneconomical in terms of man-hours and is therefore not in common agricultural use.

The objective of my thesis is to define which habitats are suitable to the coast mole, and if possible to devise a means of controlling moles through habitat manipulation. My approach was to look at molehills and not the moles themselves. It was a priori assumed that moles would push up more or fewer hills in relation to the suitability of the habitat. In order to ascertain if this relationship was present, and if so, to see if the habitat could be changed to reduce the number of molehills made by a mole, my study dealt with the following:

1. To determine where a mole will dig, by comparing habitats where moles are and are not active.
2. To determine what controls how many molehills a mole will dig per unit area.
3. To determine if there is seasonal variation in the relationship between molehill numbers and the habitat of moles.
4. To determine whether environmental factors can be manipulated to control activity producing hills.

Each chapter presented will deal with one aspect of the major work which will be discussed as a whole at the conclusion. Further studies to determine if recruitment or dispersal were responsible for the absence of moles from certain study plots rather than unsuitable habitat are included in the Appendices.

Chapter 2. Patterns of mole activity and their relationship to earthworm availability and soil characteristics

Throughout this study the habitat preference of the coast mole was estimated by its digging activity (quantified by counting molehills). It was assumed that the digging activity of moles was in some way related to the suitability of the habitat. More hills in one area than another could result from there being more individuals in the former. Godfrey (1955) found that territory size varied with the habitat. However, the relationship between molehill numbers and habitat would persist, whether or not more hills were produced by more individuals, or by more digging activity of a single individual.

The earthworm is the principal food source of the coast mole comprising 93% of its diet (Glendenning 1959), and could potentially be the sole limiting factor to mole activity. It is not a priori clear, however, which of the characteristic(s) of earthworm populations are important to moles. Therefore, earthworms were considered in terms of their numbers, mean weight, total weight, (per unit volume) and species composition which would reflect respectively the frequency of encounter, average meal size, amount of food available, and palatability. Earthworm activity, which may be an index of how frequently earthworms enter mole runs, was not considered. Earthworm activity is commonly measured by counting earthworm casts, a technique which requires considerable experience if accuracy is required, and which is unsuitable in a grazed pasture where castes are normally destroyed by livestock (Satchell 1955).

The digging activity of moles would also be expected to depend on the hardness of the ground. Godfrey (1955) mentions that shallow tunnels are made in loosely packed moist soil and deep tunnels in hard dry soil. The type of tunnel dug may be reflected in the number of molehills. The hardness of the ground in turn depends on the physical characteristics of the soil which, as a result, were given considerable emphasis in this study. The pH and mineral characteristics of the soil were also considered since they are known to relate to earthworm activity and abundance (Satchell 1955, Laverack 1961), and they may provide clues to other factors controlling mole activity with which they may covary.

There are potentially three empirical ways of determining a habitat preference in the mole. The first is to compare the habitat inside and outside its geographical range. This method would be efficient in detecting extremes and limiting factors but it would be insensitive to any synergistic or antagonistic effects. It would also be unable to detect those factors which may influence the degrees of mole activity.

A second method is to compare one field infested with moles with another devoid of them inside the geographical range. This technique has a disadvantage in that it can be argued that the field devoid of moles is inaccessible or beyond the dispersal capabilities of the species. The former is particularly pertinent in the B.C. Lower Mainland where deep drainage ditches commonly surround pastures; although moles can swim it may be incorrect to assert that they will readily take to water during dispersal. It would be extremely difficult to discredit these objections in terms of the 'normal' movements of the species.

A third method is to compare parts of one field with mole activity to other parts of the same field without moles. This was the main method used for this study. Presumably a mole has access to and is capable of entering land adjacent to its territory, and i~~t or~~ its young are in one area as opposed to another because of their habitat preferences.

Methods

A. The Study Areas

After an extensive survey of potential study areas in the farmland of the Lower Mainland, 10 fields containing a large number of molehills (qualitatively assessed) were chosen in May, 1976, as the study areas. The locations of the fields and the names assigned to them are shown in Figure 1. Fields were named after the farmer who worked the land.

The area within each field chosen for study contained the most molehills within the field. A standard 1 ha area was marked off for study. If the field was smaller than 1 ha (Gadicke, Perkin, and Campbell), the study area was limited to the size of the field. Two study areas (Laity and Judd) were oriented along a north-south (the direction was arbi-

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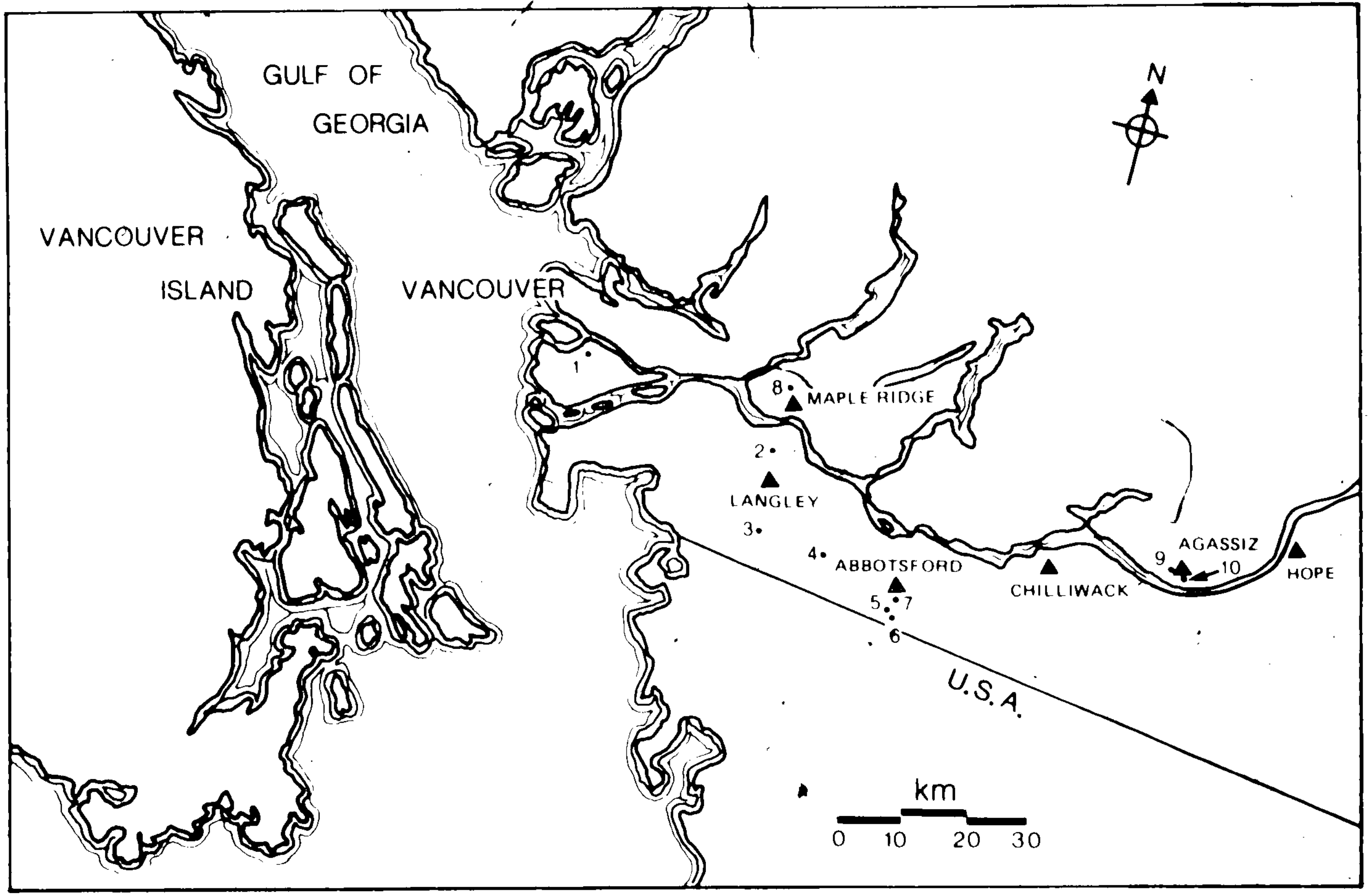
Figure 1. Map of the B.C. Lower Mainland showing the locations and names of the 10 study areas used to compare mole activity with earthworm and soil characteristics. Study areas are indicated by dots, the nearest cities by dots enclosed in a triangle.



1 KEUR
2 ROBERTSON
3 JUDD
4 GADICKE
5 CAMPBELL
6 PERKIN
7 McCONNELL
8 LAITY
9 HATT
10 BRINK

trary) axis. All others followed natural fence lines (or land features - Brink). The reason for the north-south orientation was to determine if having the study plots along the perimeters, as in most fields, in some way biased the results.

The perimeter of each study area was marked at 10 m intervals by a piece of surveyor's tape attached to a nail driven into the ground. These markers later served to divide the study areas into 10 x 10 m quadrats for enumerating molehills and taking earthworm and soil samples.

B. Enumerating Molehills

The number of molehills was counted within each of the 10 x 10 m plots in the study areas in June, 1976. The side of each hill was kicked away as it was counted so as to subsequently distinguish between old and new hills. The initial definition of a molehill was:

1) any raised mound or column of earth caused by moles, and,
2) any bare levelled circular patch of ground due to the former presence of a molehill (in subsequent counts only the first definition was used). With this definition of a molehill digging activity in the field within about the last year could be measured.

The number of molehills for each of the 10 x 10 m study plots for the 10 fields are presented in Appendices 1-10. There may have been some counting errors in Perkin and Hatt because the former was harrowed and the latter cut 2 weeks before counting; ~~the~~ numbers may be underestimated in each case. All counts were made at the end of June or the beginning of July with exact dates recorded on ~~the~~ tables.

C. Assessing Earthworm populations and soil characteristics

Lines of 10 plots were chosen on the basis of the molehill counts to run from areas of high mole activity to areas of no activity. The location of the line for each field is indicated on Appendices 1-10. In McConnell the line ran through two centers of activity. In Judd and Hatt there were many hills throughout the fields so the 10 plots within each were selected with a table of random numbers. For the latter, two control fields (containing almost no mole activity) were selected on the same farms for comparison. The control fields were about 500 m from the main study areas in each case. An area of 1 ha was subdivided into 100 plots in each control, and 10 plots were chosen at random in each from a table of random numbers.

Earthworms were sampled at the center of each study plot using the extraction technique of Raw (1959). One gallon of water containing 25 ml 40% formalin was applied to an area of 60 cm, followed by a second application when earthworms stopped surfacing. This technique is probably the best way to sample earthworms in the field (Evans and Guild 1947, Raw 1959, Svedson 1955). An area of 60 x 60 cm was treated and earthworms were removed and counted from a 50 x 50 cm central area. This procedure reduced the variability of my samples, probably because of the reduced effect of lateral seepage of the extracting solution through the ground.

Earthworms were collected with a pair of tweezers and immediately put into a preserving solution of 10% glycerin with 5% formaldehyde. Worms were weighed wet as a group for each sample and mean worm weight was computed. Total worm weight did not necessarily equal mean weight times the number of earthworms because in some instances only a fragment of a worm was collected; this was considered in worm numbers but not weights. They were later identified to species and age categories by Dr. J.W. Reynolds, Department of Forest Resources, University of New Brunswick, Fredericton, N.B.

Soil samples were either collected by an assistant at the same time as the worm samples, or immediately afterwards. The samples were collected about 2 m from where the earthworms were extracted and in a direction of equal or slightly higher slope to avoid formalin.

Soil samples were collected from a pit about 20 x 20 x 20 cm. Three stainless steel cylinders, sharpened at one end, were driven into a wall of the pit at a depth of 10 cm, and three more were driven in at 18-20 cm, depending on the soil horizons (I avoided sampling on the boundary of two horizons, and tried to remain above unconsolidated material). The cylinders were each about 4 cm long by 3 cm in diameter, and each contained an exact volume of 25.5 cc. The cylinders were removed from the ground with a garden trowel and the earth of all three from one level (total volume of 76.5 cc) was placed into a plastic bag and sealed with a tie tag.

The soil was weighed in the laboratory while still in the bag. It was then emptied onto a paper towel on a counter top, usually within 24 hours of collection to dry. The physical soil characteristics determined were:
soil moisture (wet wt-dry wt/dry wt x 100 = %),
bulk density (dry wt/vol = gm/cc),
water content (wet wt-dry wt/vol x 100 = %),
and air space (porosity-water content = %;
(porosity = 100 x specific gravity-bulk density/s.g.).
A more complete description of these characters is found in Wilde (1958), and Wilde and Voigt (1955).

Analyses of the soil were performed by the soil testing laboratory of the B.C. Department of Agriculture, Kelowna, B.C., Organic matter was determined by the Walkey-Black method; pH and nitrate by potentiometry; salts by electrical conductance; phosphorus by the acid-fluoride method; and potassium, calcium, and magnesium by atomic absorption spectroscopy. A description of these methods is in McMullan (1971). Total nitrogen was determined by the Micro-Kjeldahl method; by the Research Station, Federal Department of Agriculture, Agassiz, B.C. The soil samples tested were those used to determine the physical soil characteristics and were collected during July and the beginning of August.

D. Statistical Analyses

Statistical treatments of the data were done on the computer facilities at Simon Fraser University. Correlation coefficients (r) were obtained from the correlation matrices provided from SPSS REGRESSION. Means and standard deviations were obtained from the same program. An analysis of variance APL program ANOVAR was used instead of a t-test. The principal component analysis was done using LJIFFY. a program provided by Dr. S. Coopman of the Psychology Department at S.F.U. Nonparametric correlations were computed using SPSS NONPAR CORR, and multiple regression using SPSS REGRESSION. The Mann Whitney U statistic was computed using APL Nonpar.

Results

The number of molehills in the plots sampled for each field are given in Appendix 11. These are the values which were used in the correlation analyses. The numbers of worms for each of the plots, mean weight of worms, total weight of worms, soil moisture at 10 cm, soil moisture at 20 cm, bulk density at 10 cm, bulk density at 20 cm, water content at 10 cm, water content at 20 cm, air space at 10 cm, and air space at 20 cm are given in Appendices 12-22 respectively. The mineral contents of the plot samples from Keur, Laity, Robertson, Campbell, and Brink fields in the summer of 1976 are presented in Appendices 23-27.

For all the fields combined, mole activity was significantly correlated with the mean weight of worms, the total weight of worms ($p \leqslant .01$), soil moisture at 10 cm, negatively with bulk density at 10 cm ($p \leqslant .01$) and 20 cm, and negatively with water content at 10 cm and 20 cm ($p \leqslant .01$) (Table 1).

Only three individual fields had any significant ($p \leqslant .05$) correlations (Table 2). Of these the Keur field had five (number of worms, and soil moisture and water content at 10 and 20 cm), the Robertson field one (bulk density at 10 cm), and the Brink field one (soil moisture at 20 cm). Other fields which had nearly significant ($p \leqslant 0.10$) correlations were Laity for mean worm weight, Perkin for the number of worms, and Hatt for bulk density at 10 cm.

There were several individual fields with significant relationships between earthworm populations and the soil. In Keur soil moisture and water content were correlated with the number of worms and total weight of worms (Table 3). In Campbell, mean weight of worms was correlated with soil bulk density and air space. In Brink and Hatt the mean weight of worms was correlated with water content and soil moisture respectively. For all the fields combined the number of worms was significantly correlated with soil moisture at 10 cm, and the mean and total weights of the worms were significantly correlated with the bulk density of the soil ($p \leqslant .01$).

The earthworms sampled in the 10 fields belonged to 12 species (Appendix 28). These were: *Allolobophora chlorotica*, *Aporrectodea trapezoides*, *A. tuberculata*, *Dendrobaena octaedra*, *Denrodrilus rubidus*, *Eisenia rosea*, *Eiseniella tetraedra*, *Lumbricus rubellus*, *L. festivus*, *L. terrestris*, *Octolasion*

Table 1. Correlations (r) with all the fields combined (total of 100 quadrats) between the number of molehills and the earthworm and physical soil parameters considered. Means and standard deviations are provided.

Character	Mean	r
number of molehills	15.32	
number of worms	13.22	0.10
mean worm weight (gm)	0.50	0.25*
total worm weight (gm)	6.93	0.33**
soil moisture 10 cm (%)	35.22	0.20*
soil moisture 20 cm (%)	34.52	0.15
bulk density 10 cm (gm/cc)	0.91	-0.33**
bulk density 20 cm (gm/cc)	0.89	-0.22*
water content 10 cm (%)	29.70	0.21*
water content 20 cm (%)	29.55	0.29**
air space 10 cm (%)	35.95	0.00
air space 20 cm (%)	36.75	-0.16

*$p \leq .05$; **$p \leq .01$

Table 2. Correlations (r) by field, between the number of molehills per quadrat and the worm and physical soil parameters considered. Ten quadrats were sampled in each field.

Character	Keur	Laity	Robertson	Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt
number of worms	0.70*	-0.44	-0.16	-0.55	0.22	0.13	0.62	0.08	0.16	-0.20
mean worm weight	0.05	0.62	-0.16	0.45	0.38	-0.08	-0.30	-0.24	0.44	0.46
total worm weight	0.58	0.04	-0.19	-0.38	0.51	-0.07	0.35	0.10	0.45	0.08
soil moisture 10 cm	0.79**	0.07	0.43	0.17	0.01	0.45	-0.31	0.57	-0.59	0.36
soil moisture 20 cm	0.75*	0.16	0.44	0.10	0.05	-0.13	-0.60	0.13	-0.65*	0.36
bulk density 10 cm	-0.43	0.00	-0.67*	0.30	0.05	0.14	0.00	-0.54	0.56	-0.61
bulk density 20 cm	-0.49	0.08	-0.35	0.36	0.07	0.47	0.48	-0.17	0.53	-0.26
water content 10 cm	0.73*	0.10	0.14	0.40	0.06	0.46	-0.33	-0.02	0.21	0.53
water content 20 cm	0.75**	0.18	0.40	0.41	0.09	0.26	0.03	0.12	0.44	0.12
air space 10 cm	-0.14	-0.09	0.32	-0.50	-0.09	-0.40	0.20	0.39	-0.58	-0.27
air space 20 cm	-0.28	-0.17	-0.11	-0.54	-0.16	-0.40	-0.30	0.01	-0.61	0.02

$^{*}p \leq .05$; $^{**}p \leq .01$

Table 3. Correlations (r) by field and in total between the soil and earthworm parameters. The correlations for 20 cm of soil depth are not presented but are similar to those for 10 cm.

Correlation Tested	Keur	Laity	Robertson	Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Total
number of worms with:											
soil moisture 10 cm	0.90**	0.38	0.36	-0.32	0.38	-0.01	-0.20	0.42	0.35	0.19	0.22*
bulk density 10 cm	-0.43	-0.05	-0.13	-0.03	-0.17	0.18	-0.20	0.00	-0.43	0.33	-0.11
water content 10cm	0.84**	0.48	0.43	-0.40	0.49	0.08	-0.38	-0.45	0.18	-0.57	0.08
air space 10 cm	-0.22	-0.50	-0.39	0.40	-0.20	-0.12	0.36	-0.48	0.25	-0.56	-0.01
mean worm weight with:											
soil moisture 10 cm	0.56	-0.10	0.28	0.53	0.38	-0.39	0.08	0.27	-0.68*	-0.18	-0.03
bulk density 10 cm	-0.34	0.00	-0.49	-0.16	-0.25	-0.67*	0.40	0.20	0.50	-0.30	0.29**
water content 10 cm	0.49	-0.09	0.15	0.57	0.29	-0.58	0.46	-0.53	0.67*	0.47	-0.08
air space 10 cm	-0.05	0.10	0.17	-0.45	0.02	0.68*	-0.53	0.43	-0.80**	-0.54	-0.12
total worm weight with:											
soil moisture 10 cm	0.86**	0.10	0.41	-0.20	0.46	-0.31	-0.24	0.44	-0.20	0.12	0.19

Table 3. (Continued)

Correlation Tested	Keur	Laity	Robertson	Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Total
bulk density 10 cm	-0.47	0.11	-0.23	0.00	-0.29	-0.06	0.12	-0.02	-0.03	0.08	0.00
water content 10 cm	0.77**	0.21	0.45	-0.23	0.45	-0.26	-0.14	-0.46	0.58	-0.16	-0.07
air space 10 cm	-0.14	-0.30	-0.34	0.23	-0.08	0.23	0.01	0.50	-0.32	0.21	0.06

* $p \leq .05$; ** $p \leq .01$

cyaneum, and *O. tyrtaeum*. All of the fields contained earthworms in the genus *Lumbricus*, mainly *L. rubellus* and *L. terrestris*. Other species were found in only one or a few fields with *A. tuberculata* being the most common. Most of the individuals were juveniles, aclitellate adults were next in abundance, then clitellate adults, and finally post-clitellate adults.

It appears that there are no relationships between the number of molehills and earthworm species, mainly because the species usually changed from field to field irrespective of molehill numbers. The numbers of individuals within a species also did not appear to follow any pattern in molehill numbers.

Tables 4 and 5 present the comparison of the Judd and Hatt fields with their controls on the basis of the numbers and weights of earthworms, and physical characteristics of the soil. In the Judd field the number of worms, total weight of worms and soil moisture were significantly greater ($p \leq .05$), bulk density significantly less, and water content significantly greater than in the control. In the Hatt field the mean weight of worms, total weight of worms, and soil air space were significantly ($p \leq .01$) more, and soil moisture at 20 cm and water content at 20 cm significantly less, than in the control.

The correlations between the number of molehills in the study plots and the mineral characteristics of the soil for the summer of 1976 are presented by field in Table 6. Calcium

Table 4. Comparison of Judd field with its control (Mann Whitney U test) to determine if a field with high numbers of molehills differed from one without on the basis of the soil parameters and earthworm characteristics measured. Ten study plots were sampled in each field.

Character	Mean Judd	Mean Control Judd	U
number of worms	27.70	19.70	78.5*
mean worm weight (gm)	0.30	0.22	76.0
total worm weight (gm)	8.15	2.89	88.0**
soil moisture 10 cm (%)	52.15	34.97	97.0**
soil moisture 20 cm (%)	49.34	29.09	99.0**
bulk density 10 cm (gm/cc)	0.70	0.88	99.0**
bulk density 20 cm (gm/cc)	0.70	0.84	95.0**
water content 10 cm (%)	34.98	30.53	79.5*
water content 20 cm (%)	33.58	24.06	97.0**
air space 10 cm (%)	38.56	36.25	63.0
air space 20 cm (%)	39.80	44.18	77.0*

$^{*}p \leq .05$; $^{**}p \leq .01$

Table 5. Comparison of Hatt field with its control (Mann Whitney U test) to determine if a field with high numbers of molehills differed from one without on the basis of the soil parameters and earthworm characteristics considered. Ten study plots were sampled in each field.

Character	Mean Hatt	Mean Control Hatt	U
number of worms	22.90	28.60	65.0
mean worm weight (gm)	1.53	0.47	100.0**
total worm weight (gm)	33.79	13.38	90.0**
soil moisture 10 cm (%)	39.89	43.06	51.5
soil moisture 20 cm (%)	39.51	49.14	79.0*
bulk density 10 cm (gm/cc)	0.90	0.96	69.0
bulk density 20 cm (gm/cc)	0.87	0.93	64.5
water content 10 cm (%)	34.24	40.31	88.0**
water content 20 cm (%)	32.93	43.79	99.0**
air space 10 cm (%)	31.85	23.22	89.0**
air space 20 cm (%)	34.23	19.95	99.0**

*$p < .05$; **$p < .01$

Table 6. Correlations (r) between the number of molehills and soil pH and mineral content. Ten quadrats were sampled in each field.

Character	Keur	Laity	Robertson	Campbell	Brink
organic matter	0.34	-0.05	0.28	-0.19	-0.34
pH	-0.01	0.31	-0.54	0.49	-0.21
salts	-0.25	-0.02	-0.51	0.30	-0.44
nitrate nitrogen	-0.46	-0.03	-0.26	-0.31	0.40
phosphorus	-0.22	0.22	-0.25	-0.22	0.52
potassium	-0.20	-0.22	0.13	-0.29	-0.10
calcium	0.04	-0.02	-0.61*	0.55	-0.59
magnesium	-0.05	0.33	0.30	0.30	-0.36
total nitrogen	0.33	-0.50	0.30	0.30	-0.36

$^*p \leq .05$

was significantly and negatively correlated with the number of molehills in the Robertson field.

Correlations between molehill numbers and soil minerals for all the fields combined (total of 50 plots) show that the number of molehills was significantly positively correlated with pH (Table 7). The correlations of phosphorus and magnesium approached significance ($p \leqslant 0.10$).

Table 8 presents the correlations between the weight and number of earthworms, and the mineral content of the soil for the summer of 1976. Mean and total worm weights were significantly negatively correlated with organic matter and total nitrogen.

The five fields used in the mineral analyses were also examined for correlations between the number of molehills and the earthworm and physical soil characteristics considered as a separate group from the complete samples of the 10 fields (Table 1). The correlations of the worm parameters with the physical soil characteristics are included (Table 9). The number of molehills was not significantly correlated with the number or weight of earthworms, or the physical soil parameters. Mean worm weight was positively correlated with soil bulk density and negatively with air space at 20 cm ($p \leqslant .01$). Total worm weight was positively correlated with soil bulk density at 20 cm.

The correlations between the number of molehills and earthworms and the physical soil characteristics for the five fields not used in the mineral analyses are presented in Table 10. In

Table 7. Correlations (r) between the number of molehills and soil pH and mineral content of five fields used in the mineral analyses combined (total of 50 quadrats).

Character	Mean	Standard Deviation	r (n=50)
organic matter	7.21 %	2.58%	0.10
pH	5.75	0.39	0.31*
salts	0.14	0.03	-0.06
nitrate nitrogen	0.85 ppm	0.71 ppm	-0.05
phosphorus	40.47 ppm	28.70 ppm	0.25
potassium	63.98 ppm	60.22 ppm	-0.15
calcium	959.21 ppm	456.81 ppm	-0.02
magnesium	105.77 ppm	95.28 ppm	-0.23
total nitrogen	0.61 %	0.21 %	0.03

*$p \leq .05$

Table 8. Correlations (r) of the earthworm characteristics with soil pH and mineral content (n=50) for the five fields in Table 7.

Character	Number of worms	Mean worm weight	Total worm weight
organic matter	0.04	-0.33*	-0.28*
pH	0.13	0.03	0.03
salts	-0.03	0.09	0.07
nitrate nitrogen	0.25	0.09	0.21
phosphorus	0.24	0.24	0.10
potassium	0.07	0.21	0.14
calcium	-0.23	0.03	-0.05
magnesium	-0.26	0.13	0.08
total nitrogen	-0.12	-0.34*	-0.35*

*$p \leq .05$

Table 9. Correlations between the number and weight of earthworms and physical soil characteristics and the number of molehills in the fields used for the mineral analyses (total of 50 quadrats).

Character	Number of hills	Number of worms	Mean worm weight	Total worm weight
number of worms	0.25			
mean worm weight	0.07	0.01		
total worm weight	0.08	0.60**	0.52**	
soil moisture 10 cm	-0.01	0.04	-0.11	-0.05
soil moisture 20 cm	-0.07	0.14	-0.17	0.01
bulk density 10 cm	-0.25	-0.15	0.43**	0.26
bulk density 20 cm	-0.10	-0.09	0.39**	0.27*
water content 10 cm	0.00	0.05	0.10	-0.08
water content 20 cm	0.06	0.12	0.02	-0.01
air space 10 cm	0.17	0.05	-0.18	-0.10
air space 20 cm	0.03	-0.02	-0.33	-0.20

* $p \leq .05$; ** $p \leq .01$

Table 10. Correlations (r) of the worm and physical soil characteristics with the number of molehills in the fields not used for the mineral analyses (total of 50 quadrats).

Character	Number of hills	Number of worms	Mean worm weight	Total worm weight
number of worms	-0.10			
mean worm weight	0.46**	0.05		
total worm weight	0.33*	0.47**	0.81**	
soil moisture 10 cm	0.22	0.02	0.03	0.05
soil moisture 20 cm	0.18	-0.03	0.10	0.08
bulk density 10 cm	-0.32*	0.16	0.11	0.20
bulk density 20 cm	-0.24	0.15	0.04	0.16
water content 10 cm	0.24	-0.55**	-0.16	-0.42**
water content 20 cm	0.31*	-0.62**	0.05	-0.28*
air space 10 cm	0.02	0.41	0.06	0.25
air space 20 cm	-0.19	0.58**	0.20	-0.08

*$p \leq .05$; **$p \leq .01$

these fields the number of molehills was positively correlated with mean ($p \leq .01$) and total worm weights, negatively with bulk density at 10 cm, and positively with water content at 20 cm. The number of worms was significantly correlated with air space at 20 cm and water content, and the total weight of worms was correlated with water content, all at the 0.01 level.

A comparison of the five fields used in the mineral analyses with the five not used is presented in Table 11. They were significantly different in every characteristic except mean worm weight, soil air space, and water content at 20 cm. Those used for the mineral analyses had significantly fewer hills, fewer worms, a much less total worm weight, less soil moisture, heavier soil, and less water content at 10 cm.

The presence of a large number of zero values in the correlation analyses due to quadrats with no mole activity may mask true relationships because the number of molehills has ceased to vary, whereas the earthworms and soil characteristics have not. As a result, further correlation tests were performed omitting quadrats containing no molehills (Table 12). The number of molehills was found to be significantly and positively correlated with the total weight of worms, negatively with soil bulk density at 10 cm, positively with water content at 20 cm, and positively with pH.

The rank correlation (testing for relative, not absolute, relationships) results are presented in Table 13. Some of the data were not normally distributed so a Spearman Rho rank correlation test was used to corroborate the result of the

Table 11. Comparison of the five fields used in the mineral analyses with the remaining five fields to determine if they differ on the basis of earthworms and physical soil characteristics.

Character	Fields with no mineral samples mean	Samples SD	Fields with mineral samples mean	Samples SD	F	P
number of molehills	19.5	18.19	11.14	15.10	6.25	0.01**
number of worms	20.92	19.62	4.74	5.56	31.48	0.00**
mean worm weight (gm)	0.53	0.55	0.48	0.77	0.15	0.70
total worm weight (gm)	11.56	13.93	2.31	3.06	21.04	0.00**
soil moisture 10 cm (%)	32.86	9.10	31.18	9.60	19.24	0.00**
soil moisture 20 cm (%)	38.05	8.82	30.99	8.18	17.25	0.00**
bulk density 10 cm (gm/cc)	0.86	0.12	0.96	0.16	11.49	0.00**
bulk density 20 cm (gm/cc)	0.84	0.11	0.94	0.18	10.63	0.00**
water content 10 cm (%)	31.92	4.63	28.44	9.05	5.84	0.02*
water content 20 cm (%)	30.25	5.13	28.96	11.84	0.50	0.48
air space 10 cm (%)	35.55	5.74	35.42	12.71	12.70	0.90
air space 20 cm (%)	37.93	6.15	36.69	12.46	0.40	0.53

$^{*}p \leq .05$; $^{**}p \leq .01$

Table 12. Correlations between the number of molehills and the soil and earthworm characters with quadrats containing no molehills omitted.

Character	Fields with mineral samples (34 quadrats)		All fields (76 quadrats)	
	mean	r	mean	r
number of molehills	16.4		20.2	
number of worms	5.7	0.16	13.2	0.10
mean worm weight (gm)	0.57	-0.01	0.58	0.18
total worm weight (gm)	2.63	0.00	7.86	0.31**
soil moisture 10 cm (%)	31.99	-0.12	36.36	0.13
soil moisture 20 cm (%)	31.92	-0.23	35.56	0.07
bulk density 10 cm (gm/cc)	0.94	-0.24	0.89	-0.29**
bulk density 20 cm (gm/cc)	0.94	-0.15	0.88	-0.21
water content 10 cm (%)	24.64	0.01	30.39	0.19
water content 20 cm (%)	24.94	0.01	30.80	0.22*
air space 10 cm (%)	39.74	0.16	35.95	0.00
air space 20 cm (%)	39.41	0.11	35.84	-0.09
organic matter (%)	7.43	0.04		
pH	5.78	0.35*		
salts	0.14	-0.08		
nitrate nitrogen (ppm)	0.89	-0.13		

Table 12. (Continued)

Character	Fields with mineral samples (34 quadrats)		All fields (76 quadrats)	
	mean	r	mean	r
phosphorus (ppm)	43.56	0.24		
potassium (ppm)	66.69	-0.26		
calcium (ppm)	930.60	0.04		
magnesium (ppm)	103.53	-0.29		
total nitrogen (%)	0.62	0.02		

$^{*}p \leq .05$; $^{**}p \leq .01$

Table 13. Rank correlation results for all 10 fields combined with quadrats containing no molehills omitted (total of 76 quadrats; only the probabilities of significance are recorded).

Character	Number of hills	Number of worms	Mean worm weight	Total worm weight
number of worms	0.042^{*}			
mean worm weight	0.073	0.006^{**}		
total worm weight	0.007^{**}	0.001^{**}	0.001^{**}	
soil moisture 10 cm	0.140	0.001^{**}	0.256	0.012^{**}
soil moisture 20 cm	0.236	0.002^{**}	0.473	0.016^{*}
bulk density 10 cm	0.002^{**}	0.132	0.099	0.443
bulk density 20 cm	0.017^{*}	0.228	0.304	0.465
water content 10 cm	0.103	0.362	0.197	0.268
water content 20 cm	0.036^{*}	0.300	0.437	0.396
air space 10 cm	0.352	0.046^{*}	0.302	0.208
air space 20 cm	0.345	0.077	0.035^{*}	0.493

$^{*}p \leq .05$; $^{**}p \leq .01$

Pearson product - moment correlation, a more powerful test. Frequency distribution of the number of molehills in the plots was an exponential decay. The number of molehills was significantly correlated with the number of worms, total worm weight, soil bulk density, soil water content, and air space at 20 cm.

In the five fields used for the mineral analyses, the number of molehills per plot was found to be significantly correlated with the bulk density of the soil at 10 cm, and phosphorus (Table 14). The correlation with soil moisture at 20 cm was almost significant (p=0.065).

Table 15 presents a comparison of all plots containing molehills to those without for the 10 fields, and in the case of soil minerals, for five fields. Although some data were not normally distributed a Chi-square test for heterogeneity of variance was insignificant for all characters except mean and total weight of worms, and soil bulk density at 20 cm. A Wilcoxon two-sample test confirmed the ANOVA results in these three cases. Soil moisture at 10 and 20 cm, and water content at 20 cm, were found to be significantly more in plots with molehills than in those without, and the bulk density of the soil at 10 cm was significantly less; mean worm weight was almost significantly greater in quadrats with molehills (p=0.06).

Multiple regression analyses were used on the following combinations of the study plots:

Table 14. Rank correlation results for the five fields used in the mineral analyses with quadrats containing no molehills omitted (total of 34 quadrats; only the probabilities of significance are recorded).

Character	Number of hills	Number of worms	Mean worm weight	Total worm weight
number of worms	0.33			
mean worm weight	0.24	0.17		
total worm weight	0.39	0.001^{**}	0.001^{**}	
soil moisture 10 cm	0.102	0.41	0.048^{*}	0.205
soil moisture 20 cm	0.064	0.494	0.027	0.142
bulk density 10 cm	0.048^{*}	0.35	0.11	0.04^{*}
bulk density 20 cm	0.148	0.11	0.08	0.02^{*}
water content 10 cm	0.311	0.358	0.094	0.234
water content 20 cm	0.230	0.237	0.117	0.164
air space 10 cm	0.147	0.359	0.371	0.444
air space 20 cm	0.246	0.428	0.277	0.147
organic matter	0.43	0.13	0.105	0.015^{*}
pH	0.25	0.01^{**}	0.30	0.024^{*}
salts	0.12	0.13	0.055^{*}	0.044^{*}
nitrate nitrogen	0.14	0.44	0.24	0.054^{*}
phosphorus	0.048^{*}	0.054^{*}	0.096	0.025^{*}
potassium	0.12	0.18	0.35	0.109
calcium	0.48	0.47	0.12	0.362
magnesium	0.27	0.16	0.25	0.413
total nitrogen	0.406	0.019^{*}	0.023^{*}	0.054^{*}

$^{*}p \leq .05$; $^{**}p \leq .01$

Table 15. Comparison of quadrats with molehills and those without on the basis of earthworms and physical soil characteristics (76 quadrats with hills, 34 without), and soil minerals (34 quadrats with molehills, 16 without).

Character	quadrats with molehills		quadrats without molehills		F	P
	mean	SD	mean	SD		
Earthworms and physical soil characters						
number of worms	13.22	16.01	11.58	18.24	0.18	0.67
mean worm weight (gm)	0.58	0.74	0.28	0.28	3.73	0.06
total worm weight (gm)	7.86	12.13	4.02	5.91	2.23	0.14
soil moisture 10 cm (%)	36.36	10.28	31.62	9.67	3.98	0.05*
soil moisture 20 cm (%)	35.56	9.16	31.21	8.63	4.22	0.04*
bulk density 10 cm (gm/cc)	0.89	0.15	0.97	0.12	4.86	0.03*
bulk density 20 cm (gm/cc)	0.88	0.17	0.92	0.13	0.99	0.33
water content 10 cm (%)	30.39	8.94	27.52	8.10	1.96	0.16
water content 20 cm (%)	30.73	9.25	25.63	6.81	6.21	0.01**
air space 10 cm (%)	35.66	9.07	35.92	7.97	0.02	0.87
air space 20 cm (%)	35.84	8.65	39.63	6.45	3.91	0.05*

Table 15. (Continued)

Character	quadrats with molehills mean	quadrats with molehills SD	quadrats without molehills mean	quadrats without molehills SD	F	P
Soil mineral characteristics						
organic matter (%)	7.43	2.76	6.73	2.14	0.79	0.38
pH	5.78	0.37	5.67	0.41	0.84	0.36
salts	0.14	0.03	0.14	0.03	0.00	0.92
nitrate nitrogen (ppm)	0.90	0.79	0.75	0.52	0.45	0.50
phosphorus (ppm)	43.56	29.03	32.91	27.70	1.24	0.27
potassium (ppm)	66.69	61.03	58.22	60.01	0.21	0.65
calcium (ppm)	930.60	469.86	1020.00	436.11	0.41	0.52
magnesium (ppm)	103.53	100.21	110.53	86.76	0.06	0.81
total nitrogen (%)	0.62	0.23	0.60	0.18	0.04	0.83

* $p \leq .05$; ** $p \leq .01$

Data Available	Number of Fields	Number of Plots	Number of Characters
1. earthworm and physical soil characteristics	10	100	11
2. earthworm, physical, and mineral soil characteristics	5	50	21
3. same as '1' but only plots with molehills	10	76	11
4. same as '2' but only plots with molehills	5	34	21

The total r-squares for the four combinations were respectively 34.7%, 24.6%, 50.7%, and 65.4%. i.e. the characters were not good linear predictors of the number of molehills pushed up. When mineral characteristics were not considered the bulk density of the soil and the worm weight characters were the first three characters to enter in the stepwise regression procedure and they accounted for 26.6% of the variance when all plots were considered, and 21.3% of the variance when the plots without hills were omitted. With the mineral characteristics included, pH and magnesium together accounted for 28.6% of the variability when all plots for which mineral information was available were considered, and 38.0% of the variance when plots without molehills were omitted.

The data were further analyzed using a principal components analysis. This multivariate statistical technique has certain heuristic advantages which the other previous techniques do not have. These are: the data do not have to be linearly related (even with transformations the data may not fit a linear model); and it can accommodate synergistic effects of the data which the other techniques are simply incapable of handling. It is also easier to determine if there is direct causality between variables which can only be inferred from the previous techniques if an experimental design is not used, which is the case for this study.

The results of the principal components analysis are presented in Table 16. A five-factor rotation (rotations are used to produce the greatest predictability of the variables from the components) produced a component (4) on which mole activity loaded heavily the number of molehills correlated (r=0.83) highly with this component. Also loading heavily on the same component were the number of worms, phosphorus, total worm weight, pH, magnesium, and bulk density at 10 cm. These variables, except the number of molehills, also loaded heavily on the other components.

Discussion

A. The relationship between mole activity and the soil

The correlations obtained in Table 2 between mole activity and the physical characteristics of the soil do not appear to be meaningful except for those in the Keur field. The significant correlations obtained for the Keur field are interesting because there are 5 within that 1 field alone. Four of these are for the physical soil characteristics, soil moisture

Table 16. Results of the principal components analysis with soil minerals included. A five-factor rotation (varimax) provided the most conspicuous molehill component (4). The internal consistency value for this component was 0.39, and the sums of squares 1.87. Only those characters with the eight highest loadings are presented. A loading greater than 0.30 is considered to be significant.

Character	Loading
number of molehills	0.83
phosphorus	0.59
number of worms	0.39
pH	0.38
magnesium	-0.32
bulk density at 10 cm	-0.32
mean weight of worms	0.29
total weight of worms	0.24

and water content at 10 and 20 cm. The correlations for soil moisture at 10 cm and water content at 20 cm are significant at the 0.01 level. Looking at Appendices 15, 16, 19, and 20 it can be seen that the Keur field is the driest of all 10 fields studied. It is probable that the correlations were found to be significant with such a small sample only because the Keur field was so dry.

The significant relationship between the number of molehills and the amount of water in the soil as measured by soil moisture and water content persisted when all the 10 fields were combined (Table 1). The bulk density of the soil at depths of both 10 and 20 cm was also significantly and negatively correlated with the number of molehills. Thus, moles pushed up fewer hills in areas where the soil was dry and dense, possibly because the soil becomes more difficult to displace when it is heavier and when it is drier, and/or burrows in dense ground stay open longer in such soils and need less repair.

This relationship is also present in the comparison of the Judd field with its control (Table 4). The control field, where there were less molehills (ca 10/ha) had significantly less soil moisture and water content, and a significantly higher bulk density. There was also a significantly greater soil air space at 20 cm in the control field as well, probably because there was less water content (remember that air space= porosity-water content; as water content decreases. air space increases).

The relationship of high mole activity with a low soil bulk density is also present in the comparison of the Hatt field with its control (Table 5), but in this case it was not significant. The Hatt control field had, however, significantly more soil moisture and water content than its paired field which was the opposite of the expected result. This probably occurred because the Hatt control field was situated on low ground and subject to flooding (part of the field was flooded at the time). It is likely that, although the field appeared suitable for moles, they were not present at the time of sampling because of flooding at other times of the year. Samples were collected in August when the field was not flooded.

The significant correlations between the numbers of molehills and the bulk density and water content of the soil were still present when the quadrats without molehills were omitted from the analyses (Table 12), and when rank correlations were used (Table 13). The significance of those with soil moisture was lost. This may have occurred because the plots without molehills usually contained the lowest soil moisture content, and without this extreme in the data set the correlations were insignificant. Again, soil moisture and water content were significantly greater, and soil bulk density significantly less, in areas with mole activity compared to those with none (Table 15).

It is possible that moles were absented from certain study plots because of poor recruitment and dispersal. If this were the case the above results would not indicate that moles prefer a habitat with more soil water and a lighter soil. However, studies on the recruitment and dispersal of the coast mole (Appendices 29 and 30) indicate that recruitment and dispersal were not responsible for the absence of moles from plots in the fields used for this study.

The correlations between the number of molehills and the mineral characteristics considered by field (Table 6) produced only one significant coefficient. It is unclear why calcium is related to molehill numbers in only this one instance.

A plot of the phosphorus content of the soil versus the number of molehills (Figure 2) showed that there was a series of outlying points, all representing the study plots in the Campbell field. It appears that this one field is responsible for the significance of the correlation (Table 14) between molehill numbers and phosphorus when all fields are combined. The land owner informed me that there was a septic tank at one end of the field. This has overflowed and the sewage may have provided food for earthworms, increased their population weight, and increased the number of molehills. The sewage also increases soil phosphorus, which may have correlated with the number of molehills solely because it indirectly measured the food supply of earthworms.

Soil pH was also significantly correlated with the number of molehills (Tables 7 and 12). It is difficult to conceive how pH could be of direct importance to moles, but it can be of considerable indirect importance by its correlation with

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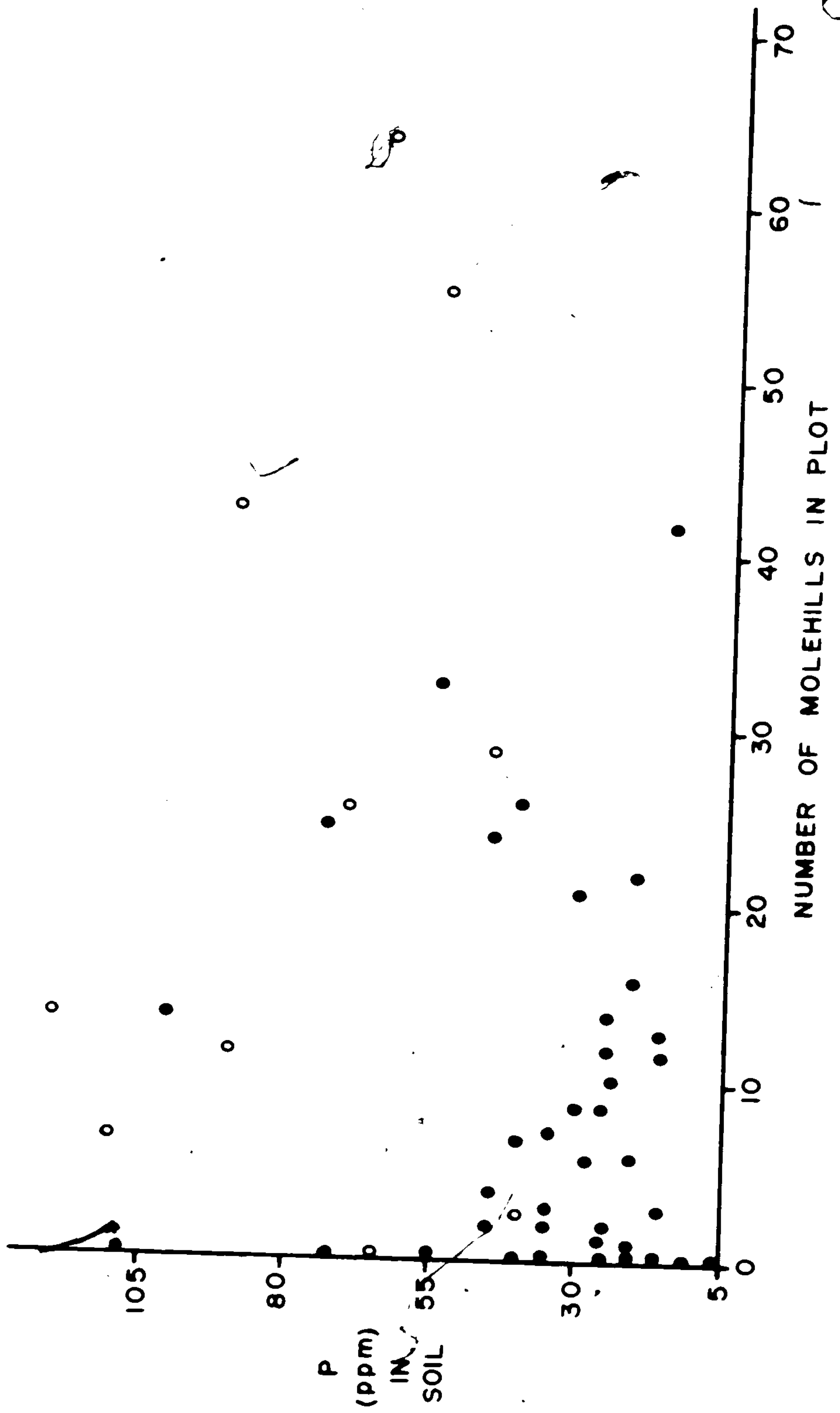
Figure 2. Plot of the phosphorus contents of the study plots in the five fields used in the mineral analyses versus the number of molehills in the plots. Points for plots in the Campbell field are indicated as hollow dots.


P (ppm) IN SOIL
5
30
55
80
105
NUMBER OF MOLEHILLS IN PLOT
0
10
20
30
40
50
60
70

earthworm populations (Table 14). As will be discussed later the number of molehills is strongly related to earthworms, and earthworms are usually reduced in numbers and weight at lower pH (Satchell 1955).

The five fields used in the mineral analyses showed no significant correlations between the number of molehills and physical soil characteristics; the remaining fields showed significant correlations between the number of molehills and soil bulk density at 10 cm and water content at 20 cm. The two groups of fields were also significantly different on the basis of every physical soil characteristic except air space and water content at 20 cm (Table 11). The fact that their correlations between the number of molehills and the soil are different is not surprising if they represent different conditions of mole activity. As stated in the Methods, the five fields used for mineral analyses were chosen because they had the most distinct gradients in mole activity. They differed in this respect from the remaining five fields, and this difference has produced a different set of correlation results.

Results shown in Table 11 are consistent with the trends so far discussed. The fields not used in the mineral analyses had significantly more molehills and had a correspondingly significantly higher soil moisture and water content, and lower bulk density.

B. The relationship ~~of~~ the number of molehills with earthworm populations

In the correlation analyses considered by field (Table 1), only the number of worms was found to be significantly correlated with the number of molehills and in the Keur field only. This may have occurred because the Keur field contained the lowest numbers of worms of all the 10 fields used in the study (Appendix 12). As the number of worms in the Keur field increased from none to a small amount, the number of molehills increased accordingly.

The following results all indicate that more molehills occur in areas with many earthworms. When all 10 fields were combined the total weight of worms and mean weight of worms were found to be significantly and positively correlated with the number of molehills. Both were significantly greater in the Hatt field than in its control (Table 5), and total weight of worms was greater in the Judd field than its control (Table 4). When all 10 fields were combined and plots without molehills were omitted (Table 10), total worm weight was significantly correlated with the number of molehills at the 0.01 level. When rank correlations were used (Table 11) the number of molehills was significantly correlated with the number of worms at the 0.05 level, and with total worm weight at the 0.01 level. In the comparison of quadrats with molehills to those without (Table 13), the mean weight of worms was found to be almost significantly greater (p=0.06) in plots with hills.

The overall picture of the relationship of earthworms with the number of molehills is that moles dig more where they have more to eat, and earthworms are more successful in soils that moles find easiest to dig. These relationships are true for correlations with mean earthworm weight, and especially total worm weight. A causal relationship can be inferred by concluding that moles dig more when they have more energy available for digging. This conclusion makes sense biologically considering the method moles use to obtain food. It must be remembered that the tunnel system acts like a pit trap. It would seem a better strategy, in terms of net energy gain, for moles to dig when they have a good food supply. If they are hungry it would be a disadvantage to expend large amounts of energy digging and extending the tunnel system (pit trap), and an advantage to conserve energy at that time and wait until more earthworms enter the tunnels.

In terms of the biological significance of the three earthworm parameters measured, it appears that the single most important factor related to the number of molehills pushed up is the total amount of food available. The average meal size appears to be next in importance (perhaps only because it is closely related to total worm weight), and the frequency of contact with food least. This last result is not surprising because a mole would have to encounter several worms of low body weight to gain the same amount of energy obtained from a larger worm. There is presumably a lower size limit to the earthworms moles will eat and the number of worms is probably a poor estimate of the amount of available food. It may be the relationship of worm number with total worm weight (Tables 9 & 14) which made the number of earthworms significant in some of the analyses.

In the five fields used in the mineral analyses no earthworm parameters were correlated with the number of molehills (Table 9), whereas in the five fields not used in the mineral analyses (Table 10) the number of molehills is significantly correlated with mean worm weight at the 0.01 level and with total worm weight. Furthermore, the number of worms and total weight of worms were significantly greater in the five fields not used for the mineral analyses (Table 11) which also contained more molehills. The explanation for this difference is a function of the data set used. The fields not used in the mineral analyses included the Judd, Perkin, and Hatt fields which contained the greatest numbers and weights of worms (Appendices 12, 13, and 14), as well as the greatest numbers of molehills (Appendix 11). It is because this extreme is present that the correlations were found to be significant.

C. The relationship of earthworm populations to the soil characteristics

Earthworms live in and are affected by the soil (Satchell . 1955). It is possible that the soil characteristics, instead of directly influencing the number of molehills, do so indirectly through their action(s) on earthworms. Table 3 shows the correlations between the earthworm parameters and the physical soil characteristics for this study. In the Keur field both the numbers of worms and total worm weight are strongly correlated ($p \leq .01$) with soil moisture and water content. In the Brink field these same two soil parameters are strongly correlated with mean worm weight. For ~~all~~ the 10 fields combined the number of worms is correlated significantly with soil moisture, and mean weight with the bulk density of the soil at the 0.01 level. The correlations were positive. In terms of the mineral content of the soil, mean and total worm weights were negatively correlated with organic matter and total nitrogen (Table 8).

It is not possible from the design of this study to statistically infer that the physical soil characteristics are related to the number of molehills indirectly through the earthworms. This possibility will have to remain open. The physical characteristics of the soil could be of direct importance by making the soil easier or harder for moles to dig. In the case of soil bulk density, furthermore, the relationship may be direct because the number of molehills is negatively correlated with the bulk density of the soil, and mean worm weight is positively correlated with soil bulk density. Because the number of molehills is positively correlated with mean worm weight, the relationship of soil bulk density with mole activity is perhaps not due to an indirect relation through earthworms.

The correlation analyses again produced different results when the data ~~were~~ subdivided into the two groups of the five fields used in the mineral analyses and the remaining five fields. In the former mean worm weight was significantly positively correlated with the bulk density of the soil and negatively with air space at 10 cm; total worm weight was significantly positively correlated with the soil bulk density at 20 cm. In the five fields not used in the mineral analyses the number of worms was significantly positively correlated with air space and negatively with water content. Total worm weight was negatively correlated with water content.

Mole activity was not correlated with either the organic matter of the soil or the total nitrogen content, as were mean and total weights of earthworms (Table 8). It would be expected that earthworms weights would be positively correlated with these characters instead of negatively, but the positive relationship is not precluded by these results since the organic matter and nitrogen above ground, available as a food source for the earthworms, was not measured.

Earthworm numbers ~~were~~ significantly correlated with soil pH, phosphorus, and total nitrogen, and earthworm weights were correlated with those factors and soil salts, pH, and nitrate nitrogen (Table 14). All these factors relate to the food supply and pH of the environment of the earthworms, all of which affect their population numbers and weights (Edwards and

Lofty 1972).

D. Multiple regression analysis

The total R-square values for the multiple regression analyses were low. The highest value for this regression analysis was for the combined mineral fields when the plots containing no molehills were omitted. It is hard to say whether the 65.4% of the variance (R^2 Total) accounted for in this analysis was due to good predictor characters, or because there were 21 characters and only 34 plots (R^2 adjusted = 8%). When the sample is increased to 50 plots with the same number of characters only 50.7% of the variance is accounted for. This inverse relationship does not occur when only the physical soil and earthworm parameters are considered. It is true that only 34.7% of the variance is accounted for when all 100 plots are considered but when the sample is reduced to 76 plots there is less variance accounted for (24.6%). Again, the bulk density of the soil and worm weight parameters were of importance, being the first 3 characters to enter in the forward stepwise regression and accounting for most of the variability explained by the regression equation. When the minerals were included, pH was again of primary importance; magnesium was secondary, perhaps because it has a strong relationship with soil bulk density (Buckman and Brady 1967).

The low R^2 totals strongly indicate that the variability in molehills is not being totally explained by the variables considered. They are a good indication that some parameter is missing. This parameter or parameters could be any of those not studied which were mentioned in the preamble, or it could be a synergistic effect of the parameters considered. Whichever the case, a regression equation cannot be formulated which could successfully predict even the majority of the number of molehills pushed up in a plot.

E. Principal component analysis

The results of the principal component analysis (Table 16) agree with those of multiple regression. The fact that there is a number of molehills component (the number of molehills weighted heavily on one component only) is encouraging. However, it is the fourth component, which explains little of the variability (8% in this case) of the data set as a whole. The variability of the other characters may be too great to infer causal relationships between them and the number of molehills.

Furthermore, the characters which heavily weight (correlated highly with the component) the molehill component also heavily weight the other components. This implies that there is no direct relationship between any one of the characters and the number of molehills. What the analysis does indicate, however, is that there is probably some character influencing not only the number of molehills, but also the other characters which loaded heavily on that component. This would favour the interpretation that it is something in the environment and not in the biology of the mole which is affecting the number of molehills. This effect in the environment could be a synergistic factor (which would be difficult to measure or compute), or some factor not measured.

F. Possible sources of error

It is possible that in suitable habitats, territory sizes can be reduced and that there would be more moles in the 1 ha areas used for study within a field. The most likely result of high densities of moles,on the number of molehills would, however, be to have molehills distributed throughout the field rather than in only one part. Secondly, if the habitat is very suitable to moles, there may be more molehills produced if two moles occupy an area usually occupied singly. This increase in molehill numbers would, however, have been counted in the study and related to the more suitable habitat. In other words, the results would be in agreement with the purpose of this study i.e. to find in which habitats there are more molehills. The number of moles is irrelevant.

Another consideration is that the environmental characteristics were measured only once whereas the molehills were actually pushed up over a broad period of time. Because the molehills represent several months of activity it is possible that the 'controlling' conditions were not measured but rather occurred during a previous time. In order to accommodate this possible error to some degree it was necessary to sample the earthworms and soil under relatively constant weather conditions, and to sample over as short a time as possible, so that at least the relative habitat differences between quadrats could be measured. This was done in the study. In the analysis it is also important to look for relative relationships between habitats and relate these to molehill numbers, which was also done.

It may not be sufficient, however, to simply look at relative relationships i.e. increasing or decreasing numbers of hills and increasing or decreasing values for the parameters considered. The absolute values of the parameters may indeed be limiting or enhancing at certain times. This possibility will be considered in the next chapter where seasonal variation in the relationship between molehills and several parameters will be considered.

Finally, the inadequacies of this sort of study acknowledged in the introduction must also be recognized. The number of molehills could vary according to the sex and/or age of the individuals, and according to whether or not the territory has recently been occupied. These factors could add variability to the number of molehills in the study plots and it is variability which cannot be accounted for by the parameters considered. Also, there were certain environmental characteristics which were not measured such as the covering vegetation, drainage patterns of the soil, etc., simply because the task was too great for a single researcher. These characteristics could again add to the unexplained variability.

Conclusion

The number of molehills present in a study plot is positively related to worm weight, soil water content, soil moisture, and pH, and negatively to the bulk density of the soil. The amount of water in the soil and pH were closely related with worm weight and it is possible that the former two are related to the number of molehills only through the latter. If such a relationship holds, then the main factors influencing the digging activity of moles are the weight of worms and the bulk density of the soil.

Chapter 3 Seasonal variation in the relationship of the number of molehills and the physical characteristics of the soil

Both the number of molehills in a particular area and the physical and biotic characters of the soil in such areas vary seasonally. Molehills and soil characters were measured at different times of the year to determine the degree of variability in each, and their relationship with each other. Moles disperse during the summer and sometimes as late as fall and winter. The environmental characteristics at these times could be expected to be of especial importance in determining where a mole will choose to settle and establish a territory. It was therefore necessary to see if the patterns of mole activity within a field changed seasonally. By following such patterns it would be possible to determine if the areas unoccupied in summer remained unoccupied after dispersal (young moles leave the territories of their mothers after May (Glendenning 1959)). If the areas unoccupied during summer were suitable they could be expected to be occupied by dispersing young moles.

Methods

The study areas were the same as those used the previous summer (1976) (Chapter 2). They were 1 ha plots within the Keur, Laity and Robertson fields. These three fields were chosen for study because they had discrete gradients of mole activity and they had empty areas that could be occupied by dispersing young.

The patterns of mole activity had been established in the summer samples (Chapter 2). The relationship of mole activity with the environment during the summer was calculated on the basis of those samples. Any effects that the changing environment may have had on the patterns of activity, or on the relationship of the activity to the environment, were studied by sampling the same study areas in September 1976 (autumn), January 1977 (winter), and April 1977 (spring). In each instance the number of new molehills per 10 x 10 m plot (100 plots per field) was counted. Again, 10 plots were chosen in a line to run through areas of high mole activity into areas of low mole activity. Soil samples were collected as in the summer of 1976. Earthworms were also sampled in September 1976 but no samples were collected afterwards to prevent damaging the earthworm populations with large amounts of formalin. New line transects were chosen for each season if the plots with the highest numbers of molehills were not in the same positions as the previous counts.

The patterns of mole activity of the three fields during the four seasons were plotted and examined for any changes. The soil and earthworm samples for the three fields were pooled, solely to increase the sample size from 10 to 30, and examined for changes in their correlations with the number of molehills over the seasons.

Results

The numbers of molehills in each of the study plots for the Keur, Laity, and Robertson fields for summer, autumn, winter, and spring are presented in Appendices 29-37 and are summarized in Table 17. The distributions of hills in the three fields over the four seasons are presented in Figure 3.

In the Keur field there was only one center of activity (shaded plots) in summer, but a second became established in autumn and expanded in winter and spring. Although this new center of activity was quite large, it did not expand into the original center of activity in the field as can be seen from the diagram for spring; an area of light activity remained between the two territories. There was some light activity in the remaining half of the field in autumn and winter which greatly decreased by spring.

A trend to more activity covering a larger part of the field in winter or spring than in summer and fall was also apparent in the Laity field. Activity was again comparatively heavy in winter. Activity was more diffuse in this field than in the Keur field. It appears that there were centers of activity in two corners; in one of those corners the activity extended towards the middle of the field. In autumn and winter these two centers expanded and a third towards another corner developed. In spring only one of the centers remained very active.

In the Robertson field there were centers of activity in each corner. The mole from the corner in the upper left was

Table 17. The numbers of molehills in the Keur, Laity, and Robertson fields in summer, autumn, winter, and spring.

	Summer	Autumn	Winter	Spring
Keur	345	355	652	666
Laity	358	533	1228	537
Robertson	712	334	396	257
Total	1415	1222	2276	1460

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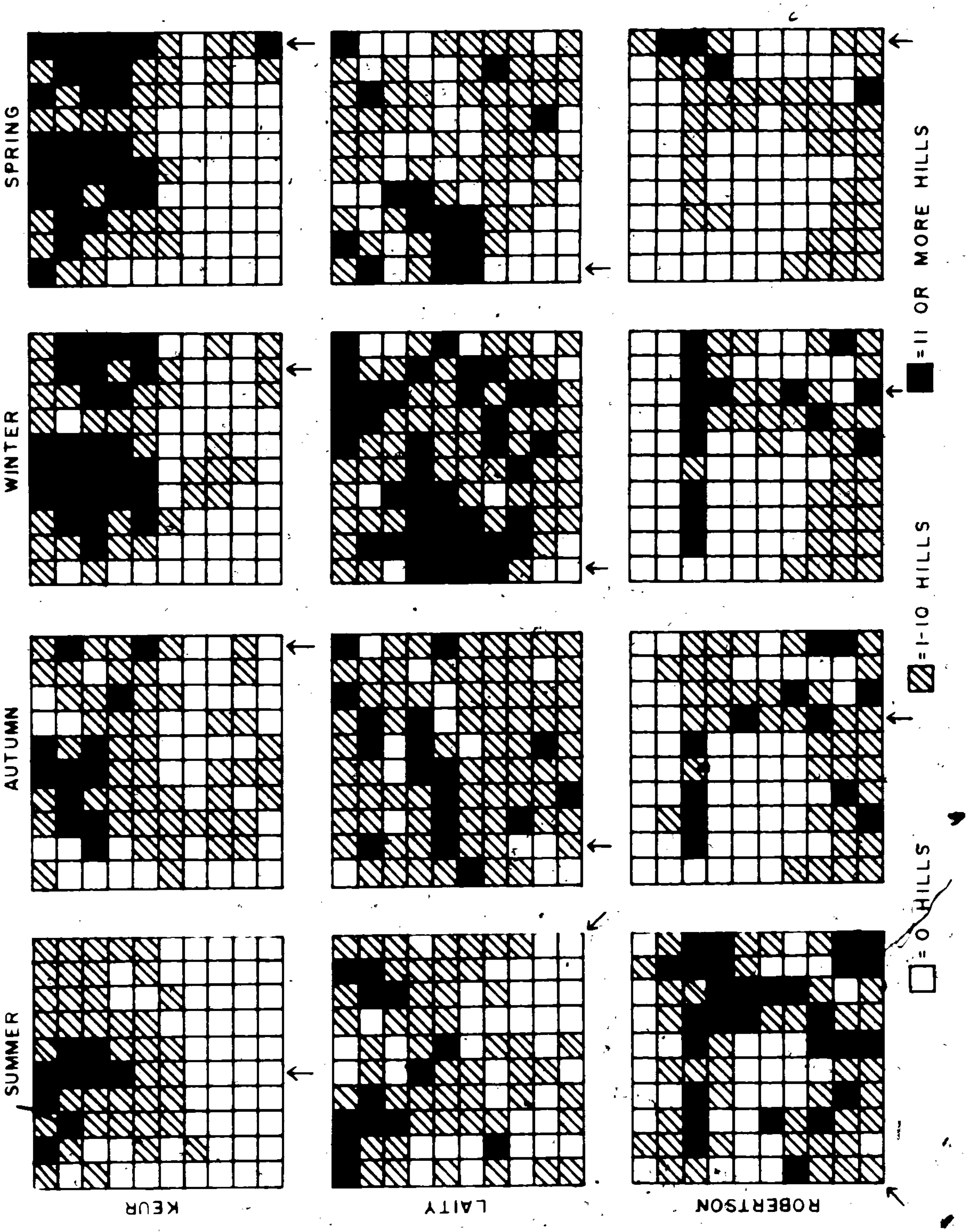
Figure 3. The distribution of molehills in the Keur, Laity, and Robertson fields during summer, autumn, winter and spring. Each diagram represents the study area, each square a study plot (10x10 m). Blank squares contained no molehills, hatched squares 1-10 hills, and solid squares 11 or more hills. The locations of the line transects used to sample soil are indicated by arrows.


SPRING
WINTER
AUTUMN
SUMMER
KEUR
LAITY
ROBERTSON
□ = 0 HILLS
▨ = 1-10 HILLS
■ = 11 OR MORE HILLS

removed by myself at the time of the counts in summer. The mole from the upper right appeared to move into the vacated area, was active in both its original territory and the vacated area in winter, and appeared to return to its original territory in spring. The activity of the other two centers appeared to decrease from summer through to spring.

There were significant negative correlations between the number of molehills and the bulk density of the soil in summer, autumn, and spring (Table 18), but not in winter. The number of molehills was also significantly correlated with the soil air space at 20 cm in spring. Again, there were also no significant rank correlations in winter (Table 19). The bulk density of the soil and soil moisture were significantly correlated with the number of molehills for the remaining three seasons. Soil air space at 20 cm was significantly correlated with the number of molehills in summer and spring.

Discussion

The changes in the distribution and numbers of the molehills over the four seasons are in agreement with Glendenning's (1959) observation that the coast mole is more active in winter than at other times of the year. The activity of the moles was heavy in autumn but this may have occurred because most of the hills had been pushed up within 2 weeks of the count. The activity of the moles was beginning to increase rapidly at this time and the autumn counts include the beginning of this

Table 18. Correlation coefficients (r) obtained between the various soil and worm parameters and the number of molehills for the Keur, Laity, and Robertson fields (total of 30 quadrats) in summer, autumn, winter, and spring.

Character	Summer	Autumn	Winter	Spring
number of worms	-0.14	0.05		
mean worm weight	0.18	0.07		
total worm weight	-0.04	-0.11		
soil moisture 10 cm	0.17	0.26	-0.09	0.29
soil moisture 20 cm	0.20	0.19	-0.22	0.24
bulk density 10 cm	-0.43*	-0.26	0.12	-0.37*
bulk density 20 cm	-0.28	-0.38*	0.19	-0.42*
water content 10 cm	0.12	0.14	-0.07	0.12
water content 20 cm	0.00	0.01	-0.19	0.01
air space 10 cm	0.04	0.01	-0.07	0.27
air space 20 cm	0.13	0.25	0.07	0.40*

$^{*}p \leq .05$

Table 19. Rank correlations (probabilities of significance) obtained in comparisons between the various soil and earthworm characters with the number of molehills for the Keur, Laity, and Robertson fields (total of 30 quadrats) in summer, autumn, winter, and spring.

Character	Summer	Autumn	Winter	Spring
number of worms	0.47	0.50		
mean worm weight	0.48	0.29		
total worm weight	0.43	0.40		
soil moisture 10 cm	0.07	0.01**	0.27	0.05*
soil moisture 20 cm	0.04*	0.02*	0.35	0.06
bulk density 10 cm	0.002**	0.02*	0.27	0.01**
bulk density 20 cm	0.02*	0.01**	0.48	0.01**
water content 10 cm	0.38	0.06	0.23	0.19
water content 20 cm	0.26	0.26	0.34	0.39
air space 10 cm	0.23	0.46	0.43	0.06
air space 20 cm	0.05*	0.25	0.34	0.01**

$^{*}p \leqslant .05$; $^{**}p \leqslant .01$

increase.

The activity of moles seemed to spread into more plots in autumn and winter, and recede from them in summer and spring. This, combined with the lack of any significant correlations of the number of molehills with soil moisture and especially the bulk density of the soil, would indicate that the environment is not limiting mole activity at this time. The bulk density of the soil does not change but the soil moisture does. The increased activity may be due to more water in the soil making it easier to dig in, allowing the moles to become more active. Alternatively, the activity of earthworms is also expected to increase in autumn and winter (optimum temperature for activity in Lumbricus is about 10.5°C (Satchell 1955)), and the increase in the digging activity of moles could simply reflect the increased activity of worms. If worms are more active, it would be expected that they would be more likely to enter mole tunnels and thus increase the mole's food supply and hence increase the number of molehills pushed up (Chapter 2).

The significance of soil air space in summer and spring could be related to other physical soil parameters. Soil air space is a covariable of soil bulk density, and is indirectly related to soil moisture through soil water content.

The lack of significant correlations between the number of molehills and the physical soil characteristics in winter, instead of indicating that these characteristics are not limiting to mole activity at this time, may simply be an artefact. There is always some destruction of the molehills by livestock and this is an error inherent in this sort of study. In winter, however, the destruction is somewhat heavier due to overgrazing and the muddy conditions created by the heavy rains. These two factors introduce a potentially severe bias in the molehill counts and they may possibly have resulted in inaccuracies in winter such that no significant correlations between the number of molehills and the physical soil characteristics were obtained. It can be assumed that the rate of destruction of molehills may have increased but the relative numbers of hills would not be expected to change; there should, therefore, have been some significant rank correlations for winter. This would imply that moles are indeed not limited by the physical soil characteristics in winter. However, the nature of the counting bias is unknown so no conclusion about the bias can be drawn.

Conclusions

There is seasonal variation in the distribution of the number of molehills. Moles were active throughout a greater part of the study areas in autumn and winter. This may have occurred because of an error in counting the number of molehills, but may instead indicate that the bulk density of the soil does not limit mole activity at this time. There were, however, parts of the fields in which moles were never active.

Chapter 4 A test of the possible effect of nitrogen fertilizer on molehill numbers

Ennik (1967) suggested that nitrogen fertilizer reduced the digging activity of the European mole. His experiment consisted of applying ammonium nitrate and limestone, either at a level of 70 kg N/ha or 140 kg N/ha, on plots which were either cut, rotationally grazed by cattle or heavily grazed. He had two replicates for each condition and application and control. He applied the yearly amount of fertilizer in two applications (spring and summer), and counted the number of molehills in each plot each year for 4 years. Continuously grazed plots only received 70 kg N/ha; two plots received a top dressing of dung after grazing, the other two did not. Moles were trapped or killed each year during the experiments. He found that the number of molehills decreased in the sequence; cut plots, continuously grazed, rotationally grazed with high nitrogen application, and rotationally grazed with low nitrogen application. Ennik calculated the mean number of molehills of the 4 years for each condition and did a range test on these four means (cut plots were not considered). He found that there was a significant (p .05) difference between the continuously grazed plots (with or without top dressing) and the rotationally grazed plots with 140 kg N/ha. There was no significant difference between the continuously grazed plots and the rotationally grazed plots with 70 kg N/ha.

Ennik attempted to determine the effect of the fertilizer on moles by looking at its effect on earthworms, the mole's main source of food. The worms in his plots were mainly *Allolobophorba caliginosa* and *Lumbricus rubellus*, with a few *A. chlorotica*. He found that his variation in earthworm numbers and weights was greater within a plot than between plots, so he could not test for any significant fertilizer effect.

Ennik concluded that within cut plots mole activity was not affected by the level of nitrogen application, and within the continuously grazed plots such activity was not affected by a top dressing of dung. He did not state that nitrogen fertilizer reduced the activity of moles in the rotationally grazed plots but the statistical analysis he presents does lead to this conclusion. He obtained no significant difference between the continuously grazed plots and the rotationally grazed plots with 70 kg N/ha, which implied that there was no effect of the grazing schedule on molehill numbers, but did obtain a significant difference between rotationally and continuously grazed plots with 140 kg N/ha. He also states that mole activity is probably related to the number of earthworms. However, he says that 'Data reported in the literature do not support the supposition that treatments with low mole activity may have been unfavourable for worm development.'

I attempted to test Ennik's 'conclusion' that nitrogen fertilizer reduces mole activity by conducting my own fertilizer experiments. Furthermore, I was interested in determining the mechanism by which the fertilizer could influence moles, so I measured the effects of the fertilizer on other aspects of the mole's environment such as the soil atmosphere.

There were four ways in which I believed nitrogen fertilizer might effect the digging activity of moles. These are:

1. The fertilizer reduces the ph of soil through the chemical reaction:

   $NH_4NO_3 + H_2O \rightarrow NH_4OH + NO_3^- + H^+$

   - there was a significant positive relation between the number of molehills and soil pH (Chapter 2).

2. The O_2 content of the soil atmosphere is decreased and CO_2 increased by increased plant growth and microbial activity.

   - moles may dig more hills to aerate their tunnels.

3. By increasing plant growth and hence evapotranspiration, soil moisture is somewhat decreased and the diffusion of soil gases and the atmosphere therefore increased.

   - moles may dig more hills if they can breathe better.

4. If the fertilizer decreases soil moisture through increased evapotranspiration moles may dig less if the soil is dry.

   - there was a significant positive correlation between the number of molehills and soil moisture (Chapter 2).

The experiments I conducted, therefore, were to test the effect of nitrogen fertilizer on mole activity, and to determine whether this effect if it exists, is due to any of the above four reasons.

Methods

A. The experimental design

Individual mole territories (as opposed to arbitrary areas) were chosen as the basic units for treatment and control units to prevent one mole from receiving two treatments. Fifteen mole territories were located on the Laity farm in Maple Ridge. (Figure 4). Territories were located by looking for centers of mole activity which appeared to form discrete units of about 30 x 40 m in area. This size is reasonable considering the results of the tracking study (Appendix 31). The shape of each rectangle included the greatest number of hills in each activity center.

This technique of delineating mole territories proved simple. There were seven territories that were under previous observation and their limits were easily recognized. For the remainder there was some doubt. In territories 4 and 5 there may have been a third individual in the area; in 14 and 15 there may have been a third individual, and; the boundary between 9 and 10 was indistinct. In each of the two instances where there may have been a third mole the territories were so plotted that the third mole could not be digging within more than 2 m of an experimental treatment. Nine and 10 received the same treatment so there was no interference.

The number of molehills in each territory was counted

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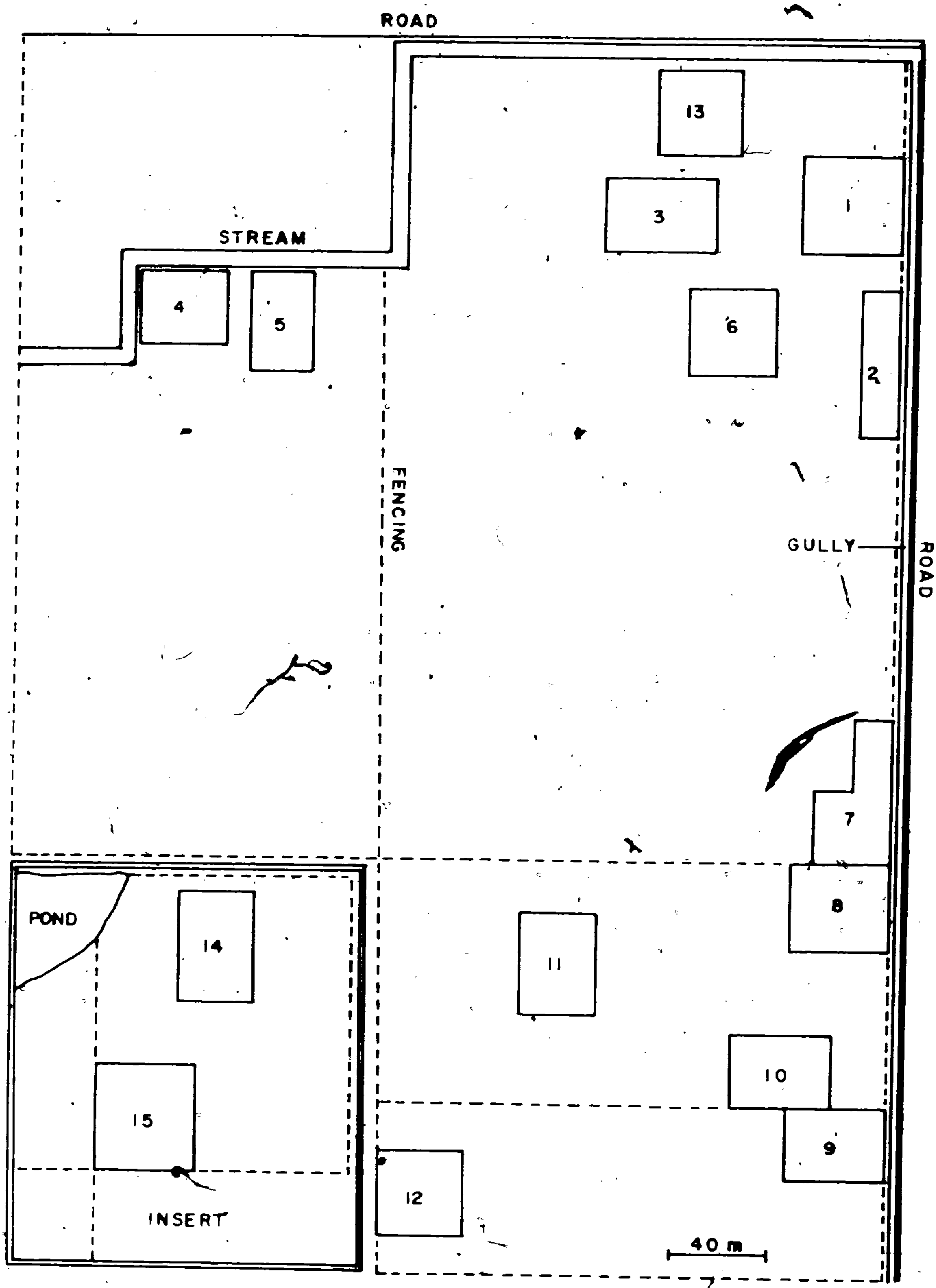
Figure 4. Schematic map showing the positions and sizes of the plots surrounding territories used in the fertilizer experiment (Laity farm, Maple Ridge).


ROAD
STREAM
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using the same method as in the habitat selection study (Chapter 2). The number of molehills initially found in each territory (6 and 7 April), and the condition each was assigned to are presented in Table 20. All fertilizer was applied using a rotary hand spreader according to the schedule in Table 21. The ammoniacal nitrogen used on 25 April was expected to lower soil pH through bacterial action according to the following chemical reaction:

$$NH_4^+ + 2O_2 \rightarrow 2H^+ + NO_3^- + H_2O$$

and would thus have the same effect as the ammonium nitrate used by Ennik (1967).

B. Measuring changes in molehill numbers and the environment

The new molehills in each of the 15 territories were counted at about 2-week intervals. Soil and air samples were collected from 3 territories only - number 4 (control), number 7 (140 kg N/ha), and number 10 (70 kg N/ha). Five soil samples were collected from each of the three territories - four from 5 m towards the center from each corner, and one from the center itself. They were collected when the molehills were counted. The moisture content of the soil was calculated after the sample was air dried. The soil was then ground with a mortar and pestle and passed through a 24 mesh sieve. The pH was determined on a 10 cc sample of this soil by adding 10 cc 0.01 M calcium chloride and stirring occasionally for 1/2 hr (McMullan 1972). The pH of the soil was read from this treated sample using a Fisher

Table 20. The 15 territories used in the fertilizer experiment. The number of molehills found in each territory on 6 and 7 April, 18 and 19 days before fertilizer was applied, are presented, as well as the treatment, dimensions, and area for each territory.

Territory	# molehills	Treatment	Dimensions(m)	Area (m^2)
1	144	140 KgN/ha	40x40	1,600
2	257	control	60x15	900
3	226	140 kgN/ha	30x45	1,350
4	348	control	30x35	1,050
5	221	140 kgN/ha	25x40	1,000
6	67	control	35x35	1,225
7	407	140 kgN/ha	30x30; 30x15	1,350
8	253	70 kgN/ha	40x35	1,400
9	355	70 kgN/ha	40x30	1,200
10	397	70 kgN/ha	40x30	1,200
11	103	140 kgN/ha	40x30	1,200
12	102	control	30x35	1,050
13	99	70 kgN/ha	35x35	1,225
14	78	control	30x45	1,350
15	90	70 kgN/ha	40x45	1,800

Table 21. Description of the fertilizer treatments for the 10 mole territories (remaining five were controls).

Fertilizer	8, 9, 10, 13, 15	1, 3, 5, 7, 11
25 April		
rate •	70 kg N/ha	140 kg N/ha
formula	41-0-0 (Scott's)	Scott's 41-0-0
composition	30% water soluble and 10.1% water insoluble nitrogen from ureas and Methylene ureas with a potential acidity equivalent of 681.8 kg (1500 lbs.) $CaCO_3$/ton	
11 July		
rate	17½ kg N/ha	35 Kg N/ha
formula	34-0-0 (Green Valley)	41-0-0
composition	50% nitrate nitrogen, 50% ammonical nitrogen.	
11 July		
rate	17½ kg N/ha	35 kg N/ha
formula +	16-16-16 (Terico)	16-16-16
composition +	nitrogen as urea, phosphorus as $P_2\ O_2$, potassium as K_2O.	

• Same as annual rate used by Ennik (1967); form of nitrogen used by Ennik (1967) was ammonium nitrate.

+ Formula and composition for phosphorus and potassium are same as used by Ennik (see Ennik (1965)); only ½ annual rate for all minerals was applied on 11 July.

ACCUMET Model-420 digital pH/ion meter.

The nitrate and ammonia contents of the soil were determined for samples immediately before and at weekly intervals after the second fertilizer application. A Simplex Soil Test Kit, Edwards Laboratory, Norfolk, Ohio, was used to determine their concentrations in ppm.

C. Sampling the air within the soil and mole tunnels

Ten air sampling sites were established in the runways of each of the three territories used to collect soil samples. Samples were collected through Tygon plastic tubing 3 mm in diameter with bore of 1 mm. The tunnel underneath a molehill was located and one end of the tubing was placed inside; the hole was then covered with earth and packed leaving about 10 cm of tubing above ground; the open end of the tubing was plugged with a toothpick. The sample tubes were placed in an approximately uniform distribution throughout each of the three territories. The average depths of the tubes were: 13.3 cm, 11.7 cm, and 12.2 cm for territories 4, 7, and 10 respectively.

At about a 1 m distance from five of the sample sites in each of the three territories I buried an inverted clay pot (5 cm bottom diameter, 10 cm high) in a hole 20 cm deep to sample air in the soil. Tygon tubing led from the pot to the surface of the ground. The device for sampling soil air described by Russell and Appleyard (1915), had been constructed but was ineffective in the soils in the Laity field. Other methods of sampling soil air require that a soil sample be removed and the air collected by water displacement. These were not used because they seemed to introduce a large sampling error due to the handling of the soil.

Air samples were collected through the tubing with 30 cc plastic disposable syringes the day following the molehill counts. The toothpick was removed from the end of the tubing and the syringe needle (20 ga) inserted. A 20 cc sample of air was withdrawn and discarded to clear the tube. A 5 cc sample of air was then withdrawn and discarded to clear the needle. Then, a 30 cc sample of air was withdrawn and later used for analysis as the tunnel or soil air.

The air samples were brought back to the laboratory and their carbon dioxide and oxygen contents determined with a Scientific Research Instruments Co. Medspect 1 medical mass spectrometer to an accuracy of ± 0.1%. All samples were collected between 0750 and 1000 hrs, and were analyzed within 4 hrs. Loss of CO_2 through the plastic is not expected to occur before 6 hrs (Consolazio 1963). Losses through the rubber stoppers used to seal the needles would be negligible.

D. Testing the effects of nitrogen fertilizer on earthworms under laboratory conditions

Ten one-gallon jars were filled with alternate layers of white quartz sand, and potting soil containing dolomite. The bodies of the jars were square (15 x 15 x 15 cm) with rounded edges. A layer of 500 ml of sand was placed into the bottom of each, followed by 500 ml of potting soil which was lightly pressed when in the jar. These were followed by layers of 250 ml sand, 500 ml potting soil, 250 ml sand, and a final 500 ml of potting soil. A layer of 500 ml of crumbled leaf litter collected in an alder thicket was then added to each jar.

Five of the jars were used as a control. For the remaining five an equivalent treatment of 140 kg N/ha (0.92 gm) of the Terico fertilizer used in the field experiment was placed uniformly under the layer of litter in each jar. Each of the 10 jars was then given 500 ml of water poured 100 ml at a time over the litter. The jars were left uncovered overnight at room temperature. In the morning they were sprinkled lightly with water to moisten the litter (about 50 ml additional water per jar).

Earthworms were obtained from a local sales merchant. They were all relatively large of the genus Lumbricus, mainly, if not all, Lumbricus rubellus from their appearance. They were brought to the laboratory, individually washed, dried, and weighed, and placed into the 10 jars, six to the jar. The tops of the jars were then covered with a paper towel fixed with a rubber band. The jars were wrapped in dark plastic and held at about 13°C for 39 days (29 September - 7 November, 1977).

On 7 November the worms were removed from the jars and individually washed, dried, and weighed. Samples of soil were collected from the three layers of potting soil in each jar (some sand was now mixed in with the soil), and allowed to air dry for 1 week. The pH of the soil was then determined in the same manner as the field soil samples except that the soil was not ground and sieved.

Results

The number of molehills, O_2 and CO_2 in the tunnels and soil, pH, and soil moisture for the territories 4, 7, and 10, are given in Appendices 49-51 respectively. In most cases it was not possible to sample the tunnel air from all 10 tubes, and the soil air from all five tubes, because some tubes were usually pulled from the ground by livestock. As a result the sample sizes for these parameters varied. In each case when a tube was pulled from the ground it was simply repositioned and left until the next sampling period. The moles themselves rarely plugged the tubes with earth.

Table 22 shows the pooled numbers of fresh molehills found in the control groups, and those treated with 70 kg N/ha and 140 kg N/ha at each sampling date. Hill counts for individual plots are in Appendix 52. It can be seen from these totals that there were no reductions in the number of molehills as a result of the fertilizer treatments. There were measurable (1-25 ppm) amounts of nitrogen in the experimental plots after the

Table 22. The number of molehills in the five territories (totals) for each treatment in the fertilizer experiment. Counts were made at approximately 2 -week intervals during the summer of 1977.

Date	Total number of hills in treated territories Control	 70 kgN/ha	 140 kg N/ha
25 April *	139	229	173
4 May	99	130	117
16 May	165	229	145
1 June	104	225	163
20 June	52	142	105
4 July	86	138	151
18 July *	68	151	99
1 August	23	90	84
15 August	3	5	20
29 August	40	105	119

* Fertilizer was applied on these dates (See Table 21).

experiment (Appendix 53).

The correlations obtained between the number of molehills and the tunnel and soil gases, and soil pH and moisture for the three territories combined where this information was available are presented in Table 23. The soil air samples for territory 7 on 20 June were omitted from the analyses because only one sample was available from that territory on that date. The samples for O_2, CO_2, soil moisture, and pH, were averaged for each territory on each date, and these means were used in the correlation analyses with the number of molehills.

Because information was not available for certain characters on certain dates, several correlation analyses were performed to provide the maximum sample size for each character. Only 23 complete samples for all characters were available (three territories over eight dates with one omitted because only one sample was available). There were 27 samples available for the tunnel gases, soil pH and moisture (soil air was only sampled starting with the second sample date); and 30 samples were available for soil moisture and pH (the mass spectrometer was broken at the time of the last sample so the air samples which had been collected could not be analyzed). The number of molehills was found to be highly correlated with the pH of the soil ($p \leq .01$), and was also correlated with soil moisture ($p \leq .05$).

The analyses were also performed on the individual territories. The number of molehills was found to be significantly

Table 23. Correlations obtained among the number of molehills, O_2, and CO_2 concentrations in the tunnels and soil, and soil pH and moisture in the three territories for which these parameters were measured. Sample sizes are included in brackets representing eight dates from each of two territories and seven for the third (n=23), all three territories for nine dates (n-27), and all three territories for 10 dates (n=30).

Character	molehills	O_2 in tunnels	CO_2 in tunnels	O_2 in soil	CO_2 in soil	pH
O_2 in tunnels	-0.25 (27)					
CO_2 in tunnels	0.16 (27)	-0.92** (27)				
O_2 in soil	-0.08 (23)	0.86** (23)	-0.95** (23)			
CO_2 in soil	0.12 (23)	-0.82** (23)	0.97** (23)	-0.97** (23)		
pH	0.69** (30)	0.00 (27)	-0.12 (27)	0.09 (23)	-0.10 (23)	
soil moisture	0.40* (30)	-0.84** (27)	0.87** (27)	-0.82** (23)	0.84** (23)	0.10 (30)

$^{*}p \leqslant .05$; $^{**}p \leqslant .01$

correlated with soil pH in territory 7 (r=0.69*), and soil moisture; in territories 4 (r=0.65*) and 10 (r=0.64*) (n=10). In no instance was the number of molehills significantly correlated with either CO_2 or O_2 in the soil or tunnels.

The percent of O_2 was negatively correlated with the percent of CO_2 in both soil and tunnel samples, and the concentrations of the gases within the tunnels were positively correlated with the concentrations within the soil.

The highest level of CO_2 found in any individual tunnel sample was 5.5%, and the lowest O_2 concentration was 14.3% (these are not in Appendices 49-51 because they are individual samples whereas those in the tables are based on averages). For the soil samples the highest level of CO_2 was 11.3% and the lowest level for O_2 was 8.3%. An analysis of variance indicated that there were significant differences in the gas concentrations among the three territories on all dates except 5 May. Territory 7 (70 kg N/ha) had significantly the highest level of O_2, and lowest CO_2, territory 4 (control) usually had the lowest level of O_2 and highest CO_2 of the three territories.

Graphs illustrating the fluctuations in the number of molehills, percent O_2 in the tunnels, and soil moisture in the three territories over time are presented in Figure 5. The pH of the soil is not included because the fluctuations were slight (this did not preclude a significant correlation between the number of molehills and soil pH). There appeared to be some correspondence between the appearance of molehills and the

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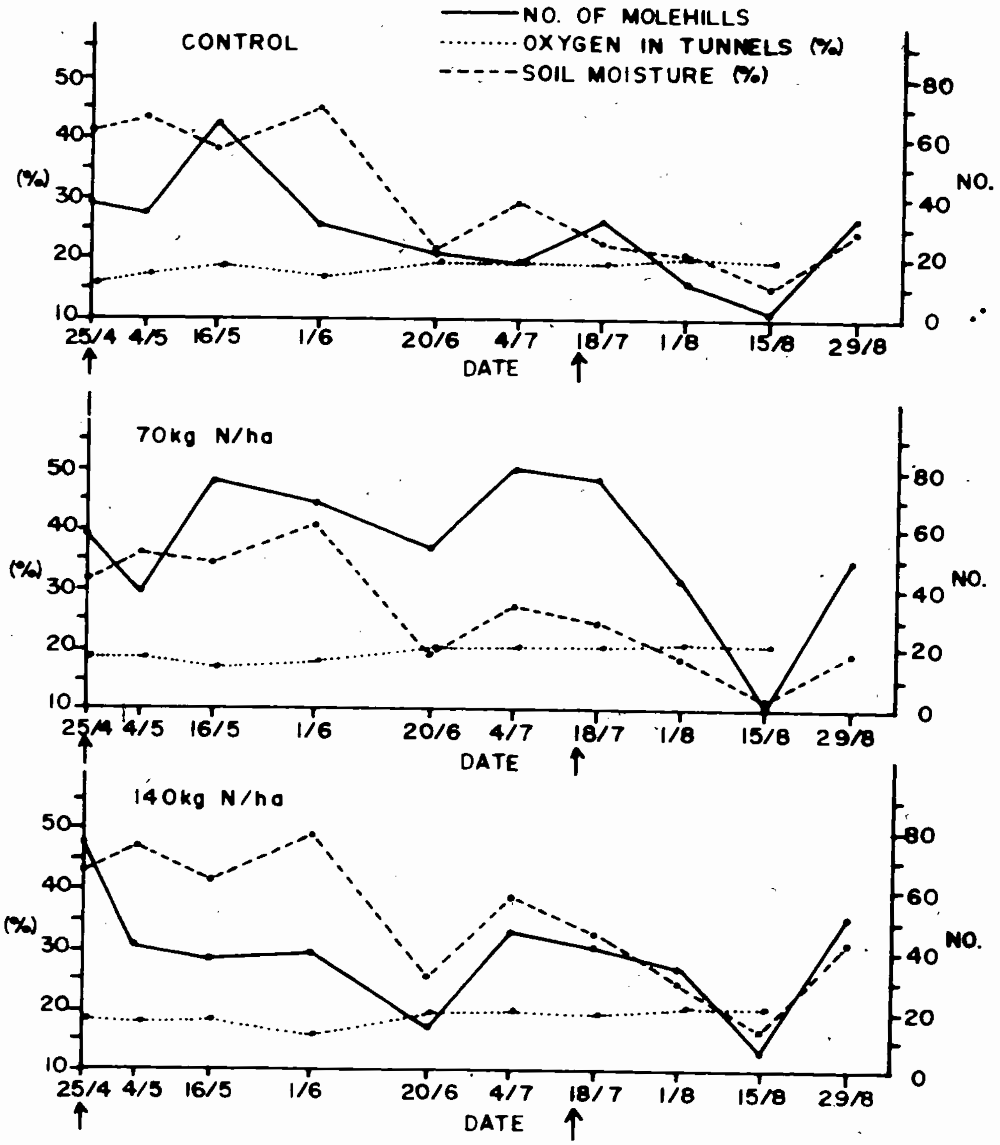
Figure 5. Graphs showing the fluctuations in the number of molehills, O_2 concentrations, and soil moisture over time in the three territories for which this information was available. The fluctuations in the number of molehills for the remaining territories were similar. The times of fertilizer applications are indicated by arrows.


NO. OF MOLEHILLS
OXYGEN IN TUNNELS (%)
SOIL MOISTURE (%)
CONTROL
70kg N/ha
140kg N/ha
(%)
10
20
30
40
50
NO.
0
20
40
60
80
25/4
4/5
16/5
1/6
20/6
4/7
18/7
1/8
15/8
29/8
DATE

occurrence of rains.

The laboratory experiment with earthworms showed that those in fertilized soil lost weight, while those untreated were gaining, thus:

	No.	Before mean wt. in g		No.	After mean wt. in g	
Experiment	31	3.58 ± 0.38	$p=0.72$	30	3.20 ± 0.38	$p \leq .01$
Control	29	3.68 ± 0.38		29	3.79 ± 0.35	

The pH of the soil in the control group after the experiment was 5.90 ± 0.12 and in the experimental group 5.61 ± 0.10 (based on three samples per jar, five jars in each group. The difference between the groups is significant ($p \leq .01$). The lower layers in all jars had higher pH values than upper layers.

Discussion

The fertilizer treatments did not appear to have any consistent effect on mole activity in the experimental plots. The fertilizer also had no measureable effect on the concentrations of O_2 and CO_2 in the soil or in the tunnels of the moles, nor on soil pH.

The number of molehills in the three territories for which the environmental parameters were measured correlated very highly with the pH of the soil and with soil moisture. These results are consistent with previous results (Chapter 2) where both these characters were correlated with the activity of moles in 10 fields. Soil pH varied from 4.41-5.20. Soil moisture was more variable, 11.90-48.98%, because of a long period of dry weather during the summer. The pH of the soil is important to earthworms (Satchell 1955) and the number of molehills could be correlated with soil pH because of its effect on a mole's food supply. Earthworm samples were collected only once before the fertilizer treatment, and twice afterwards (data not presented). There did not appear to be any relationship between the activity of moles and the number or weight of earthworms, probably due to the small sample sizes.

The CO_2 levels in the mole tunnels averaged more than 10 times that of the atmosphere, and reached levels 200 times that of the atmosphere in individual samples. Oxygen concentrations were found to be inversely correlated, but not to the same degree. These high levels of CO_2 and low levels of O_2 would normally be exaggerated for moles in deeper tunnels and further away from the molehills because there would be less aeration.

The O_2 and CO_2 contents of mole tunnels are interesting and important because the mole has a high metabolic rate, digs underground, and still manages to breathe without surfacing.

The actual levels of these gases in the tunnels has never been measured before, although Quilliam et al (1971) speculated that moles may breathe air with as much as 5% CO_2. It seems, however that the levels of these gases are of great importance to moles. This is evidenced in their various adaptions to living in O_2 deficient air. Korzujev and Koreckaja (1962) have reported that in comparison to other mammals its own size, the European mole has twice ~~the amount~~ blood, haemoglobin, and lungs. The serological composition of the bloo[illegible]f the European mole is also different from that of non-fossorial mammals of similar size (Dabrowski and Skoczen 1962, Quilliam et al 1971).

I found that CO_2 levels in the soil air are about twice as great as those within the mole tunnels. This indicates how well the mole runs are aerated, either by diffusion or by the movement of air through molehills which is related to the air movements (wind) above ground (Olzewski and Skoczen 1965), or both. The levels in the soil and tunnel samples are, however, almost perfectly correlated. Thus, although the runways are being aerated the concentrations of O_2 and CO_2 are still influenced by those in the soil air.

The CO_2 contents of the air of both the soil and tunnel increased with increasing soil moisture. This relationship is probably due to the soil air space. As soil moisture increases the soil air spaces decrease and there is less diffusion of the soil gases into the atmosphere and vice versa. As soil air space increases with decreasing soil moisture there is an almost free exchange of gases and their concentrations approach equality.

In no instance did changes in the CO_2 or O_2 concentrations correlate with changes in the number of molehills in any of the three territories observed. This occurred even though fertilizer had been applied to two of the territories. The fertilizer was also found to have no effect on the levels of the two gases.

It is apparent that the estimate of Quilliam et al (1971) of concentrations of up to 5% CO_2 in mole tunnels is too low. The coast mole is living in tunnels with as much as 5.5% CO_2 in the vicinity of a hill where the concentration is expected to be much lower than at a deeper depth and away from a hill. Laboratory experiments investigating the effects of high carbon dioxide levels on the metabolism of the California mole (Scapanus latimanus) are currently being conducted by John Nogue, Department of Physiology, San Francisco State University, San Francisco, California. The results of his experiments may help answer questions concerning any possible effects of high carbon dioxide levels on mole activity.

It is apparent from the results of other researchers that moles are well adapted to living in the type of atmosphere found in their tunnels. These adaptations include increased blood and haemoglobin weight, and serological factors.

The results of the experiments conducted on earthworms in the laboratory confirm one theoretical effect of the nitrogen fertilizer on a mole's food supply. The pH of the soil dropped as a result of the fertilizer application, and the weights of the earthworms probably decreased because they were sensitive to acidic conditions.

The effects of fertilizers on soil fauna have been considered by many researchers and their results are reviewed by Marshall (1977). The general conclusion of their work is that any non-acidifying forms of nitrogen fertilizer tend to increase earthworm populations, but the acidifying forms decrease earthworm populations. Anhydrous ammonia is lethal when earthworms come into direct contact.

However, the high levels of CO_2 and low levels of O_2 found in the mole tunnels in this study, and the fact that moles are known to be living in these tunnels, indicates that the coast mole possesses at least some adaptations similar to those found in the European mole.

The field experiment in this study did not support Ennik's (1967) hypothesis that nitrogen fertilizer reduced numbers of molehills. Neither of the fertilizer treatments had significantly fewer molehills than the controls.

Ennik's study also in itself, did not appear to support his original hypothesis for the following reasons:

1) He had no pre-treatment counts of the molehills so he had no measure of the usual distribution of molehills.
2) His cut plots were only one-quarter the size of his grazed plots. The treatments in the cut plots may

therefore have interfered with each other (cut plots were 8 m wide; European moles normally move over an area about 35 m long).

3) He only had two replicates of each condition and treatment.

4) An analysis of variance testing for differences among his combined replicates and comparing the number of molehills in the plots over a 4 year period showed that although the trend was apparently striking, it was not significant (F=2.10; p=0.25). Ennik himself used a range-test on the means; these are my results from the analysis of his data.

However, as mentioned previously it is possible that nitrogen fertilizer can, under certain circumstances, control molehills by reducing the weights of earthworms. Although Ennik's study was inconclusive and his results non-significant (by my analysis), it is possible that the fertilizer he used was successful in reducing the pH of his study plots, which resulted in the desired trend. Ennik did sample the earthworms in his plots and did not find any differences, but he used potassium permanganate as the extracting solution which is not the best of procedures (Raw 1959).

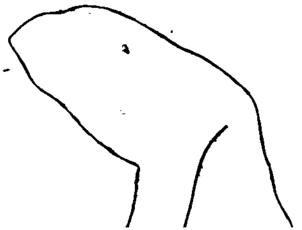
The ability of an acidifying fertilizer to reduce the pH of the soil depends on several factors. The nature of the soil is important. The composition of the soil colloids, the concentration of the cations other than hydrogen, the base saturation and the ratios of the various cations all interact in determining whether hydrogen ions will become attached to the soil colloids and thus reduce soil pH. Weather is also important. A high rainfall will tend to leach cations from the soil leaving many binding sites on the soil colloids free for the hydrogen ions to attach themselves (Buckman and Brady 1969). These factors could have been more favourable for a reduction in soil pH in Ennik's study than in mine and could have resulted in a reduction in the number of molehills after application of nitrogen fertilizer.

Ennik applied limestone along with the ammonium nitrate in his experiment - limestone increases the pH of the soil, but its ability to do so depends on the form used and the nature of its application. If it is finely ground (e.g. lime (Ca CO_3)), it will increase the pH of the soil.

If it is not it enters the ground very slowly because it depends on erosion of the mineral. Ennik does not mention the form he used. Also, when limestone is applied to a field as a top dressing as in Ennik's experiments (as opposed to being dug into the ground), it may not reduce soil pH for several years (Buckman and Brady 1969). Therefore, it seems unlikely that the limestone used by Ennik would counteract any reduction in soil pH caused by the fertilizer. In conclusion, Ennik's observation can be summarized as:

nitrogen fertilizer → reduced molehill numbers

The mechanism which I formulated for this effect is:



nitrogen fertilizer → reduced pH → reduced mean worm weight → reduced number of molehills

My experiment showed that in my study plots:

nitrogen fertilizer → reduced pH

My laboratory experimental results were:

nitrogen fertilizer → reduced pH → reduced mean weight

And the final model which I have formulated to explain why fertilizer can control molehill numbers under appropriate soil conditions is as follows:

acidifying fertilizer → reduced pH → reduced worm weight → reduced molehill numbers

I established correlations between molehills numbers with worm weight in Chapter 2. There is a good biological reason for suspecting this relationship to be causal: earthworms are the chief food source of both the European and coast moles and determine the amount of energy available for digging.

This model can be tested by using acidifying agents other than ammonium nitrate, ureau, or other nitrogen fertilizers, and see if these reduce molehill numbers. A complementary study monitoring the effects of different weather conditions, especially rainfall on the action of these agents would also be desirable. If possible, earthworm samples should also be collected in the field by sampling from plots other than those in which molehill counts are taken. The scope of such a study is large but, if weather conditions are suitable, funds are available for large amounts of fertilizer, and several people are used to collect the necessary data, it may be done within 1 year.

Conclusions

Nitrogen fertilizer may be used to control molehill numbers under certain soil and weather conditions. If it, or some other acidifying agent successfully reduces soil pH, molehill numbers may be reduced indirectly by a reduction in earthworm numbers and weights.

Chapter 5 General Discussion

The numbers of molehills on plots within fields were found to be significantly correlated with the soil parameters of bulk density, air space, and water content. Moles pushed up more hills where soils were light, wet, and with reduced air space. Plots with molehills contained more earthworms and had worms of greater mean weight than plots with no molehills in the same fields. When one field (Hatt) with many molehills was compared with a nearby control with few molehills, the mean worm weight and total weight of worms per plot were significantly heavier in the former. In a second pair of fields the mean worm weight in the Judd field was significantly heavier than in its control.

The physical and biotic environments thus apparently influence where a mole will dig. The relative importance of the physical and biotic components could not be demonstrated in this study because the major biotic component, earthworms, live in the soil and furthermore, could themselves be influenced by the digging activity of moles.

The habitat differences between areas with and without moles can be explained in part by the resistance of the soil to digging. Heavier and drier soils are more difficult to penetrate than lighter and moister soils. Moles may be digging in areas where it is easier for them to dig. This seems reasonable as the mole is a relatively small mammal with a high metabolic rate. Digging and removing earth from the tunnel system is assumed to require a great deal of energy. Digging in hard dry soils could be difficult and thus energetically uneconomical for a mole to occupy such areas permanently.

If the physical habitat is merely a covariable of the earthworm supply I conclude that moles dig most in areas where food is more available. This agrees with conclusions of previous researchers. Milner and Ball (1970) found that moles preferred mineral rich, freely drained, brown or brown podzolic soils that are greater than 1 foot in depth and with a pH greater than 4.0. They postulated that these factors were all necessary for a good earthworm population, (although they may not survive in a pH as low as 4.0), and that the digging activity of moles was only affected by the stoniness of the soil.

Funmilayo (1977) and Glendenning (1959) both concluded that the density of moles increased only with an increase in their available food supply. Funmilayo states: "... it is the soil type and soil conditions that directly determine the species distribution and abundance of earthworms and indirectly the distribution and abundance of moles".

Funmilayo (1977) also made the observation that in two study areas 'A' and 'B': "The number of molehills per hectare was 1455 in A and 292 in B or 131.1 ha and 43.6 ha per mole in A and B respectively which indicated that more molehills were made in deep heavy soils with many earthworms than in shallow light soils with a few earthworms". The results of my study agree with Funmilayo's observation that more molehills occur in areas where the earthworm supply is greater. However, in my study, and that of Arlton (1936), more molehills were found in lighter soils than in heavier. This contradicts the observations of Funmilayo and of Skoczen (1958) who found most hills in heavier soils. It should be noted that neither Funmilayo or Skoczen measured soil bulk density so that their use of the term "heavy" may be inaccurate.

The physical characteristics of the habitat may influence the number of molehills independently of the food supply. Hardy (1945) points out for example that the habitat of an animal not only provides food, but affords shelter. Moles depend on their tunnel systems for shelter - it is where they live. The species thus has certain habitat requirements which go beyond the provision of a food supply.

Perhaps the best evidence that the habitat influences directly the digging activity of moles ~~is~~ seen in the correlation analyses of Chapter 2. The number of molehills was found to be strongly correlated with the total weight of worms, negatively with the bulk density of the soil and water content, and further significantly correlated with the mean weight of worms and soil moisture. If the physical components of the habitat were influencing the number of molehills through their effects on earthworms, it would be expected that the mean and total weights of earthworms would show the same relationship to physical habitat components as did the number of molehills. None of these similarities was found (Table 1). The total weight of worms showed no significant correlation with any physical habitat parameters. Mean worm weight was found to be positively correlated with the bulk density of the soil. This correlation would have been negative if the physical habitat was exerting the same influence on earthworms as on molehills.

This is not to imply that the physical components of soil do not effect earthworms. The relationships of earthworms with the physical characteristics of the soil are well established (Satchell 1955, Edwards and Lofty 1972). In my study, however, correlations between earthworm measurements and soil characteristics were low and generally not significant.

The multiple regression analysis of the variation between plots indicates that the earthworm and physical habitat parameters measured explained only 35% of the variability in the number of molehills. I cannot account for this result in view of the significant correlation and F-test results obtained from other analyses. Correlations are no proof of causality. However, if there is a strong correlation between two variables and there are good biological reasons for suspecting a causal relationship, the correlation analyses can strongly suggest biological relationships. The F-test results are in agreement with those of the correlation analyses. The only apparent difference between the plots used to make the comparisons were the presence or absence of molehills. Therefore, I conclude that those variables found to be significantly different between the groups are of importance in determining the presence or absence of molehills.

The conclusion of the regression analysis would be that, although several of the factors were found to be significant to molehills, there may be other unmeasured factors important in the determination of their numbers. These may include surface vegetation, the sex and age of individual moles responsible for the molehills and whether or not the molehills are on newly formed or long established territories. There may also be degrees of synergism and/or antagonism between the factors measured, or between factors measured and unmeasured, which would be of importance.

I am unable to speculate on how much of the variability in the number of molehill counts is accounted for by the different individual parameters that I measured. The multiple regression analysis on the results of the present habitat selection study may be misleading because of the apparent interactions of the variables themselves and possible synergy. Therefore, it cannot be concluded from the low coefficient of differentiation that the characters I measured were of little importance to moles. The F-test results showed that the bulk density of the soil was related to the number of molehills. However, in the nitrogen fertilizer study (Chapter 6) I established that the number of molehills within the same territory varied over time as did changes in soil pH and moisture although the bulk density of the soil did not alter. This type of interaction increases the variability of my habitat measurements but at the same time decreases the total coefficient of differentiation for the data. Similarly, the mean weight of the worms was found to increase with increasing soil bulk density, and the number of molehills increased with in-increasing mean weight of the worms. However, the number of molehills decreased with increasing soil bulk density. Although, these relationships can be detected by univariate methods of data analysis they confuse a multiple regression analysis when the number of molehills is the dependent variable.

I conclude that the bulk density of the soil, soil moisture, water content, and mean and total worm weights are of importance in influencing the presence or absence of molehills in an area, and along with soil pH, the number of molehills produced.

It was a priori unclear as to whether moles dig more in suitable or unsuitable habitats. In my study moles were found to dig more in areas where there was more food than in areas where there was less food and where it was easier for them to dig. These characteristics seem biologically favourable to moles so I conclude that they dig most in a suitable habitat.

This conclusion implies that moles dig more if they have more energy available to do so, than if they have less and/or it does not require much energy to dig. Because molehills are pushed up during the construction of the deeper tunnels characteristic of permanent territories (Godfrey and Crowfoot 1960), it can be concluded that moles only establish territories where there is a good food supply and where constructing the tunnel system does not require large amounts of energy.

This deduction is consistent with Godfrey's (1955) findings on habitat differences in the types of tunnels constructed. She found that European moles in recently ploughed fields (where there are low numbers of earthworms) constructed long shallow tunnels which were shortly abandoned.

There seem, therefore, to be two hunting strategies used by moles. If there is an abundance of earthworms the mole will construct a permanent "pit trap" system. Because there are many worms the chances that they will enter the tunnels are greater than otherwise and a pit trap system is effective. If, however, there are few earthworms a pit trap system would not be expected to be effective and moles must dig after the worms and construct shallow hunting tunnels which are not permanent and must be constantly constructed anew. Moles can only use this latter strategy if they obtain more energy from their food supply than is required to constantly construct new tunnels. Thus, if there are few earthworms and the soil is hard the mole would probably lose more energy digging than it obtains from its food supply, and it is in such areas where moles are absent.

Soils may be difficult to dig at one time of the year and not at others, and soils which have few earthworms at certain times of the year may have a greater supply at other times. This may occur due to the effect of seasonal changes in soil moisture. Dry soils are more difficult to dig in and contain fewer earthworms than wet soils. In the B.C. Lower Mainland the soil is drier in the summer than in winter (Appendices 15, 16, 40-49), and I found moles entered areas in winter that were unoccupied during the summer (Glendenning (1959) observed that moles emigrated from cultivated fields to pastures in winter). I was also able to measure an increase in the number of molehills pushed up during winter, as Glendenning (1959) stated was the case. An increase in soil moisture during winter may explain why the bulk density of the soil was not significantly related to the number of molehills in winter whereas it was at other times of the year.

If moles enter a new area in winter they may be able to construct enough tunnels for the whole year by the time the soil begins to dry. If the tunnel system only requires minimal repair during the summer, the moles may be able to live in areas where the earthworm supply is less abundant at that time. Otherwise, they would expend more energy digging (due to the dry soil) than they would get from their food supply. However, the food supply may become so low in summer that the moles would be unable to sustain themselves in the areas they had invaded during the winter, in which case they must still leave the area and resume a nomadic type of existence.

It is surprising that the atmosphere in mole tunnels is so low in O_2 and high in CO_2. The CO_2 levels found in the tunnels were higher than expected, and above the extreme predicted by Quilliam <u>et</u> <u>al</u>. (1971). Moles are well adapted to living in such an environment and their digging activity did not appear to be limited by it (Chapter 4). Carbon dioxide levels may increase in the tunnels in winter, but I found that mole activity increased in winter and therefore CO_2 would not appear to limit digging at this time either.

Methods to control moles have been given considerable attention by researchers (Chapter 4). No completely successful and economic method for reducing the number of moles or molehills has been found. The mole is difficult to control because it lives under a crop which the farmer wants to protect, and it lives in the soil in which the crop grows. Introducing predators is not possible because the mole has few natural predators except for owls which feed upon young moles during dispersal. The control of the mole must therefore be accomplished by altering its environment, and in doing so the crop may be affected. Moles usually do not accept poisoned baits and setting traps for them is uneconomical on a large scale. The most effective means of control is to kill the earthworms, their major food source. This procedure, however, is detrimental to the crop because of the effects of earthworms on soil fertility (Evans 1948).

Mechanical repellents may eventually be useful in controlling moles but they have only recently been put on the market. Their efficacy in reducing mole populations has not yet been demonstrated:

Overall, the method which appears to be the most promising is the use of chemical fertilizers (Ennik 1967), or other soil acidifying agents. There is some evidence that these agents reduce the number of molehills in treated areas, and they probably produce this result by killing, or at least reducing the weights of, earthworms. The advantage of applying fertilizer is that it theoretically should not indiscriminantly wipe out the soil fauna, but should only reduce earthworm populations, and should be advantageous to the crop. Because this method appears to depend on a reduction in soil pH, only acidifying fertilizers would be effective in mole control.

The disadvantages of using fertilizers are that they depend on the specific properties of the soils to which they are applied for their ability to reduce soil pH, and as may be apparent from my study, their effect is also dependent on the weather. The latter may be indirectly related to the base saturation of the soil.

In my experimental study the application of fertilizer did not result in a statistically significant reduction in mole activity as measured by molehill numbers. Close examination of the data in Ennik's (1967) paper showed that his results may also be non-significant statistically. However, the acidifying effect of fertilization and the effect of this on earthworms in the soil has been demonstrated in the field for ammonium sulfate (e.g. Jefferson 1955, Rodale 1948). I was able to demonstrate in the laboratory that the same effects were produced by ammonium nitrate and ammonia (as urea) at a concentration of 140 kg N/ha, one of the treatments used by Ennik (1967).

It would therefore seem possible that, given the correct weather and soil conditions, application of fertilizer could result in a sufficient effect on earthworm populations to reduce mole activity.

The habitat preferences of the coast mole were studied by establishing artificial sampling grids in areas where moles were found to be digging. Plots on those grids were then used for enumerating the molehills, sampling earthworms and soil, and as units of comparison. This procedure was found to be successful in establishing relationships between the number of hills with the habitat. This technique does not take into consideration the natural distribution of molehills in the fields. A division between study plots may fall in the middle of a center of high mole activity and thereby divide this center into two parts of lesser activity.

The design of the study may be improved in certain ways. First, taking the distribution of the molehills in the field into consideration while setting up the study plots may result in establishing more accurate relationships between the number of molehills and habitat. The problem with this technique, however, is that it will require that the plots be of unequal size.

A second possible improvement to the design used in my study would be to count the number of molehills and sample the earthworms and soil at more frequent intervals over a large number of fields. This was done to some extent within the same field in three mole territories during the summer of 1977. This approach may be more useful in monitoring the relationships between the number of molehills and changes in such variables as soil air space, soil moisture (weight of water/dry weight of soil) and the earthworm population which can change fairly quickly. This technique established relationships between the number of molehills and soil moisture and pH (Chapter 4). The sampling of the earthworms may prove to be a problem because of destruction to the populations by applying large amounts of formalin extracting solution to the soil. Nevertheless, this technique may still be of some use.

An investigation into the effects of the sex and age of moles and of new territories on the number of molehills produced in a territory would seem to be a profitable line of research and would nicely complement the present study. This would involve counting the number of molehills in several territories periodically until a trend is established, and then capturing the individuals and determining their sex and age. Studying new territories may be less profitable. It would involve monitoring the activity of moles within several fields until the seasonal distribution pattern of molehills is established, and then following the progress of a new territory (most likely to appear during dispersal or winter) which may become established.

Ideally it would also be of interest to pursue the distinction between earthworms and the habitat in their effects on the number of molehills in an area. I feel that this is definitely the key question which has arisen from this thesis. Unfortunately it will be extremely difficult to answer and there is no immediate solution.

Summary

1. The relationship of the number of molehills to the food supply and physical habitat of moles was investigated in 10 fields in the B.C. Lower Mainland. Moles were found to dig most in areas of lighter, more moist soils with a greater mean weight of earthworms. Moles also showed the same relationship to their food supply and habitat in terms of the number of hills pushed up with the addition that they also pushed up more hills where the total weight of the earthworms and the soil pH were greater.

2. The number of molehills pushed up was significantly correlated with the bulk density of the soil in summer, autumn, and spring, and with soil air space in spring. The number of molehills was not significantly correlated with any of the habitat parameters measured in winter.

3. An attempt to reduce the number of molehills through the use of nitrogen fertilizer as done for the European mole by Ennik (1967) failed. In the laboratory it was determined that the fertilizer does significantly reduce soil pH and the weight of earthworms, and that it could reduce the number of molehills through this relationship. The field experiment may have failed because of weather conditions and/or soil characteristics.

4. The CO_2 content of the atmosphere in mole tunnels was found to be as high as 5.5%, and the O_2 concentration as low

as 14.3%. There was no measurable relationship between the concentrations of these gases and the number of molehills produced in a territory.

APPENDICES

APPENDIX 1. The number of molehills in the 100 study plots (10x10m) of the Keur field on 1 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8	9	10
1	10	16	7	11	21	10	2	7	2	1
2	0	4	11	7	42	23	4	1	2	9
3	1	0	4	8	16	19	3	4	2	6
4	0	0	6	4	12	5	2	0	0	9
5	0	4	6	10	6	3	1	0	4	8
6	0	0	5	1	3	1	0	1	0	0
7	0	1	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0

APPENDIX 2. The number of molehills in the 100 study plots (10x10m) of the Laity field on 2 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8	9	10
1	26	18	13	6	0	0	1	1	12	4
2	7	9	13	11	4	1	0	17	19	6
3	2	4	14	2	0	0	1	11	6	2
4	0	0	1	2	13	3	7	4	2	0
5	9	0	4	7	10	13	5	3	7	3
6	0	0	2	4	1	0	0	0	4	7
7	1	11	2	0	0	4	0	1	0	1
8	0	0	0	1	1	2	0	0	0	2
9	3	0	0	0	5	0	0	0	0	0
10	3	0	2	2	0	1	0	0	0	0

APPENDIX 3. The number of molehills in the 100 study plots (10x10m) of the Robertson field on 8 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8	9	10
1	0	3	0	0	0	0	0	0	2	0
2	6	6	5	0	1	0	7	8	13	5
3	5	14	33	18	8	11	14	9	11	16
4	0	7	0	4	8	5	22	12	20	20
5	0	0	0	0	0	0	16	15	4	6
6	0	0	11	0	0	0	7	19	0	4
7	11	3	1	0	0	0	2	21	0	0
8	8	7	24	5	0	11	29	8	0	7
9	5	2	1	17	8	22	5	0	11	38
10	3	0	9	6	4	11	4	10	16	26

APPENDIX 4. **The number of molehills in the 100 study plots (10x10m) of the Judd field on 4 June, 1976. Plots for which earthworm and soil samples were collected are outlined.**

Plot	1	2	3	4	5	6	7	8	9	10
1	7	7	15	4	23	18	14	4	23	$\boxed{37}$
2	5	23	36	$\boxed{14}$	13	1[illegible]	13	2	41	54
3	11	26	22	$\boxed{16}$	13	17	21	16	36	68
4	24	9	$\boxed{39}$	17	14	$\boxed{19}$	$\boxed{36}$	18	24	26
5	18	24	32	50	48	5	16	17	7	23
6	2	10	30	4	47	9	14	44	20	23
7	$\boxed{34}$	42	102	57	44	$\boxed{31}$	19	5	18	16
8	17	13	$\boxed{17}$	30	50	20	$\boxed{16}$	16	9	9
9	40	44	26	32	14	19	37	10	6	17
10	38	9	7	14	14	37	20	14	26	31

APPENDIX 5. **The number of molehills in the 70 study plots (10x10m) of the Gadicke field on 11 June, 1976. Plots for which earthworm and soil samples were collected are outlined.**

Plot	1	2	3	4	5	6	7	8	9	10
1	0	2	2	9	0	7	4	2	7	2
2	18	2	8	2	3	10	1	4	3	15
3	12	9	10	3	2	13	12	2	6	7
4	8	22	6	6	0	9	9	0	4	8
5	4	19	0	0	2	7	14	0	3	2
6	6	12	2	0	0	1	4	5	6	12
7	3	6	0	0	0	8	6	0	3	1

APPENDIX 6. The number of molehills in the 64 study plots (10x10m) of the Campbell field on 9 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8
1	2	6	15	7	3	0	1	9
2	2	31	22	34	41	0	0	11
3	11	17	36	12	23	0	1	4
4	3	14	43	55	29	0	7	12
5	13	6	11	28	24	11	17	26
6	13	40	17	28	64	33	17	64
7	22	17	35	41	76	28	16	18
8	7	5	15	4	15	29	8	23

APPENDIX 7. The number of molehills in the 84 study plots (10x10m) of the Perkin field on 11 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7
1	1	0	0	1	0	0	0
2	1	0	0	0	6	0	0
3	4	0	0	7	8	10	2
4	0	8	5	0	3	0	2
5	0	0	1	6	0	2	6
6	1	0	5	0	1	12	4
7	1	0	0	2	4	8	23
8	0	0	3	10	13		
9	0	0	1	10	5		
10	0	6	5	2	1		
11	1	2	3	0	1		
12	20	3	18	2	2		
13	1	23	6	0	9		
14	24	22	9	7	1		

APPENDIX 8. The number of molehills in the 100 study plots (10x10m) of the McConnell field on 12 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8	9	10
1	0	0	15	9	0	2	3	6	0	8
2	0	0	23	5	17	10	10	10	10	3
3	0	6	12	0	0	2	38	13	11	0
4	0	0	0	0	7	9	63	11	10	10
5	0	0	1	14	2	5	5	23	8	12
6	0	0	14	0	44	18	35	9	5	1
7	0	0	0	4	21	52	62	27	3	4
8	0	0	0	3	5	29	14	18	5	0
9	10	11	4	0	0	10	21	20	13	11
10	4	3	12	17	11	13	5	18	10	6

APPENDIX 9. The number of molehills in the 100 study plots (10x10m) of the Brink field on 13 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8	9	10
1	0	0	0	0	0	0	0	0	0	0
2	1	0	0	0	0	0	0	0	28	9
3	0	0	0	0	0	0	0	0	10	7
4	0	0	0	0	0	0	0	1	28	27
5	7	9	0	0	0	0	0	0	7	14
6	19	3	0	0	0	0	0	0	2	13
7	33	4	12	3	0	0	1	1	2	14
8	16	8	18	1	0	0	0	0	16	8
9	1	5	1	0	1	0	0	1	4	3
10	0	1	2	1	4	0	1	0	16	7

APPENDIX 10. The number of molehills in the 100 study plots (10x10m) of the Hatt field on 13 June, 1976. Plots for which earthworm and soil samples were collected are outlined.

Plot	1	2	3	4	5	6	7	8	9	10
1	38	45	$\boxed{23}$	17	15	10	2	2	3	14
2	41	27	24	32	23	10	12	14	0	2
3	45	41	17	18	7	19	14	7	10	0
4	14	33	27	37	$\boxed{40}$	20	17	12	11	13
5	22	40	45	$\boxed{38}$	19	33	32	21	27	31
6	22	54	29	27	31	24	$\boxed{42}$	59	51	27
7	18	24	43	26	16	26	28	42	64	52
8	$\boxed{43}$	26	$\boxed{42}$	47	37	$\boxed{67}$	48	60	59	42
9	16	$\boxed{22}$	13	19	60	29	54	42	55	48
10	14	12	9	$\boxed{15}$	$\boxed{21}$	10	20	24	33	37

APPENDIX 11. The number of molehills in each of the plots for which soil and earthworm samples were collected in the 10 study fields (summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt
1	21	26	0	36	4	64	22	5	14	22
2	42	9	13	19	19	26	23	21	2	40
3	16	14	9	39	0	12	3	14	1	38
4	12	2	22	16	0	7	2	62	1	23
5	6	10	0	17	2	0	6	35	0	15
6	3	0	0	31	7	29	0	5	0	43
7	0	0	0	34	14	55	0	63	3	67
8	0	0	24	16	0	43	0	38	12	42
9	0	0	2	37	3	14	0	10	4	42
10	0	0	3	14	2	3	0	3	33	21

APPENDIX 12. The number of worms in each of the plots sampled (summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	0	3	1	22	5	2	19	52	3	1	11	39
2	5	4	4	37	14	8	4	83	2	3	31	31
3	0	0	2	10	30	2	3	58	5	8	22	25
4	1	14	0	19	7	0	18	34	0	7	23	48
5	1	4	0	41	4	0	5	31	2	10	39	23
6	2	6	0	20	0	2	21	45	3	2	12	41
7	0	11	2	14	103	0	9	51	6	2	17	25
8	1	4	1	37	26	5	2	35	0	9	28	10
9	0	12	15	40	1	7	6	44	1	3	29	29
10	0	0	1	37	7	7	16	52	0	5	17	15

APPENDIX 13. Mean weight of worms (gm) in the plots sampled (summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	0	2.22	0.36	0.31	0.25	0.17	0.18	0.27	0.49	4.87	1.83	0.59
2	0.33	0.24	0.16	0.28	0.31	0.53	0.24	0.22	0.46	0.40	2.07	0.91
3	0	0	0.20	0.35	0.18	0.25	0.31	0.22	0.49	1.26	1.40	0.19
4	0.37	0.41	0	0.33	0.24	0	0.34	0.33	0	0.22	1.16	0.36
5	0.44	0.82	0	0.28	0.02	0	0.19	0.40	0.35	0	1.33	0.42
6	0.59	0.73	0	0.33	0	0.29	0.28	0.35	0.55	1.02	1.92	0.62
7	0	0.55	0.15	0.23	0.09	0	0.25	0.34	0.53	0.01	1.97	0.25
8	0.47	0.41	0.18	0.25	0.15	0.23	0.42	0.19	0	1.45	0.95	0.73
9	0	0.83	0.12	0.37	0.65	0.28	0.27	0.28	0.36	0.49	1.51	0.22
10	0	0	0.42	0.28	0.32	0.30	0.27	0.33	0	1.45	1.82	0.37

APPENDIX 14. Total weight of worms (gm) in the plots sampled (Summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	0	6.67	0.36	6.49	1.25	0.34	3.17	14.31	1.47	4.87	20.09	23.04
2	1.76	0.96	0.66	10.49	4.38	4.24	0.95	18.47	0.93	1.20	64.14	28.21
3	0	0	0.41	3.51	5.29	0.51	0.94	12.37	2.47	10.10	30.89	4.75
4	0.37	5.79	0	6.25	1.66	0	6.08	10.79	0	1.54	26.66	16.81
5	0.44	3.27	0	11.34	0.08	0	0.96	12.39	0.70	0	51.70	9.62
6	1.18	4.36	0	6.56	0	0.58	5.91	15.44	1.66	2.05	23.09	25.61
7	0	6.03	0.31	3.29	9.46	0	2.26	17.50	3.28	0.02	33.58	6.29
8	0.47	1.63	0.18	9.21	3.97	1.17	0.85	6.22	0	13.10	26.52	7.29
9	0	9.93	1.79	13.99	0.65	1.93	1.61	12.37	0.36	0.36	42.31	6.49
10	0	0	0.42	10.37	2,21	2.11	4.12	17.07	0	0	18.92	5.56

APPENDIX 15. Soil moisture (%) at 10 cm in the plots sampled (Summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	19.9	28.7	38.9	45.7	42.8	37.5	34.4	28.0	33.4	22.6	37.9	33.0
2	33.9	39.5	49.8	55.3	27.4	48.1	22.6	33.7	32.7	31.3	42.9	35.0
3	22.7	36.8	47.5	59.7	31.7	50.1	18.2	32.6	26.1	32.3	43.6	42.9
4	24.5	38.2	48.3	57.9	34.8	38.4	12.7	39.3	34.4	39.6	35.8	34.8
5	25.1	37.1	23.1	51.0	39.6	43.4	26.7	32.7	31.9	31.9	33.9	45.7
6	24.5	36.7	33.4	64.4	34.7	32.6	24.2	30.7	32.2	33.1	36.9	38.6
7	18.8	38.4	53.6	44.7	38.7	37.6	26.0	32.6	38.9	32.6	37.4	57.7
8	19.9	27.3	48.3	52.7	45.3	43.0	28.4	32.0	27.3	31.1	47.0	29.8
9	16.5	29.8	49.3	52.0	27.6	42.6	31.7	35.8	22.1	26.7	44.8	45.9
10	16.9	19.9	44.7	40.0	27.6	40.7	28.2	31.3	27.4	26.3	38.8	67.3

APPENDIX 16. Soil moisture (%) at 20 cm in the plots sampled (summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	23.4	31.5	31.7	50.4	40.7	46.5	32.1	27.3	31.8	18.2	36.4	38.8
2	34.1	44.3	35.4	54.1	27.6	48.8	27.8	30.1	36.8	30.9	41.5	42.7
3	23.7	47.2	39.7	53.4	32.4	49.7	22.0	29.9	23.8	33.6	38.7	64.9
4	27.0	42.9	40.8	52.7	25.6	34.6	25.8	32.6	26.2	33.0	36.8	44.6
5	30.7	41.3	24.5	49.7	29.5	45.0	32.0	31.4	30.4	30.5	36.9	42.7
6	23.0	42.6	28.1	[illegible]6.3	22.7	24.4	28.1	30.9	29.8	33.2	36.5	40.9
7	20.7	36.9	42.9	44.9	35.7	40.7	22.8	31.7	37.4	34.8	39.3	59.2
8	20.3	33.1	45.1	49.7	36.6	46.6	23.3	30.4	23.0	26.0	42.6	29.7
9	17.2	32.4	43.1	44.7	20.3	41.1	31.5	32.2	33.4	25.0	46.1	47.8
10	15.8	21.8	44.8	40.5	19.7	41.6	28.1	29.3	23.9	24.2	40.3	80.2

APPENDIX 17. Soil bulk density (gm/cc) at 10 cm in the plots sampled (Summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	0.85	0.98	0.87	0.70	0.76	0.84	0.95	0.98	0.88	1.34	0.89	1.12
2	0.80	0.87	0.80	0.68	0.95	0.78	0.91	0.95	0.94	1.24	0.87	1.04
3	0.92	0.95	0.88	0.70	0.94	0.73	0.83	0.91	0.95	1.16	0.74	0.94
4	0.81	0.94	0.83	0.67	0.87	0.90	0.82	0.92	0.80	1.10	1.06	1.03
5	0.81	0.92	1.07	0.74	0.86	0.80	0.81	1.08	0.81	1.20	1.08	0.92
6	0.78	0.81	1.08	0.63	0.81	0.99	0.73	0.97	0.86	1.15	0.93	0.99
7	0.93	0.97	0.90	0.79	0.94	0.94	0.84	0.99	0.80	1.25	0.81	0.75
8	1.05	0.95	0.78	0.62	0.81	0.91	0.71	1.01	0.92	1.20	0.90	1.15
9	1.07	1.01	0.90	0.74	0.91	0.90	0.81	0.84	0.93	1.31	0.82	0.95
10	0.84	1.06	0.86	0.72	0.93	0.84	0.89	1.07	0.84	1.30	0.88	0.75

APPENDIX 18. Soil bulk density (gm/cc) at 20 cm in the plots sampled (Summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	0.84	0.93	0.81	0.76	0.76	0.87	0.94	1.04	0.88	1.32	0.79	0.99
2	0.79	0.94	0.91	0.62	0.86	0.79	0.84	0.94	0.86	1.28	0.81	0.95
3	0.90	0.83	0.81	0.69	0.92	0.88	0.85	0.89	0.96	1.19	0.92	0.72
4	0.75	1.03	0.81	0.68	0.84	0.88	0.53	0.93	0.89	1.27	1.01	0.95
5	0.81	0.79	1.10	0.72	0.75	0.76	0.81	1.02	0.71	1.27	1.04	0.99
6	0.80	0.67	0.97	0.67	0.86	1.07	0.82	1.02	0.84	1.15	0.90	1.05
7	0.83	0.94	0.82	0.77	0.78	0.90	0.96	0.90	0.75	1.16	0.83	0.84
8	0.97	0.86	0.83	0.71	0.76	0.79	0.86	0.87	0.91	1.33	0.92	1.25
9	1.03	0.90	0.84	0.72	0.83	0.88	0.76	0.84	0.68	1.26	0.74	0.92
10	0.96	0.89	0.85	0.71	1.06	0.81	0.97	0.92	0.91	1.30	0.72	0.66

APPENDIX 19. **Water content (%) at 10 cm in the plots sampled (Summer 1976).**

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	16.3	27.0	32.7	30.9	34.0	30.3	31.5	26.3	28.4	29.1	32.5	37.6
2	26.1	32.9	38.5	34.8	26.0	36.2	19.9	30.8	29.6	37.3	36.0	36.5
3	20.1	33.7	40.2	40.4	29.7	35.1	14.6	28.5	23.8	36.1	31.0	40.2
4	19.1	34.6	38.7	37.6	29.7	33.2	10.1	34.8	26.6	42.0	36.6	36.5
5	19.7	32.8	23.8	36.5	33.9	33.6	20.8	34.1	24.8	37.0	35.2	42.1
6	18.3	28.5	34.7	38.8	28.1	31.0	17.0	28.8	26.7	36.8	32.9	38.0
7	16.8	35.7	46.6	34.1	36.3	34.1	21.1	31.2	30.0	39.1	29.3	43.4
8	20.1	25.0	36.4	31.6	36.9	37.7	19.5	31.0	24.1	35.9	40.6	34.4
9	17.0	29.1	42.6	36.9	25.0	37.0	24.8	29.1	19.8	33.5	35.4	43.6
10	13.7	20.4	37.1	27.9	25.7	32.8	24.2	32.2	22.1	32.9	32.8	50.9

APPENDIX 20. **Water content (%) at 20 cm in the plots sampled (Summer 1976).**

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	18.9	28.3	24.7	37.0	30.8	30.6	29.0	27.3	26.9	23.1	27.5	38.5
2	26.0	40.2	30.9	32.3	23.8	36.9	22.6	27.3	30.4	38.3	32.5	40.8
3	20.6	37.6	30.9	35.6	29.8	41.9	18.0	25.6	21.9	38.4	34.5	46.9
4	19.6	42.5	31.9	34.4	21.3	29.4	13.2	29.1	22.5	40.5	35.8	42.4
5	23.9	31.5	26.0	34.3	22.0	32.8	24.8	30.9	20.8	37.4	36.9	42.3
6	17.7	27.5	26.2	36.4	19.6	28.2	22.2	30.5	24.2	36.6	31.8	43.0
7	16.6	33.4	34.0	33.2	27.8	35.4	21.0	27.3	27.0	38.9	31.6	49.7
8	18.8	27.5	36.0	33.8	27.8	35.3	19.3	25.5	20.1	33.3	37.9	37.0
9	17.1	28.2	34.9	31.0	16.8	34.6	23.0	26.2	21.9	30.3	32.7	43.9
10	14.6	18.6	36.8	27.8	20.8	32.6	26.1	25.9	21.1	30.4	28.1	53.2

APPENDIX 21. Air space (%) at 10 cm in the plots sampled (Summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	51.5	36.2	34.4	42.5	36.1	37.9	32.5	36.8	38.3	20.4	33.9	19.9
2	43.7	34.4	31.1	39.5	38.1	34.2	45.6	33.4	34.8	15.9	31.0	24.1
3	45.1	30.5	26.6	33.0	35.0	37.5	53.9	37.3	40.5	20.1	41.2	24.4
4	50.5	29.8	30.0	36.9	37.5	32.7	58.8	30.4	43.1	16.4	23.3	24.7
5	49.6	32.5	35.8	35.4	33.8	36.1	48.6	25.0	44.8	17.5	24.0	22.9
6	52.4	41.0	24.5	37.5	41.3	31.8	55.6	34.5	40.7	19.7	32.0	24.7
7	48.0	27.8	19.2	35.9	28.3	30.3	47.0	31.3	39.8	13.8	40.0	28.2
8	40.2	39.0	34.0	44.8	32.4	27.9	53.6	30.9	41.2	18.7	25.6	22.1
9	42.6	32.6	23.5	35.2	40.8	28.8	44.4	39.0	45.0	17.2	33.6	20.5
10	54.5	39.4	30.3	44.8	39.2	35.5	42.2	27.4	46.2	18.1	33.9	20.5

APPENDIX 22. Air space (%) at 20 cm in the plots sampled (summer 1976).

Plot/ Field	Keur	Laity	Robertson	Judd	Control Judd	Gadicke	Campbell	Perkin	McConnell	Brink	Hatt	Control Hatt
1	49.3	36.5	44.7	34.2	40.6	36.6	35.5	33.5	39.9	27.3	42.8	24.1
2	44.0	24.2	34.9	44.3	43.6	33.4	45.5	37.1	37.2	13.2	36.8	23.1
3	45.4	31.2	38.5	38.2	35.5	25.0	50.0	40.8	41.8	16.8	30.6	15.8
4	51.9	18.7	37.3	39.9	47.0	37.3	66.8	35.8	43.8	11.4	26.0	21.5
5	45.7	38.5	32.4	38.6	49.8	38.5	44.7	30.6	52.4	14.6	23.8	20.3
6	52.1	47.1	37.3	38.3	47.8	34.2	46.8	30.8	43.9	20.1	34.1	17.3
7	51.9	31.2	34.9	37.7	42.8	30.5	42.9	38.8	44.6	17.3	36.9	18.6
8	44.7	40.0	32.8	39.5	43.6	35.0	48.1	41.7	45.7	16.5	27.1	15.8
9	43.9	37.6	33.3	41.8	52.0	32.3	48.4	41.9	52.3	22.3	39.4	21.2
10	49.2	47.7	31.1	45.3	39.1	36.7	37.4	39.4	44.4	20.5	44.6	21.7

APPENDIX 23. Mineral content of the Keur field (2/8/76).

Plot	No. of Molehills	Organic matter (%)	pH	Salts	Ni (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Total N (%)
1	21	8.7	6.1	0.18	0	28	112	1757	175	0.80
2	42	9.3	5.9	0.14	0	15	28	1305	98	0.82
3	16	7.0	5.5	0.14	0	20	34	956	156	0.68
4	12	9.3	5.8	0.16	0	16	38	1246	99	0.86
5	6	9.5	5.5	0.14	0	20	25	903	74	0.83
6	3	12.0	6.0	0.20	1	41	40	1856	125	1.07
7	0	7.8	5.9	0.16	0	17	28	1327	90	0.72
8	0	5.1	5.5	0.12	1	8	30	839	157	0.49
9	0	4.6	6.0	0.16	1	5	69	1373	117	0.43
10	0	6.4	6.3	0.22	0	110	249	1542	161	0.61

APPENDIX 24. Mineral content of the Laity field (28/7/76).

Plot	No. of Molehills	Organic matter (%)	pH	Salts	Ni (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Total N (%)
1	26	7.0	5.4	0.12	0	41	25	569	25	0.59
2	29	8.5	5.3	0.14	1	31	25	379	25	0.70
3	14	8.3	5.0	0.10	1	25	37	250	25	0.64
4	2	8.7	5.1	0.14	0	26	25	300	25	0.65
5	10	9.5	5.7	0.16	0	25	25	764	25	0.73
6	0	9.5	5.2	0.12	1	23	50	254	25	0.76
7	00	7.6	5.4	0.12	1	53	25	668	25	0.67
8	0	8.0	5.1	0.12	0	26	25	499	31	0.69
9	0	6.8	5.1	0.12	0	35	27	534	34	0.64
10	0	6.6	5.2	0.12	0	38	38	757	1	0.67

APPENDIX 25. Mineral content of the Robertson field (22/7/76).

Plot	No. of Molehills	Organic matter (%)	pH	Salts	Ni (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Total N (%)
1	0	10.0	5.6	0.12	0	22	25	803	61	0.97
2	13	11.3	5.4	0.12	0	17	98	496	45	0.98
3	9	9.5	5.5	0.08	0	26	25	490	25	0.94
4	22	9.5	5.4	0.08	0	17	25	422	63	0.89
5	0	4.9	5.7	0.16	0	22	38	1449	195	0.44
6	0	7.0	5.6	0.14	0	38	35	1192	130	0.66
7	0	9.0	5.7	0.10	0	68	25	814	28	0.79
8	24	9.0	5.5	0.10	0	43	25	468	47	0.77
9	2	11.7	5.6	0.10	1	34	25	623	25	0.89
10	3	8.5	5.3	0.10	1	37	25	395	25	0.76

APPENDIX 26. Mineral content of the Campbell field (27/7/76).

Plot	No. of Molehills	Organic matter (%)	pH	Salts	Ni (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Total N (%)
1	64	6.8	6.2	0.14	0	65	65	851	45	0.55
2	26	7.4	6.0	0.12	0	68	25	819	54	0.50
3	12	9.0	5.8	0.12	0	92	32	767	41	0.57
4	7	9.0	5.5	0.10	0	112	35	466	36	0.59
5	0	8.5	6.2	0.14	0	64	25	1041	44	0.49
6	29	7.2	6.4	0.16	1	45	28	1093	34	0.57
7	55	6.2	6.6	0.18	1	56	36	1409	26	0.52
8	43	10.0	5.8	0.12	0	89	25	774	37	0.69
9	14	8.7	5.9	0.14	1	122	56	857	42	0.60
10	3	5.2	6.0	0.16	4	41	296	348	25	0.43

APPENDIX 27. Mineral content of the Brink field (9/8/76).

Plot	No. of Molehills	Organic matter (%)	pH	Salts	Ni (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	Total N (%)
1	14	2.8	5.9	0.16	0	100	164	1065	153	0.25
2	2	3.7	6.0	0.18	0	44	135	1405	298	0.37
3	1	4.3	6.2	0.18	1	18	106	1577	321	0.29
4	1	3.7	6.2	0.22	0	23	175	1585	311	0.33
5	0	2.8	6.2	0.18	0	18	107	1477	294	0.30
6	0	3.2	6.1	0.18	2	22	133	1747	172	0.35
7	0	3.4	6.2	0.18	0	15	114	1708	300	0.37
8	12	2.9	6.0	0.16	0	25	134	1457	277	0.31
9	4	2.2	5.8	0.14	2	43	94	1102	225	0.22
10	33	2.9	6.1	0.16	3	43	104	1171	205	0.28

APPENDIX 28. The earthworm species found in the study plots used to measure soil and earthworm characteristics. The species code is as follows: ALCH=*Allolobophora chlorotica*; APTR=*Aporrectodea trapezoides*; APTB=*Aporrectodea tuberculata*; DEOC=*Dendrobaena octaedra*; DERU=*Dendrodrilus rubidus*; EIRO=*Eisenia rosea*; ELTT=*Eiseniella tetraedra*; LURB=*Lumbricus rubellus*; LUFS=*Lumbricus festivus*; LUTS=*Lumbricus terrestris*; OCCY=*Octolasion cyaneum*; OCTY=*Octolasion tyrtaeum*.

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
Keur	2								5				
Keur	4								1				
Keur	5								1				
Keur	6								2				
Keur	8								1				
Laity	1										2		
Laity	2								2				2
Laity	4								10		2		2
Laity	5								2		2		

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
Laity	6										6		
Laity	7								4		6		
Laity	9								6		6		1
Robertson	1												1
Robertson	2								2				2
Robertson	3								2				1
Robertson	7												4
Robertson	8												1
Robertson	9								2				13
Robertson	10								1				
Judd	1								19				3
Judd	2								19	7			10
Judd	3			4					5	1			
Judd	4								11	5			2
Judd	5								32				9

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
Judd	6								10	3			7
Judd	7								9	2			3
Judd	8			2					11	1			23
Judd	9			3					25				12
Judd	10								28				9
Judd (C)	1			2					1				2
Judd (C)	2			2					5				7
Judd (C)	3			25					4				
Judd (C)	4								4				3
Judd (C)	5												4
Judd (C)	7			98					4				
Judd (C)	8			19					4			1	
Judd (C)	9								2				
Judd (C)	10			4					3				
Gadicke	1								2				

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
Gadicke	2								8				
Gadicke	3								2				
Gadicke	6			1					2				
Gadicke	8								4				
Gadicke	9			3					5				
Gadicke	10			1					7				
Campbell	1								17				1
Campbell	2								4				
Campbell	3								2				1
Campbell	4								14				3
Campbell	5								5				
Campbell	6								18				4
Campbell	7								9				
Campbell	8								4				
Campbell	9								6				

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCT[illegible]
Campbell	10								11				4
Perkin	1			6					30				16
Perkin	2			6					39		3		40
Perkin	3			22					24				15
Perkin	4			14					19				
Perkin	5			7		1			23				
Perkin	6			14					31				
Perkin	7			9					28				14
Perkin	8			17					14				
Perkin	9			21					23				
Perkin	10			22					31				
McConnell	1								3				
McConnell	2								2				
McConnell	3								5				
McConnell	5								2				

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
McConnell	6								4				
McConnell	7								6				
McConnell	9								1				
Brink	1										1		
Brink	2			2					1				
Brink	3			3							5		
Brink	4			5					2				
Brink	6			2							1		
Brink	7												2
Brink	8			3							5		
Brink	9			1					1				
Brink	10			3							2		
Hatt	1						2		3		7		
Hatt	2						1				30		
Hatt	3						7				15		

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
Hatt	4						4				20		
Hatt	5						5		1		32		
Hatt	6										12		
Hatt	7						1				16		
Hatt	8		6										
Hatt	9						4				22		
Hatt	10						4				11		
Hatt (C)	1			13							26		
Hatt (C)	2						6				23	3	
Hatt (C)	3	1					12		7				
Hatt (C)	4	1					24				15	8	
Hatt (C)	5	3		3				3	13		2		
Hatt (C)	6										17	28	
Hatt (C)	7	1		9			4		11				
Hatt (C)	8								7		3		

continued ...

Field	Plot	ALCH	APTR	APTB	DEOC	DERU	EIRO	ELTT	LURB	LUFS	LUTS	OCCY	OCTY
Hatt (C)	9	1						13	15				
Hatt (C)	10			2				1	12				

APPENDIX 29. The age distribution and recruitment of a population of coast moles

When the level of mole activity is compared to physical and biological habitat components it is assumed that there are always sufficient individuals to populate the areas considered. The purpose of this study was to determine the level of recruitment of new individuals into mole populations in the latter half of 1976 and the beginning of 1977 by investigating the reproductive rate, the population age structure, and by observing the reoccupation of vacated areas. Measurements of sex ratio and body weights were also obtained.

Methods

Moles were trapped using the English scissor trap on a farm near Aldergrove, B.C. Trapping was begun on a 1.2 ha pasture on 10 July 1976, and was extended into an adjacent 3.2 ha pasture on 26 December, 1976. All trapping ended on 25 February, 1977.

The following numbers of days and trap nights were spent collecting moles:

Month	Trap days	Trap nights	No. of moles caught
July	12	194	5
August	8	96	4
September	8	64	4
October	2	16	1
December	5	125	4
January	2	50	1
February	4	100	4
Total	41	645	23

The number of traps set varied from 8-25, and they were left for 2-5 days at a time.

The uteri were removed from females and fixed and cleared after the method of Orsini (1962). They were examined under a dissecting microscope for placental scars. Ovaries were preserved in aqueous Bouins solution. They were sectioned at 7 mu and stained with eosin and haematoxylin. They were then examined for <u>corpora</u> <u>albicantia</u> as indicators of previous pregnancy.

The standard procedure for determining the age of moles has been to examine their teeth for progressive stages of wear (Deparma 1963). Keys for aging the European mole (e.g. Mellanby 1971) are available but are of little use in aging the coast mole as its dentition is markedly different. Glendenning (1959) aged 940 coast moles using skin texture and weight but he does not clearly state his method nor does he give any criteria. I devised my own key based on tooth wear (dentition formula is: I3/3, C1/1, PM4/4, M3/3), which is as follows:

Class	Estimated age	Identification of teeth
A	0-1 yrs	no noticeable wear
B	1-2	noticeable wear on the fourth premolar, 1st and 2nd molars; some wear on 2nd and 3rd premolars
C	2-3	extensive wear on 4th premolar, 1st and 2nd molars; 2nd and 3rd premolars worn to flesh
D	3-4	same as previous with the addition that canines and 2nd and 3rd incisors are also worn to flesh

The keys for the European mole extend to an age of 6 years. There appeared to be only four discrete categories of tooth wear for the coast mole. The categories of tooth wear could reflect habitat differences (Deparma 1954), so the ages should be regarded as estimates only. Four representative skulls illustrating the four categories of tooth wear are shown in Figure 6.

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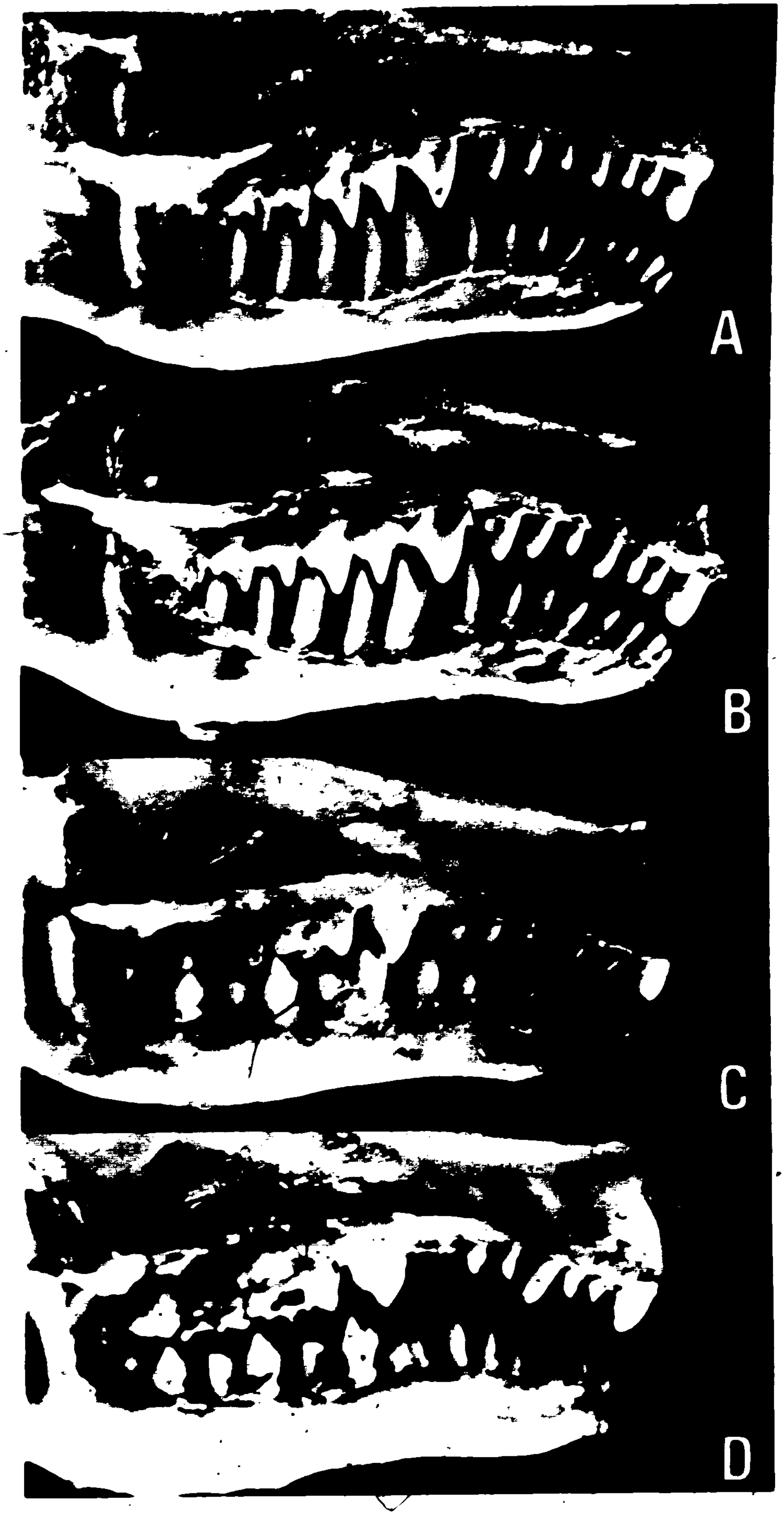
Figure 6. Photograph of four mole skulls showing the four categories of tooth wear used to assign age.


A
B
C
D

Results

A schematic map of the study area showing the relative positions of the individuals caught along with major landmarks is presented in Figure 7. Table 24 shows the dates on which the individuals were caught, their sex, weight, and estimated age.

A total of 25 moles were caught. Two were captured alive and subsequently escaped so there is no data for them. Of the remaining 23, 13 were males and 10 were females. The average weight for males was 65.32 ± 2.54 (95% confidence interval) gm (Range 63.86 - 77.38 gm) and for the females 57.22 ± 2.54 gm (Range 54.50 - 59.90 gm) for a combined average weight of 65.3 ± 3.46 gm.

Densities were computed for 24 individuals. Fifteen of the moles were caught in the 1.2 ha plot, and nine on the 3.2 ha plot. The smaller plot thus had a density of 12.5 moles/ha (5/ac), and the larger 2.8 moles/ha (1.12/ac). The overall density for the two plots combined was 5.45 moles/ha (2.18/ac). I estimated that there were 4 uncaught moles in the 3.2 ha plot which would alter the density estimate on that plot to 3.25 moles/ha (1.62/ac) and the combined estimate to 6.36 moles/ha (2.54/ac).

The smaller plot was completely trapped out by 26 October, 1976. All but one individual had been caught by 21 September, 1976. No new individuals were caught or seen to enter the area after that time. However, during the trapping

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Figure 7. Schematic map of the farm near Aldergrove, B.C., used in the recruitment study. The positions and sexes of the individuals captured are marked (identification numbers of females are circled), as well as the estimated positions of uncaught moles.

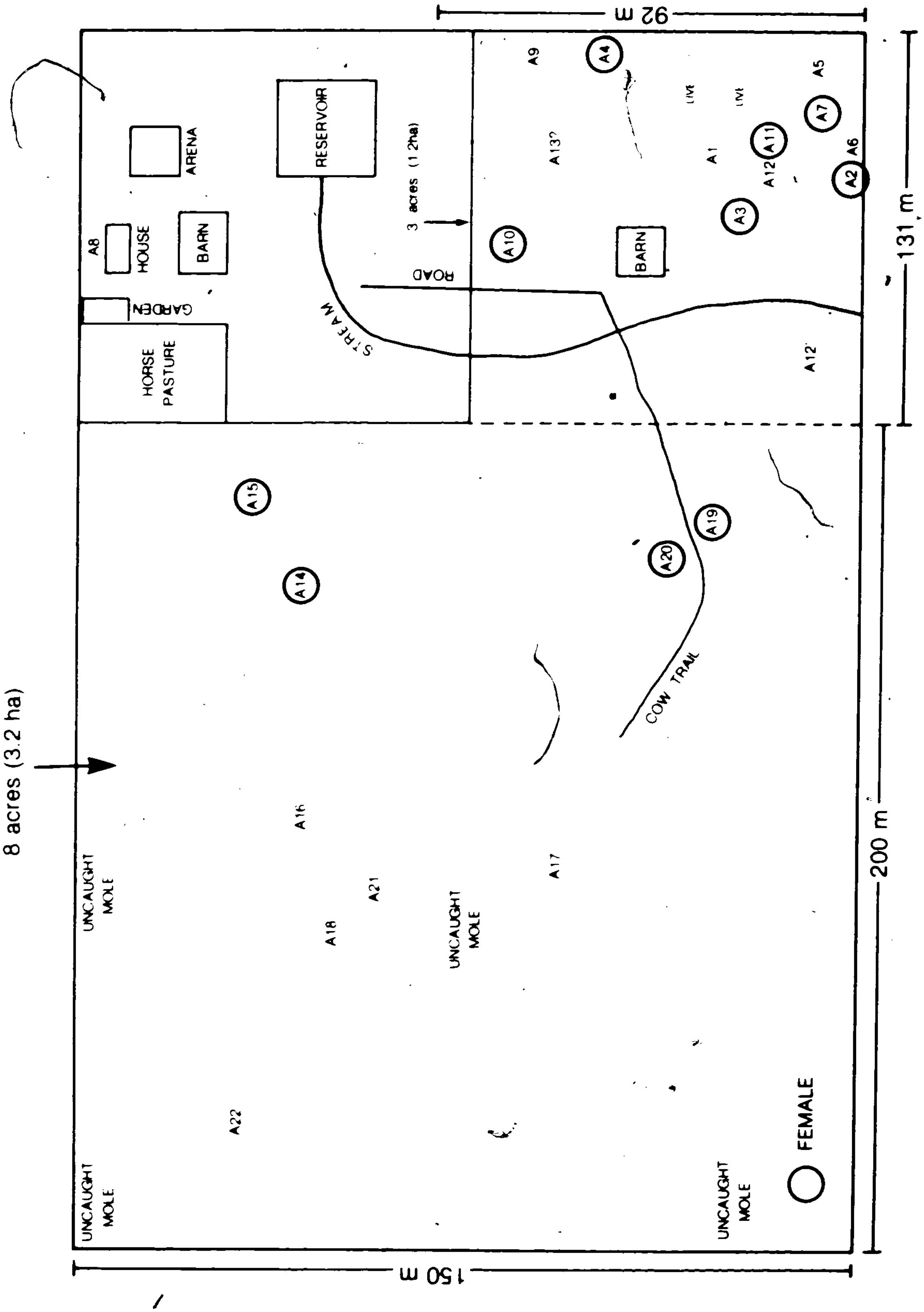
92 m
131 m
200 m
150 m
8 acres (3.2 ha)
3 acres (1.2ha)
RESERVOIR
ARENA
HOUSE
A8
BARN
GARDEN
HORSE PASTURE
STREAM
ROAD
BARN
COW TRAIL
A9
A4
LIVE
LIVE
A5
A7
A13?
A1
A11
A6
A12
A2
A3
A10
A12'
A15
A19
A20
A14
A16
A17
A21
A18
UNCAUGHT MOLE
UNCAUGHT MOLE
A22
UNCAUGHT MOLE
UNCAUGHT MOLE
FEMALE

Table 24. The moles caught in the study.

Identification	Date caught	Sex	Weight (gm)	Estimated age (yrs)
A-1	11/07/76	m	69.23	0-1
A-2	11/07/76	f	58.73	1-2
A-3	16/07/76	f	69.90	3-4
A-4	16/07/76	f	59.45	1-2
A-5	19/07/76	m	74.94	2-3
A-6	05/08/76	m	63.86	1-2
A-7	07/08/76	f	59.25	1-2
A-8	09/08/76	m	74.89	2-3
A-9	11/08/76	m	71.80	1-2
A-10	21/09/76	f	51.50	1-2
A-11	21/09/76	f	58.63	0-1
A-12	21/09/76	m	64.78	1-2
A-12'	21/09/76	m	68.61	2-3
A-13	26/10/76	m	71.23	1-2
A-14	27/12/76	f	57.29	1-2(0-1?)
A-15	27/12/76	f	55.18	1-2
A-16	27/12/76	m	73.21	2-3
A-17	30/12/76	m	76.59	2-3(3-4?)
A-18	06/01/77	m	69.62	2-3
A-19	23/02/77	f	55.40	0-1
A-20	23/02/77	f	57.84	0-1
A-21	25/02/77	m	77.38	1-2

of the smaller plot there were two instances when new moles entered the study area. Mole A-4 was active in an area which previously had no activity. It was caught almost immediately after it entered the area. Mole A-6 entered the territory vacated when mole A-2 was captured. It was active in the same runways and was caught only 2 m from where A-2 was trapped. A possible third instance occurred with moles A-12 and A-11. Both were caught within 2 m of each other on the same evening; both could not be occupying the same territory so one was probably an intruder. The new moles entered the study area from the periphery of the field from a large grassy ditch.

The ages of the 23 individuals caught were estimated to be as follows: 4 - 1 year, 12 - 2 years, 6 - 3 years, and 1 - 4 years. Males were on the average slightly older than females.

No placental scars were visible in any of the 10 uteri examined. The uteri from the two females caught in February were greatly enlarged and appeared to be in reproductive condition. Examination of the ovaries indicated that mole A-4 had bred but was inactive at the time of capture, A-11 was juvenile and had not bred, and A-4 and A-15 were entering oestrus. The breeding conditions of the ovaries of the remaining individuals could not be determined.

Discussion

The difference in the densities of the two plots studied may be due to differences in habitat. The smaller plot contains a barn which attracts cattle. The cattle were invariably on the smaller plot and stayed away from the larger even though they had unrestricted access. The smaller plot thus received larger amounts of manure. This in turn could support a larger earthworm population, and therefore should be able to support more moles. Pederson (1963) maintains that manured plots can support higher densities of Townsend mole populations than unmanured plots.

The higher density in the smaller plot could also be due to recruitment. Glendenning (1959) mentions that the density of the coast mole varies from 10.2/ha to 0.072/ha. He found that the densities of moles correlated highly with the numbers of earthworms in the fields. His highest density is still below that obtained for this study, perhaps because my study area contained more earthworms than the fields he sampled. If, however, the two moles which appeared to invade the study area are excluded from the estimate, it now becomes 10.8 moles/ha, which approximates the maximum density quoted by Glendenning (1959).

Glendenning (1959) mentions that 74 mature (over 1 year of age) male coast moles trapped over 10 years (November-April) weighed 74.3 ± 5.6 gm (64-91 gm), and 30 mature females weighed 69.8 ± 4.1 gm (61-79 gm). He further mentions that from May-September 1934, 52 adult and yearling males weighed 63.2 ± 8.0 gm (42-77 gm), and 53 adult and yearling females weighed 58.1 ± 6.6 gm (40-80 gm). He also states that the average weights for winter (November-May) were constant and that the weight records indicated that moles of all ages had an abundant food supply during ~~the~~ winter.

There does not appear to be any pattern in the distribution of males and females in the study plots (Figure 7). In the smaller plot the 2 sexes appear to be randomly distributed. In the larger plot the females are localized in the eastern half and the males in the western half, but several moles remained uncaught so any conclusion would be tentative. Similarly, there did not appear to be any pattern in the distribution of the age classes in the study plots.

Glendenning (1959) found that 45% of the coast moles which he trapped from November-April were adults over 1 year old, and 6% were adults over 3 years old (based on skin texture and weight). The remaining 55% of the individuals were less than 1 year old. In my study most of the coast moles were estimated to be 2 years old. I feel that this discrepancy may indicate that any distinction between the first two age classes was inaccurate, and in actual fact 16 of the 23 individuals in my study were 1 year old, 6 - 2 years, and 1 - 3 years.

It appears from previous work done on the coast and European moles, that recruitment is probably fairly high in moles. Perhaps the best evidence for this is presented by Glendenning (1959) where he gives the yearly number of moles he trapped in some fields. The moles were persistently successful in reinvading his trapped-out fields for the first several years whereupon after continuous trapping their numbers started to decline.

Furthermore, even though the actual ages of the moles I trapped in my study could not be determined, there were at least four moles trapped at Aldergrove in 1976-77 which showed no noticeable tooth wear, which would indicate that these moles were less than 1 year old and that some recruitment had occurred in that area in 1976.

Further evidence for recruitment is that I caught two moles within 2 m of each other, one in an area where the previous occupant had been removed a month earlier. In the instance where the resident (estimated age 1-2 yrs) was removed it was replaced by an individual of the same age. In the instance where two moles were caught within 2 m of each other on the same evening, one of the moles was estimated to be 1-2 yrs of age, and the other 0-1 yrs. One mole entered the study area producing new hills after the trapping program had begun. The estimated age of this individual was 0-1 yrs. If the estimated ages are correct it would appear, then, that the immigrant population does not consist solely of first year individuals.

The most direct way of proving recruitment would have been to find placental scars in the uteri of the females. Unfortunately, no placental scars were found in any of the 10 uteri examined, probably because most of them would have had their young by the end of April and the placental scars may have healed by July when trapping was begun. Two females and two males caught in February of 1977 all had enlarged gonads, indicating that at least the potential for breeding was present. The coast mole is known to breed at this time (Glendenning 1959).

APPENDIX 30. Movements and diel activity of the coast mole

Little is known of the movements and diel activity of the coast mole. The purpose of this section of the study was to determine the pattern of movements, home range area, and activity of a very limited number of coast moles. This information was to be compared with data for the European (Godfrey 1955) and Eastern (Harvey 1976) moles to determine if reasonable extrapolations could be made about the dispersal capabilities of the coast mole.

Methods

The capture of live coast moles proved to be difficult and time consuming. A live mole trap (Moore 1944) is described but after 2 months of daily testing it was found to be unsuitable for coast moles (moles entered the trap but did not release the trip mechanism).

After 9 field days a live mole was captured in the Laity field at Maple Ridge on 8 November, 1976. The mole was captured by monitoring the field for moles pushing up hills and then trying to flip the mole out of the ground with a shovel.

The live mole of unknown sex was brought back to the laboratory and kept overnight. In the morning it was anaesthetized with ether and a copper band (3x12 mm; wt=2gm), with 20 microcuries of Ir 192 soldered to it was attached to the left hind leg. A tail band such as was used for the European mole

(Godfrey 1955) was inappropriate because the tail of the coast mole tapers from the body to the tip; in the European mole there is a constriction at the base of the tail which prevents the band from slipping. Ir 192 was preferred over the Co 60 used by previous researchers because of its short half-life (152 days), and because it is biologically inert. The mole was then immediately taken to its point of capture and released into its runway.

The mole was followed using a Technical Associates PUG1 scintillation counter. An iodide crystal probe was mounted at the end of a 3 m boom to maintain a distance from the mole during observation to reduce disturbance.

The position of the mole was periodically marked with a small flag with the time of day recorded on it. If the mole spent more than 1 min in any position the duration of this pause was noted. At the end of each observation day the positions of the mole and the times were marked on a map of the study area.

It is difficult to determine the nature of a mole's activity. The mole was assumed to be asleep when it was at its nest (a site repeatedly used by the mole for sleep) and remained motionless for at least several min. Because the mole is underground and the scintillation counter is not sensitive enough to detect minor movements it is usually impossible to determine if the mole is feeding, sleeping away from the nest, digging, grooming, etc. As a result the data were categorized into the following activities:

1. moving - if the mole did not remain in one position for more than 1 min,
2. stationary - if it remained within monitoring distance of the probe (radius of about 15 cm) while it rested on the ground for more than 1 min,
3. digging - when the mole was actually pushing up earth; this was not recorded when the mole was heard to be digging but did not bring up soil,
4. resting - the period immediately after digging when the mole was observed to move about 30 cm from the new mound and stay in one position for several min,
5. asleep - when the mole was motionless at the nest site for more than several min, and,
6. awake - all times when the mole was not at the nest.

The nest site was defined as the place where the mole returned to sleep. It was a definite spot in the territory and was the only place where the mole slept. The term 'nest' was used by previous researchers to describe the place where moles sleep.

A second live mole was caught at the Laity farm in January, 1977 after 14 field days. It was tagged and released in the same manner as described previously except that it was not kept in the laboratory overnight. However, the mole appeared ill after the anaesthetic, and when released into the tunnel where it was caught it repeatedly came above ground, wheezing and snorting. After staying with the mole for 2 hrs in the field, continually reintroducing it into its tunnel, I left the mole for 2 days and when I returned I was unable to locate the mole again. Ten days were subsequently spent searching for the mole with a scintillation counter over a 5-ha area in detail, and cursorilly over about a 20 ha area, with no success.

Two other moles were unfortunately killed while I tried to remove them from the ground.

Results

A map showing the home range of the mole which was successfully followed is shown in Figure 8, and the activity periods are shown in Table 25. Until the beginning of December the mole confined its movements to an area of approximately 39x22 m. During December new activity was observed outside of this range and on 31 January the flagged area was 39x39 m (maximum diameters). Once the movements of the mole were known the location of the runways appeared to be well defined by the hills on the surface. However, without knowing the movements it would have been impossible to locate the runways from the hills because it is otherwise difficult to tell which hills are interconnected by a runway.

The mole spent most of its active periods in the area of the nest. The longer forays to the perimeters of its home range were infrequent. The mole did have a nest it returned to

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Figure 8. Map of the territory of the mole followed. The position of the nest is marked with an 'x'. Dots indicate places where the mole's position was recorded and usually corresponded with molehills. Lines connecting the positions of the mole are estimated positions of the mole tunnels. In a few instances the positions of the tunnels could not be determined.

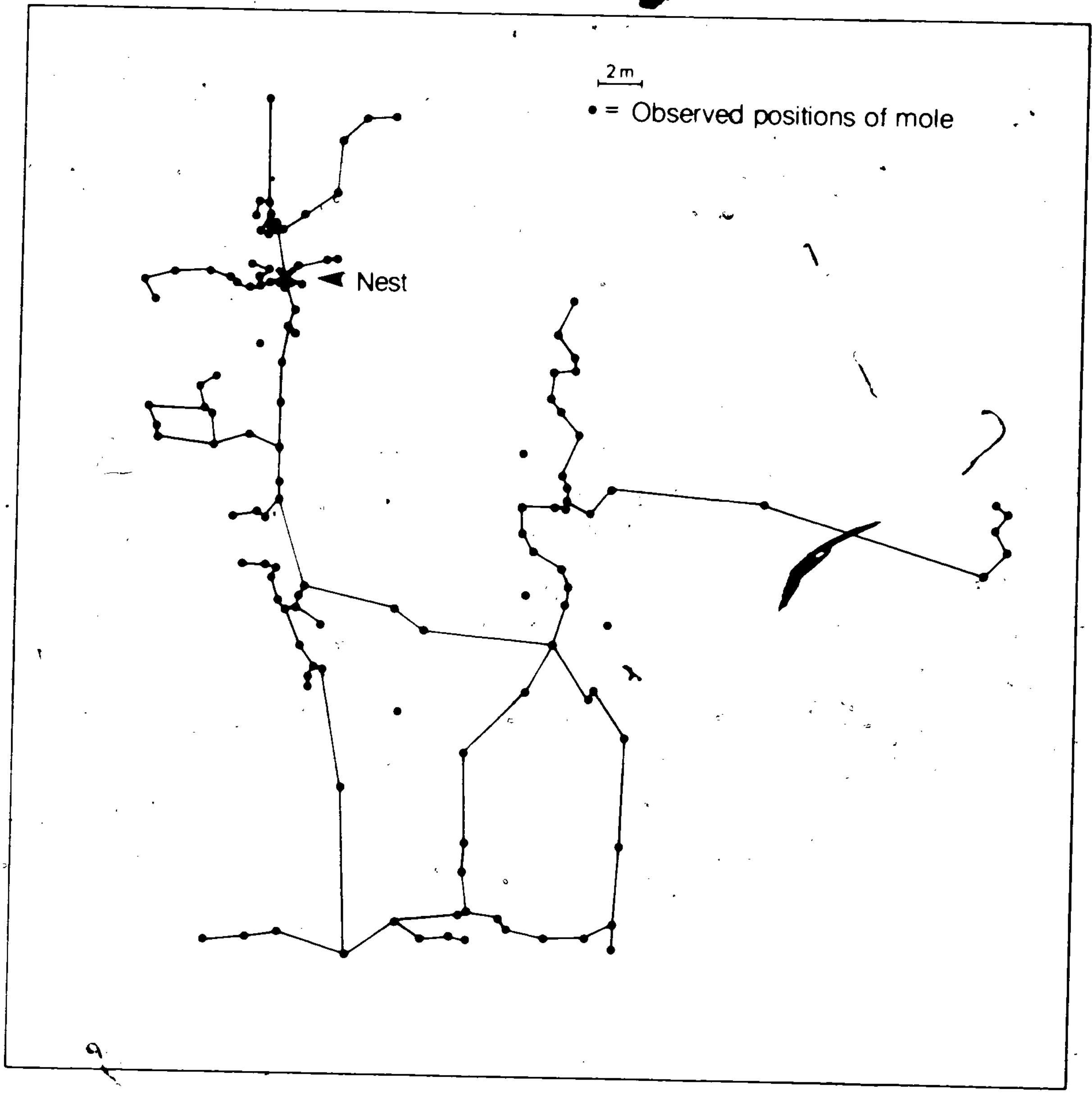
2 m
• = Observed positions of mole
Nest

Table 25. Maximum distances travelled by the mole within its territory during the periods it was followed. Observation began at the earliest times recorded on each date and the latest times were when observation ended.

Date	Time active (elapsed time (mins) in brackets)	Maximum* width (m) travelled	Maximum* length (m) travelled	Time asleep (elapsed time (mins) in brackets)
10 Nov.	1115-1124 (9)	6	2	1125-1500 (215)
12 Nov.	0935-1017 (42)	30.5	-	1018-1417 (239)
12 Nov.	1418-1533 (75)	15	13.5	
16 Nov.	1300-1519 (139)	16	13.5	0910-1259 (229)
18 Nov.	1030-1105 (35)	19.5	-	0900-1030 (90)
19 Nov.	1005-1115 (70)	21	2	1116-1530 (194)
23 Nov.	1014-1417 (243)	17	12	0900-1013 (73)
23 Nov.				1418-1445 (27)
25 Nov.	0919-1526 (367)	38	22	0900-0918 (18)
25 Nov.				1527-1535 (8)
26 Nov.	0916-1210 (176)	19	10	0910-0915 (5)
26 Nov.				1210-1235 (25)
30 Nov.	0939-1222 (163)	23	15	1223-1300 (37)
9 Dec.	0914-0923 (7)	37.5	16	0923-1250 (207)
9 Dec.	1448-1540 (52)	29	15	
22 Dec.	0905-0915 (10)	13	1.5	0915-0920 (5)
31 Jan.	0925-1413 (288)	13	34	

* after Godfrey and Crowfoot (1960)

for sleeping, and this was located in one corner of the territory (Figure 8).

The daily distances travelled by the mole are recorded in Table 25. The days of 23, 25, and 26 November contain information for what appear to be complete periods of activity (the mole was sleeping at the nest site before and after these periods). It can be seen from the movements on these days that the mole did not visit its complete home range (territory?) during one activity period, although it may do so within a 24 hr period (this was not determined).

At the beginning of an observation period the mole was located immediately if it was at its nest. Up to 1 hr was required to locate the mole if it was active when observation began. The mole did not seem to be active during any specific part of the day. For any given time the mole may have been active 1 day and asleep the next. Activity amongst moles within the field was not synchronous because other moles were observed to be digging while the mole I was monitoring was asleep.

The mole moved only for short periods of time, spending a great deal of its time stationary. Table 26 summarizes the amount of time spent by the mole at various activities. It took the mole an average of 30 min to construct a hill, and it rested about 15 min immediately afterwards. It spent a little more than 4 hr awake, and probably sleeps a little less than 4 hr (only one complete observation

Table 26. Amount of time spent by the mole at various activities (only complete periods of 'asleep' and 'awake' which were observed are recorded).

Category	Observations n	Total (min)	Mean	Maximum	Minimum
moving	34	339	9.97		
stationary	66	1124	17.08		
digging	17	563	33.12	152	5
resting	8	130	16.25	28	9
asleep	1	239			
awake	3	904	301.0	368	175

period for the latter was available).

The mole appeared to feed around the base of a hill. From monitoring its movements while it was digging it seemed that there were several blind tunnels radiating outward around the base of the hill. The mole would search these tunnels and occasionally, after a brief stationary period where I presumed it was feeding, it would let out several high pitched squeaks and sniff so loudly that I could hear it through the ground.

Discussion

The home ranges of moles are discussed in terms of maximum lengths and breadths of movements (Godfrey and Crowfoot 1960). From 10 November to 22 December 1976 the mole stayed within an area approximately 39x22 m. By 31 January 1977 the home range had extended to 39x39 m. There are several possible explanations for this increase in movement. The most obvious is that the actual home range was not accurately measured in just 1 month's observation. Second, the individual may have been a male. Male coast moles may extend their ranges during the breeding season in search of females (Glendenning 1959) as does the European mole (Larkin 1948). Third, there was a mole active previously in the area into which the mole being tracked entered in January, but this previous resident was killed in December when I attempted to remove it from the ground with a shovel. The mole being tracked may have been moving into a vacated territory. It is not possible to distinguish between these possible explanations, but an important observation is that the mole being tracked was capable of moving distances of 39x39 m.

The home range measurements for the European mole are comparable to those of the coast mole in this study. Larkin (1948) found that male European moles had home ranges about 47 m long, and females about 30 m. Godfrey (1957) found that female European moles had home ranges 37 m long. Larkin (1948) was estimating home ranges by hill patterns and trapping, Godfrey was using the radioactive isotope technique.

Glendenning's(1959) observations on the activity pattern of the coast mole are markedly different from the results of my study. From his work on caged moles he concludes that the coast mole must almost continuously be searching for food. He mentions that his caged animals rarely remained still or asleep for more than 30 min at a time, and that a mole must on the average have a worm every 10 min or starve. He extrapolates that this situation is true under natural conditions because the coast mole has been observed digging at all hrs of the day and night.

The European mole has an activity rhythm consisting of approximately 4½ hr of activity alternated with about 3½ hr of sleep (Godfrey 1955) at a nest. Only three complete periods (from the time the mole was followed after it had been asleep at the nest until it returned to the nest to sleep again), of activity were observed for the coast mole in my study but its mean duration of activity was 5 hr, roughly that of the European mole. Only one complete period of sleep was observed which was for 3 hr and 59 min, again roughly that of the European mole.

Within any one period of activity the coast mole did not travel throughout its complete home range. This was also observed for the European mole (Godfrey 1955) and the eastern mole (Harvey 1976).

This coast mole spent an average of 30 min at the base of a hill pushing up earth. This time could be considerably shorter (5 min), and in 1 instance it was longer (1½ hr). After working on a hill the mole would invariably take a brief rest averaging 17 min.

Even though only one coast mole was considered in the present study certain inferences can be made about the dispersal capabilities of the species. Clearly, the individual studied is very similar in its activity and movements to other species studied more intensively. A mole appears to inhabit a territory about 40 m long, may traverse areas three times that length if it is a male during the breeding season, and could even possibly travel distances of up to perhaps 800 m if it is young and dispersing if its movements are similar to those of the Townsend mole (Giger 1973).

It seems reasonable, therefore, to conclude that coast moles in a field are at least capable of dispersing throughout the study areas I considered in previous chapters (100 x 100 m), and that moles immediately outside of this area probably have unrestricted access to most, if not all, of the plots (10 x 10 m) in the study area. Therefore, it seems unlikely that the dispersal capabilities of the coast mole restrict it from having access to those plots in the study areas without molehills, and that they are not there for some other reason, probably because the habitat is unsuitable, at least at certain times of the year or in different years.

APPENDIX 31. The number of molehills in the study plots (10x10 m) of the Keur field in autumn (23/9/76).

Plot	1	2	3	4	5	6	7	8	9	10
1	1	0	7	8	13	17	0	0	1	2
2	0	0	12	13	21	9	0	2	4	32
3	0	11	14	6	14	13	7	2	0	4
4	0	0	8	7	3	5	9	13	2	5
5	0	1	2	3	5	1	2	1	2	16
6	1	3	9	8	0	0	0	1	0	1
7	0	0	10	0	0	0	0	0	0	0
8	0	1	2	3	2	0	1	0	0	0
9	0	1	2	0	2	0	1	0	1	3
10	0	0	0	2	1	2	0	0	0	0

APPENDIX 32. The number of molehills in the study plots (10x10 m) of the Keur field in winter (17/1/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	3	1	7	14	18	11	4	10	3	2
2	0	8	16	20	22	15	0	4	21	37
3	1	11	13	14	25	21	3	38	47	28
4	0	1	8	14	14	13	10	12	6	17
5	0	1	13	18	23	6	6	3	13	32
6	0	0	2	0	0	0	0	1	2	0
7	0	0	0	2	1	0	0	0	0	0
8	0	0	0	2	3	1	0	0	0	1
9	0	0	0	0	1	0	0	0	0	0
10	0	0	0	0	0	0	0	1	4	4

APPENDIX 33. The number of molehills in the study plots (10x10 m) of the Keur field in spring (30/3/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	14	2	9	11	24	13	5	14	9	11
2	9	16	15	14	16	16	8	8	17	39
3	2	9	15	9	13	16	4	23	32	25
4	0	1	10	12	16	16	2	24	14	21
5	0	1	5	11	14	6	7	2	8	21
6	0	1	6	0	1	0	0	4	4	8
7	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	5	7	1
9	0	0	0	0	0	0	0	0	0	4
10	0	0	0	0	0	0	0	0	5	11

APPENDIX 34. The number of molehills in the study plots of the Laity field in autumn (21/9/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	0	4	3	2	6	2	5	11	7	15
2	9	14	7	2	3	11	14	8	2	0
3	2	2	0	2	0	0	1	7	1	2
4	5	10	10	7	14	18	18	2	0	6
5	8	26	19	18	14	8	0	0	3	14
6	24	7	10	10	6	0	2	2	5	1
7	2	4	5	1	4	3	4	4	4	4
8	2	0	19	4	2	9	2	4	1	1
9	0	0	10	9	8	12	6	5	0	1
10	0	3	7	12	3	1	4	1	7	2

APPENDIX 35. The number of molehills in the study plots (10x10 m) of the Laity field in winter (19/1/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	4	8	7	1	10	18	12	14	26	27
2	5	23	4	0	3	6	14	18	1	0
3	0	14	2	34	3	19	1	11	5	0
4	21	41	31	20	51	30	7	1	24	10
5	46	28	39	27	8	1	6	10	5	26
6	59	33	24	2	3	8	4	12	29	0
7	14	32	4	0	8	13	23	5	19	8
8	2	13	21	7	37	6	1	11	8	8
9	0	1	6	5	10	24	6	13	5	0
10	0	0	3	2	2	2	9	0	1	2

APPENDIX 36. The number of molehills in the study plots (10x10 m) of the Laity field in spring (6/4/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	6	15	3	0	2	5	3	3	4	14
2	17	9	0	0	2	4	5	12	0	0
3	0	0	7	11	0	0	5	7	5	0
4	7	3	17	35	4	0	4	2	0	0
5	34	14	18	9	0	4	8	0	0	6
6	28	34	16	0	2	0	0	1	10	1
7	0	3	6	7	2	4	6	7	13	1
8	0	0	4	0	1	5	7	5	7	6
9	0	0	0	4	0	8	15	5	8	0
10	0	0	0	0	1	0	0	3	2	1

APPENDIX 37. The number of molehills in the study plots (10x10 m) of the Robertson field in autumn (24/9/76).

Plot	1	2	3	4	5	6	7	8	9	10
1	0	0	0	0	0	0	0	0	0	0
2	0	0	4	0	0	0	0	0	1	0
3	0	12	17	12	7	15	8	7	6	5
4	0	0	0	0	0	0	1	4	5	2
5	0	0	0	0	0	0	11	5	0	1
6	0	0	0	0	0	0	3	6	0	1
7	2	0	0	0	0	0	2	12	0	0
8	2	0	6	0	1	4	20	8	0	17
9	6	5	10	11	3	9	6	0	0	11
10	6	7	11	1	2	8	6	12	5	7

APPENDIX 38. The number of molehills in the study plots (10x10 m) of the Robertson field in winter (26/1/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0
3	0	15	19	14	10	11	12	13	13	12
4	0	0	0	0	0	0	7	17	8	7
5	0	0	0	0	0	0	2	1	0	3
6	0	0	0	0	0	1	1	6	0	0
7	10	0	0	0	0	0	6	13	0	0
8	10	10	10	1	0	5	21	2	0	2
9	8	2	4	4	3	9	2	0	0	15
10	5	6	10	7	4	17	1	21	9	7

APPENDIX 39. The number of molehills in the study plots (10x10 m) of the Robertson field in spring (4/4/77).

Plot	1	2	3	4	5	6	7	8	9	10
1	0	0	0	0	0	0	0	0	0	1
2	0	0	0	0	0	0	0	0	1	19
3	0	0	2	5	7	2	5	7	10	15
4	0	0	2	0	0	0	1	5	12	10
5	0	0	0	0	0	0	2	7	0	0
6	0	0	0	0	0	0	0	3	0	0
7	5	0	0	0	0	0	1	6	0	0
8	4	6	0	0	0	1	10	6	0	0
9	8	3	6	3	0	4	2	0	0	4
10	5	2	9	6	3	10	5	15	8	10

APPENDIX.40. Soil parameter values for the Keur field in autumn (30/9/76).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	2	37.1	37.1	0.75	0.75	27.9	26.5	43.8	46.7
2	32	31.6	32.6	0.91	0.78	28.8	25.5	36.9	47.6
3	4	29.9	30.8	0.95	0.88	28.3	27.2	35.8	39.6
4	5	31.8	31.1	0.76	0.81	24.2	25.3	47.1	44.2
5	16	28.4	29.4	0.94	0.89	26.6	26.3	37.9	40.1
6	1	26.1	27.7	1.01	0.95	26.3	26.4	35.5	37.8
7	0	33.2	31.7	0.93	0.94	31.0	29.9	33.9	34.6
8	0	27.2	29.3	1.04	1.03	28.3	30.3	32.4	30.8
9	3	27.4	27.3	1.05	1.11	28.7	30.3	31.7	27.8
10	0	27.1	27.4	0.97	0.96	26.3	26.2	37.1	37.6

APPENDIX 41. Soil parameters for the Keur field in winter (14/2/77).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	3	57.5	55.5	0.75	0.72	42.9	40.0	28.8	32.8
2	21	55.4	48.5	0.82	0.88	45.6	42.7	23.3	24.1
3	47	52.3	46.4	0.85	0.84	44.7	38.9	23.1	29.3
4	6	62.0	56.7	0.81	0.79	50.3	44.6	19.1	25.7
5	13	45.5	43.2	0.93	0.91	42.4	39.4	22.5	26.2
6	2	39.5	37.5	0.96	0.97	37.9	36.3	25.9	27.2
7	0	46.7	46.6	0.91	0.87	42.5	40.5	23.2	26.8
8	0	43.5	41.2	1.00	0.94	43.5	38.8	18.7	25.7
9	0	41.7	45.7	0.99	0.95	41.1	43.3	21.7	20.9
10	4	40.3	38.7	0.96	1.01	38.8	39.1	24.8	22.8

APPENDIX 42. Soil parameters for the Keur field in spring (30/3/77).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	11	68.3	63.0	0.73	0.70	49.7	44.3	22.7	29.1
2	39	54.0	54.4	0.80	0.76	43.0	41.6	26.9	29.5
3	25	55.1	47.3	0.81	0.78	44.8	36.8	24.5	33.8
4	21	49.7	44.4	0.82	0.85	40.8	37.6	28.2	30.4
5	21	60.2	51.2	0.73	0.83	43.8	42.4	28.8	26.4
6	8	52.3	45.6	0.83	0.91	43.5	41.3	25.1	24.4
7	0	48.9	51.7	0.87	0.81	42.3	41.7	25.0	27.9
8	1	43.8	39.9	0.94	0.94	41.1	37.6	23.5	26.8
9	4	44.6	40.5	0.94	0.98	42.2	39.7	22.2	23.3
10	11	38.3	39.8	1.00	0.93	38.3	36.9	23.7	28.1

APPENDIX 43. Soil parameters for the Laity field in autumn (5/10/76).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	4	30.4	35.4	1.13	0.89	34.3	31.6	23.0	34.8
2	14	46.2	46.0	0.92	0.87	42.6	40.3	22.6	26.9
3	2	39.6	44.1	0.95	0.91	37.8	40.0	26.4	25.6
4	10	43.4	41.6	0.89	0.95	38.5	39.4	27.9	24.7
5	26	43.0	42.4	0.94	0.88	40.2	37.3	24.3	29.5
6	7	41.6	41.8	1.01	1.00	41.9	41.9	19.9	19.3
7	4	37.1	41.7	1.03	0.97	38.2	40.4	33.0	23.0
8	0	36.8	32.5	1.03	1.14	37.8	37.0	23.4	20.0
9	0	35.7	40.6	1.09	0.95	38.9	38.5	20.0	25.6
10	3	26.0	24.8	1.18	1.08	30.6	26.8	24.7	32.4

APPENDIX 44. Soil parameters for the Laity field in winter (15/2/77).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	4	32.7	36.3	1.03	0.99	33.6	36.1	27.4	26.4
2	5	42.5	40.9	0.97	0.89	41.1	36.6	22.4	29.6
3	0	41.6	51.2	0.99	0.91	41.1	46.5	21.6	19.2
4	21	45.2	42.2	0.96	1.03	43.5	43.3	20.2	17.9
5	46	40.8	38.2	1.04	1.04	42.5	39.8	18.1	20.8
6	59	34.1	39.9	1.05	0.99	35.8	39.7	24.6	22.8
7	14	44.6	53.7	0.98	0.87	43.7	47.0	19.3	19.9
8	2	41.4	50.1	0.96	0.91	39.7	45.5	24.2	20.2
9	0	38.0	51.1	1.07	0.90	40.7	46.0	18.9	20.0
10	0	36.3	36.3	1.07	1.03	38.7	37.3	21.0	24.0

APPENDIX 45. Soil parameters for the Laity field in spring (6/4/77).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	6	34.0	32.0	0.92	0.96	31.2	30.9	34.1	32.7
2	17	34.5	35.7	0.97	0.94	33.6	33.6	29.5	31.0
3	0	39.1	39.7	1.01	1.06	39.5	42.0	22.3	18.0
4	7	39.6	47.3	0.96	0.82	38.0	38.6	25.8	30.5
5	34	37.4	39.8	1.02	0.95	38.0	37.8	23.6	26.4
6	28	46.8	47.9	0.90	0.86	41.9	41.2	24.3	26.4
7	0	45.1	36.7	0.90	1.03	40.7	37.8	25.2	23.2
8	0	49.4	62.7	0.87	0.70	43.0	43.8	24.0	29.8
9	0	49.6	50.3	0.88	0.90	43.8	45.2	22.9	20.9
10	0	39.4	39.5	0.96	0.97	37.8	38.5	26.0	24.7

APPENDIX 46. Soil parameters for the Robertson field in autumn (1/10/76).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	6	38.6	46.2	0.90	0.78	34.9	36.0	31.1	34.5
2	6	42.1	41.5	0.95	0.85	39.8	35.2	24.3	32.6
3	20	41.5	42.7	0.94	0.85	39.1	36.2	25.4	31.7
4	2	40.1	45.1	0.89	0.85	35.7	38.2	30.7	29.7
5	3	42.1	35.7	0.93	0.92	39.2	32.8	25.7	32.5
6	11	39.8	44.6	0.92	0.84	36.5	37.7	28.8	30.6
7	1	45.0	36.6	0.88	0.71	39.7	40.2	27.1	33.0
8	8	38.0	34.6	0.98	0.99	37.2	34.2	25.8	28.4
9	0	31.0	28.0	1.08	1.13	33.5	31.7	25.7	25.7
10	0	32.6	29.9	1.09	1.10	35.4	33.0	23.5	25.5

APPENDIX 47. Soil parameters for the Robertson field in winter (15/2/77).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	21	40.8	39.2	1.01	1.00	41.4	39.2	20.2	23.0
2	0	47.6	50.8	0.89	0.88	42.6	44.5	23.6	22.3
3	2	55.1	56.1	0.83	0.85	45.8	47.9	22.7	19.9
4	13	51.3	58.8	0.85	0.82	43.9	48.2	23.9	20.9
5	6	50.0	47.5	0.92	0.90	45.9	42.8	19.5	23.2
6	1	51.0	67.0	0.87	0.88	44.6	58.8	22.4	8.1
7	17	56.2	56.8	0.84	0.84	47.2	47.6	21.1	20.7
8	13	51.6	57.5	0.82	0.76	42.1	43.9	27.0	27.3
9	0	52.9	63.1	0.87	0.78	46.1	49.2	21.3	21.3
10	0	49.2	38.4	0.89	1.01	44.0	38.6	22.2	23.4

APPENDIX 48. Soil parameters for the Robertson field in spring (4/4/77).

Plot	No. of Molehills	Soil moisture 10 cm (%)	Soil moisture 20 cm (%)	Bulk density 10 cm (gm/cc)	Bulk density 20 cm (gm/cc)	Water content 10 cm (%)	Water content 20 cm (%)	Air space 10 cm (%)	Air space 20 cm (%)
1	1	47.6	41.8	0.89	0.98	42.2	40.8	24.3	22.1
2	19	44.5	44.7	0.87	0.97	38.6	43.2	28.7	20.4
3	15	51.2	51.2	0.87	0.84	44.4	43.3	22.9	25.1
4	10	55.9	49.5	0.81	0.86	45.4	42.5	23.8	24.9
5	0	47.4	48.3	0.88	0.90	41.8	43.7	24.9	22.2
6	0	43.5	39.5	0.93	0.96	40.6	38.0	24.0	25.8
7	0	39.0	35.6	1.01	1.02	39.3	36.2	22.7	25.4
8	0	39.0	35.0	1.00	1.03	38.9	35.9	23.5	25.4
9	4	44.7	47.4	0.87	0.87	39.1	41.2	27.9	25.5
10	10	51.2	47.4	0.85	0.88	43.8	41.7	24.0	25.1

APPENDIX 49. Number of molehills, O_2, CO_2, pH and soil moisture for mole territory #4 during the nitrogen fertilizer experiment (summer 1977).

Date	No. of molehills	n for tunnel gases	O_2 in tunnel (%)	CO_2 in tunnel (%)	n for soil gases	O_2 in soil (%)	CO_2 in soil (%)	pH	Soil moisture (%)
25/4	38	10	16.0	3.8				4.66	41.49
4/5	35	10	17.25	2.38	5	15.04	3.98	4.55	43.54
16/5	65	9	18.93	2.0	5	17.0	4.2	4.69	38.10
1/6	31	9	16.78	2.94	4	11.12	6.72	4.62	45.15
20/6	22	8	19.6	0.92	4	18.87	1.77	4.56	21.64
4/7	19	9	19.7	1.03	4	18.95	1.9	4.61	29.56
18/7	32	9	19.52	1.2	4	18.62	2.07	4.41	22.96
1/8	11	6	20.23	0.67	5	19.40	1.5	4.67	20.93
15/8	2	8	19.76	0.75	5	19.24	1.18	4.44	14.95
29/8	33							4.63	25.00

APPENDIX 50. Number of molehills, O_2, CO_2, pH, and soil moisture for mole territory #7 during the nitrogen fertilizer experiment (summer 1977).

Date	No. of molehills	n for tunnel gases	O_2 in tunnel (%)	CO_2 in tunnel (%)	n for soil gases	O_2 in soil (%)	CO_2 in soil (%)	pH	Soil moisture (%)
25/4	58	10	18.8	1.4				4.82	31.81
4/5	39	8	18.57	1.74	5	18.06	2.2	4.77	36.05
16/5	76	9	16.93	1.13	4	19.35	1.42	5.05	34.35
1/6	69	9	17.97	1.82	3	17.0	2.47	4.94	40.77
20/6	54	9	20.12	0.31	1	20.2?	0.7?	4.91	19.19
4/7	80	9	20.18	0.52	5	19.92	0.78	5.20	27.61
18/7	77	9	20.22	0.53	5	19.76	1.02	4.88	24.46
1/8	43	8	20.66	0.24	5	20.46	0.46	4.88	18.47
15/8	1	9	20.65	0.1	5	20.54	0.16	4.79	11.90
29/8	49							4.85	19.23

APPENDIX 51. Number of molehills, O_2, CO_2, pH and soil moisture for mole territory #10 during the nitrogen fertilizer experiment (summer 1977).

Date	No. of molehills	n for tunnel gases	O_2 in tunnel	CO_2 in tunnel	n for soil gases	O_2 in soil (%)	CO_2 in soil (%)	pH	Soil moisture (%)
25/4	75	10	18.0	2.0				4.66	42.70
4/5	41	10	17.76	2.24	5	13.02	4.92	4.77	47.14
16/5	37	10	18.24	2.57	5	14.82	5.14	4.85	41.63
1/6	39	10	15.8	3.59	5	10.22	6.26	4.70	48.98
20/6	14	10	19.65	0.73	5	19.3	1.38	4.56	25.44
4/7	46	10	19.91	1.0	5	19.38	1.56	4.81	38.87
18/7	41	9	19.42	1.22	5	18.28	2.18	4.60	32.74
1/8	34	7	20.39	0.56	4	20.32	0.57	4.76	24.69
15/8	6	9	20.55	0.15	5	20.52	0.18	4.44	16.48
29/8	51							4.69	31.60

APPENDIX 52 The number of molehills in the individual territories during the nitrogen fertilizer experiment.

Territory/date Controls	Apr. 25	May 4	May 16	Jun 1	Jun 20	Jul 4	Jul 18	Aug 1	Aug 15	Aug 29
2	19	18	40	17	8	48	17	3	0	3
4	38	35	65	31	22	19	32	11	2	33
6	13	6	8	8	13	10	3	1	0	0
12	39	29	41	15	0	0	7	1	0	3
14	30	11	11	33	9	9	9	7	1	1
	27.8	19.8	33.0	20.8	10.4	17.2	13.6	4.6	0.6	8.0
kg N/ha										
8	32	8	23	61	35	15	43	19	3	19
9	99	50	87	41	17	24	16	15	0	23
10	58	39	76	69	54	80	77	43	1	49
13	24	18	16	18	19	12	3	5	1	2

APPENDIX 52 (Continued)

Territory/date	Apr. 25	May 4	May 16	Jun 1	Jun 20	Jul 4	Jul 18	Aug 1	Aug 15	Aug 29
15	16	15	27	36	17	7	12	8	0	12
	45.8	26.0	45.8	45.0	28.4	27.6	30.2	18.0	1.0	21.0
140 kg N/Lu										
1	20	24	40	32	35	39	3	29	13	21
3	33	27	39	58	31	52	50	18	1	21
5	11	12	7	2	0	8	1	2	0	20
7	75	41	37	39	14	46	41	34	6	51
11	34	13	22	32	25	6	4	1	0	6
	34.6	23.4	29.0	32.6	21.0	30.2	19.8	16.8	4.0	23.8

APPENDIX 53. Mean nitrate and ammonia content (ppm) in the territories of the fertilizer experiment. The second application of fertilizer was applied 11 July after the soil samples were collected on that date.

Date/ Treatment	Control (Territory 4)		70 kg N/ha (Territory 10)		140 kg N/ha (Territory 7)	
	NO_3	NH_4	NO_3	NH_4	NO_3	NH_4
11/7	2	0	7	0	0	4
18/7	0	0.2	0	0	4	0.6
25/7	0	0.4	0	0	4	0.4
1/8	0.4	0.4	6	0	0.6	2
8/8	0.2	2	0	0	0	0
15/8	2	0	0	0	7	0.4
29/8	0	0	2	0.4	3.4	0

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