

Population Studies on the Distribution of Moles  
(Talpa europaea L.) relative to food supply  
and general habitat

by

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## SUMMARY

1. Preliminary investigations of the stomach contents of moles in 1967/68 winter showed that earthworms were the main food of moles and that the percentage weight of earthworms in the diet might vary in different localities.

2. The distribution, population densities and biomass of earthworms were determined in Boghall glen and the results were related to the habitat and the distribution and abundance of moles. The distribution and abundance of earthworms were found to be directly influenced by the habitat particularly soil and soil conditions. Moles lived in the areas with the highest populations of earthworms and the abundance of moles was influenced by the abundance of earthworms.

3. The population densities of insect larvae and slugs were determined in Boghall glen and the results were related to the distribution of moles. The results showed that the distribution of moles was not related to those of insect larvae and slugs.

4. A study of the distribution and abundance of moles in relation to the habitat at Boghall glen showed that the habitat had no direct effect on the distribution of moles but the abundance of moles was directly related to the habitat.

5. Studies on the distribution and abundance of moles and earthworms in relationship to soil and soil conditions showed that soils which were suitable for earthworms were also suitable for moles, and that the abundance of earthworms, and as a result that of moles, were influenced by soil and soil conditions.

6. Results of investigations of the diet showed that invertebrates were the only food eaten by moles and that moles did not have any major preferences for particular items of food. The composition of the diet reflected mainly the distribution and relative abundance of the moles' potential foods in the soil.

7. The monthly variations in the body weight, weight of stomach contents, weight of stomach contents expressed as a percentage of body weight and the composition of the diet of moles were studied from March to August 1969. The body weight did not undergo any major monthly fluctuations except in the breeding season. Males were significantly heavier in May than in March and July and females were significantly heavier in each of April, May and June than in March. There were no significant monthly differences in the weight of stomach contents and the weight of stomach contents expressed as a percentage of body weight in males. The food consumption of females was significantly higher in May than in March and the weight of stomach contents expressed as a percentage of body weight (less the weight of stomach contents) was significantly higher in May than in March and July and in June than in July. The relative weight of earthworms in the diet did not undergo any major monthly variations but insect larvae contributed relatively more weight to the diet than earthworms in May to July.

Males were significantly heavier than females both as adults and as juveniles. Juveniles were lighter than adults in June but they grew to adult sizes in July though they were still sexually distinguishable from adults. There were no significant differences

between males and females and adults and juveniles in the weight of stomach contents, weight of undigested food in the stomachs and the weight of stomach contents expressed as a percentage of body weight. The weight of full stomachs (stomach contents + empty stomachs) and the weight of empty stomachs of males were significantly higher than those of females, on average and in January 1970. There were no major differences in the qualitative composition of the diet of males and females and of adults and juveniles.

8. The body weight and feeding habits of moles collected in pastures at different localities in January 1970 were compared. There were no significant differences in the body weight, stomach weight, weight of stomach contents, weight of stomach contents expressed as a percentage of body weight and the relative weight of earthworms in the diet of moles in the different pastures. Slight differences in the composition of the diet were observed between localities.

9. Four moles were each fed in captivity for 10 weeks. Males ate 73-75% of their body weights and females ate 85-89% of their body weights daily when fed on earthworms.

10. Investigations carried out on wild and captive moles showed that captive moles stored earthworms from mid-September to end of November and wild moles stored earthworms probably from after mid-October to mid-January.

11. Three methods were used to estimate the population density of moles in Boghall glen. Only 23% of moles built fortresses and

only 43% built nests that could be located from surface evidences. Reliable estimates of the number of moles present were obtained in the spring when all mole-hills and ridges were flattened on two areas and the number of areas with fresh diggings were counted on the second and third days.

12. The age of moles was assessed by measuring the length of the second upper molar teeth. The age structure of a mole population depends on the history of the population. The maximum life span of a mole was found to be four years but only 3 moles (1.7%) in the populations studied (N = 181) was of this age. The age distribution was similar in both males and females.

13. Investigations carried out on a small population of moles on Leip field from July 1969 to January 1970 showed that the sex ratio in an undisturbed population in July was 1:1. Evidence was obtained which suggested that moles were usually solitary and aggressive in the presence of other moles. Only one of six moles marked on Leip field in mid-August 1969 survived till January 1970. The other moles probably died during the severe drought and soil desiccation at the end of August to early September and in October 1969.

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## INTRODUCTION

The common mole, Talpa europaea L., is one of the best known mammals and it can survive in a wide range of habitats. Its presence is indicated by mole-hills and the raised ridges of surface runs.

The status of the mole as a pest is a matter of controversy but moles and their mole-hills are regarded as a nuisance in gardens, seed beds, golf courses and in grass fields. The numbers of moles in arable land are kept down by cultivation practices and by pest control officers. In many old established permanent pasture lands and other similar relatively stable habitats however, the numbers of moles have been increasing steadily since the decline in the mole-fur trade and the reduction in the number of professional mole-catchers. On pasture land with severe infestation, the combination of mole-hills and surface burrows lowers the quality and reduces the quantity of grass, interferes with mowing and encourages the growth of weeds such as the thistle.

The fortress, nest and tunnel systems of the mole have been extensively studied but little has been written about the social organization in the species. The types of food eaten by the mole in the various parts of its range have also been very well studied but the factors determining the composition of the diet, e.g. abundance of food, season, and habitat conditions have not been fully explained, neither has the role of the habitat on the distribution of the mole been described for any particular mole populations.

A clear understanding of their habitat preferences, the factors influencing their distribution and abundance and the minimum biomass

necessary for their existence will help in the effective control and management of moles. The present investigation is a study of the physical and general habitat conditions of a mole population and the relationship between moles and their food, particularly earthworms, in a reseeded semi-upland pasture field.

SECTION 1      LITERATURE REVIEWPART A - THE MOLE (Talpa europaea Linnaeus)Distribution

Macgillivray (1845), Matthews (1952) and Godfrey and Crowcroft (1960) reported that the mole is distributed throughout most of Europe and its range extends to the southern shores of the Mediterranean. In Britain it occurs all over the mainland but is absent from Ireland and some of the smaller islands. Harvie-Brown and Buckley (1892) stated that the mole was extending its range (in Scotland) both in existing areas and in accidental colonization of areas originally devoid of moles. Their observations were later confirmed by MacDougal (1942). The mole is able to inhabit rich and poor soils alike and in Britain it has been reported from habitats ranging from rich woodlands, pastures and meadows to dry sandy soils both at sea shores and at the summit of high hills (Adams, 1920; Heath, 1932; MacDougal, 1942; Mellanby, 1967). Folitarek (1932) observed the habitat preferences of Russian (Ukraine) moles and noted that moles were more abundant in forests, fields and meadows. Kruishtal (1934) also studied the distribution of moles in Ukraine and concluded that the distribution and abundance of moles are governed by a complex of factors, one of which is the presence of invertebrates of a particular size. The influence of food on the distribution of moles was also reported by Mellanby (1966, 1968) who concluded that the mole is indigenous to woodlands but has

successfully colonized man-made environments. He also noted that the patchy distribution of moles in the Pennines was related to the patchy distribution of their food in the area. However, no investigations have so far been conducted to measure quantitatively the factors responsible for the distribution of moles.

The mole's domain and the social relationship of moles.

Macgillivray (1845) described the fixed arrangement of the internal structure of the mole's fortress. His account was taken from that of Geoffrey St. Hilaire (1829) which was based on the work of Henri Le Court. Evans (1892) excavated a number of fortresses and found that the positions of tunnels in the fortresses were not disposed with mathematical exactitude as was earlier believed. Adams (1903, 1910) was the first to dissect and draw the internal structure of many fortresses and he found that the internal structure of the fortresses was variable. He found the complicated galleries to be purely accidental and without reference to premeditated escape except in the case of the bolt runs. Evans (1907) made further dissections and confirmed his own earlier observations and those of Adams. Adams found that fortresses were built at the end of autumn and their construction was completed in a day. He described the nest cavity as roughly spherical and the nest as a ball of grass or leaves or a mixture of both. Ford (1935) suggested that it is only old males that build fortresses and that the building of fortresses is determined by habitat conditions.

Burton (1950) found that fortresses were not built by all moles. He observed two nests  $3\frac{1}{2}$  ft. and  $2\frac{1}{2}$  ft. each below the surface and without fortresses above them. Godfrey and Crowcroft (1960) found that fortresses were built by both sexes and that in pasture, nests are often built beneath the unbroken turf and that more than one nest may be present within a tunnel system. There were early controversies about the methods and organs employed by the mole in digging. Macgillivray (1845) and Bell (1837) supposed that the muzzle of the mole contained a special digging bone while Adams (1906) and Folitarek (1932) assumed that the mole lifted the soil with its head and shoulders. Conclusive evidence about the methods and organs of digging in the mole was provided by Skoczen' (1958). He made observations on moles both under artificial and natural conditions and found that the mole uses only its front paws for digging. All previous workers agree that the mole makes three types of tunnels - deep permanent tunnels with associated mole-hills, shallow tunnels with the displaced soil formed into a ridge and open trenches called rutting runs or traces d'amour. Adams (in Barrett-Hamilton, 1911) concluded that the tunnels of males were different from those of females. Macgillivray (1845) and Bell (1874) found no differences in the tunnel system of males and females, but Larkin (1948) observed a tendency on the part of juvenile males to start the construction of their permanent tunnel systems by digging a single tunnel in a comparatively straight line while the tunnel systems of juvenile females lacked apparent design.

Adams (1903, 1910) observed that rutting runs could be found any time in the year but that they were more abundant in the reproductive period. Barrett-Hamilton (1911) suggested that rutting runs are probably made by moles that are searching for a new territory. Larkin (1948) found rutting runs only in the reproductive season. The rate of burrowing was studied by Godfrey and Crowcroft (1960) who found that in pasture, a male constructed 22 yards of surface runs in the first 24 hours, 4 yards in the second 24 hours and 26 yards in the following 4 days and that up to 40 yards of open runs could be made overnight by a single mole. They found that the amount of tunnel constructed depended on the time devoted to digging which is mainly influenced by the relative abundance of the food.

The social relationship of moles within a population is not conclusively known. Barrett-Hamilton (1911) and Ford (1935) suggested that old males are solitary while females and juveniles are comparatively sociable. Larkin (1948) and Godfrey (1957) also reported the close association between females and their offsprings. Multiple catches of moles in the same tunnel has been reported by some authors (MacDougal, 1942; Larkin, 1948; Stein, 1950; Mellanby, 1966). Larkin found only single females in his multiple catches and he explained that multiple catches is due to the larger home ranges and greater activity in males relative to females. Stein (1950) explained multiple catches as "changes of shift" or "day shift" in the group based on the fact that the absence of synchrony in the activity rhythm of different individuals makes it possible for many

moles to use the same tunnel. Godfrey and Crowcroft (1960) believed that the "changes of shift" envisaged by Stein could occur in overcrowded habitats but that moles are solitary and aggressive by nature. They pointed out that the use of common runways under certain conditions, particularly during migrations, is not inconsistent with territorial behaviour. Some authors have commented that the mole is prone to cannibalism (Barrett-Hamilton, 1911; MacDougal, 1942) but only Larkin (1948) has reported a case of cannibalism involving a male and a juvenile and he commented that females may have to defend their offsprings from males. He believed that territorial behaviour helps to stabilize the population density over large areas in the early winter. Godfrey (1957b) reported a number of fights between moles and Godfrey and Crowcroft (1960) suggested that fights help to preserve the isolation and territorial rights of individuals and do not generally lead to deaths unless an individual is frequently attacked.

#### The food of the mole

Macgillivray (1845) wrote that the food of the mole is mainly earthworms and insect larvae but it will occasionally eat frogs, lizards and birds. The first significant comparative qualitative work on the food of moles was that of White (1914). He examined the contents of a large number of selected stomachs and found that the mole was carnivorous and that earthworms and insect larvae were the main foods. Adams (1920), Folitarek (1932), and MacDougal (1942) also examined stomach contents and found that the mole is

completely carnivorous and that plant remains in the stomachs were accidental. No systematic food preference tests have been done on the common mole. Kruishtal (1934) studied the food preference by combining an examination of stomach contents with an investigation of the invertebrates in the soil and he found that the mole's food included nearly all groups of animals that inhabit the soil it occupies and that the smaller invertebrates occurred less frequently in stomach contents than in soil samples. He regarded all the vertebrates he found in the stomachs as incidental prey. The local, seasonal and yearly variations in the diet of the mole have been observed by many workers. Ford (1935) examined the stomach contents of moles captured near Oxford and found that the proportion of earthworms to insect larvae in the stomachs depended on the habitat. Larkin (1948) examined stomach contents from three different localities over two winters and found that the proportion of earthworms and insects in the diet show great monthly, yearly and local variations and that in an abundance of food earthworms make up to 90% or more of the total diet. He found that the proportion of insects in the diet increases from November to June. Godfrey and Crowcroft (1960) examined the contents of stomachs collected from November (1953) to October (1954). They found no significant monthly differences in food consumption except that the stomachs of females in May contained significantly more food than in any other month. They found that the qualitative composition of the diet varied considerably from month to month and concluded that this was mainly related to the reproductive cycles of the animals preyed upon. They examined

stomachs collected in one month from two localities, one mile apart, and found that earthworms and insect larvae occurred in approximately the same percentage number of stomachs in the two localities and that all other food items showed great local variations in their percentage occurrences in the stomachs. They explained that the composition of the diet of the mole in any locality is related to the distribution and abundance of its food in the soil it occupies. Skoczeń (1966) examined stomachs from three localities and found that the weight of stomach contents of moles collected at the same locality does not undergo any major fluctuations except in the breeding season. He found that the consumption of certain food items depends on season and habitat and that insects occurred in the diet only slightly in the cold seasons but more abundantly as the soil gets warmer. 'Stomach stones' have been reported to occur in the stomach contents of moles. Godfrey (in Godfrey and Crowcroft, 1960) found them in various stages of formation in fifteen out of 702 stomachs. Skoczeń (1966) found the occurrence of 'stomach stones' in the stomachs to be related to habitat and the sex and age of moles and he commented that their presence in the stomachs is supposed to influence the mortality of moles. He described them as, "balls of loose or compact plant fragments mixed with mole hairs and parts of arthropodal armour".

Little work has been done to determine the quantity of food eaten by moles. Macgillivray (1845) wrote about the excessive voracity of the mole and the fury of a hungry mole and added that a mole will die quickly if deprived of food. Matthews (1952)

explained that the observed voracity was related to the necessity for the mole to maintain a high body temperature. Skoczeń (1957) found that when captive moles are fed on earthworms males eat 50% of their body weight, and females eat 100% of their body weight daily. The food consumption of moles under natural conditions was estimated theoretically by Godfrey and Crowcroft (1960) who found that the maximum weight of food in a full stomach was 16 g. They estimated that if the stomach was filled near the beginning and end of the three daily periods of activity it will receive a maximum of 96 g. of food daily which is roughly equivalent to the body weight of the whole animal. They assumed, however, that in unfavourable habitats like arable fields the stomachs will be full or nearly full only three times daily and 40-45 g. (about 50% of the body weight) will represent a more probable subsistence level. Hawkins and Jewell (1962) experimented with two captive moles. Each mole was kept in captivity for at least two weeks before its daily food consumption was recorded. They found that moles eat about one-third to half their body weight daily when fed on earthworms and that the amount of food eaten depended on the calorific value of the food. Mellanby (1967) fed one captive mole on earthworms and found the daily food consumption to be approximately equal to half the body weight. He suggested that the mole's food consumption is overestimated because of the habit of the mole of storing excess food which could easily be overlooked.

Sexual differences in diet and food consumption have been

reported for the mole. Folitarek (1932) found that females eat 43.3% less food than males. Larkin (1948) found no significant qualitative differences in the diet of males and females but he found both slight and significant monthly differences in the quantitative analysis of the food of males and females. Godfrey and Crowcroft (1960) found the stomachs of males to be significantly heavier than those of females in February, March, August, October, November and on the average. They found the stomachs of females to be significantly heavier than those of males in May and explained that this was due to the extra-nutritional demands of lactation in females.

The methods employed by the mole in locating and capturing its prey is still a matter of conjecture. Folitarek (1932) reported that the tunnel of moles acts like a pit-fall trap for earthworms and active insects in favourable conditions but that in unfavourable conditions the mole deliberately hunts for its food by extending its burrows. Godfrey and Crowcroft (1960) suggested that the mole obtains its food by searching within the soil, throughout its existing tunnels and above the ground. They believed that surface feeding is the least important method and is caused by unfavourable conditions below the ground. Mellanby (1966, 1967 and 1968) also suggested that the mole's tunnel acts like a pit-fall trap and that digging is done mainly to extend tunnels that are not sufficiently productive and to repair damaged tunnels. There is some evidence however, to show that digging and feeding are related. Godfrey (1955) found that moles in arable land spent two-thirds of the active

period in digging while those in pastures spent considerably less time. She believed that this was related to the abundance of food in the two habitats but that the ease of capture of different species of prey might also be an important factor. She observed moles digging very close to the surface in pasture seizing earthworms and fly larvae.

The mole is known to store excess of food particularly earthworms. Barrett-Hamilton (1911) stated that there was not sufficient evidence of storage of earthworms by moles and that the injuries inflicted on stored earthworms are liable to kill them quickly and make them worthless as food. Adams (1920) observed the tendency to store earthworms in captive moles. MacDougal (1942) reported the storage of earthworms by moles and explained that the earthworms were more easily caught in periods of hard frost. Conclusive evidence about storage of earthworms was supplied by Evans (1948) who examined a large number of stores from several soil types. He concluded that moles have preference for storing L. terrestris and a few larger types of earthworms which were probably caught while crawling in the mole's tunnels. He regarded the smaller earthworms as accidental members of the stores. Larkin (1948) found no stores in the Oxford area. Skoczeń (1961a) investigated the food-storing habit of moles by making observations on captive and wild moles and he found that earthworm stores were associated with winter nests and were collected during digging activities in the first cold days in autumn and in mild winter. He also found that earthworms in

autumn stores have mutilated and decapitated bodies while those in winter and spring stores have regenerated heads and that the smaller earthworms in the stores were eaten first.

### Reproduction

It is difficult to determine the sex of a mole on the basis of external morphological characters since non-breeding females have a superficial resemblance to males in this respect. Matthews (1935) put forward a method of sex determination based on the quantitative measurements of some external features. Skoczeń (1958) also described a similar method. Macgillivray (1845) and MacDougal (1942) reported the numerical superiority of males over females. Folitarek (1932) suggested a sex ratio of 1:1. Larkin (1948) found the sex ratio from litter and juveniles to be approximately 1:1 and claimed that the sexes occur in approximately equal numbers if all the moles in a population are caught. Godfrey and Crowcroft (1960) found the sexes to occur in approximately equal numbers except in the breeding season when males outnumber females because of the greater activity of males. Skoczeń (1966) stated that the sex ratio depended on season, method of catching and the history of the population. He showed that there are more juvenile males than females but the excess males are killed during migrations since males are relatively more migratory than females. The seasonal cycle in the reproductive systems of males and females has been described by Matthews (1935), Larkin (1948) and Godfrey and Crowcroft (1960). Juvenile moles do not breed in their first year of birth and the reproductive organs

in both sexes are at their maximum development in February and early March. Adams (1903), Wood-Jones (1914) and Matthews (1935) reported that the female vagina opens spontaneously in March prior to mating but it is not definitely known whether copulation takes place inside the tunnels or above the soil. Adams (1920) suggested that rutting runs are used in search for mates but Larkin (1948) stated that the presence of rutting runs during the breeding season suggested that mating takes place in them. Adams (1920) stated that mating is confined to the end of March to early April and perhaps occasionally in May, but Larkin (1948) stated that copulation takes place in March in the Oxford area and that peak pregnancy was in late March. Godfrey and Crowcroft (1960) estimated the breeding season to last from February to late June in Britain and reported peak pregnancy in early April in Suffolk. Adams (1920) estimated the gestation period to be approximately six weeks, Matthews (1935) gave an estimate of four weeks and Larkin (1948) gave an estimate of four to five weeks. Adams (1903), Evans (1907), Larkin (1948), and Godfrey and Crowcroft (1960) reported the number of embryos to be an average of approximately four. Adams (1903, 1910) examined litters and found no nestling mortality, but Godfrey and Crowcroft (1960) reported instances of nestling mortality. Adams (1903, 1910), Evans (1907) and Matthews (1935) reported the number of litters<sup>s</sup> per year to be one but Larkin (1948), and Godfrey and Crowcroft (1960) found evidence of second litters. Adams (1903) estimated lactation to last for three weeks but Larkin (1948) estimated it to last for

four to five weeks. Godfrey (1957a) marked litters with radioactive rings and found that they left the nest after thirty-three days. Adams (1920) and Godfrey and Crowcroft (1960) studied the rate of growth of nestling moles and found it to be very rapid. The weight of juveniles at weaning is not definitely known but Larkin (1948) trapped a male and a female weighing 48 g. and 44 g. respectively.

### Mole populations

Since live-trapping techniques have not been developed for the mole, census counts of mole populations usually involved killing the whole populations (complete "trapping-out") or at least some of the moles in the populations ("trapping-out" of quadrats) and it was usually assumed that reliable population estimates could be based on the results obtained from the trapping. Larkin (1948) attempted to estimate the population density of moles in an area of 123 acres by trapping-out sixteen small quadrats whose combined area equalled 2.28 acres. His attempt failed because he underestimated the home ranges of the moles. Godfrey and Crowcroft (1960) pointed out that unless the dead moles are needed for other purposes, trapping-out is unsuitable for field investigations as it wipes out the population which is being studied. According to them, estimates of mole numbers obtained from trapping-out data are subject to errors arising from births, deaths and migrations. This was also shown by Mellanby (1966) who estimated the population density of moles in an area of 387 acres by trapping-out a compartment of eleven acres.

He assumed that four out of eighteen moles trapped in the compartment immigrated into the area during the trapping. Some authors have suggested other methods by which the estimate of mole numbers could be made. Kruishtal (1934) suggested that there is a direct relationship between the numbers of mole-hills and the numbers of moles and he attempted to use this relationship to estimate the densities of moles. Popov and Falkenshtein (1939) pointed out that the numbers of mole-hills depend on soil type and weather and are not a reliable index of the number of moles. They recommended a census of the permanent soil passages which moles use for reaching their feeding grounds from their permanent shelters and claimed that an experienced person could distinguish these runs from other types. As pointed out by Godfrey and Crowcroft (1960) there is no evidence that the feeding and sleeping quarters are widely separated in moles or that moles regularly use communal runs. They suggested that if all mole-hills and ridges in a field are flattened and the field inspected again the following day, the numbers of areas with fresh diggings is a fairly reliable index of the number of moles. Larkin (1948) found that the population density in an area after January does not exceed four per acre. He found the population density to be eight per acre just after the juveniles of the year have been born, six per acre by November and a maximum of 4 per acre after the end of December, and he concluded that the enforced migration of juveniles from their places of birth helps to maintain a stable density in the population.

The age structure of mole populations and the life-span of the mole have been worked out from the examination of tooth wear. Larkin (1948) drew the profile of a second upper molar tooth from each skull by means of a camera lucida and compared the drawings with that of a standard tooth showing little or no wear. He used the measurements of the wear on the two highest inner cusps to obtain segregation into age groups and he found that the maximum life-span of the mole is three years. His material contained 46.8% juveniles, 42.6% one to two year old, and 13% two to three year old. He found no significant differences in the age distribution of the sexes. He found approximately 50% of juveniles in established colonies, over 90% in recently colonized areas and 87.9% in arable fields and he concluded that the age structure of a population depends on the history of the population. He failed to obtain clear segregation into age groups in a population from one locality and he explained that this was due to differential tooth wear caused by heterogenous soil. Stein (1950) aged moles on a combination of criteria and concluded that the maximum life-span of a mole is three years. His material contained two-third one year old and one-third more than one year old of which moles more than two years old formed only four per cent. Deparma (1954) aged moles by describing and comparing the wear on teeth. She suggested that the method is reliable only when not less than 40-45 moles are collected from the same population within two to three months. Her material contained 60-65% juveniles. She concluded that three-quarters of juveniles die in the first year and that the maximum life-span of the mole is on

the average four years, and never more than five years. Godfrey (unpublished work in Godfrey and Crowcroft, 1960) examined 800 mole skulls from Suffolk using a cusp of the second molar of the lower jaw as an indicator of tooth wear. She obtained evidences of three age groups in a sample from one locality in May but not later in the year. She explained that the failure to obtain clear segregation into age groups after May was due to differential tooth wear. She also failed to obtain segregation into age groups in a small sample from a homogenous soil. Godfrey and Crowcroft (1960) suggested that a few moles might live longer than three years but that owing to severe tooth wear a mole is not likely to live as long as five years. In their opinion every 100 moles in an undisturbed population will consist of 67 aged one year, 22 aged two years, 7 aged three years, 3 aged four years and 1 aged five years. Skoczeń (1966) also determined the age of moles by a combination of criteria and concluded that only a few moles can live as long as five years. He suggested counting the number of nests in a fortress in autumn as an ancillary method to tooth wear and claimed 95% agreement between the results of the two methods. His materials contained 45.74% juveniles, 27.19% one year old, 13.65% two year old, 9.73% three year old and 3.7% four year old. He found the percentage of middle age moles to be relatively high, and that of old moles to be relatively low in the optimum habitats.

Seasonal migrations and surface activities in moles have been described by many authors. Adams (1920) and MacDougal (1942)

reported that moles come to the surface in summer and early autumn to search for food and water. Bennett et al. (1942) described the seasonal migrations of mole colonies from dry soils to damp soils in summer and from flooded soils to relatively drier soils in autumn. Larkin (1948) found that movements are normally largely restricted to juvenile moles which are forced out of their birth places. He also found that mole colonies remain fairly static in the winter after the juveniles have constructed permanent homes. Stein (1950) described the migration of moles from exposed habitats to protected areas during frosts in autumn and winter and added that the overcrowding of moles in such areas leads to death from food shortage. Godfrey (1957a) described the partial migration of two females from dry soils to damp soils in May. Mellanby (1966) described how moles left a flooded area and returned to the same area when the water level subsided. Morris (1966) believed that moles normally spend a part of their active periods on the surface. He reported that several moles were trapped on the surface in a hot, dry summer during an expedition (in France) in 1964. Godfrey and Crowcroft (1960) believed that mole's appearance on the surface is usually caused by adverse conditions in the soil. They suggested that detailed investigation might show that migrating mole colonies do not always survive but are replaced by a new generation of moles.

The causes of death or mortality factors in moles are fairly well known. The mortality rate is supposed to be highest in juveniles. Adams (1903) mentioned reports of foxes digging out

nests. Folitarek (1932) and Godfrey and Crowcroft (1960) believed that juveniles are very vulnerable to predation when they have just been dispersed and have not mastered the art of digging, and Godfrey and Crowcroft (1960) added that after the juveniles are able to dig properly, the various causes of death affect adults and juveniles equally. Widespread mortality of moles during hot, dry summers has been reported by Adams (1920) and Elton (1931). Larkin (1948) reported that cultivation kills a large number of moles in arable fields especially when the soil is shallow. He believed that diseases and predation might also be important factors in the population ecology. Godfrey and Crowcroft (1960) believed that shortage of food brought about by adverse weather can kill moles but that the winter is seldom severe enough in Britain to cause widespread mortality. They also believed that flooding can cause deaths because although moles may swim to dry areas but once there they may find other moles in residence or conditions to be unsuitable for them. Although many potential predators of moles are known (Adams, 1903; Folitarek, 1932) it is generally believed that their predation is incidental and does not have any significant effect on population numbers. The only predator believed to be capable of lowering the numbers of moles is man who, according to Adams, is probably partly motivated by commercial gains. Dogs and cats may kill some moles particularly in areas near human settlements. Ford (1935) reported a case of sixteen moles picked up by a dog in the course of a single morning. Some predators may be of importance in the population ecology especially in summer and autumn. Southern (1954) reported

the remains of moles in the pellets of Tawny owls and showed that moles constituted 40-50% of the total food of this species in June to August. Skoczeń (1962) reported the findings of moles in the food of the buzzard (Buteo buteo L.). His collections were made from May to July and they contained 86.4% juveniles.

#### PART B - EARTHWORMS (Lumbricidae)

Darwin (1881) wrote the first important account of the biology of earthworms. Evans (1910) gave a list of the Oligochaeta (earthworms and their allies) in the Forth area of Scotland with a general note on the distribution of each species. Evans (1946) wrote a paper on the distribution of the number of segments in earthworms and their use in identification of immature earthworms. Evans and Guild (1947) developed the technique for the extraction of earthworms with potassium permanganate solution ( $\frac{1}{4}$  oz. of potassium permanganate in 1 gallon of water sprayed over 2.7 square feet) and they later used this technique extensively in a series of investigations on the factors affecting the general ecology of earthworms in the field (Evans and Guild 1947, 1948a, 1948b; Evans, 1948; Guild 1948). They found that earthworms were most active in spring and autumn when soil conditions were most favourable and that the two factors which mainly determine activity are temperature and moisture but that the occurrence of an obligatory diapause in A. longa and A. nocturna may be a contributory factor. They also found that the population density and species composition of earthworms on a field depends on the agricultural history of the field and on

soil types (Evans and Guild 1947, 1948). In a study of the earthworm populations in the Carse of Stirling, Guild (1948) found that light and medium loam soils carry a higher population of earthworms than clay, gravelly sand and alluvial soils and that the typical species in areas of acid natural pastures are B. eiseni and Dendrobaena sp. Further work on the population density of earthworms in some parts of Scotland and the variations in the local populations of earthworms within a field were carried out by Guild (1951a, 1951b, 1951c, 1952). He found that earthworm populations vary considerably both in total numbers and in species composition within small areas of a field and that these local variations are related to soil and soil conditions. He identified 10 species of earthworms in a series of samples taken on the rough hill grazing in a part of Boghall glen towards the eastern part of the area where the present investigations were carried out. He found high population numbers and more species in the lower south-end of the site where the herbage was fine and the soil was moist than in the upper part where the herbage was matted and the soil was drier and possibly more acid. He concluded that soil moisture, soil temperature and acidity are ecological factors which affect population numbers and that each of these factors could act as complete limiting factors at its extreme limits. He suggested that soil depth, soil texture, food supply, herbage cover, basal mat and exposure can affect populations to some extent.

Guild (1955) found that a field population of earthworms usually contained (a) deep burrowing species and (b) shallow

burrowing or sub-surface species, and listed A. longa, A. nocturna, O. cyaneum, L. terrestris (and probably A. caliginosa and O. lacteum) among deep burrowers which make well-defined burrows and form casts. He sub-divided the shallow working species into burrowers and 'non-burrowers' and he listed A. caliginosa, A. chlorotica and E. rosea as shallow-working burrowers which make well-developed burrows penetrating the top 6 in. of soil. He included Dendrobaena sp., L. castaneus, L. festivus and L. rubellus among shallow-working species which form no well-defined burrows and penetrate only the top 3 in. of the soil. He concluded that all species of earthworms prefer dung and succulent herbage remains to fibrous and lignified types of organic matter. Satchell (1955) investigated the distribution of earthworm populations on grass plots receiving various manures and related the differences in earthworm populations between the plots to soil pH and exchangeable calcium ions, soil moisture and vegetation. He found that the differences between plots in percentage moisture contents were very small and did not affect earthworm populations. He found the occurrence of five grasses (Arrhenatherum avenaceum, Agrotis vulgaris, Anthoxanthum odoratum, Dactylis glomerata and Holcus lanatus) and clover (Trifolium repens) to be indirectly correlated with earthworm populations and that moles tended to be present where earthworm were most abundant. He found that in a laboratory experiment earthworms were able to distinguish between solutions whose differences in pH were less than half a unit. He concluded that soil pH plays an important role in determining the distribution of

earthworms and he classified earthworms into three categories with regard to their limits of pH tolerance. The three categories were (a) acid tolerant (B. eiseni, D. octaedra and D. rubida with pH range of 3.5 to 5.0), (b) Ubiquitous (D. subrubicunda, L. castaneus, L. rubellus, L. terrestris and O. cyaneum with pH range of 3.5 to 7.0) and (c) acid intolerant (A. caliginosa, A. chlorotica, A. longa and A. nocturna with pH range of 4.5 - 7.0. The group included by Satchell in acid-tolerant species were those described by Guild (1948) as typical of acid natural pastures.

Svendsen (1955) found that estimates of earthworm populations made by potassium permanganate were consistently and comparatively lower than those made by hand-sorting and he suggested that the permanganate method was unsuitable for comparative studies. Raw (1959) estimated populations by permanganate method, formalin method and hand-sorting method. He used a solution of 25 ml. of 40 per cent formalin in one gallon of water which he applied to 4 sq. ft. with a second application in about 20 minutes after the first application. He found that estimates of L. terrestris populations made with formalin approximated closely to those obtained by counting the number of L. terrestris burrows and that the proportion of species extracted by formalin varies consistently from about 60% for A. chlorotica to 20 - 30% for E. rosea. Gerard (1960, 1967) investigated the effect of environmental factors on the activities of earthworms and found that earthworms go deeper into the soil under unfavourable conditions in winter and summer, if the condition

is mildly unfavourable earthworms become quiescent but if the conditions become extreme they usually die without coiling up. He found that in June and July 1959 most newly hatched earthworms died when the surface soil fluctuated from wet to dry within a few days. He also found that diapause did not occur in earthworms living in soils kept at field capacity with water in summer and concluded that under this condition temperature seems to be the one factor affecting earthworm activity in summer.

## SECTION 2. DESCRIPTION OF SITE

The present investigations were carried out at a site in Boghall glen, Midlothian, on a piece of land belonging to the Edinburgh College of Agriculture. Appendix 1 is a map showing some of the general physical features of the site and the distribution of moles in March 1968 and in March 1969. The geographical location of the site is indicated by the grid references shown on the edges of the map; the grid references were taken from Ordnance Survey map sheet NT26NW.

The site was at an altitude of 950 ft. to 1225 ft. above sea level in a valley slope with open exposure and no trees. On the basis of topography, the site could be divided roughly into 3 parts - a steep-sloped upper part, a gently sloping middle part and a level or near level bottom part. The location of the site in this semi-upland area made the habits and ecology of the mole easier to study because there was less likelihood of disturbances to the habitat. The original vegetation of the site was mainly gorse (Ulex europaeus), thistles (Carduus sp.) and wild grasses (mainly Nardus stricta, Deschampsia flexuosa and Agrostis tenuis) and this could still be observed on the rough hill grazing surrounding the site on its eastern part. The site was ploughed in 1962 and reseeded with a seed-mixture of Rye-grass (Lolium perenne) Cock's foot (Dactylis glomerata), Clover (Trifolium sp.) and Rape (Brassica sp.) The total area of the site was 33 acres (13.4 hectares) and this was divided into four fields by means of fences for the regulation of grazing which was fairly extensive on the south and middle parts

of the site (section A) but much less so on the upper part of the site (Section B). The site received a total weight of 59.6 tons of fertilizers between 1962 and 1968. The fertilizers applied were 3.1 ton of Nitrochalk (Nitrate of ammonia mixed with fine chalk), 7 ton of S.A.I. No. 2 (High nitrogen fertilizer containing 23% nitrogen, 10.2% soluble phosphate, 0.8% insoluble phosphate and 11.0% potash), 0.6 tons of phosphate of ammonia, 0.9 tons of slag (11-13% phosphate) and 48 tons of lime. Since it was reseeded the site has been under permanent pasture for grazing of sheep and cattle and confirmation was obtained from the management authorities that the site would remain under permanent pasture for the duration of the experiments.

A stream originating from a natural spring outside the western part of the site flowed down the whole length of the lower south end of the site in a west to east direction and was fed at intervals along its course by a number of smaller streams and hill drains. The water table was high in many parts of the site reaching the surface or near surface in many places and the natural drainage was very poor giving rise to flooded or waterlogged soils in many places especially in wet periods and in such areas there was a copious growth of rushes (Juncus sp.). To lower the water table on the site, artificial drainage cuttings were made; the locations of these cuttings are shown in Appendix 1.

Efforts were made to obtain a second site on which comparative studies could be made but none was available because the sites at convenient distances to the college were either used for intensive

agricultural practises or were subject to serious human interference. The large area of the present site, however, offered sufficient opportunities for the study of the relationship between mole populations, invertebrate populations and soil conditions in the different parts of the site. The site was subdivided into two parts - Section A and Section B based on topography, origin of soil and local variations in the soil such as depth, organic matter content, and pH. The microscale variations due to cultivation and grazing also had a marked effect on the vegetation and these were also taken into account in making the divisions. It must be stressed that the site was a single habitat with wide local variations and this division was made mainly for the convenience of the interpretation of the data on the relationship between mole populations, earthworm populations and habitat conditions. Section A was 27 acres (10.94 hectares) and it occupied the south bottom and middle parts of the site while Section B (6 acres = 2.43 hectares) occupied the northern top end of the site (see Appendix 1). The various features of the soils and vegetation on the site as a whole and in the two subsections are discussed below. Section A was at an altitude of 950 ft. to 1150 ft. above sea level while Section B was at an altitude of 1100 ft. to 1225 ft. above sea level.

#### Soils and soil conditions.

The soil in the lower and middle parts of the site (Section A) was Gleys derived from lower Carboniferous sediments and Old Red Sandstone sediments and lavas. It was poorly drained though local

conditions like vegetation, artificial drainage and topography produced different types of soil conditions. The soil on the north end of the site (main part of Section B) was derived mainly from fine-grained riebeckite, trachytes and allied acid igneous rocks which have suffered frost shattering and solifluction. The main constituents of the rock were quartz and felspar. Appendix 2 is a map showing the depth of soil (surface of soil to parent material) in the various parts of the site. The soil was deepest at the bottom of the site (1ft.5in-1ft.6in.deep) and it contained few stones but the depth decreased gradually and the soil became more stony as the distance from the bottom increased, until at the extreme north end the soil was only 9 in. - 11 in. deep and was very stony. The soil depth in Section A varied from 1 ft. 6 in. to 1 ft. 3 in. and in Section B it varied from 1 ft. 2 in. to 9 in. Appendix 3a is a map showing the areas where soil samples were taken for the investigations of the texture of the surface soil and for measurements of the percentage organic matter contents. The results are shown in a table in appendix 3b. There were local variations in the soil texture over the site as a whole but generally the soil was heaviest at the bottom of the site and lightest at the upper end of the site, the soil texture varying from loam at the bottom of the site to sandy-loam in the middle and coarse sand in the extreme north end of the site. The percentage organic matter contents of the soil also showed wide local variations over the site but generally it was higher in the north end than in the south end of the site. The mean (± S.E.) percentage soil organic

matter contents was  $23.4 \pm 11.1$  in Section B and it was  $12.8 \pm 3.4$  in Section A. The organic matter contents of the soil was significantly higher in Section B than in Section A, the mean ( $\pm$  S.E.) difference in organic matter contents between the two sections being  $10.6 \pm 5.1$  giving an estimated t value of 2.1 (t at P 0.05 = 2.04). The higher organic matter contents of the soil in Section B was probably related to the soil pH and the vegetation which are discussed later.

The soil pH was measured at various locations on the site and its immediate environs and the results are shown on a map in Appendix 4. The soils under natural and semi-natural conditions in the immediate vicinities of the site were strongly acid (mean ( $\pm$  S.E.) soil pH =  $4.9 \pm 0.5$ ) while the soils on the site have pH varying from 5.3 to 6.5 (P = 0.05). The mean ( $\pm$  S.E.) soil pH on the site was  $5.9 \pm 0.6$  which was approximately one unit higher than that outside the site. The mean ( $\pm$  S.E.) difference in pH between the soils on the site and those in its surroundings was  $1.1 \pm 0.26$  which was highly significant (estimated t value for the difference = 4.2, and t at P0.01 = 2.7) and this suggested that the high lime status of the soils on the site was due to artificial liming. The wide local variations in soil pH on the site are probably related to both the natural acidity of the soils and to the uneven nature of the fertilizer applications due to the nature of the land surface which made it difficult for tractors to reach some parts of the site. The soil pH was higher in the south bottom parts of the site and decreased progressively northwards. The

mean ( $\pm$  S.E.) soil pH in Section A was  $6.0 \pm 0.6$  and that in Section B was  $5.3 \pm 0.2$  giving a mean ( $\pm$  S.E.) difference in soil pH of  $0.7 \pm 0.4$  between the two sections. The estimated t value for this difference was 1.9 which was not significant ( $P = 0.05$ ) but nearly so ( $P = 0.10$ ) [ $t$  at  $P0.10 = 1.7$  and  $t$  at  $P0.05 = 2.06$ ]. The soil pH in Section B was approximately the same as that in the immediate environs of the site. The mean ( $\pm$  S.E.) difference in soil pH between Section B and the surroundings of the site was  $0.4 \pm 0.3$  with an estimated t value of 1.67 which is lower than the value of t at  $P0.05$  [ $t$  at  $P0.10 = 1.74$  and  $t$  at  $P0.05 = 2.1$ ]. The similarity in soil pH in these two areas suggested that the habitat conditions in Section B was very similar to that in the rough hill grazing surrounding the site. The percentage soil moisture content was determined over the whole site on 9/8/68 and in five series of sampling between 29/1/69 and 11/6/69 and the results are given in a table in Appendix 5.

The soil moisture content was very variable over the site as a whole but the mean ( $\pm$  S.E.) soil moisture content was consistently higher in Section B than in Section A of the site though the difference was significant ( $P = 0.05$ ) only in two series of samples taken on 29/1/69 and on 12/3/69. The significantly higher value of the soil moisture contents on Section B when it was wet was mainly a function of the higher organic matter contents of the soils in this section which conferred on the soils a high capacity for holding water. Section B had a better drainage and the subsoil was drier than that in Section A. The measurements of percentage

soil moisture contents given here mainly relates to the water-holding capacity of the surface (7 in. deep) soil.

### Vegetation.

A list of plants identified on the site is given in Appendix 6a. The vegetation showed wide local variations which were probably related to soil, soil conditions and cultivation. In most parts of Section A, the former plough layer could still be observed 5 in. - 6 in. below the soil surface forming a thick grass mat which was nearly decomposed in some areas but much less so in other areas. No plough layer was observed in any part of Section B which indicated that this section was probably not ploughed in 1962. Broadly speaking Sections A and B carried different types of vegetation (with particular reference to dominant grasses) though local variations occurred in Section A. Appendix 6b is a map showing the distribution of gorse (Ulex europaeus) and rushes (Juncus sp.) on the site. Rushes were found in flushed areas and along the edges of streams and drainage lines. Other plants found abundantly in association with rushes were grasses (Anthoxanthum odoratum, Cynosurus cristatus, Deschampsia caespitosa, Festuca rubra and Holcus lanatus), thistles (Carduus sp.), creeping buttercup (Ranunculus repens) and white clover (Trifolium repens). Other grasses found commonly in this community were Agrostis tenuis, Lolium perenne and Poa pratense. Dry conditions on steep slopes and in a few other places produced the growth of a variable amount of gorse (Ulex europaeus). The main grasses found in association

with gorse were Nardus stricta, Agrostis tenuis, Deschampsia flexuosa and occasionally H. lanatus. Bluebell (Campanula rotundifolia) was frequently found growing among gorse stems. The rest of the site (areas free of gorse and rushes) was divided into areas with similar vegetation. The parts of Section A labelled A<sub>1</sub> (between the stream and the south boundary of the site) was dominated by rushes in wet places. In drier areas the vegetation was mainly grasses of which the most abundant ones were Nardus stricta, Deschampsia flexuosa and Anthoxanthum odoratum. Common herbaceous plants in this area were Potentilla erecta, Ranunculus repens, Myosotis hispida and Lychris flos-cuculi. Bilberry (Vaccinium myotillus) was common. Two species of moss (Polytrichum commune and Rytidiadelphus squarrosus) were frequently found among grass roots and bases. The main part of Section A is labelled A<sub>2</sub> (Appendix 6b). This was the well-grazed part of the site and, here, the vegetation was fine, luxuriant and deep green. The main grasses in this area were Lolium perenne (the most abundant grass), Cynosurus cristatus, Dactylis glomerata, Festuca rubra, Holcus lanatus and Poa trivialis. Poa annua was locally abundant particularly in depressions and Phleum pratense and Deschampsia caespitosa were common. White clover (Trifolium repens) was abundant and mouse-ear chickweed (Cerastium vulgatum) and Creeping Buttercup (Ranunculus repens) were common. Stinging nettles (Urtica dioica) were frequent and thistles (Carduus sp.) were abundant in areas with old mole-hills but few in other areas. The areas in Section A labelled X1 to X6 were small patches which carried a

vegetation similar to that on Section B where the vegetation was matty (top  $\frac{1}{2}$  - 1 in. of soil was made up<sup>of an</sup> undecomposed mat of dead grass), tussocky and very pale green. Section B was floristically much poorer than Section A and basically similar to the rough hill grazing outside the eastern parts of the site. The most abundant grass in this section was Nardus stricta whose large bases formed tussocks. Other grasses found commonly were Agrostis tenuis, and Deschampsia flexuosa, while Cynosurus cristatus, Festuca ovina, Festuca rubra and Holcus lanatus were frequent. Clover and thistles were common but stinging nettles were rare. Frequent weeds were Campanula rotundifolia, Cerastium vulgatum and Potentilla erecta. Bilberry and a species of moss (Polytrichum commune) were common on the floor. The poor vegetation in Section B was due mainly to the fact that the area has never been ploughed because it was relatively inaccessible and difficult to farm mechanically.

The two subdivisions of the site even though they belonged broadly to the same habitat have some differences in soil conditions and vegetation. In area Section A, the soil was relatively heavier (loam to sandy-loam), deeper (1 ft. 3 in. to 1 ft. 6 in. deep), contained less organic matter contents ( $P = 0.05$ ) and was slightly less acid ( $P = 0.10$ ) than the soil in area Section B which was lighter (sandy-loam to coarse sand), shallower (1 ft. 2 in. to 9 in.) and was peat-like. The vegetation in the main part of area Section A was composed mainly of grasses of high value for grazing while the vegetation in

area Section B was basically similar to a rough hill grazing and was dominated by Nardus stricta which is of poor value for grazing. The differences in habitat conditions between the two area sections are related to mole populations and earthworm populations in the results and discussions in Sections 5 and 6.

SECTION 3. PRELIMINARY INVESTIGATIONS

Preliminary investigations were carried out in 1967/68 winter to determine the major items of the food of moles and to study the distribution of the potential food of moles in Boghall glen as a guide to the planning of the main experiments on the relationship between the mole and its food.

Investigation of stomach contents

The types of food eaten by moles and the most important food in their diet were determined by examining stomach contents. 50 moles were trapped from Boghall farm (semi-upland pasture), Bilston field and Roslin field (Low land pasture, Langhill farm) and a Garden (Loanhead). Boghall farm is about one-and-a-half miles from Langhill farm and about two-and-a-half miles from Loanhead, while Langhill farm and Loanhead are about one mile apart. Each stomach was first preserved in 5% formalin (to harden the contents) and later examined. The method of examination is given in the main text under investigation of stomach contents (Section 4B.2c). The percentage number of stomachs containing each food item was calculated for each site and for all sites. The mean ( $\pm$  S.E.) weight of stomach contents and the percentage weight of earthworms in the stomach contents were also computed from the data. Local and sexual differences in these quantities were estimated.

## Results

The percentage occurrence of food items in stomachs is shown in Appendix 7. Earthworms occurred in 100% of stomachs from Boghall and Garden, 90% of stomachs from Bilston and 66.7% of stomachs from Roslin. This probably reflected the differences in the abundance of earthworms in the different localities. The percentage occurrence of insect larvae in stomachs was lower than that of earthworms on each site. It was high in stomachs from Boghall (84%) and relatively low and approximately the same in stomachs from Roslin (55.6%), Bilston (50%) and Garden (50%) which showed that the proportion of moles that consumed insect larvae was higher in semi-upland areas than in lowland areas. This probably also reflected the relative abundance of insect larvae in semi-upland and lowland areas. The remaining food items in the stomachs showed wide variations in their occurrences in stomachs in the different localities. The percentage occurrence of adult insects varied from 11.1% in stomachs from Roslin to 33.3% in stomachs from Garden and that of earthworm cocoons varied from 16.7% in stomachs from Garden to 40% in stomachs from Bilston. Centipedes were absent in stomachs from Bilston but they were present in 82.2% of stomachs from Garden, 12% of stomachs from Boghall and 10% of stomachs from Bilston. Plant materials were found only in stomachs from Bilston (20%) and Boghall (12%) and one stomach stone was found in one stomach from Bilston. In the whole material, earthworms occurred in 92% of stomachs, insect larvae in 68% of stomachs, earthworm cocoons in 32% of stomachs, adult

insects in 20% of stomachs and slugs and centipedes in less than 20% of stomachs. This suggested that earthworms were the main food of moles and that insect larvae were supplementary food. The other food items were casual or minor food items.

The mean ( $\pm$  S.E.) weight of stomach contents was  $6.9 \pm 0.94$  g. for moles from Garden,  $5.6 \pm 0.75$  g. for moles from Bilston,  $5.4 \pm 0.46$  g. for moles from Boghall and  $4.8 \pm 0.77$  g. for moles from Roslin. There was no significant difference ( $P = 0.05$ ) in the weight of stomach contents of moles from any two sites which indicated that the food consumption of moles was not significantly affected by the local habitat conditions. The mean ( $\pm$  S.E.) percentage weight of earthworms in the stomach contents was  $98.0 \pm 11.0\%$  for moles from Garden,  $84.0 \pm 5.4\%$  for moles from Boghall,  $81.8 \pm 8.8\%$  for moles from Bilston and  $62.1 \pm 9.0\%$  for moles from Roslin. The percentage weight of earthworms in the diet was significantly higher ( $P = 0.05$ ) in moles from Garden and Boghall than in moles from Roslin which suggested that the relative weight of earthworms in the diet might depend on the habitat. The observed differences probably reflected the relative abundance of earthworms in the different localities. Earthworms constituted more than 80% by weight of the total food in stomachs in three localities, 62.1% by weight in one locality and 81.5% by weight in the whole material. This showed that earthworms were the main food of moles in the locality in which these investigations were carried out. The mean ( $\pm$  S.E.) weight of stomach contents of males ( $6.3 \pm 0.46$  g.) was higher than that of females ( $5.0 \pm 0.55$ ) but

the difference was not significant ( $P = 0.05$ ). The mean ( $\pm$  S.E.) percentage weight of earthworms in the diet of males ( $83.1 \pm 5.4\%$ ) was approximately equal to that of females ( $79.8 \pm 6.5\%$ ). These showed that the food consumption, and the composition of the diet with respect to earthworms were basically the same in both sexes and that the results for the various sites have not been influenced by sexual differences in food consumption and the composition of the diet.

These results should, however, be interpreted with regard to the winter conditions because the food consumption and the composition of the diet of moles are known to be influenced by seasonal changes in their sexual cycle and in the weather.

#### Investigation of the distribution of earthworms at Boghall glen

30 Samples were taken in Section A and 10 samples in Section B (total 40 samples for the whole site). Earthworms were extracted with dilute formalin (25 ml. in one gallon of water). The method of sampling for earthworms is explained in the main investigations (Section 4.A.1). Earthworms from each sample were collected in a bottle of 5% formalin and were counted, identified and weighed in the laboratory. Mature earthworms were identified to species but immature ones were not subdivided further. The investigation was started on 4/12/67 but only one series of extractions were made on each area section because the soil was frozen and the scarcity of earthworm casts showed that earthworms were not active at that time. Attempts made later to get better results did not succeed until mid-April when the main sampling was started.

## Results

45% of the samples yielded no earthworms and the rest yielded only a few ranging from 1 to 39 per sample. 214 earthworms were extracted from Section A, and 76 from Section B which gave a total of 290 earthworms for the whole site of which 101 were adults and 189 were immatures. The percentage of the adult populations formed by each of the 7 species that were identified is shown in brackets after the name of the species. A. caliginosa (38.6%), A. chlorotica (5.9%), E. rosea (4.0%), D. octaedra (2.0%), D. rubida (1.0%), L. castaneus (5.9%) and L. rubellus (42.6%). L. rubellus was the most abundant species and it was found on all parts of the site. A. caliginosa was nearly as numerous as L. rubellus and was found only in Section A. All other species occurred in relatively low numbers and their distribution was also very localised. A. chlorotica and E. rosea were found only in Section A and D. octaedra, D. rubida and L. castaneus were found only in Section B. The results indicated that the distribution of earthworms in Boghall glen showed considerable local variation which was probably related to the habitat conditions, particularly soil types and soil conditions. However, it was expected that more species would be found, and that the present species ~~would~~ be found in new areas on the site when the soil conditions become more favourable for earthworm activity, particularly in spring and autumn.

## SECTION 4. METHODS

The methods used in the investigations are explained in this section. The results of each investigation are given in Section 5 under the same subheadings used in this section.

### 4.A. INVESTIGATION OF THE POTENTIAL FOOD OF MOLES

#### 1. EARTHWORMS

##### Introduction.

As noted in the literature review, many workers investigating the food of moles have found that earthworms were the main item of the diet with insect larvae as supplementary food. The preliminary investigations of the present work (ref. Section 3) confirmed that in the locality in which it was done, earthworms were the main food of moles and so earthworms (Lumbricidae) were chosen as the main subject for investigation in relation to the distribution of moles. The three main aspects of earthworm ecology studied were (i) the distribution of species, (ii) the seasonal "activity" trend of populations and (iii) the relative population density and biomass in different parts of the experimental site. The results were related to the distribution and abundance of moles and to habitat conditions.

The method used for sampling was the formalin extraction method of Raw (1959). The concentration of formalin used throughout the investigations was 25 ml. of 40% formalin in one gallon of water. The sensitivity of this method was improved by a second application of dilute formalin to each sample unit 10-15 minutes

after the first application. Handsorting was not employed because the investigations were concerned with relative populations and the seasonal fluctuations in the active populations. The population figures obtained were therefore comparative and equal to the active populations but not to the absolute populations.

### Sampling and extraction

The sample unit for all earthworm sampling was one square yard. Two series of samplings were made for the initial investigations. In the first series of sampling, 30 random samples were taken in area Section A and 10 samples in area Section B (total of 40 samples for the whole site). These 40 samples were taken at approximately monthly intervals and under similar weather conditions. The purpose of these monthly totals of 40 samples was to estimate the population density, biomass and species distribution of earthworms in each area section and over the site as a whole. In the second series of sampling, 9 samples were taken in area Section A and 3 samples in area section B at fortnightly intervals (total of 12 samples for the whole site) all being taken on the same day. This was to give the "activity" trend of earthworm populations throughout the whole period of the investigations and if possible to reveal any sudden fluctuations in the population numbers. The labour and time involved in taking 40 samples precluded the larger samples from being taken at sufficiently close intervals.

By the end of 1968, the local variations in the populations, biomass and species distribution of earthworms on the site were well

known. It was then decided to combine the initial two series of samplings into one series but to reduce the number of samples so that the sampling could be done at fortnightly intervals. Area Section A was subdivided into 20 units and area Section B was subdivided into 6 units with fairly uniform habitat conditions. Half of the subdivisions in each area section were in mole-infested areas and the remaining half were in areas free of moles. One sample was taken in each subdivision which made 20 samples in area Section A and 6 samples in area Section B (total 26 samples for the whole site). Since equal number of samples were taken in mole-infested areas and the areas free of moles it was easy to relate earthworm populations and biomass to the distribution of moles. This sampling was completed in June 1969 when, as a result of management requirements moles were trapped out from most parts of the experimental site.

The extraction of earthworms from each one square yard sample unit was done by cutting and removing the surface vegetation without disturbing the soil and the roots of the plants. One gallon of dilute formalin (25 ml. of 40% formalin in one gallon of water) was sprayed uniformly over the quadrat. Earthworms emerging from the soil were collected in a bottle of 5% formalin. A further gallon of dilute formalin was sprayed over the quadrat 10 - 15 minutes after the first application. Collection of earthworms from a sample continued until no earthworms emerged.

Identification of earthworms and treatment of results

Earthworms were identified, counted and weighed in the laboratory. Earthworms from each sample were first divided into (a) adults and near-adults and (b) immatures. The adults and near-adults were identified to species and the number of each species was counted. In the first sampling the identification of immatures was not attempted. In all subsequent samples, however, the immatures were subdivided into 4 groups - (a) A. caliginosa, E. rosea and O. cyaneum; (b) A. chlorotica; (c) Dendrobaena species; and (d) Lumbricus species. These subdivisions were on the bases of colour, size, shape of prostomium and number of segments where applicable. Earthworms from each sample were weighed as a unit.

The species composition was calculated for (i) each series of sampling, (ii) each section (areas Sections A and B) separately and the whole site for the whole sampling period. The population density and biomass on the site as a whole were calculated for each series of sampling and two graphs were drawn one to show the population trend ("activity curve") and the other to show the biomass. The population density and biomass for the whole sampling period were compared between area Sections A and B. The population density and biomass were compared between mole infested areas and the areas free of moles for samples taken between January and June 1969. Each population estimate was calculated by using the log (Number + 1) transformation of the numbers of earthworms extracted from samples and the results were expressed as mean (± S.E. of the mean) number of earthworms per unit area. The biomass of earthworms

was estimated without transforming the numbers and the results were expressed as mean ( $\pm$  S.E. of the mean) weight of earthworms per unit area.

To relate earthworm populations to soil conditions particularly soil temperature and moisture, spot temperatures were measured at 4 in. depth. Estimates of soil moisture contents were made by taking soil samples with an auger. The samples were dried to constant weight in the laboratory and the weight of water in the soil was calculated as the difference between the wet and dry weights of the sample. The weight of water in each sample was recorded as percentage moisture content of the sample. The weekly rainfall was calculated from records of rainfall kept on the farm to supplement the soil moisture data which proved relatively inadequate. The soil temperature readings also proved inadequate relative to the earthworm population trends so official meteorological records from the nearby Bush estate were used. Soil temperatures from this station approximated closely to the readings obtained at the experimental site so the fluctuations in the soil temperature readings at Bush were considered to be similar to those which would occur at the experimental site. It was realised that the soil temperature and moisture data could have been better collected by continuous recordings but the human interference on the site was such that valuable instruments could not be left there.

#### 4.A.2 SOIL INVERTEBRATES

A study of the population numbers, species composition and the distribution of such invertebrates that could serve as moles'

food in the experimental site was made in June 1968 and again in May 1969. The aim was to relate the distribution of invertebrates to the distribution of moles.

The unit of sampling was a soil core 4 in. in diameter by 7 in. deep taken with a steel corer. The cores were taken to 7 in. depth because mole tunnels were seldom more than 7 in. deep (except in Section A) and the vertical distribution of most invertebrates on the site (except large earthworms) did not appear to extend beyond this level. In the 1968 sampling 165 cores were taken in area Section A and 35 cores were taken in area Section B (total 200 cores for the whole site). Samples were taken randomly in mole-infested areas and the areas free of moles. The number of samples taken in each area was proportional to the relative size of such areas on each field. Each sample was taken when the soil was moist and without removing the surface vegetation. The cores were examined in the laboratory and the invertebrates were extracted from each core in two stages. Each core was first broken down and hand-sorted to extract earthworms and the larger insect larvae. The soil was then washed through 4 sieves of diminishing mesh size. The invertebrates extracted from each core were collected in 70% alcohol and were later identified and counted. Insect larvae were identified to families and earthworms and slugs were identified to species. The population density of each group of invertebrates was estimated for each section and for the site as a whole. The population densities of earthworms, all insect larvae, Elaterid larvae, Tipulid larvae and slugs were compared between mole-infested areas and the areas free of moles.

In the 1969 sampling it was also intended to study the relationship between the available food in the soil and the food actually eaten by the moles in the experimental site. The methods of sampling, number of samples per section and the extraction and identification of invertebrates were the same as in 1968. The percentage number of soil samples containing each species or family of invertebrates (frequency of occurrence of invertebrates in soil samples) was calculated and the figures obtained were compared with the percentage number of moles' stomachs containing each food item (frequency of occurrence of invertebrates in stomach contents of moles) during the same period.

#### 4.B. INVESTIGATION ON THE HABITS OF MOLES

##### 1. DISTRIBUTION AND ACTIVITY

Map shows the distribution of moles on the experimental site in March 1968 and March 1969 (Ref. map of site - Appendix 1). A mole infested area was defined as an area having mole-hills or surface tunnels of moles in the form of raised ridges. The outermost mole-hills or surface tunnels in a particular area were usually taken as the boundary of the mole infestation. This criterion might exaggerate the area actually explored and exploited by the mole in the course of its daily activities but it was the only objective method that could be employed in drawing a map of the distribution. Rutting runs or roofless tunnels were made by moles at certain times in the year. Such runs were not permanently occupied by the mole and they were not considered as

part of the mole's range unless they were made among the existing mole-hills and surface tunnels. The distribution and abundance of moles on the site are reported in the results section.

Observations on the activity were made from January 1968 to January 1970 both on the experimental site and in its immediate environs. The index of mole activity was the amount of digging carried out. Notes were kept of (i) migratory movements caused by changes in soil conditions, (ii) the period when fortresses were built, (iii) the types of tunnels constructed and the time of the year when they were constructed and (iv) the dispersal movements and the period of recolonization of trapped-out areas and the colonization of new areas.

#### 4.B.2. THE FEEDING HABITS OF MOLES

Observations were made on (a) method of gathering food, (b) food storage, (c) the actual diet and (d) local variations in the body weight and diet.

##### (a) Method of gathering food

Several yards of mole tunnels were opened up and examined at different times in the year to see if the tunnels acted as pit-fall traps in which case some invertebrates might be found lying freely in the tunnels. Examination of tunnels were also made before traps were set in them and whenever moles were dug out alive their tunnels were also examined. A number of fresh mole-hills were also examined on various occasions to see if they contained invertebrates. Observations were made on moles engaged in digging

to see how earthworms and insect larvae reacted in response to the digging.

(b) Food storage

The first two dissections of fortresses were made on 23/4/68. Each fortress was dissected with a spade. On 15/10/68 two fortresses constructed on area Section A in December 1967 were dissected. On 28/2/69 5 fortresses were dissected. Only half of each fortress was dissected and the nest was left intact in each case to facilitate further observations. The soil was frozen hard and covered with snow when the fortresses were dissected. Earthworms collected from each fortress were identified to species in the laboratory and the species composition and the conditions of each earthworm in the stores were recorded. On 10/3/69 the remaining half of each of the 5 fortresses was dissected. All the fortresses except one had been repaired at this time but no stores were found in them. 4 Fortresses were dissected on 12/5/69 and 2 others on 19/5/69. On 28/7/69 tunnel systems were examined in areas with fresh diggings on Leip field. Observations were also made on captive moles to see if they stored excess food.

(c) Body weight and diet of moles

The diet of the mole was studied by examining stomach contents. Duffus and Scissor traps were used on each section of the site from March to early August 1969 after which there were no more moles on the site. The traps were inspected daily and records were kept of the field, site and date on which each mole was trapped. Each dead mole was weighed (to 0.1 g.) and measurements (in inches)

were made of the lengths of its body, tail (minus the terminal hairs) and hind-leg (minus the claws). The distance between the anus and the external genitalia was also recorded for each mole. The average testis weight was recorded for each male. The state of the vaginal orifice, the mammary glands and the reproductive tract were recorded for females. The weight of the uterus and the ovaries was recorded from April to August.

#### Investigation of stomach contents.

Stomachs were first preserved in formalin to harden the contents (see also Section 3 - Preliminary investigation of stomach contents). Each stomach was later washed in water and weighed (to 0.1 g.). It was then opened up along its greater curve and the contents emptied into a fine-meshed sieve which was covered to prevent drying. The empty stomach was rinsed in water, dried on filter paper and weighed (to 0.1 g.). The weight of the stomach contents was calculated. The aggregate of food in the stomach was loosened with a pincette and a fine jet of water was used to wash away the sediments and leave the undigested and indigestible components of the contents on the sieve. The fraction of the contents left on the sieve was emptied into water in a petri dish and examined. The material was first sorted into the following food categories: (i) earthworms, (ii) insect larvae, (iii) adult insects, (iv) earthworm cocoons, (v) slugs, and (vi) centipedes. Each food category was weighed (to 0.01 g.) when present in sufficient quantities but otherwise only its occurrence was recorded. The numbers of adult insects, slugs, earthworm cocoons and

centipedes were recorded. Insect larvae were identified to families and slugs were identified to species. Earthworms were further subdivided into genera and species where possible. Sometimes small earthworms like A. caliginosa, A. chlorotica, Dendrobaena sp. and the immature stages of the larger earthworms were swallowed whole by the mole and were present in the stomachs in more or less unchanged form. Since an earthworm could not be conclusively identified without the head and the anterior segments (up to and including the region of the tubercula pubertatis) of the same individual being available, the identification of earthworm fragments in the stomachs could only be regarded as approximate. Only occurrence was recorded for plant materials but stomach stones were weighed.

The following data were computed from the records of mole trapping and those of investigation of stomach contents: (i) the total number of moles trapped in each section and the population density of moles based on the actual area of land surface infested with moles, (ii) the sex ratio of moles on the site, (iii) the body weight of moles, (iv) the body weight - the weight of stomach contents, (v) the weight of stomach contents (full stomach - empty stomach), (vi) weight of stomach contents expressed as a percentage of body weight, (vii) the weight of stomach contents expressed as a percentage of body weight less the weight of stomach contents, (viii) the percentage number of stomachs containing each food item and the percentage weight of earthworms in the stomach contents. Monthly and sexual differences in body weight and diet were estimated and the differences in body



weight and diet of adults and juveniles in June and July were also estimated. In addition to these, the body weight, food consumption, and the composition of the diet of moles caught in areas Sections A and B [from the beginning of trapping to 15/4/69 when the last mole on Section B was caught] were compared.

(d) Local variations in the body weight and diet of moles

These investigations were carried out in January 1970. It was intended that the results would reveal the variations in the body weight and diet of moles in different localities. 33 Moles were trapped on Leip field and environs (including Fulford field) at Boghall farm. 13 other moles were trapped on Bilston field at Langhill farm. Boghall farm is about one-and-half miles from Langhill farm and both trapping sites were under permanent pasture. The moles were treated as reported for Boghall glen and the same data were computed from the results.

4.B.3. FOOD CONSUMPTION OF CAPTIVE MOLES

The aim of this investigation was to assess the maximum daily food (earthworms) consumption and the variations in different moles and to compare the results with the results of field experiments on the food consumption.

Mole cages: Two wooden cages were constructed based on the design of Skoczen (1961) and Rudge (1966). Each cage was in two parts: (a) a sleeping cage and (b) a feeding cage. The sleeping cage was 24 in. long by 18 in. wide and 9 in. high and it was filled with moist compact soil to a depth of 4 in. A wooden box (6 in. x 6 in. x 6 in.) with two openings each 2 in. in diameter

was placed at one of the far end corners. The box served as a nest chamber for the mole and was filled with dry grass. The feeding cage was 12 in. long by 12 in. wide and 9 in. high. At its far end corners two dishes were placed for holding earthworms and for holding water. Each cage was fitted with a locking lid to prevent escape, the lids being made of zinc wire mesh to provide adequate aeration. The two cages (a) and (b) were linked together by two tunnels 2 in. in diameter made of zinc metal cloth 1 mm. thick with 0.5 sq. cm. mesh. To prevent injuries to the mole, the metal cloth was sewn with the cut edges facing outwards. The incorporation of junctions and mazes in the system made it possible to vary the length and shape of the tunnel system for each mole. However, it was soon discovered that two straight tunnels each  $2\frac{1}{2}$  ft. to 3 ft. long were adequate for each mole. The tunnels were raised off the floor to allow waste products from the mole to drop through. The soil in the sleeping cage was kept constantly moist and changed as soon as it was fouled. Fouling of the soil usually occurred when the mole dragged large earthworms into the sleeping cage and consumed them there, leaving their gut contents in the cage. The tunnels and the feeding cage were also cleaned regularly to avoid unpleasant odours.

Method of obtaining live moles: Killing traps with the springs weakened to convert them to holding traps were first used. These needed constant attention and were not very efficient, only 2 moles being obtained. The digging of moles was used instead. An area with fresh diggings was kept under observation until the mole was

observed to be moving the soil. The tunnel system was quickly blocked behind the mole and then opened up until the mole was caught. This method was also time-consuming and its efficiency depended on practice and experience. Four moles were caught by using this method. (The method was later employed in counting the numbers and ringing the moles on Leip field). One mole was picked up on the surface at dawn by a shepherd and given to me in the morning on 12/8/68.

Method of obtaining earthworms: In the initial stages of the experiment earthworms were dug up from garden soils. It was soon obvious however that a constant supply of earthworms could not be maintained by this method. Electrical shock extraction was considered impracticable. Earthworms extracted with formalin were considered to be dangerous as food for moles because of possible toxic effects. Eventually earthworms were extracted with dilute formalin (25 c.c. of 5% Formalin in one gallon of water) on some of the college lawns. They were washed in water as soon as they emerged from the soil, and then placed in a soil culture. It was found that the earthworms regained their vigour very quickly in the soil culture. Dead and extremely sluggish earthworms were not fed to the mole and the healthy ones were washed thoroughly in water before they were fed to the mole.

Method of feeding moles: Each mole was fed twice daily at 9 a.m. and 6 p.m. When a mole was brought into the laboratory it was provided with a quantity of earthworms equal to its own body weight, or 100 gm. if its body weight was less than 100 gm. When the daily

food consumption of a captive mole was approximately known the food fed to it was decreased or increased accordingly. The weight of food fed to the mole was recorded and before the next feeding, the weight of food left in the cage was also recorded. Care and patience were needed in recording the weight of food left in the cages because some earthworms were stored by the mole while others crawled to various parts of the cages. The daily food consumption of each surviving mole was recorded for a period of 10 weeks from the second day of capture.

The following data were computed from the results:-

(i) the daily food consumption on weekly basis and (ii) the daily food consumption for the last 8 weeks in captivity and this was compared for all surviving moles. Observations were made on the feeding behaviour, food storage and the causes of death in captive moles.

The two major factors limiting the number of moles used in this experiment were lack of space and lack of time to obtain a continuous and sufficient quantity of earthworms to feed many moles. The method employed to obtain earthworms could only be satisfactorily used when earthworms were active in the autumn and spring.

#### 4.B.4. MOLE POPULATION STUDIES

Three aspects of mole populations were investigated:

(a) the estimation of the population density of moles on the experimental site, (b) the age structure of mole populations and the life span of the mole and (c) the social organization, sex-ratio, and the changes in numbers and distribution of a small population

of moles on Leip field. In addition the sex-ratio was recorded for all sites on which trapping was carried out.

(a) Estimation of the population density of moles at Boghall glen

The population of moles at Boghall glen was determined from trapping records. The experiments recorded in this section were attempts to develop methods of determining the population density of moles without killing the moles so that records could be kept of the seasonal, annual and local changes in numbers. The first attempt to count the number of moles was made by constructing three different types of live-capture mole traps. Each trap was on trial for a period of several hours daily for more than one month but no moles were caught in any of them. The second attempt was made by weakening the springs of 10 killing traps and converting them to holding traps. When these traps were first tried on the field, one mole was killed on the upper part of area Section A on 24/1/69 and two other moles escaped. The method was discontinued.

The number of fortresses in area Section A and area Section B was counted and recorded as a possible means of estimating mole numbers. The method of counting nests was also used. All fortresses were opened up and confirmed to be inhabited by moles. All other large mole-hills were opened up and the number of nests was recorded and noted on a map. The experiment was continued until only very small mole-hills were left unopened on the site.

The next method used to estimate numbers was employed only on two areas in Section A. All mole-hills and surface ridges in the first selected part were flattened on a Friday.

The number of areas with fresh diggings were counted and noted on a map on the second day and traps were set in such areas. On the second selected part all old mole-hills and surface ridges were flattened on a Saturday and the number of areas with fresh diggings were counted the following Monday when traps were set in such areas. The investigations were done at the end of April (1st part) and in early May (2nd part), when moles were active in digging. The number of areas with fresh diggings and the number of moles trapped in such areas were compared. The number of mole-hills on each field was counted before the beginning of trapping experiments. The mole-hills referred to in this section included fresh mole-hills and old mole-hills with no plants growing on or over them. Each area section was subdivided into sub-units of mole-areas where possible and the number of mole-hills and the number of moles trapped in such areas were recorded. The number of mole-hills per acre in each section of the site was calculated. The correlation between the number of mole-hills and the number of moles was calculated for (a) similar areas (similar soils) and (b) the whole site.

(b) The age structure of populations and the life span of moles.

The head of moles whose stomachs had earlier been used in the investigations of the mole's diet were cleared and cleaned by boiling them in water for 15 minutes to remove the skin and flesh. The lower jaw was removed from each head and the brain was blasted out by means of a strong jet of water. Each skull was thoroughly cleaned, dried to constant weight in the oven and

labelled to show the site on which the mole was trapped. Skulls from Leip field and environs, Fulford field and Bilston field were also labelled to show the sex. In the Boghall glen series only the left second upper molar teeth were measured but in the Leip field and environs, Fulford field and Bilston field series both left and right second upper molar teeth were measured.

Method of measuring tooth: Ten left second upper molar teeth were chosen for examination under the binocular microscope (at x 12.5 magnification). These included 2 teeth from juveniles and 8 teeth from adults. Each tooth was cleaned and mounted in plasticine on a slide so that its inner cusps were all visible. Drawings were made to show the wear surfaces on each tooth. A comparison of the drawings of the adult teeth with those of the juveniles showed that there were four main wear surfaces on each tooth - the 3 inner cusps and the central ridge between them. It was possible to measure the length of the 3 inner cusps but the wear on the central ridge could not be measured. Drawings were made of tooth at different stages of wear.

A microscope micrometer eye-piece was used to measure the length of each of the 3 inner cusps from the lowest point on the neck of the tooth to the summit of each cusp. A fourth measurement was taken from the highest point on the neck of the tooth to the summit of the highest inner cusp. The mean of the 4 measurements was calculated for each tooth. In the Leip field, Fulford field and Bilston field series, the average mean measurements of the left and right teeth was calculated. The moles were classed into

age groups using the micrometer measurements of the teeth directly. The mean measurement had a range of 2.41 to 2.70 for juvenile moles (in June to early August). 0.3 Class interval was therefore used to classify the measurements into age groups.

The micrometer readings were converted into millimeters by using an objective graticule with 100 division each equal to 0.01 mm. Each division on the micrometer was calculated to be equal to 0.857 mm. This was used to calculate the magnification of teeth in drawings. Tables were made of the age structure of the mole populations on each site and histograms of the age distribution were made.

(c) Studies on a small population of moles on Leip field

This short investigation was carried out on Leip field, Boghall farm between June 1969 and January 1970. Leip field is situated 850-950 ft. approximately (above sea level) and covers 4 acres of sloping ground. The field is permanent grass with a uniform, well-grazed sward which is almost free of weeds. The aspect is open. A small stream flows from north to south just outside the field on its eastern side and this joins a larger stream at the lower south-end of the field. Across the gully is Fulford field which is surrounded on all 4 sides by a plantation of trees and on two sides by marshy ground. Leip field was trapped free of moles in the winter of 1967-1968 but was recolonized again in the autumn of 1968. The tunnels of moles on Fulford field extend to the bank of the stream at many points while the tunnels of moles on Leip field extend to the bank of the stream at only one point.

During the present investigation, the tunnel system of moles on Leip field were studied. In the early summer, the temporary tunnel system of 2 juvenile males and 1 juvenile female were drawn. Measurements were made of the dimensions of the tunnels of adult and juvenile moles of both sexes and the changing pattern of the tunnel distribution was studied from the end of June 1969 till January 1970.

The population of moles on the field was determined by digging each mole up. This method was effective and practicable in the early summer because moles made shallow tunnels (4-6 in. deep) and it was easy to spot where a mole was digging. The tunnel system of a newly dispersed juvenile mole was usually small and discrete and it was possible to open up the whole system and capture the mole. The moles were aged on the basis of size (juveniles at this stage are much smaller and slimmer than adults) and sexed on the basis of the distance between the anus and external genitalia. (In males this was between 0.35 - 0.5 in. while in females it was between 0.15 - 0.2 in.). A numbered aluminium ring was attached to the narrow base of the tail of each mole that was captured and the mole was released back into its own tunnel except in the case of one juvenile female which was released into an uninfested area to facilitate the measurements of the length of tunnel it could dig in a day and to draw its tunnel system. Whenever the whole tunnel system was destroyed before a mole was captured, the mole was released at one end of a destroyed tunnel. A wooden peg bearing the same number as the one on the tail-ring

of the mole was pushed into the ground at the point of release of each mole. All moles on the field were ringed on the tail within 3 days. Two captive moles (Nos. C<sub>1</sub> and C<sub>2</sub>) had originally been released into the field in December 1968. The male (No. C<sub>1</sub>) was recaptured in a tunnel 80 yards south of its original point of release but the female (No. C<sub>2</sub>) was never recaptured.

A map was drawn to show the distribution of moles. The restriction of a mole to its own territory was occasionally confirmed by digging the mole out and checking the number on its tail-ring with that on the wooden peg. A shepherd accidentally killed 4 of the moles (Nos. 1, 3, 7 and 8) on 12/7/69 when he observed them digging shallow tunnels. All the moles were very active at this time.

Two captive moles were released into uninfested areas on Leip field on 16/7/69. One was a female (No. C<sub>3</sub>) and the other was a male (No. C<sub>4</sub>). Their points of release and the location of the 4 moles killed by a shepherd are shown on <sup>a</sup>map.

Extensive digging continued on all parts of the field and the tunnel systems of moles on the south-end of the field began to lose their solitary nature and merge into one another. By 30/7/69, the tunnel system of No. C<sub>1</sub> and No. 6 had merged together. The mole digging on the part of the tunnel originally belonging to No. 6 was captured and identified to be No. C<sub>1</sub>. Mole No. 6 was later captured at the northern-end of the field, 135 yards away from its original territory on 5/8/69. Checks made on the tail-rings of the other moles on the field showed that they had remained

in their tunnels. The distribution of moles on the field on 5/8/69 is shown on map.

The distribution was not checked after the middle of August and there were no signs of fresh diggings on the field at the end of August when the field was inspected. The soil was very dry at the end of August and the only slight mole activity observed was around the streams where the soil was relatively moist.

Further observations were made in December 1969 and January 1970 and the distribution of moles on the field on 14/1/70 is shown on map. It was not possible at this time to catch the moles alive by the method used the previous summer, so the moles were trapped-out. The trapping included Leip field and all the isolated mole colonies in its immediate environs. The tail of each mole trapped was examined for ring or the marks left by a dislodged ring. The moles were aged as described previously.

## SECTION 5. RESULTS

### A.1. EARTHWORMS

#### Distribution in Boghall glen

11 Species of earthworms belonging to 5 genera were identified and they included the 7 species identified in the preliminary investigations. The species identified were: A. caliginosa (Savigny 1826), A. chlorotica (Savigny 1826), D. octaedra (Savigny 1826), D. rubida (Savigny 1826), E. rosea (Savigny 1826), L. castaneus (Savigny 1926), L. festivus\* (Savigny 1826), L. rubellus (Hoffmeister 1843), L. terrestris\* (Linnaeus 1785), O. cyaneum\* (Savigny 1826) and O. lacteum\* (Oerley 1881). A = Allolobophora, D = Dendrobaena, E = Eisenia, L = Lumbricus, O = Octolasion (\* Species not identified in the preliminary investigations).

Appendix 8 and Table 1 show the species composition and the percentage number of each species in (a) adult populations and (b) total populations on each section (areas Sections A and B) and on the site as a whole. The A. caliginosa group of immatures included E. rosea and O. cyaneum but as E. rosea and O. cyaneum occurred in very low numbers in the adult (2.3% and 1.4% of total populations respectively compared with 37.8% of A. caliginosa) the group could be taken to represent A. caliginosa fairly accurately. So also the Lumbricus sp. group of immatures included L. castaneus, L. festivus, L. rubellus and L. terrestris but L. rubellus formed 45.8% of the total adult populations compared with 1.2% of L. castaneus, 0.6% of L. festivus and 0.5% of L. terrestris and the

group could be taken to represent L. rubellus fairly accurately. The Dendrobaena sp. group of immatures included D. octaedra and D. rubida.

Fig. 1 is a map showing the distribution of A. caliginosa, A. chlorotica, L. festivus, L. rubellus and L. terrestris on the site as a whole. A. caliginosa occurred abundantly in all parts of Section A but was absent from Section B. The distribution of E. rosea, O. cyaneum and O. lacteum was very similar to that of A. caliginosa [except that they occurred in very low numbers]. A. chlorotica was distributed mainly in the lower south-end of Section A where it occurred in low numbers except in a few places where it was relatively abundant in the spring and autumn. Altitude might be a limiting factor to its distribution since it was restricted to the areas below 1075 ft. (above sea level). D. octaedra and D. rubida were distributed over the whole site but they occurred in relatively low numbers except that the populations of D. rubida were sometimes high in the north-end of Section A and in some parts of Section B. L. castaneus was found over the whole site but its numbers were low. L. festivus was found in low numbers in some restricted parts of Section A. L. rubellus was distributed abundantly over the whole site. L. terrestris was found consistently only in a small area in the south-western part of Section A but it was found once in the near-adult form in the south middle part of Section A. Its numbers were low in all cases.

The two most abundant species in Section A were L. rubellus and A. caliginosa. The mean ( $\pm$  S.E.) population density (No. per

sq. yd.) was  $8.0 \pm 4.9$  for adult L. rubellus and  $7.9 \pm 5.3$  for adult A. caliginosa. L. rubellus formed 42.9% of the adult populations and 45.9% of the total populations while A. caliginosa formed 41.5% of the adult populations and 47.8% of the total populations. The other species in Section A occurred in relatively low numbers of between 4.0% of the adult populations and 3.2% of the total populations for A. chlorotica to 0.6% of the adult populations for each of L. festivus and L. terrestris. The most abundant species in Section B was L. rubellus (Mean  $\pm$  S.E. population density of adults in No. per sq. yd. =  $4.5 \pm 2.9$ ) which formed 75.7% of the adult populations and 87.1% of the total populations. The other three species (D. octaedra, D. rubida and L. castaneus) found in this section formed 4.7%, 15.7% and 3.9% of the adult populations respectively. On the site as a whole, L. rubellus formed 45.8% of the adult populations and 50.3% of the total populations while A. caliginosa formed 37.8% of the adult populations and 42.4% of the total populations. The numerical superiority of L. rubellus over A. caliginosa was due mainly to the absence of the latter from Section B which showed that the numerical importance of each species in the total populations depended on its local abundance and the pattern of its distribution over the site as a whole.

11 Species were found in Section A but only 4 species were found in Section B which suggested that the habitat influenced the distribution of earthworms. The few number of species on Section B was probably due to the fact that some species could not live in the

relatively shallow, sandy and fairly acid soils in that section. The relatively higher altitude on Section B and the poorer herbage cover were also ecological factors which could make conditions unsuitable for certain species of earthworms. The number of species on Section B was not only limited but the population density of the main species (L. rubellus) in the section was significantly lower ( $P = 0.05$ ) than in Section A. The mean ( $\pm$  S.E.) population density (No. per sq. yd.) of adult L. rubellus was  $8.0 \pm 4.9$  in Section A and  $4.5 \pm 2.9$  in Section B. The mean ( $\pm$  S.E.) difference in the population density of adult L. rubellus between Sections A and B was  $3.1 \pm 1.46$  which was significant (estimated  $t = 2.12$  and  $t$  at  $P0.05 = 1.96$ ) and suggested that the abundance of this species was considerably reduced in this relatively unfavourable habitat. The population densities (mean  $\pm$  S.E. number per sq. yd.) of L. castaneus ( $0.2 \pm 0.2$ ), D. octaedra ( $0.3 \pm 0.4$ ) and D. rubida ( $0.6 \pm 1.2$ ) in Section A was approximately equal to those obtained ( $0.2 \pm 0.5$  for L. castaneus,  $0.3 \pm 0.4$  for D. octaedra and  $0.9 \pm 1.1$  for D. rubida) on Section B which suggested that these species were probably more able to withstand the ecological conditions in Section B than L. rubellus could. The results on the distribution showed that fewer species of earthworms lived in the relatively unfavourable habitat in Section B and that in this habitat the abundance of the main species was considerably reduced in comparison with its abundance in the more favourable habitat in Section A.

TABLE 1

## SPECIES COMPOSITION OF THE EARTHWORMS AT BOGHALL GLEN

Species Composition of earthworms																						
		Adults										Immatures					Adults and Immatures					
Total Number		Percentage number of:										Total	Percentage number of:				Total	Percentage number of:				
Section	All species	A. caliginosa	A. chlorotica	D. octaedra	D. rubida	E. rosea	L. castaneus	L. festivus	L. rubellus	L. terrestris	O. cyaneum	All species	A. caliginosa (and E. rosea and O. cyaneum)	A. chlorotica	Dendrobaena sp.	Lumbricus sp.	All species	A. caliginosa (and E. rosea and O. cyaneum)	A. chlorotica	Dendrobaena sp.	Lumbricus sp.	
A	8985	41.5	4.0	1.7	3.6	2.5	0.9	0.6	42.9	0.6	1.6	9803	49.8	2.5	1.0	46.7	18788	47.8	3.2	3.1	45.9	
B	877	-	-	4.7	15.7	-	3.9	-	75.7	-	-	1369	-	-	8.1	91.9	2246	-	-	12.9	87.1	
A & B	9862	37.8	3.7	2.0	4.7	2.3	1.2	0.6	45.8	0.5	1.4	11172	43.7	2.2	1.9	52.3	21034	42.7	2.9	4.1	50.3	

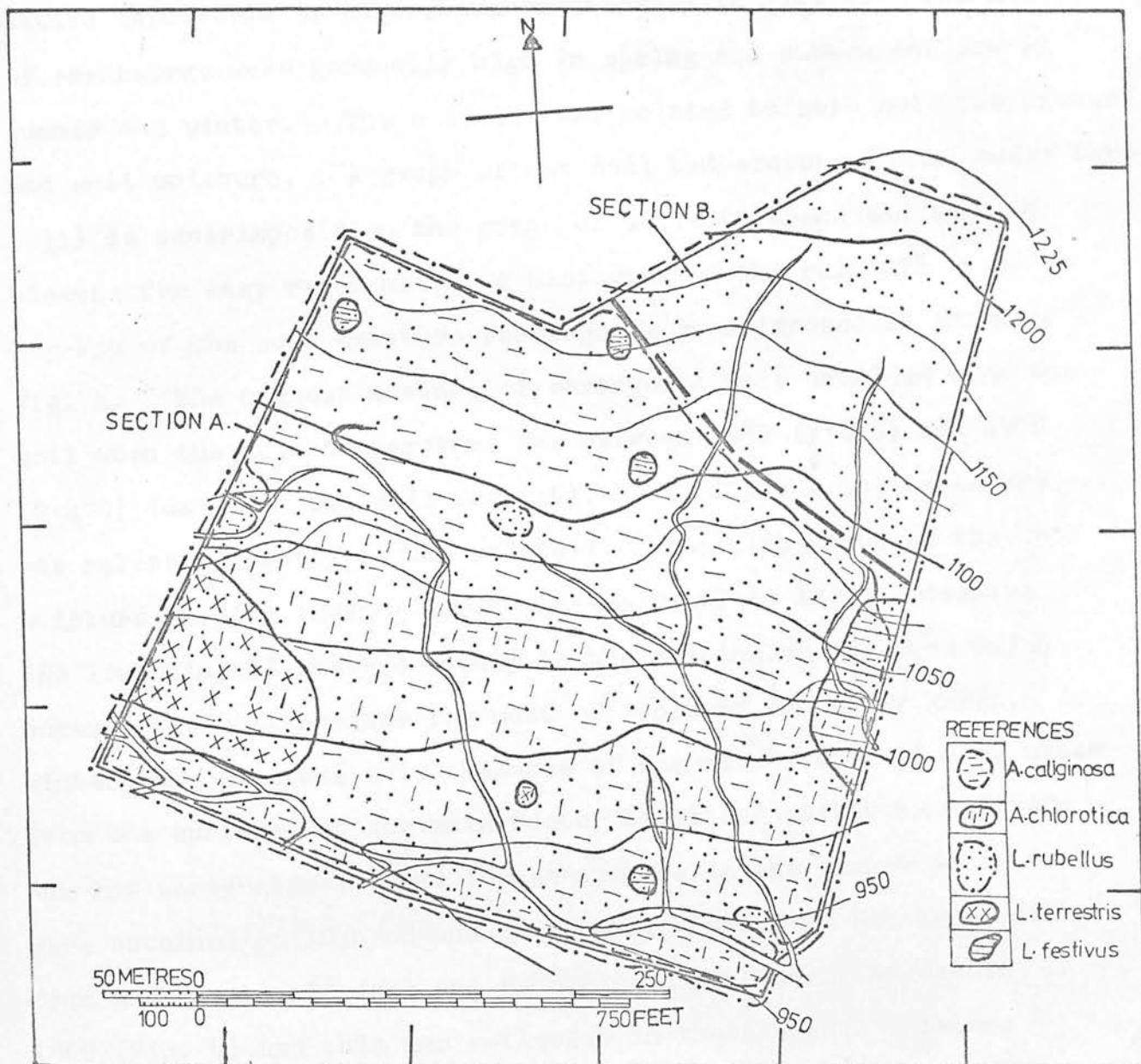


Fig. 1. Distribution of earthworms at Boghall glen.

"Activity" trend of Populations: Appendix 9 shows the numbers and weight (in g.) of earthworms extracted from each sample. The seasonal trend in the activity of earthworms on the site as a whole is shown graphically in Fig. 2 and the trend in biomass of active earthworms is also shown graphically in Fig. 3. The numbers of earthworms were generally high in spring and autumn and low in summer and winter. The activity was related to both soil temperature and soil moisture. A graph of the soil temperature (4 in. under bare soil) is superimposed on the graph of activity trend and that of biomass for easy reference. A histogram of the rainfall on which a graph of the soil moisture readings is superimposed is shown in Fig. 4. The highest numbers of earthworms were obtained from the soil when the soil temperature was between  $46^{\circ}\text{F}$  ( $7.8^{\circ}\text{C}$ ) and  $49^{\circ}\text{F}$  ( $9.4^{\circ}\text{C}$ ) (and when the soil was wet). Usually the soil moisture was related directly to the rainfall. The high value of the soil moisture reading (mean  $\pm$  S.D. =  $38.3 \pm 9.6\%$ ) on 12/3/69 despite the low rainfall was due mainly to the melting of the snow which covered the soil surface for most of February and early March. In winter, the soil was moist because of the slow evaporation of water from the surface, so the main factor affecting earthworm activity was low temperature. The lowest numbers in the summer of 1968 were obtained on 10/6/68 and on 5/8/68. Rainfall was very low from mid-May to mid-June and from mid-July to early August in 1968 (Fig. 4) and this was reflected in the low soil moisture readings (mean  $\pm$  S.D. =  $32.0 \pm 10.4\%$ ) obtained on 6/8/68. The

soil temperature at these periods was also above 50°F (10°C). The soil was hot and dry and there was a marked decrease in the numbers of active earthworms. Few earthworms were also obtained on 8/6/69 when the soil conditions were the same as on 10/6/68 and 5/8/68.

The activity trend of A. caliginosa, A. chlorotica and L. rubellus (Fig. 5) showed that soil desiccation and high soil temperatures in summer affected A. caliginosa and A. chlorotica more than L. rubellus. The active populations of A. chlorotica dropped virtually to zero under adverse soil conditions in summer and winter. The population ("activity") trend of L. rubellus indicated a real decrease in the populations of this species from January 1969 to the end of the investigations. Fig. 6 is a graph of the percentage number of adults in the populations. The adverse soil conditions in the summer of 1968 affected the immatures more than the adults and the percentage of adults in the populations rose to above 50% under these conditions as against the value of below 50% in the previous spring. It was possible that the immatures lived nearer to the surface than the adults in which case soil desiccation would affect a relatively higher proportion of immatures. It was also possible that some of the immatures (and probably some adults also) were not only inactive but were actually killed so that the low populations in summer 1968 reflected both a decrease in activity and a decrease in population numbers.

Fig. 7 is a graph of the "activity" trend of earthworms populations in each of Sections A and B (the population figures

are given in Appendix 10). The effect of high soil temperatures and soil desiccation on earthworm activity was relatively more severe in Section A than in Section B. The populations of active earthworms in Section A were usually much higher ( $P = 0.05$ ) than in Section B but on 10/6/68, and on 24/6/68 the population densities of active earthworms in Section B were significantly higher ( $P = 0.05$ ) than those in Section A, and on 4/7/68 and on 11/7/68 the population densities of active earthworms were approximately equal in Sections A and B. Also, in 9/6/69 sampling earthworm activity fell in Section A but rose in Section B. The higher activity of earthworms in Section B relative to Section A when the soil was dry was probably related to the sponge effect of the higher soil organic matter contents in Section B which made the surface soil relatively moister than in Section A. (ref. Appendix 5).

Population density and biomass of earthworms in areas Sections A and B of Boghall glen: The relative population densities (in thousands per acre) and biomass (in Kg. per acre) of earthworms in Sections A and B and the differences between the two sections for each series of samples are shown in Appendices 10 and 11. The population density of earthworms in Section A was significantly higher than in Section B. The mean ( $\pm$  S.E.) population density (numbers per square yard) was  $23.3 \pm 2.2$  in Section A and  $8.8 \pm 2.4$  in Section B. The mean ( $\pm$  S.E.) difference in population density between Section A and B was  $14.5 \pm 1.0$ . The estimated t value for this difference was 14.50 which was highly significant [t at  $P0.01 = 2.58$ ]. The biomass

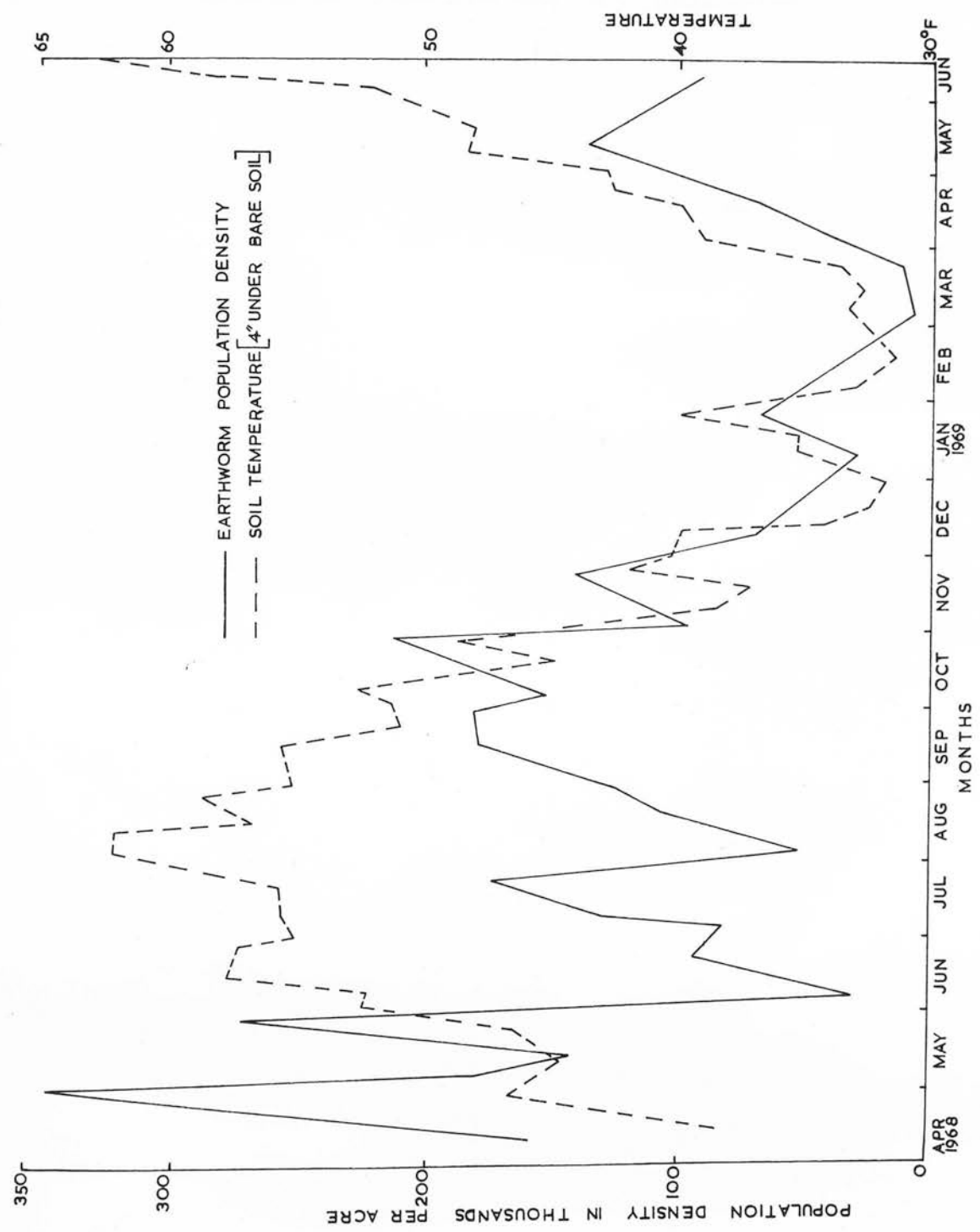


Fig. 2. Earthworm population ("activity") trend.

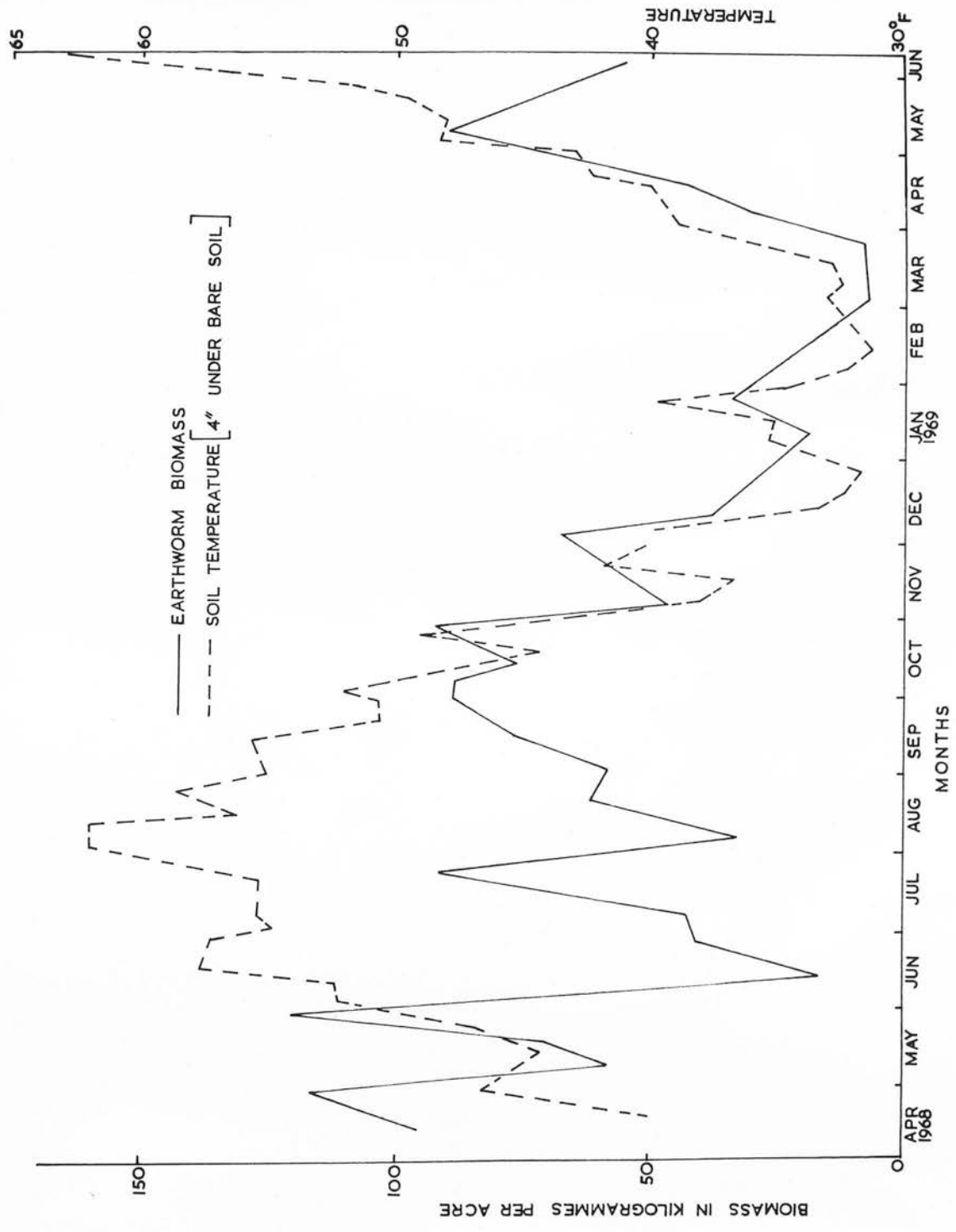


Fig. 3. Earthworm biomass.

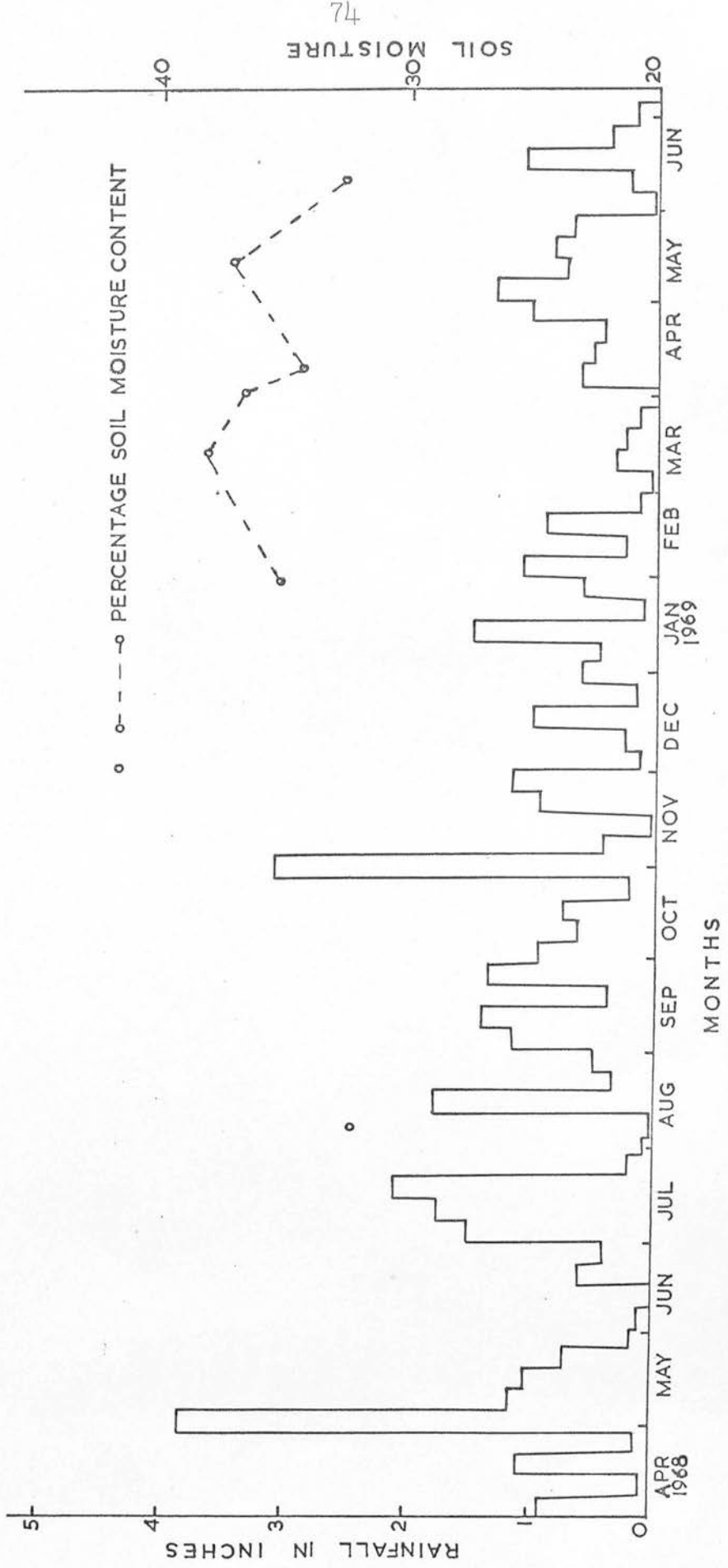


Fig. 4. Rainfall and percentage soil moisture content.

— L RUBELLUS  
 - - - A CALIGINOSA  
 - · - · - A CHLOROTICA

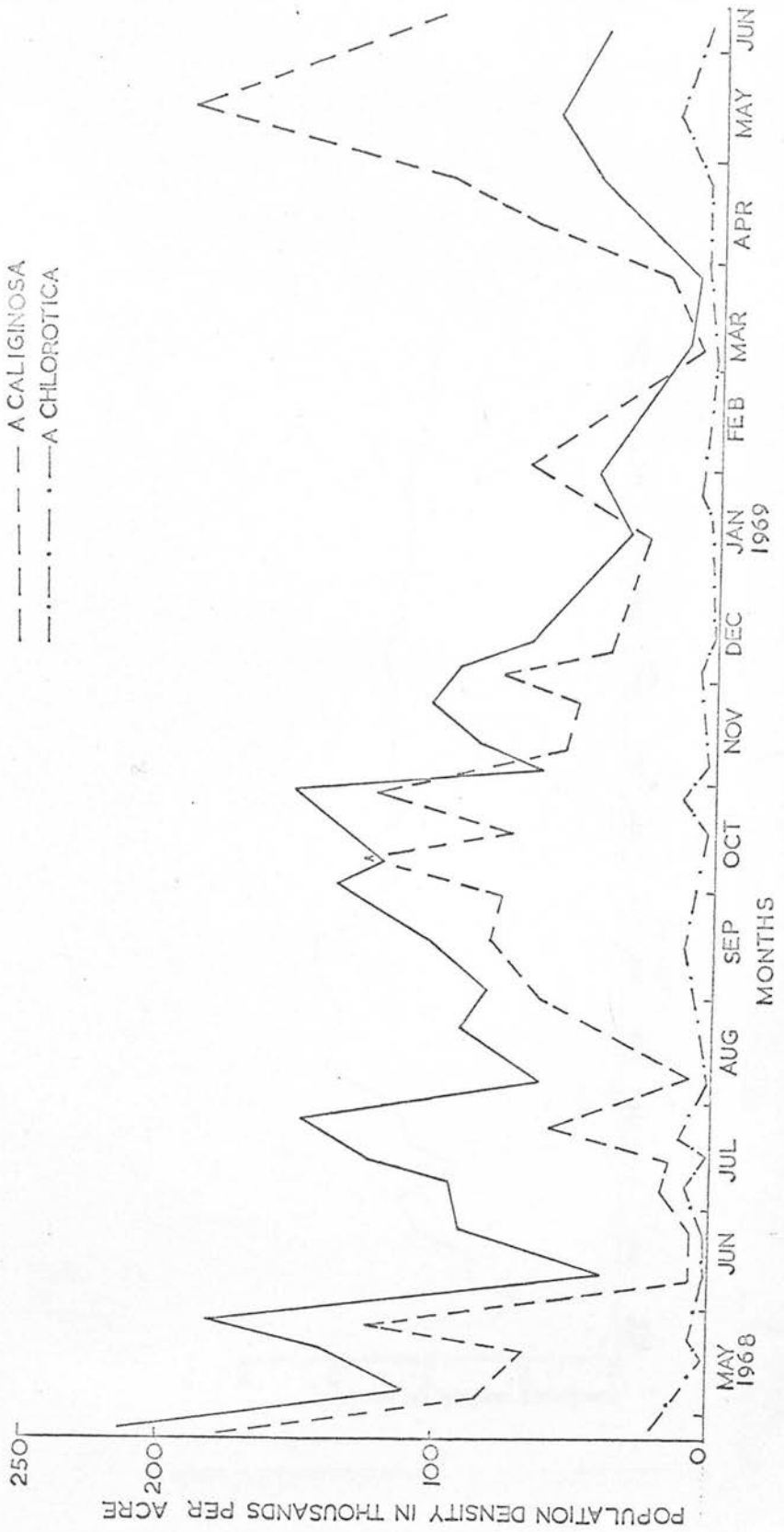


Fig. 5. Population ("activity") trend of A. caliginosa, A. chlorotica and L. rubellus.

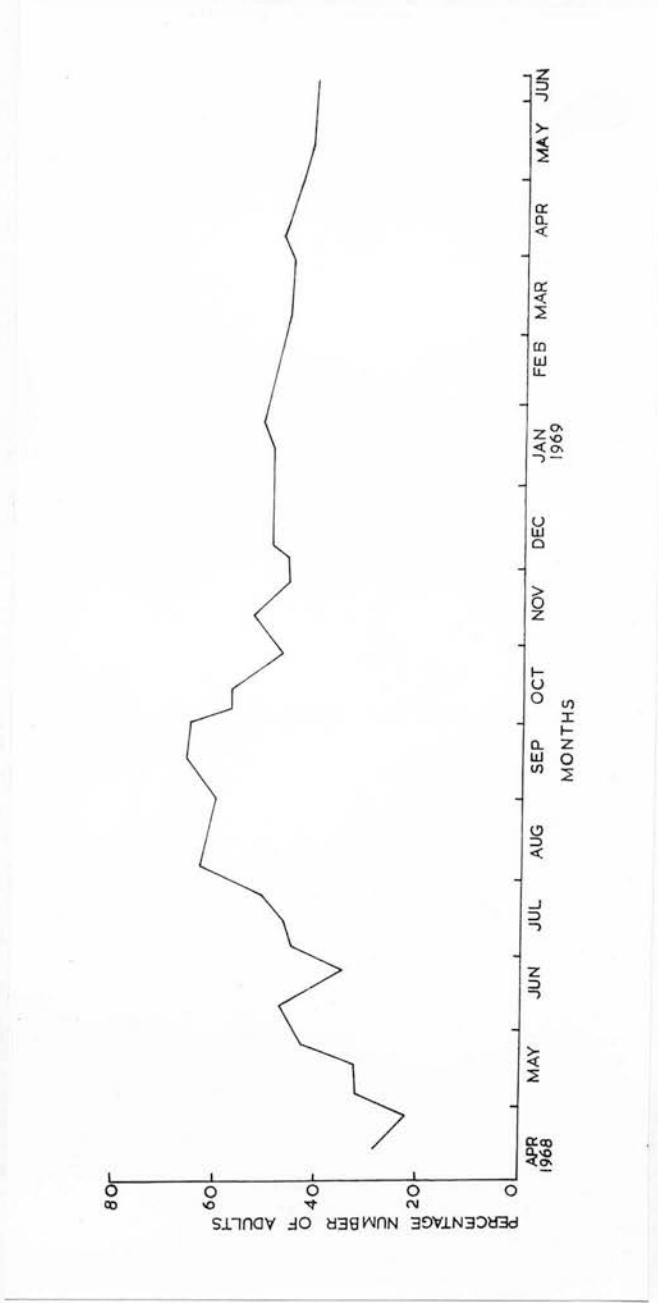


Fig. 6. Percentage number of adults in earthworm populations.

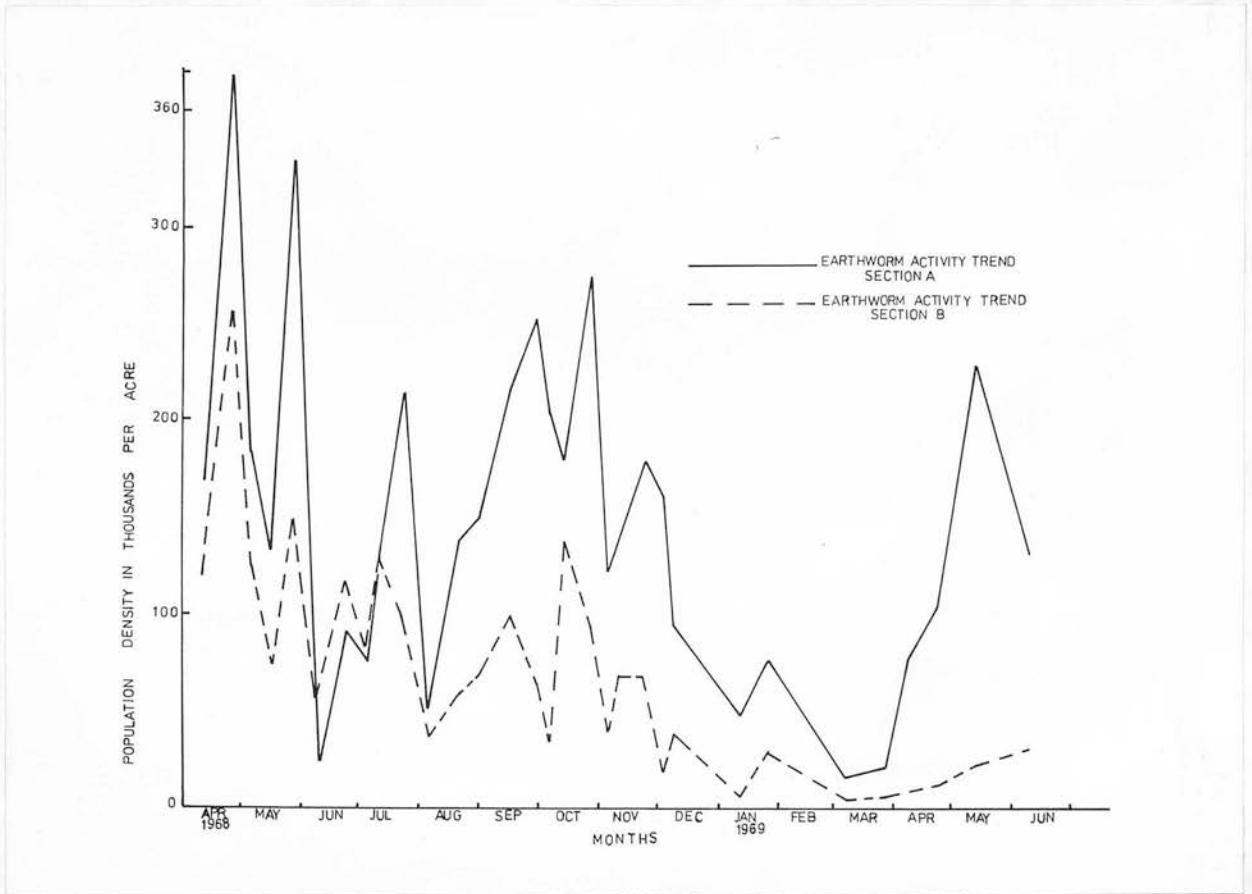


Fig. 7. "Activity" trend of earthworm populations in areas Sections A and B of Boghall glen.

followed the same pattern of distribution as the population density. The mean ( $\pm$  S.E.) biomass (in grammes per square yard) was  $13.98 \pm 0.71$  in Section A and in Section B it was  $6.20 \pm 0.74$ . The mean ( $\pm$  S.E.) difference in biomass between Sections A and B was  $7.8 \pm 1.003$ . The estimated t value for this difference was 7.78 which was highly significant (t at  $P=0.01 = 2.58$ ). The population density and biomass of earthworms in each section reflected the distribution and abundance of earthworms in that section. The low population density and biomass of earthworms in Section B were probably due to the small number of species in that section. It was shown in the section on the distribution of species that L. rubellus formed the main species in Section B but that its population density was significantly lower ( $P = 0.05$ ) in Section B than in Section A. The populations of the other 3 species in Section B were similar to their populations in Section A. It was possible to have a small number of species but for these species to occur in large numbers, but in Section B the number of species were small and the most important species occurred in relatively low numbers. The relatively low population density and biomass in Section B can therefore be regarded as due mainly to the small number of species and also partly to the decrease in the populations of L. rubellus in Section B as compared with Section A.

#### Earthworm distribution and mole distribution

Table 2 shows the population density of earthworms in mole infested areas and in areas free of moles for 7 series of samples

taken between 13/1/69 and 9/6/69. The populations of earthworms were higher in mole-infested areas than in the areas free of moles in all cases but significantly so ( $P = 0.05$ ) only in 6 cases and on average. In the one case in which the difference in the population density of earthworms in the two areas was not significant, the populations of earthworms were generally very low because earthworms were inactive at the time of sampling (ref. Fig. 2 and Appendix 10). Table 3 shows the biomass of earthworms in mole infested areas and in areas free of moles for the same 7 series of samples given above. The biomass of earthworms was higher in mole-infested areas than in the areas free of moles in all cases but significantly higher ( $P = 0.05$ ) only in 3 cases and on average. The lack of significance in the differences in biomass of earthworms between the two areas in 4 cases was also due mainly to low population numbers.

The relationship between the population density of earthworms and the population density of moles.

The density of moles was related to the density of earthworms. The population density of moles (in March 1969) in area Section A where the population density of earthworms was high was 4.5 moles per acre but in area Section B where the population density of earthworms was comparatively low the population density of moles was 2.7 moles per acre. This suggested that the abundance of moles might be influenced by the abundance of their food. The area of land occupied by a mole (in March 1969) was approximately

TABLE 2

Population density of earthworms in mole infested areas  
and areas free of moles at Boghall glen

Date of Sampling	Mean (+ S.E.) population density of earthworms (in numbers per square yard)	
	Mole infested areas	Areas free of moles
1 13.1.69	11.50 ± 1.26	3.71 ± 1.26
2 27.1.69	32.42 ± 1.26	6.23 ± 1.26
3 10.3.69	2.92 ± 1.26	1.30 ± 1.26
4 28.3.69	5.45 ± 1.26	1.65 ± 1.26
5 23.4.69	37.64 ± 1.26	4.46 ± 1.26
6 13.5.69	59.95 ± 1.26	11.79 ± 1.26
7 9.6.69	42.85 ± 1.26	8.40 ± 1.26
1-7 13.1.69 - 9.6.69	18.54 ± 1.09	4.41 ± 1.09

Differences in the population density of earthworms in mole infested  
areas and areas free of moles

Date of sampling	Mean (+ S.E.) population density of earthworms [in Log (No. + 1) per square yard]		
	Mole infested areas	Areas free of moles	Critical Difference
1 13.1.69	2.5223 ± 0.22775	1.5467 ± 0.22775	0.9756*
2 27.1.69	3.5047 ± 0.22775	1.9760 ± 0.22775	1.5287*
3 10.3.69	1.3631 ± 0.22775	0.8295 ± 0.22775	0.5336
4 28.3.69	1.8613 ± 0.22775	0.9717 ± 0.22775	0.8896*
5 23.4.69	3.6496 ± 0.22775	1.6955 ± 0.22775	1.9541*
6 13.5.69	4.1044 ± 0.22775	2.5449 ± 0.22775	1.5595*
7 9.6.69	3.7766 ± 0.22775	2.2388 ± 0.22775	1.5378*
1-7 13.1.69-9.6.69	2.9689 ± 0.08608	1.6862 ± 0.08608	1.6862 <sup>⊕</sup>

\* Difference highly significant (Critical difference at P0.01 = 0.8742)

<sup>⊕</sup> Difference highly significant (Critical difference at P0.01 = 0.5307.)

TABLE 3

Biomass of earthworms in mole infested areas and areas  
free of moles at Boghall glen

Date of Sampling	Mean ( $\pm$ S.E.) biomass of earthworms (in grammes per square yard)		
	Mole infested areas	Areas free of moles	Critical Difference
1 13.1.69	6.0 $\pm$ 2.68	2.2 $\pm$ 2.68	3.8
2 27.1.69	10.0 $\pm$ 2.68	4.6 $\pm$ 2.68	5.4
3 10.3.69	2.3 $\pm$ 2.68	0.7 $\pm$ 2.68	1.6
4 28.3.69	2.8 $\pm$ 2.68	0.8 $\pm$ 2.68	2.0
5 23.4.69	14.0 $\pm$ 2.68	3.7 $\pm$ 2.68	10.3*
6 13.5.69	24.2 $\pm$ 2.68	12.2 $\pm$ 2.68	12.0*
7 9.6.69	18.7 $\pm$ 2.68	5.2 $\pm$ 2.68	13.5*
1-7 13.1.69 - 9.6.69	11.1 $\pm$ 1.85	4.2 $\pm$ 1.85	6.9 <sup>⊕</sup>

\* Differences significant (Critical difference at  $P0.05 = 7.8$ ).

<sup>⊕</sup> Difference significant (Critical difference at  $P0.05 = 3.3$ ).

0.22 acres in Section A and 0.37 acres in Section B and the percentage increase in area infested with moles between March 1968 and March 1969 was 12.9% in Section A and 44.4% in Section B which showed that the home ranges of moles in Section A were smaller than those of moles in Section B and that moles in Section B had to search over a relatively larger area of land for their food than moles in Section A. The number of mole-hills per acre at the start of trapping in March 1969 was 589 in Section A and 118 in Section B which suggested that more mole-hills were made in deep soils with high populations of invertebrates than in shallow soils with low populations of invertebrates.

#### 5A.2 DENSITIES AND SPECIES COMPOSITION OF INVERTEBRATE POPULATIONS EXTRACTED FROM SOIL CORES

Appendix 12 shows the population densities of invertebrates in Boghall glen in June 1968. The total earthworm populations (157.0 per sq. yd.) were higher than those obtained when formalin was used. The population density of adult L. rubellus (10.9 per sq. yd.) was low compared with that of A. caliginosa (33.3 per sq. yd.) Adult L. terrestris were not found in soil cores. It was possible that some earthworms retreated deeper into the soil in response to vibrations caused by sampling and this might partly explain why adult L. terrestris were absent in the soil cores. Earthworms cocoons were about twice as abundant as earthworms but the populations of insect larvae (40.6 per sq. yd.) were much lower than those of earthworms. Larvae of 3 families of insects (Elateridae,

Muscidae and Tipulidae) were identified and each of them was found in each section of the site. The populations of Tipulid larvae (17.2 per sq. yd.) were higher than those of Elaterid larvae (12.5 per sq. yd.) and Muscid larvae (10.9 per sq. yd.). It was possible that some insects had passed their larval stages at the time of sampling and this might explain why only three families of insect larvae were found. The populations of slugs (3.1 per sq. yd.) were low and only 2 species, Agrolimax reticulatus and Arion fasciatus were found.

Appendix 13 shows the population densities of invertebrates in Boghall glen in May 1969. The populations of earthworms (206.4 per sq. yd.) were higher than in June 1968. O. lacteum was identified for the first time in many parts of Section A. There was a further decline in the population density of L. rubellus (2.1 per sq. yd.) and this trend was also observed when formalin was used (Fig. 5). The three large species, L. festivus, L. terrestris and O. cyaneum were absent from soil cores. The distribution of earthworms and the relative populations in each section were similar to those obtained in June 1968 and those obtained when formalin was used. The number of families (12) and the populations of insect larvae (274.6 per sq. yd.) were higher than in June 1968. The insect larvae identified included one family of Hymenoptera (Formicidae), one family of Lepidoptera (Noctuidae), 4 families of Coleoptera (Carabidae, Curculionidae, Elateridae and Scarabaeidae) and six families of Diptera

(Bibionidae, Dolichopodidae, Empididae, Muscidae, Rhagionidae and Tipulidae). Bibionidae had the highest populations (150.3 per sq. yd.) but they were found only in the earlier series of samples taken in Section B and the upper part of Section A and their high population density was due to their aggregation in the soil (1-177 per soil core) and not to a wide distribution. The most abundant and widely distributed larvae were Tipulid larvae (49.4 per sq. yd.) Dolichopodid larvae (25.5 per sq. yd.) and Elaterid larvae (18.2 per sq. yd.). The populations of the other insect larvae were relatively low. The two species of slugs identified in 1968 were also identified in this series.

There were differences between areas Sections A and B in the population densities of invertebrates both in 1968 and in 1969 samples. Appendix 14 shows the mean ( $\pm$  S.E.) population densities (in number per sample) of all invertebrates, earthworms, earthworm cocoons, all insect larvae and elaterid larvae in Sections A and B for June 1968 and Appendix 15 shows similar figures for May 1969. The differences between Sections A and B are also shown. The population densities of all invertebrates, earthworms and earthworm cocoons were significantly higher ( $P = 0.05$ ) in Section A than in Section B while the population density of elaterid larvae were significantly higher in Section B than in Section A in 1968. The population density of all insect larvae was approximately the same in the two sections. Similarly, in 1969 samples the population densities of earthworms and earthworm cocoons were significantly higher in Section A than in Section B but the population densities

of all invertebrates, insect larvae and elaterid larvae were approximately equal in the two areas. The relative abundance of earthworms in areas Sections A and B in soil cores agreed with the results for earthworm populations obtained with formalin extraction.

#### Invertebrate distribution and mole distribution

Table 4 shows the population densities of earthworms, insect larvae, Elaterid larvae, Tipulid larvae and slugs in mole-infested areas and in areas free of moles in June 1968 and Table 5 shows similar results for May 1969. In both years, the population density of earthworms was significantly higher ( $P = 0.05$ ) in mole infested areas than in areas free of moles while the population densities of all insect larvae, elaterid larvae, tipulid larvae and slugs were approximately the same in the two areas. The results suggested that the distribution of moles was related to the distribution of earthworms and that moles lived in the areas with the highest populations of earthworms in Boghall glen. The distribution of moles was, however, not related to the distribution of any group of insect larvae, all insect larvae, and slugs.

#### 5B HABITS OF MOLES

##### 1(a) THE DISTRIBUTION AND ABUNDANCE OF MOLES IN RELATIONSHIP TO THE HABITAT AT BOGHALL GLEN

The distribution of moles on the site in March 1968 and in March 1969 has been shown (Appendix 1). The site was divided into

TABLE 4

Population density of invertebrates in mole infested areas and areas free of moles at Boghall glen in June 1968

Soil Invertebrates	Mean population density (in numbers per square yard)	
	Mole infested areas	Areas free of moles
Earthworms (Lumbricidae)	159.8	51.9
All insect larvae	24.7	25.0
Elaterid larvae	6.5	8.3
Tipulid larvae	9.4	9.2
slugs	3.1	0.8

Comparison of the population density of invertebrates in mole infested areas and areas free of moles

Soil Invertebrates	Mean population density [in Log (No. + 1) per sample area of sample = 0.0097 square yard]				
	Mole infested areas	Areas free of moles	Difference	S.E. Difference	t
Earthworms	0.9352	0.4074	0.5278	0.0866	6.09*
All insect larvae	0.2147	0.2156	0.0009	0.0572	0.016
Elateridae	0.0608	0.0611	0.0003	0.0337	0.009
Tipulidae	0.0872	0.0853	0.0019	0.0362	0.052
Slugs	0.0304	0.0081	0.0223	0.0169	1.32

\* Difference significant (t at P0.05 = 1.96)

TABLE 5

Population densities of invertebrates in mole-infested areas and area free of moles at Boghall glen in May 1969

Invertebrates	Mean population density (in numbers per square yard)	
	mole infested areas	Areas free of moles
Earthworms (Lumbricidae)	178.4	53.8
All insect larvae	98.4	96.2
Elaterid larvae	9.7	16.5
Tipulid larvae	35.3	28.2
Slugs	2.7	4.1

Comparison of the population density of invertebrates in mole infested areas and the areas free of moles

Soil Invertebrates	Mean population density (in Log (No. + 1) per sample. Area of sample = 0.0097 square yard)			S.E. Difference	t
	Mole infested areas	Areas free of moles	Difference		
Earthworms	1.0035	0.4191	0.5844	0.1027	5.690*
All insect larvae	0.6690	0.6582	0.0108	0.1136	0.095
Elaterid larvae	0.0893	0.1476	0.0583	0.0420	1.390
Tipulid larvae	0.2933	0.2410	0.0523	0.0657	0.800
Slugs	0.0244	0.0396	0.0152	0.0220	0.691

\* Difference significant (t at  $P0.05 = 1.96$ )

areas occupied by moles and areas free of moles as indicated by mole-hills and surface ridges. Some areas not occupied in 1968 were later occupied in 1969 showing that the distribution of moles was not static. The spreading was however along the margins of existing areas showing that they were mainly increases in home ranges in existing areas and not the choice of new homes in the uninfested areas. Samples of soil invertebrates taken in areas with no moles were taken not in the immediate edges of areas occupied by moles but in the middle of mole-free areas. It was possible that the invasion of the habitat was still in progress and not yet complete but no information was available as to the precise time of invasion of the site by moles. The distribution of mole-hills could be divided into three fairly distinct types: (i) mole-hills were numerous and clumped together (Plate I), (ii) mole-hills were less numerous and were evenly distributed (Plate II), and (iii) mole-hills were few and widely dispersed (Plate III). In any of the three types of distribution, the mole-hills could be large or small. When mole-hills were large and distributed as in (i) and (ii) above or were small and distributed as in (i) above, the effect on the surface vegetation was severe, the quantity and probably also the quality of grass were considerably reduced and the growth of weeds was encouraged. This happened in early 1969 particularly in Section A and caused the management to demand the killing of all moles on the site. The distribution of moles in Boghall glen showed no apparent distinction into suitable or unsuitable habitats except that moles were absent



Plate I. Clumped mole-hills.



Plate II. Evenly distributed mole-hills.



Plate III. Widely-dispersed mole-hills.

in very dry soils and in soils that were frequently flooded. Moles were found in all soil types and from the lowest point to the highest point on the site which showed that soil types and altitude did not influence their distribution. The mean ( $\pm$  S.E.) soil pH was  $6.1 \pm 0.6$  in mole-infested areas and  $5.7 \pm 0.3$  in mole-free areas. The mean ( $\pm$  S.E.) difference in soil pH between the two areas was  $0.4 \pm 0.58$  which was not significant. (The estimated t value for the difference was 0.7 and t at  $P0.05 = 2.06$ ). The mean ( $\pm$  S.E.) soil organic matter contents in mole-infested areas was  $14.8 \pm 8.5$  and in areas free of moles it was  $15.5 \pm 5.8$ . The mean ( $\pm$  S.E.) difference in soil organic matter contents between the two areas was  $0.7 \pm 3.8$  which was not significant (The estimated t value for the difference was 0.2 and t at  $P0.05 = 2.04$ ). The results showed that soil pH and the percentage organic matter contents of soils did not influence moles in their choice of habitats. The surface vegetation did not appear to have any direct significant influence on the distribution of moles. Moles were found in most places where rushes (Juncus sp.) were found except that where the soils were flooded rushes were present but moles were absent. The relationship between mole distribution and the distribution of rushes appeared to be an indirect one and was probably due to a mutual preference for damp soils. Mole-hills were found among gorse (Ulex europaeus) in a few cases but the number of mole-hills in such areas were usually few. It was observed that moles usually built their fortresses and nests among rushes and gorse whenever these plants were present. There appeared to be a concentration of

moles along drainage lines particularly in Section A of the site. The relative abundance of thistles (Carduus sp.) in areas with old mole-hills was probably due to the fact that this species is a colonizer of the bare soil surfaces created by mole-hills. The abundance of moles was related to the habitat. Moles were more abundant in Section A than in Section B of the site. The number of moles on the site in 1968 was not known so that the population density of moles and the increase in numbers between 1968 and 1969 could not be estimated. This meant that the increase in the area occupied by moles from March 1968 to March 1969 could not be correlated with the increase in the number of moles in each section between that period. The area occupied by moles in Section A in March 1968 was 16.3 acres and the area occupied in March 1969 was 18.4 acres representing an annual increase of 12.9% in the foraging area of moles in this section. The area occupied by moles in Section B in March 1968 was 1.8 acres and the area occupied in March 1969 was 2.6 acres which meant an annual increase of 44.4% in the foraging area of moles in the section. The increase in area occupied by moles would be affected by the number of offspring produced in each section in Spring 1968 but there was no indication that more offspring per pair of moles would be produced in Section B than in Section A, and no migration of moles into Section B was observed. This meant that the relatively larger annual increase in areas occupied by moles in Section B was probably related to the poorer ecological conditions on this section. The most important ecological factor in this respect was food supply which has already

been discussed (Section 5A.1)

The population density of moles was calculated as the "highest density" i.e. number of moles per area of actual land surface occupied by moles. The population density of moles in April 1969 was 4.5 moles per acre in Section A and 2.7 moles per acre in Section B which showed that the abundance of moles was related to the habitat. The number of mole-hills per acre at the start of trapping in March 1969 was 589 in Section A and 118 in Section B which suggested that more mole-hills were made in relatively deeper soils with high populations of invertebrates than in shallow soils with low populations of invertebrates. The large number of mole-hills in Section A was related to the mole's food supply. In this section there are both deep-burrowing and surface burrowing species of earthworms and the moles worked deep to obtain the former category of earthworms. Also the population density of invertebrates was high so digging would provide much food. In Section B moles made mainly shallow tunnels because only surface living species of earthworms were present. It was also more rewarding to make surface tunnels in this section because of the low population density of invertebrates.

#### 5B. 1(b) MOLE ACTIVITY

##### Tunnels

Four main types of tunnels were observed: permanent tunnels, surface tunnels, rutting runs and raised ridges with no through passages under them. Permanent tunnels were between  $4\frac{1}{2}$  in. to

12 in. deep and the spoils of earth from their excavations were thrown up as mole-hills. Surface tunnels were usually not more than 3 in. deep and the displaced soil was formed into a ridge. They lacked mole-hills and their roofs sometimes collapsed. Tunnels intermediate between surface and permanent types were also observed. They were usually between 3 in. to  $4\frac{1}{2}$  in. deep and the displaced soil was thrown up as small mole-hills. Rutting runs were grooves in the soil usually never more than 1 in. deep (Plates IV and V). They were observed to last for about one week and were probably never revisited by the moles which made them. They were abundant in March 1968 and March 1969 but they were also observed in the north-end of Section B of Boghall glen in November 1968 and at other times on Leip field. These **furrows** were probably made by moles searching for food or new territories or escaping from flooded soils. Raised ridges with no through passages under them (Plates VI and VII) were observed in May 1968 and in May and June 1969. Strictly speaking, these are not tunnels; they are wider than the normal surface tunnels and in some cases up to one square foot of the soil surface was covered by them. They collapsed when touched but if undisturbed they lasted for about three weeks. There were differences between Section A and B of Boghall glen in the types of predominant tunnels. In Section A, deep permanent tunnels and the associated large mole-hills predominated although surface tunnels were also common. The permanent tunnels were up to 12 in. deep and in many places they penetrated below the original plough layer of the soil and bits of



Plate IV. Rutting runs.



Plate V. Rutting runs under snow.



Plate VI. Raised ridges with no through passages under them.



Plate VII. Raised ridges with no through passages under them.

decaying vegetation could be seen in the mole-hills. In Section B surface tunnels predominated and the permanent tunnels in this section were seldom more than 5 in. deep and only small mole-hills were made. The differences in the types of predominant tunnels in Sections A and B was probably related to the depth of the surface soil.

#### General activity

The seasonal activity of moles was recorded from January 1968 to January 1970. The relative activity in the sexes during the period of trapping was also noted. Sexual activity in males relative to females was judged on the basis of the ratio of each sex caught in traps and the weight of the reproductive organs. The weight of reproductive organs in males and females are shown in Appendices 16 and 17. In mild weather in January 1968, 1969 and 1970, moles built permanent tunnels and surface tunnels. The surface tunnels of males were long, relatively straight and led away from their homes while those of females were winding and confined to their homes (sexes confirmed by trapping). The long tunnels of males were probably used to search for females. In periods with severe ground frost in January, February and March, only deep tunnels were made and these too were very few. Digging was carried out in existing tunnels and the spoils of earth from such diggings were forcibly discharged over or under existing mole-hills which sometimes cracked in many places. It was not known if the diggings represented searching within the tunnels or very short

extensions not necessitating the formation of new mole-hills. In March 1968 and 1969, rutting runs were built in flooded areas and these probably served as exploratory routes. In most of February and in early March 1969, the soil was covered with snow and rutting runs which had originally been built between the soil and snow interface were observed as the snow melted in early March (Plate V). The mean ( $\pm$  S.E.) weight of testis of males was at a maximum ( $783 \pm 106$  mg.) in March 1969 and decreased gradually to the lowest level in July ( $170 \pm 28$  mg.). Two females were trapped in March of which one had closed vagina and the other had opened vagina, this evidence was fragmentary but it would appear that the female vagina opened in late March. Males were slightly more active than females in March. The sex ratio in trappings was  $4\sigma:1\text{f}$  which was not significantly different from a 1:1 ratio ( $\chi^2 = 3.6$ ,  $\chi^2_{[1]}$  at  $P0.05 = 3.8$  and at  $P0.1 = 2.7$ ). Multiple catches in March involved more than one male but only one female was involved in multiple catches. It would appear that the relative activity in the sexes was an important factor in the occurrence of multiple catches. In April 1968 and 1969 moles were more active than in March. There were increases in digging coupled with a slight increase in home ranges. Moles trapped in areas with fresh diggings in April were usually females. It was possible that such females were enlarging their homes in preparation for the birth of offspring. The mean ( $\pm$  S.E.) weight of the reproductive tract in females was at a maximum in April ( $760 \pm 170$  mg.) and decreased gradually to a minimum in June ( $210 \pm 46$  mg.) and July

(236 ± 96 mg.). Only one of 9 females caught in April was visibly pregnant (with 3 embryos) but it was possible that there were cases of non-visible pregnancies. The vagina was open in all females. The sex ratio in trappings in April (1.9 male:1 female) was not significantly different from a 1:1 ratio ( $\chi^2 = 2.5$  and  $\chi^2_{[1]}$  at  $P0.05 = 3.8$  and at  $P0.1 = 2.7$ ). Multiple catches in April involving more than one female was recorded once and that involving more than one male was recorded once. It appeared that activity in the sexes was approximately the same in April.

In May 1968 and 1969 moles were more active than in April. Multiple catches were recorded for both males and females. The sex ratio in trappings in May was 1.8 males to 1 female which was not significantly different from a 1:1 ratio ( $\chi^2 = 2.4$  and  $\chi^2_{[1]}$  at  $P0.05 = 3.8$ ) showing that activity was equal in the sexes. One female was pregnant with 4 embryos but most females caught in May had very prominent mammary glands showing that they were lactating. One lactating female with three babies in her nest was caught on 12/5/69. The 3 placentae were still in her uterus.

Raised ridges with no through passages under them were made in May. In wet periods in June and July activity was similar to that in May except that the raised ridges with no through passages under them were not made in July. Surface tunnels predominated in wet periods in June, July and August but in dry periods as occurred in June, end of July and early August 1968, moles migrated into adjacent moist soils that had been too wet for them in normal times. The moles returned to their original homes when the soil

became moist again. Whenever the adjacent areas were equally dry, moles migrated vertically by digging deeper tunnels. The construction of surface tunnels was restricted to the beds of dried up streams and drainage lines, river banks, and among thick vegetation of grasses and rushes whenever these existed. In extremely exposed areas no diggings were observed. Three moles were caught on the surface in dry periods in August 1968, and one of them was kept in captivity where it later died.

#### Dispersal and population movements

Dispersal and population movements constituted the most important aspects of mole activity from mid-June to early January. The activity in adult male and female moles in June was the same. The sex ratio was (0.9 male:1 female) not significantly different from a 1:1 ratio ( $\chi^2 = 0.1$  and  $\chi^2_{[1]}$  at  $P0.05 = 3.8$ ). Only one of 10 females caught in June (on 11/6/69) was pregnant (with 4 embryos) but the others had prominent mammary glands and the vaginal orifice was closing gradually in some. The results indicated that juveniles were born at different times within the reproductive period and this would lead to differences in their body weights, time of weaning and tooth length. The first juvenile, a female weighing 61 g., was trapped on 5/6/69. Adults and juveniles of both sexes were trapped in the same tunnels and within 24 hours from early June to mid-July indicating that adult and juveniles were sociable for a short period after the juveniles were weaned until they were dispersed. Juveniles were significantly smaller ( $P = 0.05$ ) than adults in June (Table 23) and the weight of their

reproductive organs was much smaller than those of adults (Appendices 16 and 17). The differences in body weight of adults and juveniles disappeared in July (Table 26) but juveniles were still sexually undeveloped in July. Juveniles establishing their own homes were observed on Leip field at the end of June 1969. Dispersal of juveniles took two forms. (a) The juveniles built their homes as extensions to the homes of their parents in summer and later moved further away but without breaking the tunnel links when they constructed their permanent homes in the autumn. This was the only type of dispersal observed at Boghall glen and this explained why the distribution of moles in 1969 (Appendix 1) appeared to be a marginal extension to the distribution in 1968. (b) The juveniles built their homes at some distance away from their parents' homes and the two sites were not connected by tunnels. This type of dispersal (or migration) involving movements above the surface and leading to the infestation of areas originally devoid of moles was described as "jump-spreading" and was probably characteristic of habitats in which the available favourable areas had been occupied. Juveniles dispersed by the jump-spreading method invariably built some length of rutting runs in the sites of their new homes. Such runs were probably built for a quick exploration of the new site. In summer juveniles built small nests of balls of grass under the unbroken turf and the increases in their home ranges were relatively greater than the increases in the home ranges of adults.

The soil was flooded in September and October 1968 and at the

end of January 1969. Moles deserted flooded runs but damp runs were used as fresh feet-marks were found in them and damaged ones were repaired. When an area was completely flooded, moles left such areas and built new tunnels in drier areas, the migration to the new areas being accomplished by building tunnels between the old and new areas. The moles usually returned to their original homes when the soil conditions became favourable again. Migrations and population movements were observed from November till the beginning of January in 1968 and 1969. Many cases of jump-spreading occurred and resulted in the infestation of new areas and the recolonization of trapped-out areas. Some areas were observed to be recolonized every autumn despite repeated trapping out of moles from such areas each winter. Extensive digging occurred in December 1968 and December 1969 as moles invading unoccupied areas built new homes and established moles enlarged their old homes. The shallow summer tunnels were wholly or partially abandoned and were replaced with deep permanent tunnels. Fortresses were built between the end of December and early January. Large-scale population movements stopped in early January in both years but extensive diggings continued till mid-January.

The possible relationship of digging activity particularly to feeding habits is discussed further in Section 6 (Discussions).

5B. 2. THE FEEDING HABITS OF MOLES(a) Method of gathering food

No invertebrates were found lying freely in mole tunnels but on three occasions the rejected gut contents of earthworms were found which indicated that feeding took place in the tunnels. It was possible that the invertebrates which fell into the tunnels were eaten within a very short time or that such invertebrates escaped back into the soil very quickly. On two occasions earthworms were seen to have emerged from the soil where a mole was digging and on each occasion the mole emerged to the surface groping for the earthworms. On another occasion one L. rubellus with a fresh wound on its head was found buried in the floor of a freshly dug tunnel. These observations suggested that digging could take place in conjunction with feeding. The inability of the mole to catch an escaping prey showed the short range of its sensory organs. Earthworm cocoons were found in fresh mole-hills on two occasions which suggested that moles were not very efficient at locating cocoons or that cocoons were not a favourite item of their diet.

(b) Food storage

No stores of earthworms were found in any of the fortresses dissected on 23/4/68 and 15/10/68 which indicated that stores were not laid until late in the autumn. The 5 fortresses dissected on 28/2/69 included the two dissected on 15/10/68 which were rebuilt at the end of December 1968. All 5 fortresses contained stores of earthworms which were decapitated or mutilated. The wounds on

the earthworms had healed up which indicated that the injuries were inflicted much earlier. Moles probably laid their stores from about mid-October to mid-January. On 10/3/69 the remaining half of each of the fortresses dissected on 28/2/69 were dissected but no stores were found in them indicating that the stores had been eaten, possibly transferred or that the earthworms crawled away. All fortresses dissected after this time contained no stores but findings of invertebrates included (i) 2 Tipulid larvae under a nest containing three baby moles and 2 dead D. rubida in another fortress on 12/5/69, and (ii) 2 immature A. caliginosa in a fortress on 19/5/69 all of which indicated that a mole could hoard a little amount of food any time in the year.

Species composition and the conditions of earthworms in the 5 fortresses dissected on 28/2/69: Appendix 18 shows the species composition of earthworms in each fortress. The number of species in each store reflected the species composition of the earthworm populations in the area in which each fortress was located which suggested that each mole collected its food only in the immediate vicinity of its home. The proportion of each species in the stores did not correspond to the relative abundance of the species in the soil. L. terrestris and O. cyaneum formed 43.1% and 21.6% respectively of the total number of earthworms in Fortress 1. The field populations of each of these two species (as estimated with formalin) were relatively very low compared with those of A. caliginosa and L. rubellus. The preponderance of L. terrestris and O. cyaneum in Fortress 1 and also of O. cyaneum (6.7%) in Fortress 2 suggested that these species

were more suitable for storage whenever they were present. Table 6 shows the species composition and the percentage number injured or dead in the 5 fortresses. The percentage number of each species in the field populations of earthworms is also shown for comparison with their abundance in the stores. Only two earthworms (one A. caliginosa and one L. castaneus) were dead and they were apparently uninjured. The healed injuries of the surviving earthworms showed that the treatment they received from the moles would not normally kill the earthworms. The presence of both injured and uninjured earthworms in the stores suggested that the members of the stores came from two sources - those deliberately bitten and stored by the moles and those that wandered accidentally into the stores. The smaller earthworms (A. chlorotica, D. rubida, E. rosea) occurred in very low numbers in the stores and they were not injured which suggested that they were mainly accidental members of the stores. It was also possible that some A. caliginosa wandered into the stores. This was indicated by the presence of some members of this species which were knotted together in typical hibernation posture. The percentage number injured in L. terrestris (95.2%) and O. cyaneum (90.9%) was relatively higher than that in L. rubellus (85.7%) and in A. caliginosa (81.5%) which also indicated that almost all the larger species were deliberately stored while some of the smaller species probably wandered into the stores.

#### Food storage by captive moles.

Two moles kept in captivity in 1968 mutilated and stored the

TABLE 6

Numbers and condition of each species in earthworm stores from five mole fortresses  
at Boghall glen on 28.2.69.

Species of earthworms	Numbers and condition of each species in stores from five mole fortresses										Percentage number of each species in field populations of adult earthworms
	Number of adults	Number of immatures	Total Number	Number injured	Number not injured	Percentage number injured	Number (and percentage) dead	Percentage number in store	Number in store populations		
A. caliginosa	209	61	270	220	50	81.5	1 (0.4%)	83.1	45.7		
A. chlorotica	1	-	1	-	1	0	-	0.3	9.5		
D. rubida	1	-	1	-	1	0	1	0.3	1.7		
E. rosea	2	-	2	-	2	0	-	0.6	4.2		
L. castaneus	1	-	1	-	-	-	1 (100%)	0.3	0.6		
L. rubellus	5	2	7	6	1	85.7	-	2.2	32.8		
L. terrestris	12	10	22	20	2	90.9	-	6.8	1.7		
O. cyaneum	17	4	21	20	1	95.2	-	6.1	1.7		
All species	248	77	325	267	58	82.2	2 (0.6%)	100.0			

excess of earthworms fed to them. The habit was first observed on 15/9/68 and it lasted till the end of November. The stores were always laid in the same places mainly at the corners of the sleeping cages. In a few instances a mole pushed soil from the sleeping cage and used it to bury earthworms in the feeding cage. Observations showed that some of the earthworms were deliberately stored by the moles while some earthworms crawled into the sleeping cage and were hoarded by the moles. Captive moles eventually ate their stores unless they were always provided with excess earthworms as was the case before the stores were discovered. This suggested that wild moles too would probably eat their stores eventually. Other moles kept in captivity occasionally stored a few earthworms that crawled into their sleeping cages but mass storage was observed only from mid-September to the end of November.

(c) Body weight and diet of moles

The body weights, stomach weights and the results of the analysis of the stomach contents of moles trapped in Boghall glen from March till early August 1969 are shown in Appendix 19. The results of the investigation of the body weight and diet are given under 4 subdivisions: (i) all moles (males and females combined), (ii) males and females separately, (iii) adults and juveniles separately in June and July and (iv) moles trapped in areas Sections A and B of Boghall glen in March to mid-April. The body weight of moles was given under this section because it was found to be directly related to the feeding habits.

(i) All moles (males and females combined)

Table 7 shows the monthly mean ( $\pm$  S.E.) body weight of moles and the differences between months from March to August 1969. The body weight increased from March to the highest value in May after which it declined gradually to the lowest level in August. It was significantly higher ( $P = 0.05$ ) in April than in June, July and August and in May it was significantly higher than in June, July and August. The low body weight in June was due to the low body weight of juveniles and partly to a slight decrease in the body weight of adults at the end of the reproductive season. Only juvenile moles were caught in August. Table 8 shows the mean ( $\pm$  S.E.) body weight less weight of stomach contents and the differences between months from March to August 1969. The results were similar to those obtained when the body weight was analysed without removing the weight of the stomach contents except that the difference in body weight between April and July was no longer significant ( $P = 0.05$ ). The results showed that the weight of stomach contents might not contribute significantly to the body weight and that the increases in body weight in April and May were real increases and were not due to increases in the weight of stomach contents. Table 9 shows the mean ( $\pm$  S.E.) weight of stomach contents and the differences between months from March to August 1969. There were no significant differences ( $P = 0.05$ ) between months in the weight of stomach contents which showed that the food consumption was not significantly affected by seasonal changes in food availability. The monthly mean ( $\pm$  S.E.)

TABLE 7

Monthly variations in the body weight of (male and female) moles at Boghall glen

Month	Mean ( $\pm$ S.E.) body weight (in g.)
March	96.5 $\pm$ 16.5
April	99.0 $\pm$ 11.3
May	107.7 $\pm$ 12.2
June	89.5 $\pm$ 16.5
July	86.1 $\pm$ 8.9
August	81.8 $\pm$ 9.3

Mean ( $\pm$  S.E.) differences between months in body weight

Months	Mean ( $\pm$ S.E. difference in body weight (in g.))	t	t at P0.05
March-April	2.5 $\pm$ 7.87	0.32	2.07
March-May	11.2 $\pm$ 7.87	1.42	2.06
March-June	7.0 $\pm$ 8.60	0.81	2.01
March-July	10.4 $\pm$ 7.28	1.43	2.03
March-August	14.7 $\pm$ 12.21	1.20	2.18
April-May	8.7 $\pm$ 4.80	1.81	2.01
April-June	9.5 $\pm$ 4.47	2.13*	2.00
April-July	12.9 $\pm$ 4.02	3.21*	2.01
April-August	17.2 $\pm$ 8.40	2.05*	2.05
May-June	18.2 $\pm$ 5.23	3.48*	2.00
May-July	21.6 $\pm$ 4.12	5.24*	2.01
May-August	25.9 $\pm$ 8.77	2.95*	2.05
June-July	3.4 $\pm$ 4.69	0.72	2.00
June-August	7.7 $\pm$ 10.39	0.74	2.02
July-August	4.3 $\pm$ 7.48	0.57	2.04

\* Difference significant at P0.05

TABLE 8

Monthly variation in body weight - weight of stomach contents of  
(male and female) moles at Boghall glen.

Month	Mean ( $\pm$ S.E.) body weight - weight of stomach contents (in g.)
March	90.4 $\pm$ 13.7
April	93.3 $\pm$ 10.2
May	101.8 $\pm$ 11.9
June	84.2 $\pm$ 15.5
July	81.3 $\pm$ 7.6
August	77.3 $\pm$ 7.4

Mean ( $\pm$  S.E.) differences between months in weight of body - weight  
of stomach contents

Months	Mean ( $\pm$ S.E.) difference in weight of body-weight of stomach contents.	t	t at P0.05
March and April	2.9 $\pm$ 3.42	0.85	2.07
March and May	11.4 $\pm$ 7.07	1.61	2.06
March and June	6.2 $\pm$ 7.55	0.82	2.01
March and July	6.08 $\pm$ 6.00	1.01	2.03
March and August	13.1 $\pm$ 9.85	1.33	2.18
April and May	8.5 $\pm$ 4.47	1.90	2.01
April and June	9.1 $\pm$ 4.80	1.90	2.00
April and July	12.0 $\pm$ 2.35	5.11*	2.01
April and August	16.0 $\pm$ 6.48	2.47*	2.05
May and June	17.6 $\pm$ 5.00	3.52*	2.00
May and July	20.5 $\pm$ 3.78	5.42*	2.01
May and August	24.5 $\pm$ 7.81	3.14*	2.05
June and July	2.9 $\pm$ 4.36	0.67	2.00
June and August	6.9 $\pm$ 8.77	0.79	2.02
July and August	4.0 $\pm$ 6.08	0.66	2.04

\* Difference significant at P0.05

TABLE 9

Monthly variations in the weight of stomach contents of (male and female) moles at Boghall glen

Months	Mean ( $\pm$ S.E.) weight of stomach contents (in g.)
March	6.2 $\pm$ 3.5
April	5.4 $\pm$ 3.6
May	5.7 $\pm$ 1.3
June	5.2 $\pm$ 2.4
July	4.8 $\pm$ 2.2
August	4.3 $\pm$ 3.2

Mean ( $\pm$  S.E.) differences between months in weight of stomach contents

Months	Mean ( $\pm$ S.E.) difference in weight of stomach contents (in g.)	t	t at P0.05
March and April	0.8 $\pm$ 1.95	0.41	2.07
March and May	0.5 $\pm$ 1.47	0.34	2.04
March and June	1.0 $\pm$ 1.57	0.64	2.01
March and July	1.4 $\pm$ 1.60	0.88	2.03
March and August	1.9 $\pm$ 3.25	0.58	2.18
April and May	0.3 $\pm$ 1.08	0.28	2.02
April and June	0.2 $\pm$ 1.11	0.18	2.00
April and July	0.6 $\pm$ 1.17	0.51	2.01
April and August	1.1 $\pm$ 1.98	0.56	2.05
May and June	0.5 $\pm$ 0.69	0.72	2.00
May and July	0.9 $\pm$ 0.71	1.27	2.01
May and August	1.4 $\pm$ 2.02	0.69	2.05
June and July	0.4 $\pm$ 0.81	0.49	2.00
June and August	0.9 $\pm$ 2.10	0.43	2.02
July and August	0.5 $\pm$ 2.10	0.24	2.04

Differences not significant at P0.05

weight of undigested food in stomach contents is shown in Table 10. The differences between months are also shown. The trend in the weight of undigested food in stomach contents was the same as the trend in the weight of stomach contents which showed that the weight of undigested food in the stomach was a reliable index of the food consumption of moles. Table 11 shows the monthly mean ( $\pm$  S.E.) weight of stomach contents as a percentage of the body weight and the differences between months from March to August 1969. There were no significant ( $P = 0.05$ ) monthly differences in the weight of stomach contents as a percentage of the body weight which shows that the food consumption was directly related to the body weight in all months. Table 12 shows the monthly mean ( $\pm$  S.E.) weight of stomach contents as a percentage of the body weight - weight of stomach contents. The results were similar to those obtained when the food consumption was considered in relation to the body weight without subtracting the weight of stomach contents. This again suggested that the body weight of moles might reliably be analysed with respect to food consumption without removing the weight of the stomach contents.

A list of invertebrates identified in the stomach contents of moles from Boghall glen is shown in Appendix 20 and the percentage number of stomachs containing each food item from March to August 1969 is shown in Appendix 21. The results in Appendix 21 are also represented graphically (Fig. 8) for earthworms, insect larvae, earthworm cocoons, slugs and adult insects. The composition of the diet varied very much from month to month with particular regards

TABLE 10

Monthly variations in the weight of undigested food in the stomach contents of (male and female) moles at Boghall glen

Month	Mean ( $\pm$ S.E.) weight of undigested food in the stomach contents (in g.)
March	2.9 $\pm$ 2.4
April	1.9 $\pm$ 2.0
May	1.6 $\pm$ 0.7
June	1.3 $\pm$ 0.8
July	1.2 $\pm$ 0.8
August	1.3 $\pm$ 0.6

Mean ( $\pm$  S.E.) differences between months in the weight of undigested food in stomach contents

Months	Mean ( $\pm$ S.E.) difference in weight of undigested food in the stomach contents (in g.)	t	t at P0.05
March and April	1.0 $\pm$ 1.3	0.77	2.07
March and May	1.3 $\pm$ 1.0	1.30	2.06
March and June	1.6 $\pm$ 1.0	1.60	2.01
March and July	1.7 $\pm$ 1.0	1.70	2.03
March and August	1.6 $\pm$ 1.7	0.94	2.18
April and May	0.3 $\pm$ 0.7	0.43	2.01
April and June	0.6 $\pm$ 0.6	1.00	2.00
April and July	0.7 $\pm$ 0.6	1.17	2.01
April and August	0.6 $\pm$ 1.4	0.43	2.05
May and June	0.3 $\pm$ 0.3	1.00	2.00
May and July	0.4 $\pm$ 0.3	1.33	2.01
May and August	0.3 $\pm$ 0.8	0.38	2.05
June and July	0.1 $\pm$ 0.3	0.33	2.00
June and August	0 $\pm$ 0.8	0	2.02
July and August	0.1 $\pm$ 0.9	0.11	2.04

Differences not significant at P0.05

TABLE 11

Monthly variations in weight of stomach contents as a percentage of the body weight in (male and female) moles at Boghall glen

Months	Mean ( $\pm$ S.E.) % food consumption per unit of body weight
March	5.9 $\pm$ 3.0%
April	5.3 $\pm$ 3.5%
May	5.3 $\pm$ 1.9%
June	5.8 $\pm$ 2.4%
July	5.5 $\pm$ 2.5%
August	5.0 $\pm$ 4.0%

Mean ( $\pm$  S.E.) differences between months in weight of stomach contents as a percentage of the body weight

Months	Mean ( $\pm$ S.E.) difference in weight of stomach contents as a percentage of the body weight	t	t at P0.05
March and April	0.6 $\pm$ 1.75%	0.34	2.07
March and May	0.6 $\pm$ 1.34%	0.45	2.04
March and June	0.1 $\pm$ 1.37%	0.07	2.01
March and July	0.4 $\pm$ 1.42%	0.28	2.03
March and August	0.9 $\pm$ 3.87%	0.23	2.18
April and May	0 $\pm$ 1.11%	0	2.02
April and June	0.5 $\pm$ 1.04%	0.48	2.00
April and July	0.2 $\pm$ 1.20%	0.17	2.01
April and August	0.3 $\pm$ 3.60%	0.08	2.05
May and June	0.5 $\pm$ 0.78%	0.64	2.00
May and July	0.2 $\pm$ 0.87%	0.23	2.01
May and August	0.3 $\pm$ 3.32%	0.09	2.05
June and July	0.3 $\pm$ 0.87%	0.34	2.00
June and August	0.8 $\pm$ 3.32%	0.24	2.02
July and August	0.5 $\pm$ 3.46%	0.15	2.04

Differences not significant at P0.05

TABLE 12

Monthly variations in weight of stomach contents as a percentage of the body weight - weight of stomach contents in (male and female) moles

Month	Mean ( $\pm$ S.E.) % food consumption per unit of body weight
March	6.3 $\pm$ 4.4%
April	5.7 $\pm$ 4.0%
May	5.8 $\pm$ 2.5%
June	6.6 $\pm$ 2.8%
July	5.9 $\pm$ 2.8%
August	5.3 $\pm$ 3.3%

Mean ( $\pm$  S.E.) differences between months in weight of stomach contents as a percentage of the body weight - weight of stomach contents

Months	Mean ( $\pm$ S.E.) difference in weight of stomach contents as a percentage of the body weight - weight of stomach contents.	t	t at P0.05
March and April	0.6 $\pm$ 2.32%	0.26	2.07
March and May	0.5 $\pm$ 1.97%	0.25	2.06
March and June	0.3 $\pm$ 1.93%	0.16	2.01
March and July	0.4 $\pm$ 2.01%	0.20	2.03
March and August	1.0 $\pm$ 3.61%	0.28	2.18
April and May	0.1 $\pm$ 1.36%	0.07	2.01
April and June	0.9 $\pm$ 1.27%	0.71	2.00
April and July	0.2 $\pm$ 1.38%	0.14	2.01
April and August	0.4 $\pm$ 3.01%	0.13	2.05
May and June	0.8 $\pm$ 0.95%	0.84	2.00
May and July	0.1 $\pm$ 1.05%	0.10	2.01
May and August	0.5 $\pm$ 2.45%	0.20	2.05
June and July	0.7 $\pm$ 0.99%	0.71	2.00
June and August	1.3 $\pm$ 2.48%	0.54	2.02
July and August	0.6 $\pm$ 1.90%	0.32	2.04

Differences not significant at P0.05

to adult insects, individual families of insect larvae, earthworm cocoons, slugs, centipedes and plant materials but the percentage number of stomachs containing earthworms, insect larvae and Tipulid larvae did not vary very much from month to month. Tipulid larvae were abundant in the surface layers of the soil from March to early August and the relative abundance of this species in stomach contents during that period was related to their ecology and life cycle. The occurrence of the larval forms of other insects in stomach contents was probably similarly related to the ecology and life cycles of the insects. It was possible that the occurrence of adult insects in the stomachs reflected the extent of surface activities in moles since adult insects would most probably be caught on the surface. Appendix 22 shows the monthly mean ( $\pm$  S.E.) percentage weight of earthworms in the stomach contents and the differences between months from March to August 1969. The percentage weight of earthworms in the diet was highest in August and lowest in July but there were no significant differences ( $P = 0.05$ ) between months which showed that the relative weight of earthworms in the diet was not significantly affected by the changes in soil conditions and the activity of earthworms. The results in Appendix 22 are represented graphically in Fig. 9. The percentage weight of earthworms in the diet was inversely related to that of insect larvae since earthworms and insect larvae constituted the main components of the food. A comparison of Fig. 8 and Fig. 9 showed that the percentage occurrence of food items in

the stomachs did not reflect the relative importance of the various food items in the diet. Thus, the percentage occurrence of earthworms in stomach contents was lower than that of insect larvae in March, April, June and July and equal to that of insect larvae in May and August which suggested that relative to insect larvae earthworms contributed less weight to the food in March, April, June and July and as much weight in May and August. However, the results of analysis by weight showed that earthworms contributed relatively more weight to the diet in March, April and August while insect larvae contributed relatively more weight to the diet in May, June and July. The results showed that a more reliable indication of the relative importance of food items in the diet of moles was obtained when food items were weighed. The disparity between the results of the two analyses was due to the fact that the analysis of the percentage occurrence of food items in the stomachs did not take the relative weights of the different species of prey into account and this could lead to serious errors. The mean ( $\pm$  S.E.) weight of earthworms in Boghall glen was  $0.40 \pm 0.01$  in area Section A and  $0.45 \pm 0.02$  in area Section B (The low mean weight of earthworms in Boghall glen was due to the preponderance of the smaller species and the low mean weight of earthworms in area Section A relative to Section B was due to the relative abundance of the smaller species in Section A while L. rubellus formed the main species in Section B). The mean ( $\pm$  S.E.) body weight was  $0.15 \pm 0.09$  for Tipulid larvae (leatherjackets),  $0.03 \pm 0.02$  for Elaterid larvae (wireworms),  $0.29 \pm 0.10$  for slugs (Agrolimax

reticulatus) and  $0.027 \pm 0.01$  for earthworm cocoons. These figures indicated that in relationship to the moles' food requirements, one earthworm was at least approximately equal to three full-grown Tipulid larvae, or two full-grown Agrolimax reticulatus, or more than ten elaterid larvae or earthworm cocoons. It could be seen from this that the importance of earthworms in the diet of moles was due both to their high frequency of occurrence in the stomachs, and to their larger biomass relative to the other items of the moles' diet.

#### Food preferences

Table 13 shows the percentage occurrence of food items in the stomach contents and in soil samples for the period 15/5/69 to 15/6/69. All invertebrate foods of moles which were found in soil samples were also found in stomach contents except Curculionid and Scarabaeid larvae which were found in one soil sample but were absent from stomach contents. The results showed that moles ate nearly all the invertebrates they could find in the soil. It also suggested that invertebrates that occurred in very low numbers in the soil were likely to be missed out by moles. Muscid larvae were not found in stomach contents during the period covered by the investigations but they were found in the contents at other times (Appendices 19-21). The six most widely distributed food items in the soil were earthworm cocoons (76.5% occurrence), earthworms (62.0% occurrence), insect larvae (59.5% occurrence), Tipulid larvae (30.5% occurrence), Dolichopodid larvae (17.0% occurrence) and

Elaterid larvae (14.0% occurrence). The percentage occurrence of these food items in stomach contents were - insect larvae (100%), earthworms (98%), Tipulid larvae (89.8%), Elaterid larvae (55.1%), Dolichopodid larvae (42.6%) and earthworm cocoons (6.1%). These showed that the various food items occurred in the same general proportions in both soil samples and stomach contents except earthworm cocoons which were abundant in the soil but were found only in a small proportion of stomachs. The low occurrence of earthworm cocoons in stomachs suggested that they were not a favourite item of the diet. The results showed that wide distribution and abundance in the soil of a prey species were important factors in the frequency of its selection for food by moles. There were indications that the size of prey and the relative activity of different species of prey might also be of some importance in their selection for food by moles. Noctuid larvae were found only in two soil samples but they occurred in a relatively high proportion of stomach (26.5% of stomachs) which suggested that their large size might make them easier to locate by moles. Carabid larvae were found in 4.0% of soil samples and in 44.9% of stomachs. This species was very active and its low occurrence in soil samples might indicate that they escaped from the samples. If, however, invertebrates fell into mole tunnels, many of this active species would fall into the tunnels and this might explain why a high percentage number of stomachs contained them.

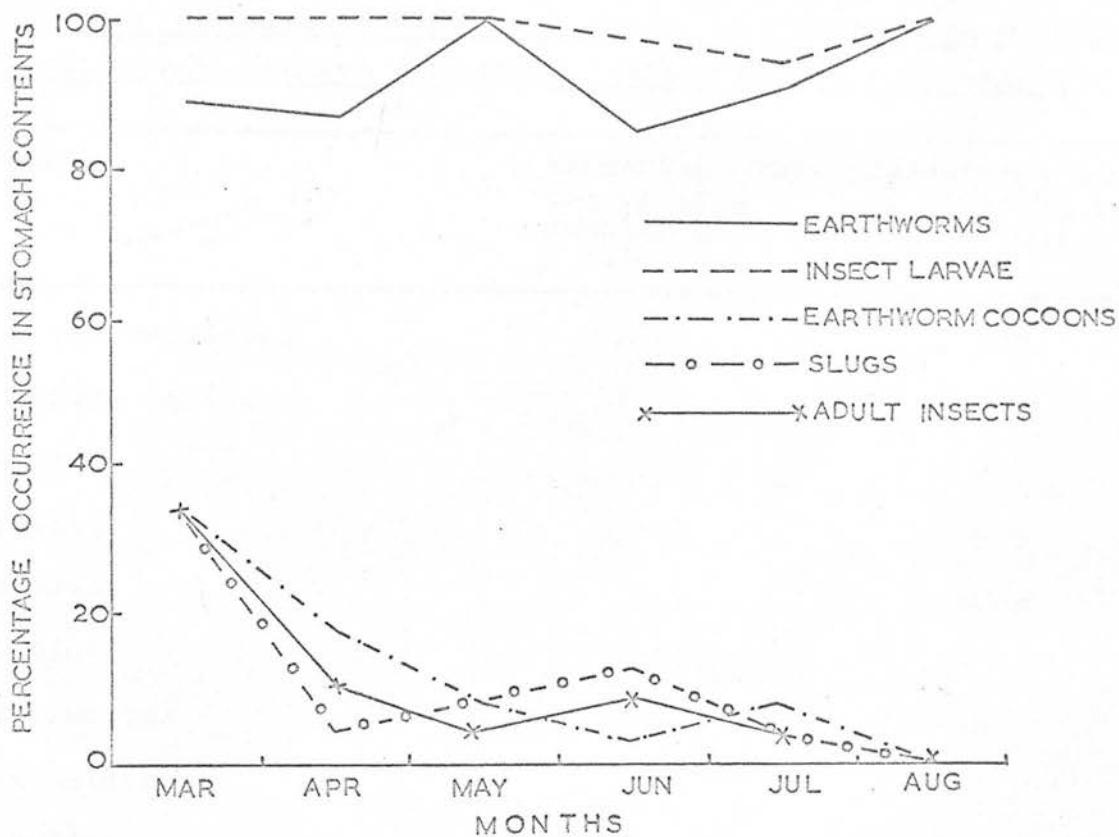


Fig. 8. Percentage occurrence of food items in stomach contents of moles.

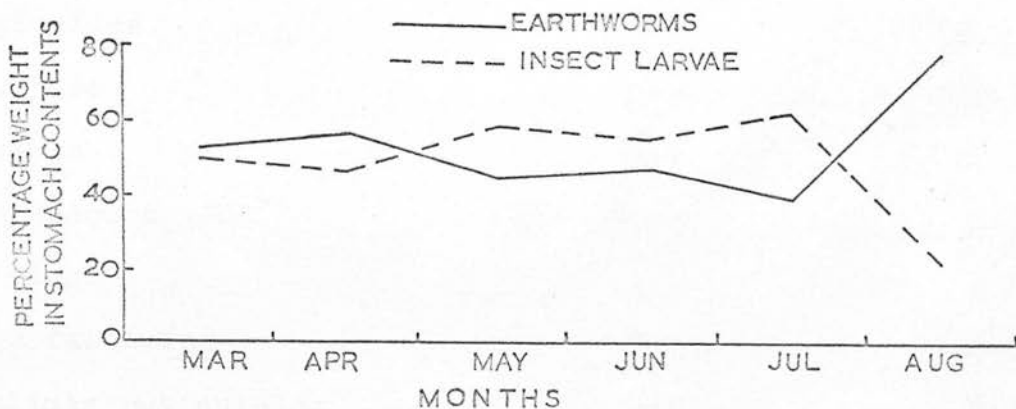


Fig. 9. Percentage weight of earthworms and insect larvae in stomach contents of moles.

TABLE 13

Food preferences in moles from Boghall glen: the percentage occurrence of food items in the stomach contents of moles and in soil samples.

Food Items	Percentage number of soil samples containing:	Percentage number of stomachs containing:
Earthworms (Lumbricidae)	62.0	98.0
All insect larvae	59.5	100.0
Formicidae	0.5	2.0
Noctuidae	1.0	26.5
Carabidae	4.0	44.9
Elateridae	14.0	55.1
Curculionidae	0.5	0
Scarabaeidae	0.5	0
Bibionidae	4.5	28.6
Dolichopodidae	17.0	42.9
Empididae	5.5	34.7
Muscidae	7.0	0
Rhagionidae	2.5	24.5
Tipulidae	30.5	89.8
Adult insects	1.5	10.2
Earthworm Cocoons	76.5	6.1
All slugs	4.0	8.2
Arion fasciatus	2.0	2.0
Agrolimax reticulatus	2.5	8.0
Centipedes (geophilidae)	0	2.0

(ii) Comparison of the body weight and diet of male and female moles

The monthly mean ( $\pm$  S.E.) body weight of males and females and the differences between the sexes from March to August 1969 are shown in Table 14. Males were significantly heavier ( $P = 0.05$ ) than females in all months and on average. Only one male was caught in August so sexual differences could not be estimated. The increase in body weight from March to May were more marked in females (67.5 to 95.3 g.) than in males (103.8 to 115.4 g.) and this reflected the relative increase in activity in the sexes during this period. Adult males were significantly heavier in May than in March and July. The mean ( $\pm$  S.E.) increase in body weight of adult males between March and May was  $11.6 \pm 5.4$  g. which was significant ( $t = 2.15$  and  $t$  at  $P0.05 = 2.07$ ). The mean ( $\pm$  S.E.) decrease in body weight of adult males between May and July was  $16.4 \pm 5.7$  which was significant ( $t = 2.93$  and  $t$  at  $P0.05 = 2.12$ ). Differences in body weight between other months in males were slight ( $P < 0.05$ ). Adult females were significantly heavier in April than in March (mean ( $\pm$  S.E.) difference =  $18.3 \pm 6.16$ ,  $t = 2.97$  and  $t$  at  $P0.05 = 2.31$ ), in May than in March (mean ( $\pm$  S.E.) difference =  $27.8 \pm 6.40$ ,  $t = 4.34$  and  $t$  at  $P0.05 = 2.12$ ) and in June than in March (mean ( $\pm$  S.E.) difference =  $26.1 \pm 7.94$ ,  $t = 3.29$  and  $t$  at  $P0.05 = 2.33$ ). The seasonal trend in the weight of the reproductive organs in males and females has been shown (Appendices 16 and 17). It appeared that there was a difference or delay of two months between the time of maximum development of testis in males and the time of maximum body weight, and in females there

appeared to be a difference of one month between the time of maximum weight of uteri and ovaries and of body. The difference in females was not apparent as females were not significantly heavier in April than in May but in males the difference in body weight between March and May was significant. Table 15 shows the monthly mean ( $\pm$  S.E.) body weight - weight of stomach contents in males and females and the differences between the sexes from March to August 1969. The trend in body weight - weight of stomach contents was similar to that in body weight when the weight of stomach contents was not removed. Table 16 shows the mean ( $\pm$  S.E.) weight of stomach contents in males and females and the differences between months from March to August 1969. The time of maximum food consumption in males corresponded approximately with the time of maximum development of testis while the time of maximum food consumption in females corresponded with the period of lactation. There were no significant differences ( $P = 0.05$ ) between males and females in the weight of stomach contents in any month and on average indicating that food consumption was approximately equal in the sexes. There were no significant monthly differences in the weight of stomach contents of males but the stomach contents of females were significantly heavier ( $P = 0.05$ ) in May than in March though there were no significant differences between other months in females as well. Table 17 shows the weight of full stomachs (empty stomach + stomach contents) in males and females and the differences between the sexes from March to August 1969. The results are also expressed as a histogram in Fig. 10. The trend in the weight of full stomach was the same as that in the weight of

TABLE 14

Comparison of the body weight of male and female moles

Month	Mean $\pm$ (S.E.) body weight in gm.			t	t at P0.05
	Male	Female	Difference		
March	103.8 $\pm$ 9.3	67.5 $\pm$ 2.4	36.3 $\pm$ 8.31	4.37*	2.31
April	105.3 $\pm$ 6.8	85.8 $\pm$ 6.5	19.5 $\pm$ 4.36	4.47*	2.07
May	115.4 $\pm$ 7.3	95.3 $\pm$ 7.1	20.1 $\pm$ 4.24	4.74*	2.06
June	98.3 $\pm$ 12.6	80.7 $\pm$ 15.3	17.6 $\pm$ 6.48	2.72*	2.03
July	91.7 $\pm$ 6.9	78.8 $\pm$ 7.0	12.9 $\pm$ 3.87	3.33*	2.06
August	96.0	77.0 $\pm$ 5.1	-	-	-
March - August	102.5 $\pm$ 11.8	83.0 $\pm$ 12.7	19.5 $\pm$ 3.16	6.17*	1.98

TABLE 15

Comparison of the body weight - weight of stomach contents in male and female moles

Month	Mean $\pm$ (S.E.) body weight - weight of stomach contents (in g.)			t	t at P0.05
	Male	Female	Difference		
March	96.6 $\pm$ 6.2	65.5 $\pm$ 2.4	31.1 $\pm$ 7.94	3.92*	2.31
April	98.9 $\pm$ 4.5	81.4 $\pm$ 8.4	17.5 $\pm$ 4.36	4.01*	2.07
May	109.9 $\pm$ 6.4	88.9 $\pm$ 5.6	21.0 $\pm$ 3.60	5.83*	2.06
June	92.6 $\pm$ 11.8	75.9 $\pm$ 14.0	16.7 $\pm$ 6.00	2.78*	2.03
July	86.3 $\pm$ 7.0	74.6 $\pm$ 7.4	11.7 $\pm$ 4.00	2.88*	2.06
August	88	73.7 $\pm$ 4.5	-	-	-
March - August	96.6 $\pm$ 11.3	78.7 $\pm$ 11.6	17.9 $\pm$ 2.81	6.37*	1.98

\* Differences significant at P0.05

stomach contents. There were no significant monthly differences in the weight of full stomachs of males and females but, on average, the weight of full stomach was significantly higher ( $P = 0.05$ ) in males than in females. The mean ( $\pm$  S.E.) weight of empty stomachs in males was  $0.98 \pm 0.17$  g. and that in females was  $0.86 \pm 0.20$  g. The mean ( $\pm$  S.E.) difference in weight of empty stomachs between males and females was  $0.12 \pm 0.047$  g. which was significant ( $t = 2.55$  and  $t$  at  $P0.05 = 1.98$ ). The discrepancy between the results of analysis of weight of stomach contents and the weight of full stomachs was due to the fact that the weight of empty stomachs of males was, on average, significantly higher than that of females. This suggested that the weight of empty stomachs should be taken into consideration in any comparative analysis of the food consumption of males and females. Table 18 shows the monthly mean ( $\pm$  S.E.) weight of undigested food in the stomach contents of males and females and the differences between the sexes from March to August 1969. The weight of undigested food in the stomach contents of males was approximately equal to that in the stomach contents of females in all months and on average which again showed that the food consumption was approximately equal in the sexes. Table 19 shows the monthly mean ( $\pm$  S.E.) weight of stomach contents as a percentage of the body weight in males and females and the differences between the sexes from March to August 1969. The weight of stomach contents as a percentage of the body weight was approximately equal in the sexes in each month and on average indicating that the relationship between food consumption and body

TABLE 16

Comparison of the weight of stomach contents of male and female moles

Month	Mean ( <u>±</u> S.E.) weight of stomach contents (in g.)			t	t at P0.05
	Male	Female	Difference		
March	7.3 <u>±</u> 3.1	1.9 <u>±</u> 0.25	5.4 <u>±</u> 2.66	2.03	2.31
April	5.9 <u>±</u> 3.6	4.3 <u>±</u> 3.3	1.6 <u>±</u> 2.22	0.72	2.07
May	5.4 <u>±</u> 2.1	6.2 <u>±</u> 1.94	0.8 <u>±</u> 1.22	0.66	2.06
June	5.5 <u>±</u> 2.4	5.0 <u>±</u> 2.3	0.5 <u>±</u> 1.10	0.45	2.03
July	5.3 <u>±</u> 2.3	4.1 <u>±</u> 1.8	1.2 <u>±</u> 1.17	1.03	2.06
August	8.2	3.0 <u>±</u> 1.8	-	-	-
March - August	5.8 <u>±</u> 2.8	4.7 <u>±</u> 2.5	1.1 <u>±</u> 0.67	1.65	1.98

Differences not significant at P0.05

TABLE 17

Comparison of the weight of full stomach (empty stomach + contents) in male and female moles

Month	Mean ( <u>±</u> ) weight of stomach (in g.)			t	t at P0.05
	Male	Female	Difference		
March	8.4 <u>±</u> 3.2	2.7 <u>±</u> 0.2	5.7 <u>±</u> 2.59	2.20	2.31
April	6.9 <u>±</u> 3.7	5.3 <u>±</u> 3.3	1.6 <u>±</u> 2.14	0.75	2.07
May	6.5 <u>±</u> 2.2	7.4 <u>±</u> 2.1	0.9 <u>±</u> 1.27	0.71	2.06
June	6.5 <u>±</u> 2.4	5.4 <u>±</u> 2.4	1.1 <u>±</u> 1.10	0	2.03
July	6.2 <u>±</u> 2.3	5.0 <u>±</u> 1.2	1.2 <u>±</u> 1.02	1.18	2.06
August	8.9	3.6 <u>±</u> 1.8	-	-	-
March - August	6.7 <u>±</u> 2.7	5.4 <u>±</u> 2.5	1.3 <u>±</u> 0.64	2.03	1.980*

\* Difference significant at P0.05

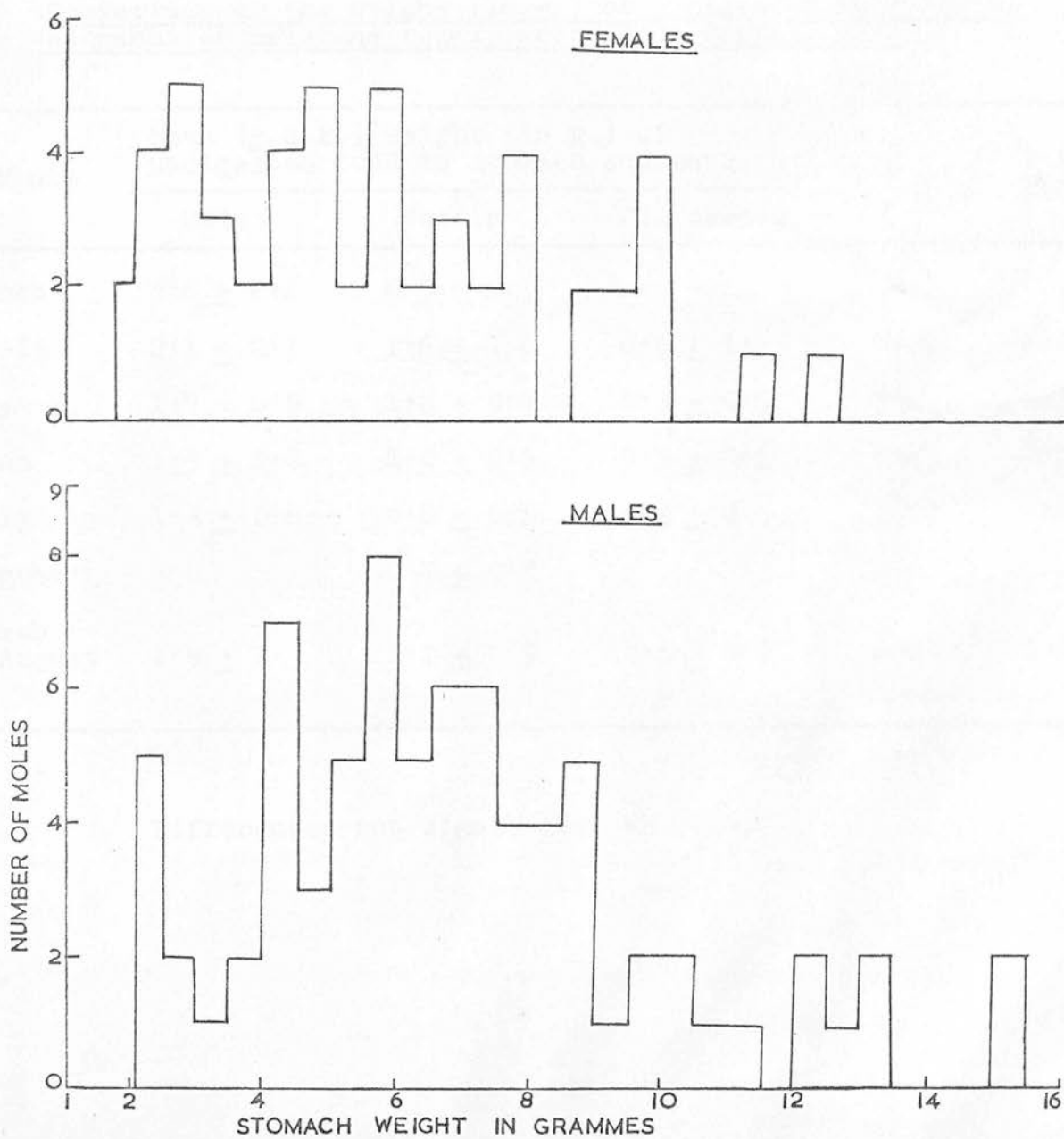


Fig. 10. Stomach weight of male and female moles.

TABLE 18

Comparison of the weight (in g.) of undigested food in the stomachs of male and female moles from Boghall glen

Month	Mean ( $\pm$ S.E.) weight (in g.) of undigested food in stomach contents			t	t at P0.05
	Male	Female	Difference		
March	3.6 $\pm$ 2.2	0.5	-	-	
April	2.1 $\pm$ 2.1	1.6 $\pm$ 1.8	0.5 $\pm$ 1.3	0.38	2.07
May	1.7 $\pm$ 0.9	1.4 $\pm$ 0.7	0.3 $\pm$ 0.5	0.60	2.06
June	1.5 $\pm$ 0.9	1.0 $\pm$ 0.6	0.5 $\pm$ 0.4	1.25	2.03
July	1.3 $\pm$ 0.6	0.8 $\pm$ 0.5	0.5 $\pm$ 0.3	1.67	2.06
August	3.0	0.7 $\pm$ 0.7	-	-	
March - August	1.9 $\pm$ 1.3	1.1 $\pm$ 0.9	0.8 $\pm$ 0.9	0.89	1.98

Differences not significant at P0.05

weight was the same in the sexes. The weight of stomach contents as a percentage of the body weight was approximately the same in all months in males but in adult females it was significantly higher in May than in March (mean ( $\pm$  S.E.) difference =  $3.9 \pm 1.51$ , estimated t value = 2.52 and t at P 0.05 = 2.23) and slightly higher in June than in March (mean ( $\pm$  S.E.) difference =  $3.6 \pm 1.75$ , estimated t value = 2.06 and t at P 0.1 = 1.72). The differences between other months in females were slight. The relatively higher food consumption by females in May was probably related to the fact that most females were lactating in May. Table 20 shows the monthly mean ( $\pm$  S.E.) weight of stomach contents as a percentage of the body weight less weight of stomach contents in males and females and the differences between the sexes from March to August 1969. There were no significant differences between males and females in the weight of stomach contents as a percentage of body weight - weight of stomach contents. There were no significant differences between months in this quantity in males but significant monthly differences occurred in adult females. The weight of stomach contents as a percentage of body weight - weight of stomach contents was significantly higher in May than in March and in July and also in June than in July. The mean ( $\pm$  S.E.) difference in this quantity between May and March was  $4.6 \pm 1.67$  (t = 2.75 and t at P 0.05 = 2.23), that between May and July was  $3.6 \pm 1.42$  (t = 2.54 and t at P 0.05 = 2.18) and that between June and July was  $3.7 \pm 1.33$  (t = 2.78 and t at P 0.05 = 2.10). The results of the last analysis suggested that in relation to their body weight females consumed significantly more food in May

TABLE 19

Comparison of the weight of stomach contents as a percentage of the body weight in male and female moles

Month	Mean ( $\pm$ S.E.) weight of stomach contents as a percentage of the body weight			t	t at P0.05
	Male	Female	Difference		
March	6.8 $\pm$ 2.6%	2.5 $\pm$ 0.5%	4.3 $\pm$ 2.24%	1.92	2.31
April	5.4 $\pm$ 3.1%	5.1 $\pm$ 4.1%	0.3 $\pm$ 2.14%	0.14	2.07
May	4.8 $\pm$ 1.8%	6.3 $\pm$ 1.7%	1.5 $\pm$ 1.04%	1.44	2.06
June	5.5 $\pm$ 2.5%	6.1 $\pm$ 2.2%	0.6 $\pm$ 1.10%	0.55	2.03
July	5.8 $\pm$ 2.4%	5.2 $\pm$ 2.5%	0.6 $\pm$ 1.38%	0.43	2.06
August	9.0 %	3.7 $\pm$ 2.4%	-	-	-
March - August	5.6 $\pm$ 2.6%	5.5 $\pm$ 2.7%	0.1 $\pm$ 0.66%	0.15	1.98

TABLE 20

Comparison of the weight of stomach contents as a percentage of the body weight (- weight of stomach contents) in male and female moles

Month	Mean ( $\pm$ S.E.) weight of stomach contents as a percentage of the body weight [body weight - weight of stomach contents]			t	t at P0.05
	Males	Females	Difference		
March	7.3 $\pm$ 4.4%	2.5 $\pm$ 0.5%	4.8 $\pm$ 3.94%	1.22	2.31
April	5.8 $\pm$ 3.6%	5.5 $\pm$ 4.8%	0.3 $\pm$ 2.65%	0.11	2.07
May	4.9 $\pm$ 1.9%	7.1 $\pm$ 1.9%	2.2 $\pm$ 0.92%	2.39	2.06
June	6.1 $\pm$ 2.9%	7.1 $\pm$ 2.6%	1.0 $\pm$ 1.25%	0.80	2.03
July	6.3 $\pm$ 2.8%	5.4 $\pm$ 2.7%	0.9 $\pm$ 1.57%	0.57	2.06
August	-	4.0 $\pm$ 2.8%	-	-	-
March - August	6.0 $\pm$ 3.1%	6.2 $\pm$ 3.1%	0.2 $\pm$ 0.56%	0.36	1.98

Differences not significant at P0.05

than in March and July and in June than in July. The heavy food consumption in adult females at these times was related to their reproductive activities, particularly lactation.

Table 21 shows the percentage number of male and female stomachs containing each food item from March to August 1969. Earthworms, insect larvae, adult insects, earthworm cocoons, slugs and plant materials occurred in approximately equal proportions of male and female stomachs. Bibionid larvae, empidid larvae and Elaterid larvae were found in a relatively higher proportion of male stomachs but the other families of insect larvae occurred in approximately the same proportion of stomachs in the sexes. The results revealed no major differences in the qualitative composition of the diet of males and females. Table 22 shows the monthly mean ( $\pm$  S.E.) percentage weight of earthworms in the diet of males and females and the differences between the sexes from March to August 1969. There were no significant differences ( $P = 0.05$ ) between the sexes in the proportion of earthworms in the diet in any month and on average which showed that the proportion of earthworms in the diet was approximately the same in both sexes at all times.

(iii) Comparison of the body weight and diet of adult and juvenile moles in June and July 1969.

Table 23 shows the mean ( $\pm$  S.E.) body weight, body weight - weight of stomach contents, weight of stomach contents, weight of stomach contents as a percentage of the body weight, weight of stomach

TABLE 21

Qualitative differences in the composition of the food of male and female moles from Boghall glen in March to August, 1969.

Sex of Moles	Percentage stomachs containing:																		
	Number of stomachs examined	Families of insect larvae											Adult Insects	Earthworm cocoons	Slugs	Centipedes (Geophilidae)	Plant materials	Stomach stones	
		Earthworms (Lumbricidae)	All insect larvae	Formicidae	Noctuidae	Carabidae	Elateridae	Bibionidae	Dolichopodidae	Empididae	Muscidae	Rhagionidae							Tipulidae
Males	77	90.9	97.4	1.3	23.4	41.6	42.9	22.1	28.6	24.7	3.9	10.4	90.9	7.8	9.1	10.4	2.6	7.8	10.4
Females	54	88.9	98.1	0	24.1	46.3	31.5	11.1	22.2	5.6	1.9	13.0	85.2	7.4	9.3	7.4	0	11.1	13.0

TABLE 22

Percentage weight of earthworms in the diet of male and female moles at Boghall glen

Month	Mean ( $\pm$ S.E.) Percentage weight of earthworms in the diet			t
	Male	Female	Difference	
March	68.7 $\pm$ 12.1	33.9 $\pm$ 24.3	34.8 $\pm$ 27.2	1.28
April	46.6 $\pm$ 8.9	62.6 $\pm$ 13.0	16.0 $\pm$ 15.7	1.02
May	49.3 $\pm$ 8.1	35.5 $\pm$ 10.9	13.8 $\pm$ 13.5	1.02
June	40.5 $\pm$ 7.7	50.7 $\pm$ 7.7	10.2 $\pm$ 10.9	0.94
July	27.1 $\pm$ 8.9	48.1 $\pm$ 9.9	21.0 $\pm$ 13.3	1.58
August	88.3 $\pm$ 34.4	66.7 $\pm$ 19.8	16.6 $\pm$ 39.7	0.42
March - August	53.4 $\pm$ 6.7	49.6 $\pm$ 6.3	3.8 $\pm$ 9.2	0.41

Difference not significant in any of the six months and on the average (t at P0.05 = 1.980)

contents as a percentage of the body weight - weight of stomach contents, and the weight of undigested food in the stomach contents of adult and juvenile males and adult and juvenile females in June 1969. (Table 26 shows similar results for July 1969). The differences between adults and juveniles of both sexes in the size of their reproductive organs have been shown (Appendices 16 and 17). Juveniles were much lighter than adults in June and their reproductive organs were much smaller than those of adults. The weight of stomach contents was approximately equal in adults and juveniles. The weight of undigested food in the stomachs was also equal in adults and juveniles. The weight of stomach contents as a percentage of the body weight with or without the weight of stomach contents was slightly higher in juveniles than in adults but the differences were not significant. The results indicated that the food consumption of adults and juveniles were not significantly different in June and that the ratio of stomach weight to body weight was approximately equal in adults and juveniles in June. Table 24 shows the mean ( $\pm$  S.E.) body weight, body weight - weight of stomach contents, weight of stomach contents, weight of undigested food in the stomachs, weight of stomach contents as a percentage of the body weight and the weight of stomach contents as a percentage of the body weight - weight of stomach contents. of juvenile males and females in June 1969. The body weight of juvenile males (with or without the weight of stomach contents) was significantly higher ( $P = 0.05$ ) than that of juvenile females, which showed that the difference in body size between males and females was apparent very early in life. The weight of stomach contents, the weight of undigested food in stomach contents and the weight of stomach contents as a percentage of the body weight

TABLE 23

Comparison of the body weight and food consumption of adult and juvenile moles in June

Month	Measurements	Mean ( $\pm$ S.E.)			t	
		Sex	Adults	Juveniles		Difference
June	Body weight (in g.)	Male	108.7 $\pm$ 6.6	89.7 $\pm$ 9.7	19.0 $\pm$ 5.56	3.42*
		Female	93.8 $\pm$ 9.1	67.6 $\pm$ 7.0	26.2 $\pm$ 5.5	4.76*
	Body weight - weight of stomach contents (in g.)	Male	102.7 $\pm$ 5.6	84.4 $\pm$ 9.0	18.3 $\pm$ 4.63	3.95*
		Female	88.5 $\pm$ 6.8	63.2 $\pm$ 5.2	25.3 $\pm$ 4.05	6.25*
	Weight of stomach contents (in g.)	Male	5.7 $\pm$ 1.7	5.3 $\pm$ 2.9	0.4 $\pm$ 1.50	0.27
		Female	5.5 $\pm$ 2.3	4.5 $\pm$ 2.2	1.0 $\pm$ 1.50	0.67
	weight of stomach contents as a percentage of the body weight	Male	5.1 $\pm$ 0.7%	5.9 $\pm$ 3.1%	0.8 $\pm$ 1.58%	0.51
		Female	5.7 $\pm$ 1.8%	6.4 $\pm$ 2.3%	0.7 $\pm$ 1.40	0.50
	weight of stomach contents as a percentage of the body weight - weight of stomach contents	Male	5.7 $\pm$ 1.5%	6.4 $\pm$ 3.6%	0.7 $\pm$ 1.84%	0.38
		Female	7.2 $\pm$ 2.0%	7.0 $\pm$ 3.0%	0.2 $\pm$ 1.73%	0.12
	Weight of undigested food (in g.) in stomach contents	Male	1.4 $\pm$ 0.9	1.6 $\pm$ 0.9	0.2 $\pm$ 0.4	0.50
		Female	1.2 $\pm$ 0.7	0.8 $\pm$ 0.4	0.4 $\pm$ 0.3	1.33

\* Difference highly significant (t at P0.01) = 2.88)

TABLE 24

Comparison of the body weight and food consumption of male and female juvenile moles in June

Measurements	Mean $\pm$ S.E.			t
	Male	Female	Difference	
Body weight (in g.)	89.7 $\pm$ 9.7	67.6 $\pm$ 7.0	22.1 $\pm$ 5.48	4.03*
Body weight - weight of stomach contents (in g.)	84.4 $\pm$ 9.0	63.2 $\pm$ 5.2	21.2 $\pm$ 4.80	4.42*
Weight of stomach contents (in g.)	5.3 $\pm$ 2.9	4.5 $\pm$ 2.2	0.8 $\pm$ 1.63	0.49
weight of stomach contents as a percentage of body weight	5.9 $\pm$ 3.1%	6.4 $\pm$ 2.3%	0.5 $\pm$ 1.77%	0.28
weight of stomach contents as a percentage of body weight - weight of stomach contents	6.4 $\pm$ 3.6%	7.0 $\pm$ 3.0%	0.6 $\pm$ 2.16%	0.28
Weight of undigested food in stomach contents (in g.)	1.6 $\pm$ 0.9	0.8 $\pm$ 0.4	0.8 $\pm$ 0.5	1.80

\* Difference highly significant (t at P0.01 = 2.88)

(with or without the weight of stomach contents) were approximately equal in juvenile males and females which showed that, like in adults, there were no sexual differences in food consumption, and the weight of stomach contents as a percentage of the body weight between juvenile males and females in June. The percentage number of adult and juvenile stomachs containing the various food items in June 1969 is shown in Table 25. Earthworms, insect larvae, Tipulid larvae, adult insects and stomach stones occurred in approximately equal proportions of adult and juvenile stomachs. The proportion of adult stomachs containing some food items (slugs, Noctuid and Carabid larvae) was relatively higher than that of juvenile stomachs. Juveniles did not eat earthworm cocoons and relative to adults more juveniles had plant materials in their stomachs suggesting a slightly greater surface activity or less expertise in food sorting in juveniles relative to adults. The mean ( $\pm$  S.E.) percentage weight of earthworms in the diet in June 1969 was  $41.4 \pm 8.0\%$  for adults and  $50.2 \pm 8.4\%$  for juveniles which indicated that the proportion of earthworms in the diet of juveniles was slightly higher than that in the diet of adults. The mean ( $\pm$  S.E.) difference in the percentage weight of earthworms in the diet of adults and juveniles was  $8.8 \pm 11.7\%$  which was not significant (estimated t value = 0.75 and t at  $P0.05 = 2.02$ ). The results indicated that the composition of the diet and in particular the proportion of earthworms in the diet was basically the same in adults and juveniles.

The differences in the body weight of adults and juveniles

TABLE 25

Qualitative differences in the diet of adult and juvenile moles at Boghall glen in June 1969

'Age' of mole	Number of stomachs examined	Percentage stomachs containing:																	
		Insect larvae																	
		Earthworms (Lumbricidae)	All insect larvae	Hymenoptera (Formicidae?)	Noctuidae	Carabidae	Elateridae	Bibionidae	Dolichopodidae	Empididae	Muscidae	Rhagionidae	Tipulidae	Adult insects	Lumbricid cocoons	Slugs	Centipedes	Plant materials	Stomach stones
Adult	19	84.2	100	5.3	31.6	68.4	26.3	10.5	10.5	-	10.5	5.3	94.7	5.3	5.3	21.1	-	5.3	5.3
Juvenile	21	85.7	95.2	-	4.8	33.3	14.3	-	4.8	9.5	-	4.8	85.7	9.5	-	4.8	-	9.5	4.8

of each sex (Table 26) were no longer statistically significant in July. The slight difference between the body weight of adults and juveniles was produced by two processes - a slight decrease ( $P < 0.05$ ) in the body weight of adults at the end of the reproductive season and a slight increase ( $P < 0.05$ ) in the body weight of juveniles. The mean ( $\pm$  S.E.) decrease in body weight was  $9.7 \pm 5.839$  for adult males and  $7.0 \pm 8.7$  g. for adult females while the mean increase in body weight was  $1.4 \pm 4.9$  g. for juvenile males and  $8.2 \pm 4.2$  g. for juvenile females. The weight of the reproductive organs in juveniles was still significantly smaller ( $P = 0.05$ ) than in adults in July (Appendices 16 and 17). The measurements showed that juveniles grew to adult sizes by the end of July but were still sexually distinguishable from adults. There were no significant differences ( $P = 0.05$ ) between adults and juveniles in each sex in the weight of stomach contents, weight of undigested food in the stomach contents, and the weight of stomach contents as a percentage of the body weight with or without the weight of the stomach contents.

(iv) Comparison of the body weight and diet of moles trapped in areas Sections A and B of Boghall glen.

Table 27 shows the mean ( $\pm$  S.E.) measurements of body weight (with and without the weight of stomach contents), weight of stomach contents, weight of undigested food in stomach contents, weight of empty stomach, weight of stomach contents as a percentage of the body weight (with or without the weight of stomach contents) and the percentage weight of earthworms in the stomach contents of moles trapped in

TABLE 26

Comparison of the body weight and food consumption of adult and Juvenile moles in July

Month	Measurements	Mean ( $\pm$ S.E.)			t	
		Sex	Adults	Juveniles		Difference
July	Body weight (in g.)	Male	99.0 $\pm$ 1.0	90.6 $\pm$ 6.8	8.4 $\pm$ 5.4	1.56
		Female	84.9 $\pm$ 7.6	75.8 $\pm$ 4.0	9.1 $\pm$ 6.2	1.47
	Body weight - weight of stomach contents (in g.)	Male	96.0	84.9 $\pm$ 6.4	11.1	-
		Female	81.8 $\pm$ 7.9	71.0 $\pm$ 3.8	10.8 $\pm$ 6.15	1.76
	Weight of stomach contents (in g.)	Male	2.9 $\pm$ 0.8	5.6 $\pm$ 2.2	2.7 $\pm$ 2.24	1.21
		Female	2.9 $\pm$ 0.8	4.3 $\pm$ 1.8	1.4 $\pm$ 1.9	0.74
	weight of stomach contents as a percentage of the body weight	Male	3.0 $\pm$ 1.0%	6.1 $\pm$ 2.3%	3.1 $\pm$ 2.12%	1.46
		Female	3.3 $\pm$ 0.8%	6.1 $\pm$ 2.5%	2.8 $\pm$ 2.25%	1.24
	weight of stomach contents as a percentage of the body weight - weight of stomach contents	Male	3.0 $\pm$ 1.0%	6.7 $\pm$ 2.7%	3.7 $\pm$ 2.37%	1.56
		Female	3.5 $\pm$ 1.1%	6.4 $\pm$ 2.8%	2.9 $\pm$ 2.01%	1.44
	Weight of undigested food (in g.) in stomach contents	Male	0.9 $\pm$ 0.4	1.6 $\pm$ 0.4	0.7 $\pm$ 0.5	1.40
		Female	0.6 $\pm$ 0.3	1.0 $\pm$ 0.7	0.4 $\pm$ 0.5	0.80

Differences not significant (t at P0.05 = 2.15 and 2.23 for adult and juvenile males and adult and juvenile females respectively)

Sections A and B of Boghall glen in March to mid-April 1969. There were no significant differences ( $P = 0.05$ ) between the moles caught in the two sections in any of the measurements taken which suggested that the differences in habitat conditions did not have any significant influence on the weight of body and the food consumption of moles in the two sections. The moles in Section A had a slightly higher ( $P < 0.05$ ) proportion of earthworms in their diet than those in Section B and this might be related to the fact that earthworms were more abundant in Section A relative to Section B. Table 28 shows the qualitative composition of the diet in areas Sections A and B. There were no major differences in the composition of the diet of moles in the two sections with regards to earthworms, all insect larvae, Tipulid larvae, adult insects, earthworm cocoons and slugs. Noctuid and Carabid larvae were found in stomach contents in Section A but not in Section B. This might not mean any major difference in the composition of the diet since the number of moles ( $N = 20$ ) considered was small. Bibionid larvae were found in 8 stomachs in Section B but only in 3 stomachs in Section A. It was probable that the proportional occurrence of Bibionid larvae in the stomach contents was related to the fact that these larvae were slightly more abundant in Section B than in Section A (see Appendix 13).

(v) Local variations in body weight and diet of moles

Appendix 23 shows the body weight, stomach weight and the results of the analysis of stomach contents of moles trapped in Leip field and environs (including Fulford field) and Bilston field in January 1970. Table 29 shows the mean (+ S.E.) measurements

TABLE 27

Comparison of the body weight and food consumption of moles caught in areas Sections A and B of Boghall glen between March and mid-April, 1969

Measurements	Mean (+ S.E.)			t
	Section A	Section B	Difference	
Body weight (in g.)	100.3 ± 15.4	97.8 ± 14.3	2.5 ± 10.00	0.25
Body weight - weight of stomach contents (in g.)	94.2 ± 12.5	90.7 ± 12.7	3.5 ± 7.87	0.44
Weight of stomach contents (in g.)	6.2 ± 3.9	7.1 ± 4.3	0.9 ± 2.76	0.33
Weight of undigested food in stomach contents (in g.)	2.5 ± 2.3	3.4 ± 2.4	0.9 ± 1.58	0.57
Weight of empty stomach (in g.)	1.1 ± 0.2	1.0 ± 0.2	0.1 ± 0.13	0.77
weight of stomach contents as a percentage of the body weight	5.8 ± 3.1%	6.9 ± 4.3%	1.1 ± 2.51%	0.44
weight of stomach contents as a percentage of the body weight - weight of stomach contents	6.1 ± 3.0%	7.7 ± 4.9%	1.6 ± 2.54%	0.63
% weight of earthworms in stomach contents	64.4 ± 31.6%	54.0 ± 33.4%	10.4 ± 21.95%	0.47

Difference not significant (t at P0.05 = 2.10)

TABLE 28

Qualitative differences in the composition of the diet of moles in areas Sections A and B at Boghall glen in March to mid-April 1969

		Percentage number of stomachs containing:																
Section	Number of stomachs examined	Families of insect larvae																
		Earthworms (Lumbricidae)	All insect larvae	Noctuidae	Carabidae	Elateridae	Bibionidae	Dolichopodidae	Empididae	Muscidae	Rhagionidae	Tipulidae	Adult insects	Earthworm cocoons	Slugs	Centipedes	Plant materials	Stomach stones
A	10	90	100	30	50	40	30	30	10	10	10	70	20	30	20	10	10	10
B	10	80	100	-	-	30	80	30	20	10	20	90	10	20	20	-	20	30

of body weight (with and without stomach contents), weight of full stomach, weight of empty stomach, weight of stomach contents, weight of stomach contents as a percentage of the body weight and the percentage weight of earthworms in the diet of moles from Leip field and environs and Bilston field. The differences between localities and between males and females from both localities are shown. There were no significant differences ( $P = 0.05$ ) in the body weight, weight of stomach contents, weight of empty stomach, and the weight of stomach contents as a percentage of the body weight of moles from the two localities. The mean ( $\pm$  S.E.) percentage weight of earthworms in the stomach contents was slightly higher in moles from Bilston field ( $96.2 \pm 6.1\%$ ) than in moles from Leip field and environs ( $88.9 \pm 4.0\%$ ) but the difference was not significant ( $P = 0.05$ ) which showed that the relative proportion of earthworms in the diet was not significantly influenced by the habitat. All the moles in this series were collected from pasture lands and the effect of habitat on the composition of the diet might be slight but it was possible that the effect of habitat would be greater if moles were collected from two different types of habitats, e.g. pastureland and arable land. The body weight was significantly higher ( $P = 0.05$ ) in males than in females but the weight of the stomach contents was approximately equal in the sexes. The mean ( $\pm$  S.E.) weight of full stomach (empty stomach + contents) was significantly higher in males than in females. So also the mean ( $\pm$  S.E.) weight of empty stomach was significantly higher in males than in females. The significantly higher weight

of the full stomach of males relative to females was due to the effect of the weight of empty stomach which was significantly higher ( $P = 0.05$ ) in males than in females. The result of the analysis indicated that the weight of empty stomachs could have a significant effect on the results of comparative analysis of the food of moles. The percentage weight of earthworms in the stomach contents was approximately equal in males and females indicating that the relative weight of earthworms in the diet was approximately equal in the sexes. The weight of stomach contents as a percentage of body weight was also equal in the sexes indicating that the relationship between food consumption and body weight was the same in both sexes.

Table 30 shows the qualitative composition of the food of moles in Leip field and environs and Bilston field in January 1970. The frequency of occurrence of food items in the stomachs is shown separately for males and females from each site and for all moles on each site. The percentage number of stomachs containing earthworms (100%) was the same on both sites but the percentage number of stomachs containing insect larvae was relatively higher in moles from Leip field and environs (84.8%) than in those from Bilston field (61.5%). Certain food items (Noctuid and Carabid larvae, adult insects and slugs) found in stomachs from Leip field did not occur in stomachs from Bilston field while Bibionid larvae, Dolichopodid larvae and plant materials were found in stomachs from Bilston field but not in those from Leip field and environs. There

TABLE 29

Body weight and diet of moles trapped during January 1970 in Leip field and environs and Bilston field

Measurements	Mean ( $\pm$ S.E.)		t	
	Leip field & environs	Bilston field		
Body weight (in g.)	82.5 $\pm$ 1.2	83.4 $\pm$ 1.8	0.9 $\pm$ 2.2	0.41
Body weight (less weight of stomach contents) (in g.)	77.6 $\pm$ 1.1	77.9 $\pm$ 1.6	0.3 $\pm$ 2.0	0.15
Weight of stomach (contents + empty stomach)	5.5 $\pm$ 0.4	6.5 $\pm$ 0.6	1.0 $\pm$ 0.8	1.14
Weight of stomach contents	4.8 $\pm$ 2.2	5.4 $\pm$ 2.2	0.6 $\pm$ 1.1	0.55
Weight of empty stomach	1.00 $\pm$ 0.03	1.00 $\pm$ 0.04	0 $\pm$ 0.05	0
Wt. of stomach contents as a % of body weight	6.6 $\pm$ 0.4%	7.7 $\pm$ 0.7%	1.1 $\pm$ 0.8%	1.38
% weight of earthworms in stomach contents	88.9 $\pm$ 4.0%	96.2 $\pm$ 6.1%	7.3 $\pm$ 7.4%	0.99

Differences between males and females on both sites

Measurements	Mean ( $\pm$ S.E.)		t	
	Males	Females		
Body weight (in g.)	94.4 $\pm$ 1.4	71.5 $\pm$ 1.6	22.9 $\pm$ 2.10	11.39*
Body weight (less weight of stomach contents) (in g.)	88.3 $\pm$ 1.2	67.2 $\pm$ 1.4	21.1 $\pm$ 1.8	11.7*
Weight of full stomach (empty stomach + stomach contents) (in g.)	6.8 $\pm$ 0.5	5.2 $\pm$ 0.6	1.6 $\pm$ 0.70	2.29*
Weight of stomach contents (in g.)	5.5 $\pm$ 2.5	4.3 $\pm$ 1.8	1.2 $\pm$ 0.9	1.33
Weight of empty stomach (in g.)	1.1 $\pm$ 0.03	0.9 $\pm$ 0.03	0.2 $\pm$ 0.04	5.0*
Weight of stomach contents as a percentage of the body weight	7.2 $\pm$ 0.5%	7.2 $\pm$ 0.6%	0 $\pm$ 0.7%	0
% weight of earthworms in stomach contents	92.4 $\pm$ 4.7%	92.6 $\pm$ 5.3%	0.2 $\pm$ 6.8%	0.03

\* Differences significant (t at P0.05 = 2.02)

TABLE 30

Qualitative Composition of the Diet of Moles from Leip Field and Environs (Hill pasture) and Bilston Field (Lowland pasture) in January 1970

site of Trapping	Sex of moles	Number of stomachs examined	Percentage stomachs containing:													
			All earthworms	All insect larvae	Families of insect larvae							Adult Insects	Earthworm cocoons	Slugs	Centipedes	Plant materials
					Noctuidae	Carabidae	Elateridae	Bibionidae	Dolichopodidae	Empididae	Tipulidae					
Leip field and environs	males	22	100	86.4	36.4	13.6	54.5	0	0	45.5	27.3	4.5	72.7	4.5	4.5	0
	females	11	100	81.8	0	9.1	63.6	0	0	45.5	18.2	9.1	45.5	9.1	18.2	0
	male and female	33	100	84.8	24.2	12.1	57.6	0	0	45.5	24.2	6.1	63.6	6.1	9.1	0
Bilston field	males	6	100	50.0	0	0	16.7	16.7	0	33.3	16.7	0	66.7	0	16.7	16.7
	females	7	100	71.4	0	0	14.3	14.3	14.3	42.9	28.6	0	57.1	0	14.3	28.6
	male and female	13	100	61.5	0	0	15.4	15.4	7.7	38.5	23.1	0	61.5	0	15.4	23.1
Leip field and environs and Bilston field	males	28	100	78.6	28.6	10.7	46.4	3.6	0	42.9	25.0	3.6	71.4	3.6	7.1	3.6
	females	18	100	77.8	0	5.6	44.4	5.6	15.6	44.4	22.2	5.6	50.0	5.6	16.7	11.1

were no major differences in the percentage number of male and female stomachs containing the various food items on each site and on both sites combined except that Noctuid larvae were found in male stomach but not in female stomachs on Leip field and environs and Dolichopodid larvae were found in female stomachs but not in male stomachs on Bilston field. The results indicated that the composition of the diet varied slightly with the habitat but that the composition of the diet is nearly the same in males and females in each habitat.

### 5B.3 FOOD CONSUMPTION OF CAPTIVE MOLES

7 Moles were fed in captivity but 3 of them lived for only between four to twelve days each. The stomach of one of them was empty but the stomachs of the remaining two contained balls of grass which might have influenced their death. The daily consumption of earthworms was recorded for 10 weeks for each surviving mole and the results are shown in Appendix 24. Mole No. 1 was an adult male fed from 30/7/68 to 8/10/68. It weighed 107.7 g. on the day of captivity and its weight fluctuated between 102.0 to 118.0 g. during the experiments. Mole No. 2 was a juvenile female fed from 13/9/68 to 22/11/68. It weighed 76.5 g. on the first day of captivity and this fluctuated between 73.0 to 79.0 g. during the experiments. Mole No. 3 was an adult female fed from 9/4/69 to 8/6/69. It weighed 81 g. on the first day of captivity and this fluctuated between 77.5 to 104.0 g. during the experiments. Mole No. 4 was an adult male fed from 30/4/69 to 9/7/69. It

weighed 95.0 g. on the first day of captivity and this fluctuated between 93 to 105 g. during the experiments.

Table 31 shows the daily mean (± S.E.) food consumption of each mole for 10 weeks. The differences in food consumption between moles are also shown for the last 8 weeks in captivity. The daily food consumption was highest in the first week in captivity in all moles and it was equally relatively high in the second week for moles Nos. 2, 3 and 4. The daily food consumption varied less in the last 8 weeks which justified the exclusion of the first two weeks from the main data computed from the results. The food consumption of mole No.1 was significantly higher ( $P = 0.05$ ) than that of any of the other moles while the food consumption of mole No. 2 was significantly lower than that of any of the other moles. Moles No. 3 and 4 ate approximately the same amounts of food. The food consumption of each mole was related to its body weight (which was also related to its sex and sexual condition). Mole No. 1 was heavier than any of the other moles and this explained its higher food consumption. Mole No. 2 was also lighter than any of the other moles and it ate less food than any of them. The results of field investigations showed that males and females ate approximately the same amounts of food in April, May and June. Similar results were also obtained in the food consumption of captive moles (No. 3 and No. 4) during this period which indicated that the food consumption of captive moles was basically similar to that of wild moles. The food consumption per unit of body weight (using the body weight on first day of captivity) was 0.73,

0.84, 0.89 and 0.75 for moles Nos. 1, 2, 3 and 4 respectively which showed that captive moles ate a quantity of earthworms equal to between 73% to 89% of their body weights when fed on unlimited supplies.

#### General observations on captive moles

Captive moles showed similar pattern of behaviour when searching for food. When a hungry mole woke up, it would run to the feeding cage and when it approached the entrance it would lift up its head and sniff the inside of the cage for food. If food was not available it would sniff, search and scratch every bit of the food dish, the water dish and the whole of the feeding cage. It would then run back into the tunnels and return to repeat its search for food. When it had searched unsuccessfully a few times it might drink some water and go back into its nest but it usually came back after a short interval. If food was available the mole haphazardly picked the first earthworm it could catch. If it caught a small earthworm it usually consumed it on the spot, but if it caught a large one it would run backwards with it into the tunnel or in some instances into the sleeping cage where it consumed the earthworm. The mole catches an earthworm with the mouth and holds it down with the two forelegs (between the fourth and fifth fingers of each foreleg) and pulls it into the mouth by raising and lowering its head alternately. During this process the gut contents of large and medium-sized earthworms are squeezed out and rejected. Small earthworms like A. caliginosa, A. chlorotica,

TABLE 31

Daily food consumption of captive moles

Mean ( $\pm$ S.E.) daily food consumption (in grammes)				
Weeks	Mole 1 (adult male) body-weight = 107.7 g	Mole 2 (juvenile female) bodyweight = 76.5 g	Mole 3 (adult female) body weight = 81.0 g	Mole 4 (adult male) body weight = 95.0 g
1	91.0 $\pm$ 4.3	84.6 $\pm$ 2.2	85.6 $\pm$ 2.2	89.3 $\pm$ 3.2
2	77.2 $\pm$ 4.5	74.0 $\pm$ 2.4	85.3 $\pm$ 4.2	82.9 $\pm$ 4.3
3	76.2 $\pm$ 1.8	62.4 $\pm$ 1.1	65.4 $\pm$ 5.3	66.9 $\pm$ 2.9
4	82.0 $\pm$ 2.2	60.0 $\pm$ 1.0	74.6 $\pm$ 4.7	67.3 $\pm$ 3.2
5	82.9 $\pm$ 1.8	65.1 $\pm$ 1.6	75.9 $\pm$ 3.9	67.6 $\pm$ 2.7
6	79.3 $\pm$ 4.7	67.0 $\pm$ 1.4	72.3 $\pm$ 3.7	67.0 $\pm$ 2.7
7	80.0 $\pm$ 1.9	65.0 $\pm$ 1.5	68.1 $\pm$ 7.5	68.1 $\pm$ 1.5
8	81.0 $\pm$ 2.7	65.0 $\pm$ 1.5	67.0 $\pm$ 0.6	71.0 $\pm$ 2.4
9	76.0 $\pm$ 1.9	62.3 $\pm$ 1.8	73.4 $\pm$ 2.0	76.4 $\pm$ 2.5
10	75.1 $\pm$ 1.7	65.3 $\pm$ 1.4	77.0 $\pm$ 2.1	76.1 $\pm$ 2.5
3-10	79.06 $\pm$ 1.22	64.02 $\pm$ 0.56	71.71 $\pm$ 1.49	70.05 $\pm$ 1.00

Differences in mean ( $\pm$  S.E.) daily food consumption in the third week to tenth week in captivity

Pairs of moles	Differences in mean ( $\pm$ S.E.) daily food consumption	t
No.1 and No.2	15.04 $\pm$ 1.34	11.224*
No.1 and No.3	7.35 $\pm$ 1.93	3.808*
No.1 and No.4	9.01 $\pm$ 1.57	5.739*
No.2 and No.3	7.69 $\pm$ 1.59	4.836*
No.2 and No.4	6.03 $\pm$ 1.14	5.289*
No.3 and No.4	1.66 $\pm$ 1.79	0.927

\* Differences significant (t at P0.05 = 1.980)

Dendrobaena sp., E. rosea and the small immature stages of the larger earthworms were swallowed whole, rapidly and from either end. Large earthworms were eaten from the head end but if the mole failed to locate this end after a few attempts, it either picked another earthworm or took one or two bites from the tail end before the search for the head end was resumed. No part of an earthworm (except the gut contents) was rejected by moles. Moles did not appear to eat between meals. When earthworms were offered to satiated moles, the earthworms were either pushed aside, dragged about and later abandoned or buried in the soil. All moles drank water readily. Attempts made to keep two moles (an adult male and an adult female in one instance, and one adult and one juvenile male in another instance) in a large cage with separate nest chambers failed because the moles fought fiercely using the front paws to scratch the underside of the other's body. These observations suggested that moles were solitary and quarrelsome. The phenomenon of earthworm storage by captive moles has been described under food storage by moles.

#### 5B.4. MOLE POPULATION STUDIES

##### (a) Estimation of the population density of moles at Boghall glen

Appendix 25 is a map showing the distribution of fortresses and nests in Boghall glen in April 1969. A fortress is a relatively large mole-hill containing one or more nests. Plate VIII shows the size of a fortress relative to that of other mole-hills, Plate IX shows an undissected fortress and Plate X shows a

fortress dissected to show the nest. There were no fortresses on the site in October 1967 but two fortresses were built on Section A in December 1967. There were 21 fortresses in April 1969 and there were 90 moles which showed that only 23<sup>6</sup>/<sub>100</sub> of moles built fortresses. This showed that the number of fortresses was not a reliable index of the number of moles. All the fortresses were on Section A and none was on Section B which showed that the building of fortresses was related to the habitat and particularly their absence from Section B suggested that they were not built in shallow soils. 57.1% of the fortresses were built among gorse (Ulex europaeus) and rushes (Juncus sp.) and 42.9% were built in areas where these plants were absent which indicated that moles were inclined to build fortresses in the protected parts of their habitats.

Plate XI shows a simple mole-hill which was dissected to show the nest. The nests referred to in this section included those in fortresses and those found inside simple mole-hills as shown in Plate XI. A total of 39 nests were excavated which showed that only 43<sup>9</sup>/<sub>100</sub> of moles on the site built nests that could be located from surface evidences and that the number of such nests was not a reliable indication of the number of moles. All the nests were located in Section A and no nests were found in Section B. Mole-hills with nests were invariably built in protected places among gorse and rushes. On a part of Section A the number of nests was 91.3% the number of moles. If it was assumed that each nest was occupied by only one mole then the number of nests approximated



Plate VIII. Size of a fortress relative to that of other mole-hills.



Plate IX. An undissected fortress.



Plate X. Fortress dissected to show the nest.



Plate XI. Simple mole-hill dissected to show nest.

very closely to the number of moles in this area which suggested that the number of nests might be a useful indication of the number of moles in some habitats. It was found that nests were sometimes deserted especially when they became damp and that when two nests were situated very close to each other they were probably built by the same mole. When whole discrete tunnel systems were excavated it was found that juvenile moles built simple nests under the unbroken turf and the spoils of soil from the excavation of the tunnels and nest cavity were discharged as one or a few large mole-hills a few feet away from the nests. The disparity between the number of nests and the number of moles was also partly due to the fact that these types of nests could not easily be discovered from surface evidences.

The number of areas with fresh diggings (6) and the number of moles trapped in such areas (6) were equal on the first part of Section A where the number of areas with fresh diggings was counted on the second day after the destruction of the old mole-hills and surface tunnels. On the second part of Section A where the number of areas with fresh diggings was counted on the third day, the number of moles trapped (22) was slightly lower than the number of fresh diggings (27). This showed that the counts of areas with fresh diggings must be made on the second day after the destruction of the existing mole-hills before accurate figures could be obtained. When the two parts were considered together, the number of areas with fresh diggings was 17.9% more than the number of moles. The results showed that it was possible to obtain a fairly accurate

estimate of the population density of moles in the spring without killing the moles.

The relationship between the number of moles and the number of mole-hills

Appendix 26 shows the number of mole-hills and the number of moles. The correlation coefficient ( $r$ ) between the number of mole-hills and the number of moles was 0.995 in similar habitat (similar soil types on Section A) and 0.841 in dissimilar habitats (different soil types on the whole site). Both figures showed that the number of mole-hills increased as the number of moles increased. The high correlation between the number of moles and the number of mole-hills in similar habitats showed that the number of mole-hills was a reliable index of the number of moles when similar habitats were considered while the low correlation in dissimilar habitats showed that the number of mole-hills depended on both the number of moles and the habitat and could not be used as an index of mole numbers when considering a large area with diverse habitats.

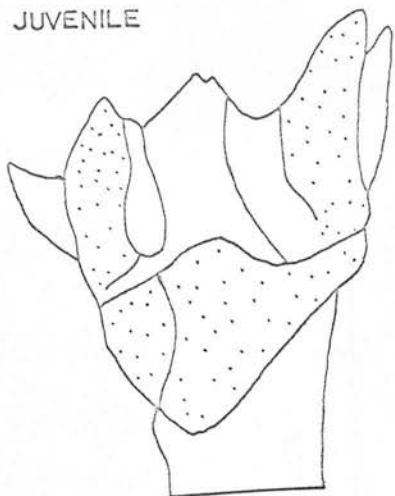
(b) Age structure of mole populations and the life span of the mole

The tooth measurements of moles from Boghall glen are shown in Appendix 27 and the tooth measurements of moles from Leip field and environs, Fulford field and Bilston field are shown in Appendix 28. Appendix 29 is a drawing of the left second upper molar tooth of a juvenile mole showing the method of tooth measurements. The letters a, b, c, d in the drawing represent the

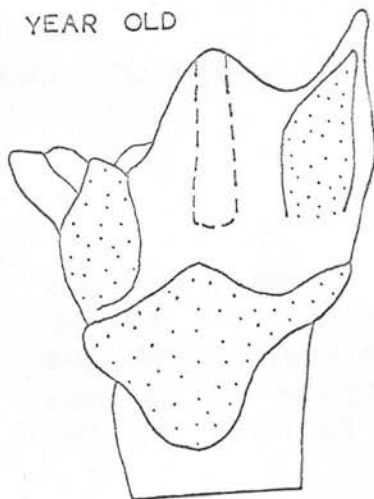
distances shown in the tables of tooth lengths. The left second upper molar tooth of moles aged between 0 (juveniles) and 4 years are shown in Fig. 11. The shaded areas are the wear surfaces. The inner cusps were robust and pointed in juveniles but they thinned down and became blunted in older moles. The space between the cusps was raised into a ridge in juveniles but in adults the ridge disappeared and was replaced by a furrow which widened and deepened with age. The extent of the furrow is indicated by broken lines in Fig. 11. In moles aged  $3\frac{1}{2}$  to 4 years the cusps had disappeared almost completely and the tooth was thin with a big hollow in its inner surface. The rate of wear of individual cusps was different in each tooth: in some teeth the anterior cusp wore down quicker than the posterior cusp while the reverse procedure took place in others. This indicated that a clear segregation into age groups might not be obtained by using a single cusp of one tooth as an indicator of tooth wear. There was no great difference between the mean measurements of the left and right tooth of the same mole but the use of the average mean measurements of the right and left teeth was considered more reliable for classification into age groups. The number of moles in each tooth length and age group in the different localities are represented in a histogram in Fig. 12.

Boghall glen: There were 5 age groups of which juveniles formed 35.6%, one year old 31.9%, two year old 25.2%, three year old 6.7% and four year old 0.7%. The number of moles decreased as the age

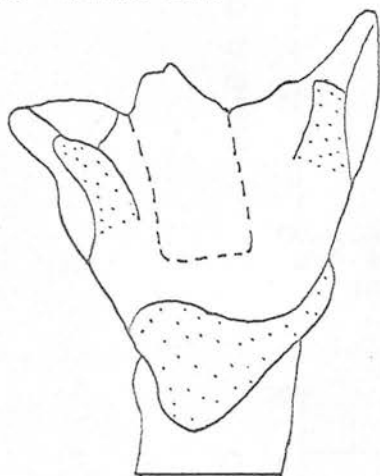
JUVENILE



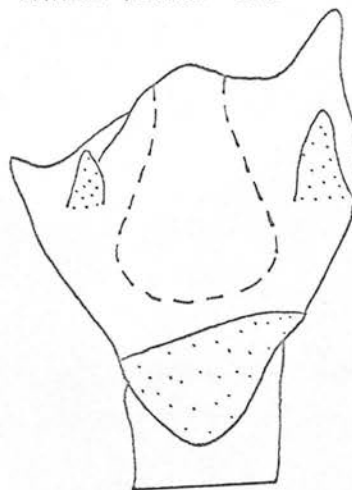
ONE YEAR OLD



TWO YEARS OLD



THREE YEARS OLD



FOUR YEARS OLD

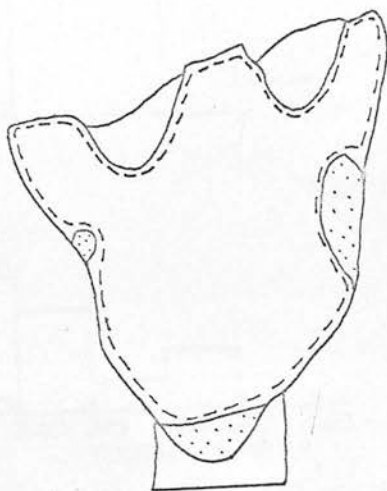


Fig. 11. Left second upper molar tooth of moles (x 25).

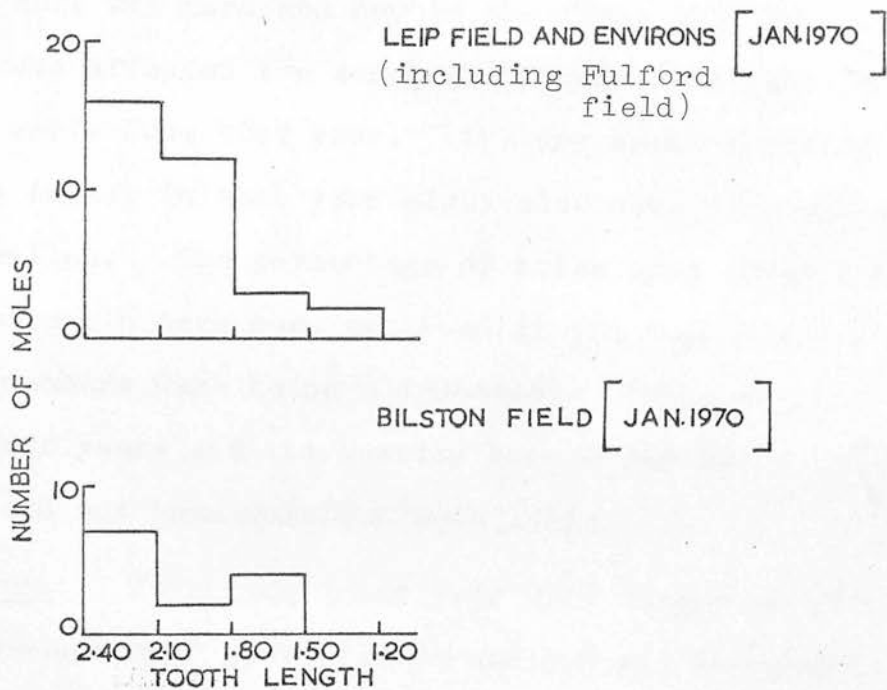
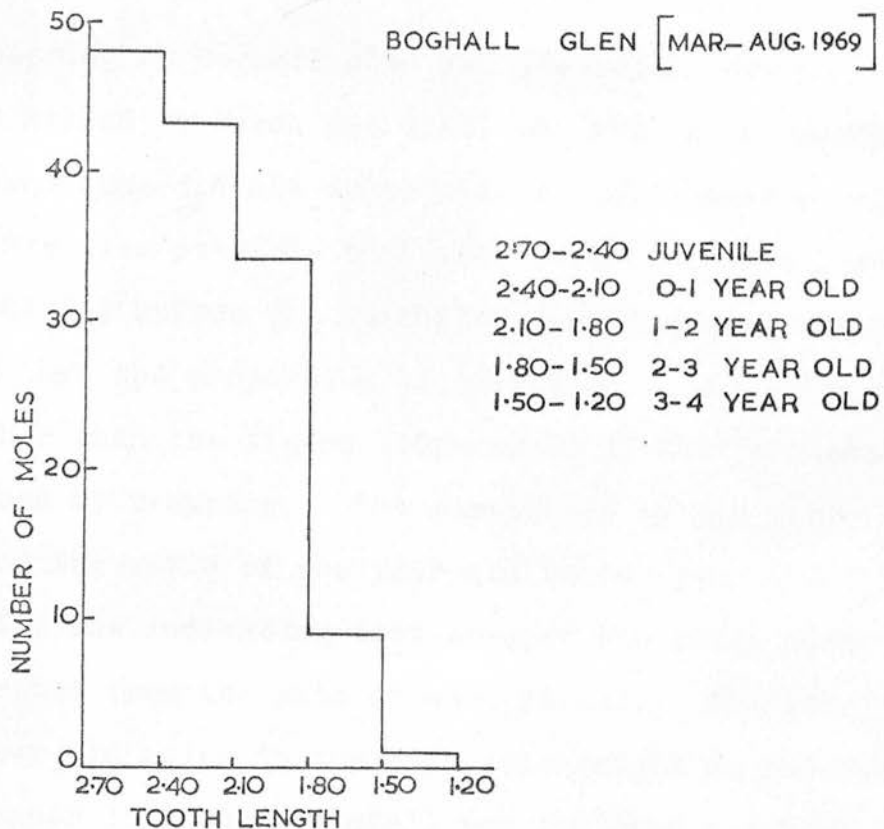


Fig. 12. The age structure of mole populations.

increased. The trapping at Boghall glen was started in March so that all females killed in March and April and the two pregnant ones killed in May and June did not contribute to the annual crop of offspring. It was also possible that some juveniles died because their mothers were killed before the juveniles were weaned. Consequently this showed that the proportion of juveniles in the population would have been higher than the figure shown above if the population had not been disturbed by trapping. The percentage of one year old moles was low and the ratio of one year old to two year old moles was consequently low indicating that some of the moles born in 1968 spring emigrated from the site or were killed. The low proportion of one year old moles in the population might be related to the weather in summer 1968 when rainfall was low from mid-May to mid-June and the soil was hard and dry in the first half of June. This might have affected the survival of moles that should have been weaned in early June that year. The dry spell from the end of July to early August in that year might also have contributed to the death of juveniles. The percentage of moles aged three and four years was low as could have been expected if the population was growing and old members were being eliminated. There was only one mole aged four years and its heavily worn molar tooth indicated that it could not have survived much longer.

Leip field and environs: Juveniles (half year old) formed 66.7% of the population, one-and-half year olds formed 25% and two-and-half year olds formed 8.3%. This area was a partially recolonized area and this accounted for the high percentage of juveniles in the population.

Fulford field: Juveniles (half year old) constituted 38.1% of the population, one-and-half year olds constituted 42.9% and two-and-half year olds and three-and-half year olds each constituted 9.5% of the population. The number of juveniles was lower than the number of one-and-half year old indicating that there had been a reduction in the number of the former. The reduction was probably caused by enforced dispersal of juveniles into less densely populated areas in the surroundings which included Leip field and environs. When the moles from Fulford field were considered together with those from Leip field and environs, a more balanced age distribution (48.5% juveniles, 36.4% one-and-half year olds, 9.1% two-and-half year old and 6.1% three-and-half year olds) was obtained indicating that the moles on these two sites were probably derived from a single population. Each of the two moles aged three-and-half years could probably have lived to be four years old but their heavily worn teeth indicated that a longer survival was very unlikely.

Bilston field: The population was made up of 53.8% of juveniles (half year old), 15.4% one-and-half year olds and 30.8% two-and-half year olds. The low percentage of moles aged one-and-half years indicated a reduction in the number of moles born in 1968 spring. The reduction in number of this age group was probably caused by the same conditions as explained for Boghall glen. The absence of moles aged three-and-half years was probably due to the trapping-out of this field in 1967/68 winter (preliminary investigations) and if the field was recolonized by juvenile moles in 1968

Spring such moles would be two-and-half years old by January 1970.

Life-span of the mole: Only one mole aged four years was caught in summer 1969. In winter 1970 two moles aged three-and-half years were caught. If moles aged four years had survived through autumn 1969 moles aged four-and-half years should have been caught in winter 1970 and since none was caught, the maximum life span of the mole in this locality was most likely to be four years. The results showed that only 1.7% of moles could live up to four years in this locality.

The age distribution of moles at Boghall glen was not analysed with respect to sex but this was done with moles from the other sites and the result is shown in Appendix 30. The percentage of females in the population was 39.1%. Females constituted 34.5% of the juveniles and this was only slightly lower than its percentage in the population. The percentage of females in one-and-half year old was 50% and this was higher than the percentage in the population suggesting the possibility of a slight wastage of males relative to females in this age-group. The percentage of females in two-and-half year old moles was 42.9% which was only slightly higher than its percentage in the population. The two moles aged three-and-half years were males. The results showed that the age distribution was similar in the sexes. The absence of female moles aged three-and-half years indicated that there was a slight possibility that males might live longer than females. A clear segregation into age groups was not obtained

when the weight of skulls was plotted in histograms first for all moles and separately for males and females and this suggested that the weight of skull was not related to age in moles. The weight of skull was found to be related to the sex of moles but not to the habitat. The mean ( $\pm$  S.E.) weight of skull for moles from Leip field and environs ( $0.55 \pm 0.01$  g.) was equal to that of moles from Bilston field ( $0.55 \pm 0.01$ ). When males and females from the two sites were considered separately the mean weight of skull was  $0.6 \pm 0.01$  for males and  $0.5 \pm 0.01$  for females. The mean ( $\pm$  S.E.) difference in skull weight between the sexes was  $0.1 \pm 0.01$  which was highly significant (estimated t value = 10.0 and t at  $P0.01 = 2.70$ ). The results indicated that moles could not be aged accurately on the basis of their skull weights.

(c) Studies on a small population of moles on Leip field

Tunnels: Figs. 13 and 14 show the drawings of the temporary tunnel systems of two juvenile males in July and Fig. 15 shows the tunnel system made in four days by a juvenile female. It appeared that there were no fundamental differences in designs between male and female tunnel systems at this time of the year. The measurements of the dimensions of adult and juvenile tunnels are shown in Appendix 31. The depth of tunnels was typical for that time in the year when the soil was moist and warm and invertebrates were abundant in the surface layers. The tunnels of adults seemed slightly deeper than those of juveniles. The tunnels of adult males were wider than those of adult females and juveniles but there was not much difference between the width of the tunnels of adult females and juveniles.

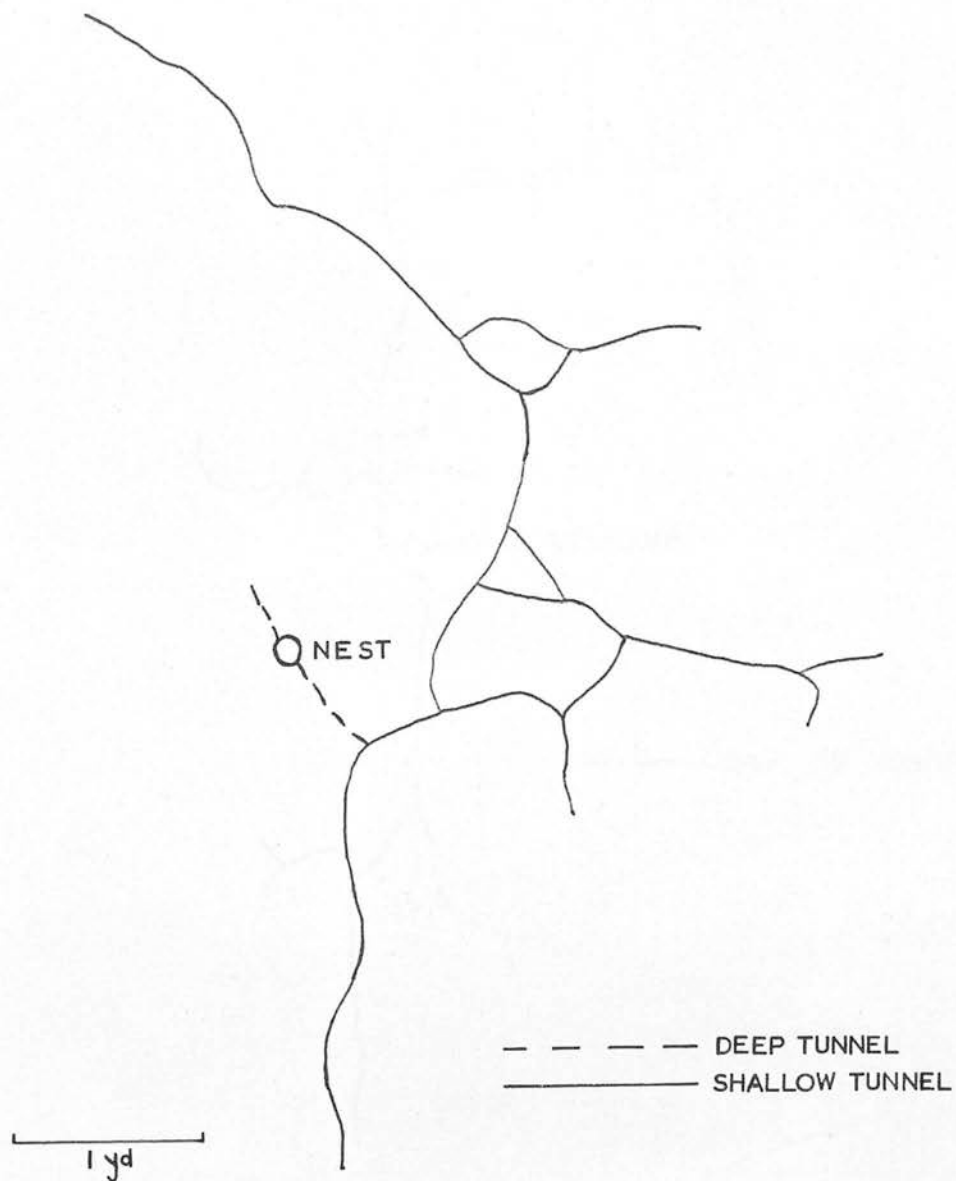


Fig. 13. Tunnel system of a juvenile male.

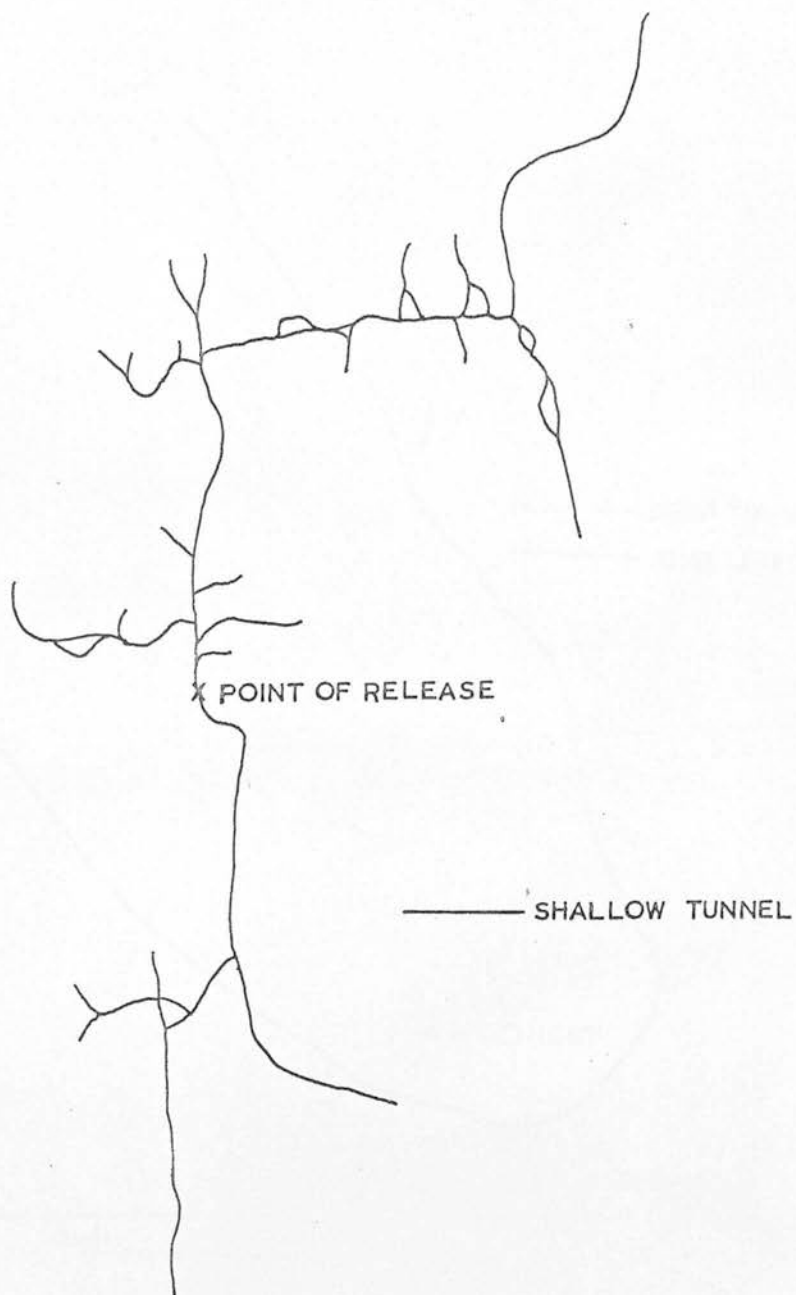


Fig. 14. Tunnel system of a juvenile male.

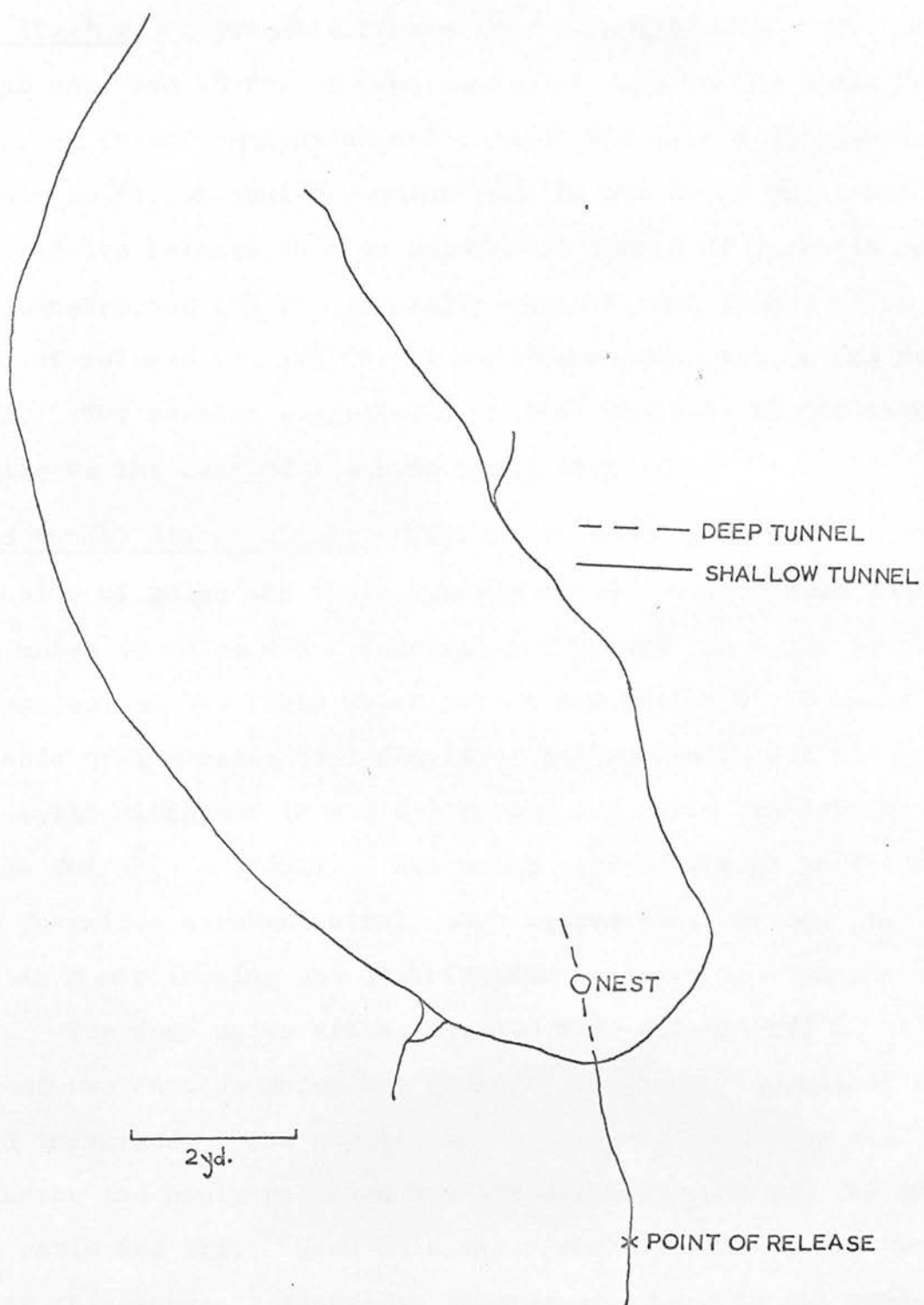


Fig. 15. Tunnel system of a juvenile female.

Rate of digging: A juvenile female (No. 1) constructed 9 ft. of permanent runs and 18 ft. of semi-permanent runs in the first 24 hours, 24 ft. of semi-permanent runs in the second 24 hours, 16 ft. and 10 ft. of semi-permanent runs in the third and fourth 24 hours of its release into an uninfested area. A juvenile male (No. 6) constructed  $47\frac{1}{2}$  ft. of semi-permanent runs in the first 48 hours of release and  $17\frac{1}{2}$  ft. of semi-permanent runs in the next 24 hours. The results suggested a gradual decrease in the amount of digging as the size of the home range increased.

Mole and tunnel distribution: Fig. 16 is a map showing the distribution of moles and their tunnels on 10/7/69. There were 5 adult moles (3 males and 2 females) and 5 juvenile moles (3 males and 2 females) on the field which gave a population of 10 moles and a sex ratio of 1.5 males to 1 female. The sex ratio was not significantly different ( $P = 0.05$ ) from a 1:1 ratio (estimated  $X^2 = 0.40$  and  $X^2_{[1]} = 3.841$ ). All moles were active at this time but the juveniles were relatively more active than the adults. Fig. 17 is a map showing the distribution of moles and tunnels on 16/7/69. The four moles killed accidentally and the points of release of two captive moles are shown. The tunnel system of each mole had increased. The population of moles at this time was 8 (including the newly released captive moles Nos. C3 and C4) and the sex ratio was 1:1. Each mole was restricted to its own tunnel system at this stage. Extensive digging continued in all parts of the field and the tunnel systems in the bottom south end of the field began to lose their individualities and merge into one another.

By 30/7/69, the tunnel systems of No. C<sub>1</sub> and No. 6 had merged together. The mole digging on the part of the tunnel originally belonging to No. 6 was captured and found to be No. C<sub>1</sub>. No. 6 was recaptured 7 days later at the top north end of the field 135 yards away from its original home. Its short tunnel system indicated very recent arrival and since there were no tunnel connections between the two sites it must have travelled above the soil surface to reach its new home. Both moles had severe lacerations on their chests indicating that they fought. This single observation suggested that moles were solitary and that weaker moles were expelled from overcrowded areas. It was possible that the solitary habit was one of the factors preventing the overcrowding of moles in the favourable parts of the habitat. The captive moles Nos. C<sub>3</sub> and C<sub>4</sub> each made a few feet of semi-permanent and rutting runs before abandoning their points of release on the second day after their release. No. C<sub>4</sub> was recaptured on 22/7/69 in the built-up part of the south-end of the field 85 yards away from where it was originally released. It left this site again on the second day and it was not recaptured afterwards. It was most probably expelled from the site by the resident moles which again indicated that the solitary behaviour of moles was a major factor in preventing overcrowding in the favourable parts of the habitat. Checks on the tail rings of other moles showed that they had remained in their existing homes. The distribution of moles on 5/8/69 and the point of recapture of No. C<sub>4</sub> on 22/7/69 are shown in a map in Fig. 18.

The distribution was not checked after the middle of August but all moles retained their rings till that time. Observations made at the end of August showed that there were no fresh diggings on the field. The soil was hard and extremely dry at this time and the only diggings observed were along the banks of streams and in marshy areas. Exposed areas like Leip field were more adversely affected by the drought than other areas with trees. Soil conditions improved slightly in September but October was dry. Observations made in December 1969 and in early January 1970 showed that moles were active on the field once more.

Fig. 19 is a map showing the distribution of moles on Leip field and environs on 14/1/70. The summer tunnel systems of juveniles were temporary and the only ringed mole caught on the field had abandoned its summer tunnels. 7 moles were trapped on Leip field and 5 moles were trapped in its environs. Only one mole (No. 2) had a ring. The trapping-out and checking of moles around Leip field for rings ensured that no surviving ringed mole had been missed out. The 7 moles on Leip field were made up of 5 males and 2 females giving a sex ratio of 2.5 males to 1 female. Age determination results showed that 6 of the 7 moles were juveniles (half year old) born in the previous spring while one was a one-and-half years old adult born in 1968 spring. The results showed that only one of the six moles on Leip field in mid-August 1969 survived till January 1970. The other moles were probably killed during the drought and soil desiccation which occurred at the end of August and in October 1969. The mole population on

Leip field in January 1970 were probably derived from the protected areas of Fulford field. 83.3% of the new moles on Leip field were juveniles which suggested that migration and dispersal movements concerned mainly juveniles which could not find a home in their places of birth. 83.3% of the new moles on Leip field were males indicating that males might be more adventurous than females.

Behaviour of captive moles released into the field: Of the two captive moles released into Leip field in December 1968, the male (No. C<sub>1</sub>) successfully established a home 80 yards away from its point of release, but the female (No. C<sub>2</sub>) was never recaptured. The two captives (Nos. C<sub>3</sub> and C<sub>4</sub>) released on 16/7/69 were eventually lost even though the male was recaptured on 22/7/69 85 yards away from its point of release. The fact that these moles left their points of release for other areas suggested that moles exercised some preferences in their choice of habitat. Newly released captive moles always constructed rutting runs suggesting that this type of tunnel served for exploratory purposes. The recapture of captive moles at considerable distances from their points of release suggested that migrating moles could cover considerable distances above the surface.

Sex ratio in moles: Appendix 32 shows the number of males and females, the sex ratio and the estimated  $\chi^2$  of the sex ratio for each mole population. There were more males than females in all cases except on Bilston field where there were 6 males and 7 females.

In Boghall glen the sex ratio was approximately 1:1 when adults and juveniles were considered separately but the number of males was significantly higher ( $P = 0.05$ ) than that of females when adults and juveniles were considered together. This was due to the cumulative effect of a slight excess of males in both adults and juveniles. The sex ratio on Leip field in July 1969 was approximately 1:1 and this probably approximated to the true sex ratio in an undisturbed population at that time of the year. The number of males was significantly higher ( $P = 0.05$ ) than the number of females on Fulford field. This was probably related to the emigration of moles from that field. The sex ratio approximated to a 1:1 ratio when moles from Leip field and environs and Fulford field were considered together which indicated that the moles were probably derived from a single population. The number of males was significantly higher ( $P = 0.05$ ) than the number of females when moles from all sites were considered together which reflected the cumulative effect of an excess of males in a majority of the populations. The results indicated that there was a slight excess of males in most populations and that this could lead to males being numerically superior to females when many populations are considered together.

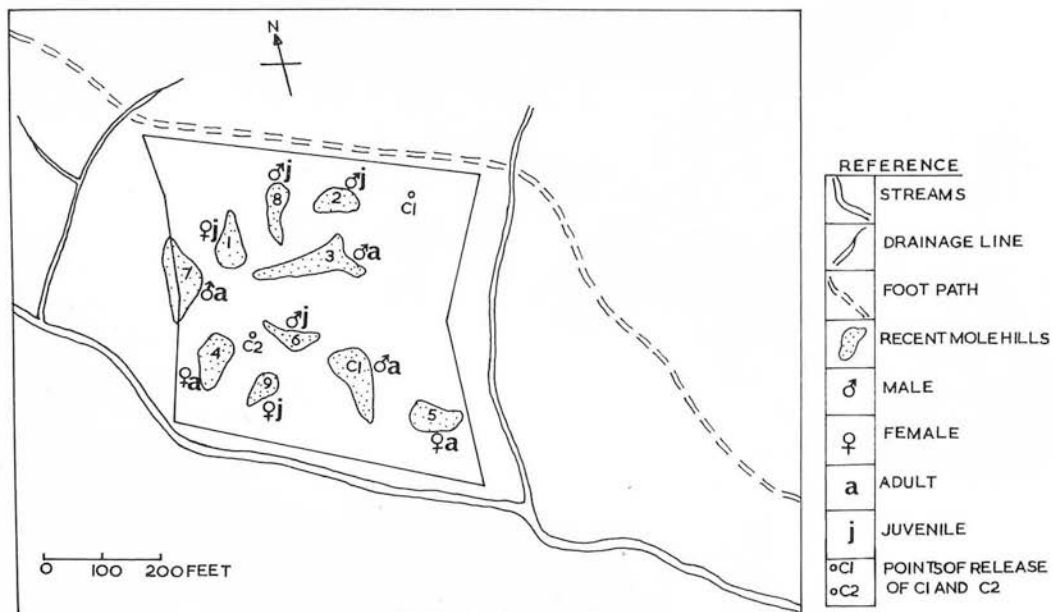


Fig. 16. Distribution of moles in Leip field on 10.7.69.

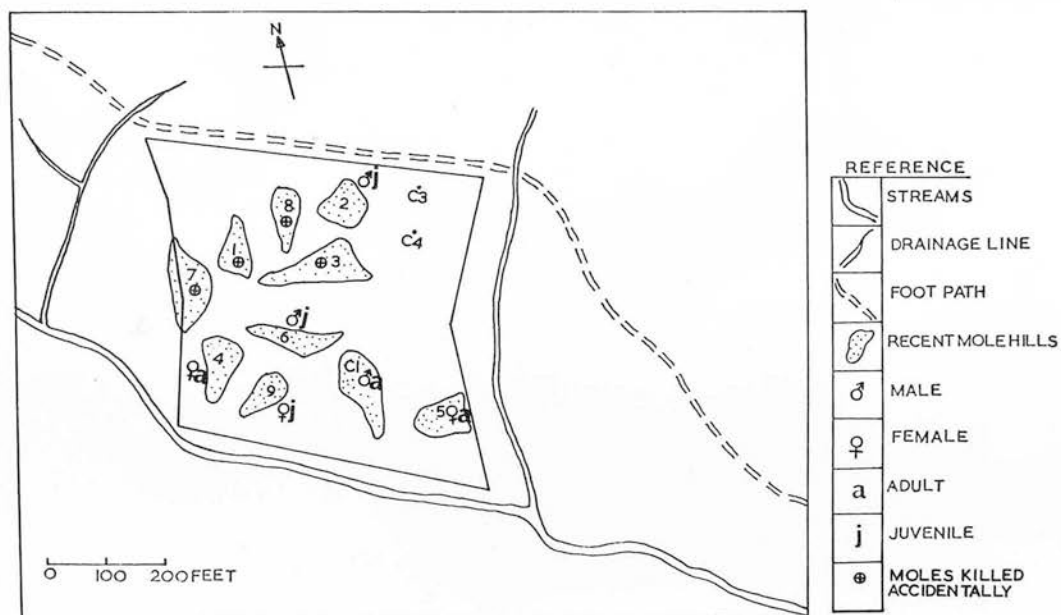


Fig. 17. Distribution of moles in Leip field on 16.7.69.

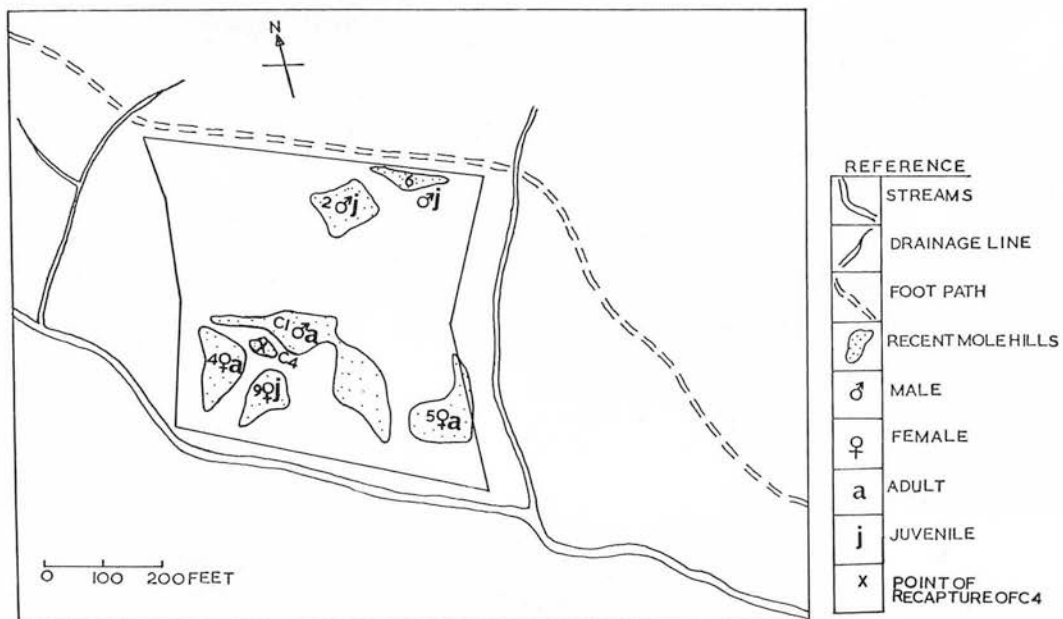


Fig. 18. Distribution of moles in Leip field on 5.8.69.

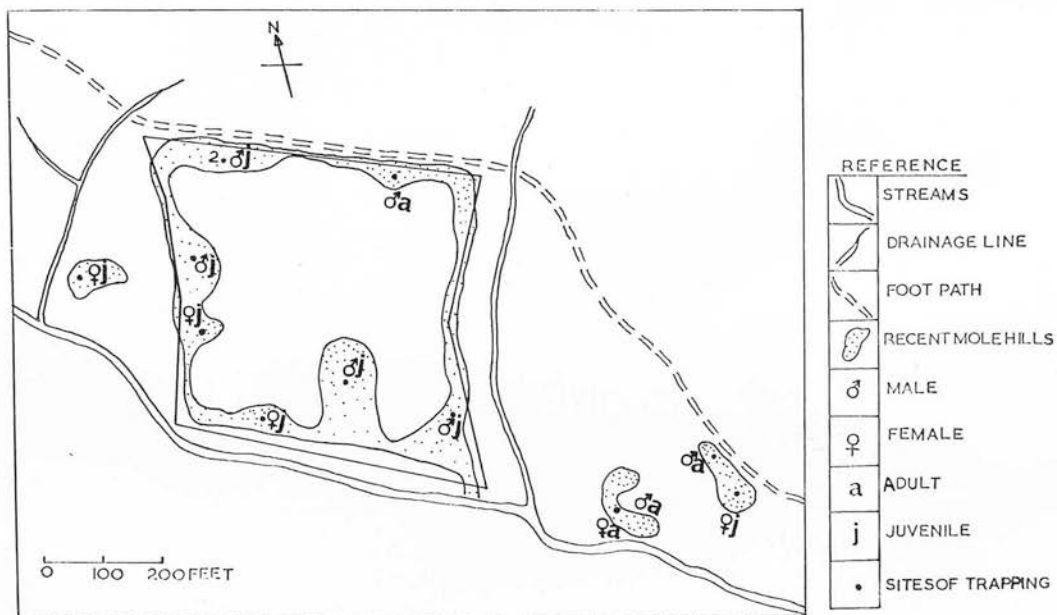


Fig. 19. Distribution of moles in Leip field on 14.1.70.

SECTION 6. DISCUSSIONS AND CONCLUSIONS

It was shown in the results that the number of species and the population density of earthworms in Boghall glen were higher in the lower south-end of the site than in the upper north-end of the site which agreed with the findings of Guild (1952) in an area east of the present site. The differences in species distribution and abundance of earthworms on the site were related to the local variations in soil type, soil conditions, altitude and herbage cover. It was shown that the relatively heavier soil in the south and middle parts of the site (area Section A) carried a higher number of species and higher populations of earthworms than the lighter soil at the top end of the site. Guild (1948) obtained similar results in samples taken from the Carse of Stirling. The role of a relatively higher altitude on the distribution of earthworms could not be assessed clearly because of other ecological factors which also varied as the altitude increased. A. chlorotica was found only in areas below 1075 ft. (above sea level) and A. caliginosa, E. rosea, O. cyaneum and O. lacteum were found only in areas below 1175 ft. (above sea level) and it was suggested that the relatively higher altitude on area Section B might be a limiting factor to the distribution of these species. Only four species were found in Section B which was still more or less a semi-natural (uncultivated) rough hill grazing. The four species (D. octaedra, D. rubida, L. castaneus and L. rubellus) belonged to the group classified as shallow-working 'non-burrowers' by Guild (1955). These species are thought to utilize only the

top 3 in. of the soil and it was quite possible that the relatively shallow top soil in area Section B was a limiting factor to most of the other species found in area Section A but absent from area Section B. Those species found in area Section A but absent from area Section B were all (except L. festivus) burrowers. In effect, only the shallow-working 'non-burrowing' species were found in area Section B while both 'non-burrowers', shallow-burrowers and deep burrowers were found in area Section A.

The soil in area Section B was slightly more acid than that in area Section A though the soil pH could not, in relation to earthworm distribution, be described as very extreme in any part of the site. The differences in earthworm distribution on the site may however be related to the local variations in soil pH. Two (D. octaedra and D. rubida) of the four species found in area Section B belonged to the category described as acid-tolerant while the other two (L. castaneus and L. rubellus) belonged to the category described as ubiquitous by Satchell (1955). The presence in area Section A of two species (A. caliginosa, A. chlorotica) described as acid-intolerant (Satchell 1955) and their absence from area Section B suggests that soil pH was a limiting factor to their distribution on the present site. While the soils on the site were not as acid as the lower limits of pH suggested by Satchell, it was possible that the acid-intolerant and ubiquitous species found in Section A but absent from Section B preferred the less acid soils in Section A. The poorer vegetation in Section B might have both direct and indirect effects on population numbers

and species distribution since vegetation is an index of soil conditions. This relationship has been shown by Satchell (1955). The vegetation in Section A was fine and composed mainly of nutritive grasses while that in Section B was matty, tussocky and composed mainly of Nardus stricta which is a hard grass and of little nutritive value. As Guild (1955) pointed out earthworms prefer to feed on soft plant remains and dung. The soil organic matter content in Section B was much higher than in Section A but it was possible and indeed very likely that the type of soil organic matter contents in Section B, being derived mainly from dead roots and leaves of Nardus stricta and in fairly undecomposed form, was not of the type suitable as food for earthworms. It was therefore likely that the food level for earthworms in Section B was low and this might in effect contribute to the low populations of earthworms in that section. The differences between Sections A and B in each of the factors enumerated above might not be so great as to account wholly for the observed disparity in earthworm distribution between the two areas but since each of these factors could affect species distribution to some extent, the observed differences in species distribution in the different parts of the site might be due to the combined effect of all the factors. It was also possible that the invasion of the site by the normal pasture species of earthworms started in the south-end of the site and was still progressing. This might explain the very localized distribution of L. terrestris and the absence of A. longa.

The population density and biomass of earthworms were

significantly higher in Section A than in Section B and it was suggested that the differences in abundance and biomass of earthworms in the two sections were caused by the same ecological factors responsible for the differences in the distribution of earthworms between the two sections. It was also shown that the relatively low populations in Section B were due mainly to the lower number of species and also to a decrease in the population density of the main species in that section as compared with Section A. The results suggest that fewer species of earthworms are found in the less favourable habitats and that in these habitats the population density of certain species may be reduced which in effect produces a relatively low population density and biomass of earthworms in such habitats.

It was shown in the results that the soil, vegetation and altitude did not have any major influence on the distribution of moles. This confirmed the views of all previous workers. It was also shown that the distribution of moles was not related to that of insect larvae even though they formed the main food of moles at certain times in the year. Of all the insect larvae found in Boghall glen, only wireworms have a larval life of up to and more than one year but the biomass of these larvae was too low to provide enough food for moles. The most important larvae in the food of moles were leatherjackets whose larval life lasts from about November to July. They were found in mole stomachs from January but they did not attain a position of relative importance in the diet till April. It is not surprising then that the

distribution of moles was not related to that of insect larvae since none of them can form a sufficient and continually available source of food for moles either because of their small biomass (wireworms) or because they were not always available in the soil (leatherjackets and others). In contrast to insect larvae however, earthworms have a large biomass and they were always available.

It was shown that the distribution of moles was intimately related to that of earthworms and that in the habitats studied, moles lived in the areas with the highest populations of earthworms. The distribution of earthworms was found to be influenced by soil and soil conditions. Since the distribution of moles was related to that of earthworms, and the distribution of earthworms was influenced by the soil and soil conditions, it was to be expected that the distribution of moles would also be influenced by the soil and soil conditions, but this was not so. This can be explained from the fact that the distribution of moles was related to that of earthworms as a group (Lumbricidae) and not to that of any single species of earthworm. This introduces some elasticity into the distribution of moles which is particularly important in assessing the ways in which the habitat influenced the distribution of earthworms, but not that of moles. It was shown in the present work that more species of earthworms lived in deep, loamy soils with high lime status (in Section A) than in shallow, sandy, fairly acid soils (in Section B) in Boghall glen and that the habitat influenced the distribution of earthworms by limiting the number of species that could live in certain soils and soil conditions. If the distribution of moles was related to that of any particular

species of earthworm, moles would be absent from all soils from which that species was absent and in that case the soil would limit the distribution of earthworms and that of moles. Since the distribution of moles was related to that of Lumbricidae as a whole any soil that can accommodate some species of earthworms is likely to be able to support some moles, although the reduction in the number of earthworms may lead to a corresponding reduction in the number of moles. It was also shown in the results that the population densities of earthworms and those of moles were higher in the deep loamy soils than in the shallow sandy soils. The explanation given above on the distribution of earthworms and moles in relation to the soil now makes it clear that it is in fact the soil which influences the abundance of earthworms and consequently that of moles. The general conclusion is that in the area under consideration the presence of earthworms determines to a large extent where moles can be found, and that the number of earthworms and as a result that of moles are controlled by soil and soil conditions. This suggests that at any given time in an area supporting the maximum number of moles, the number of earthworms and the number of moles have to be in equilibrium with the habitat. However, the number of moles varies from the highest in spring to the lowest in winter.

The seasonal changes in the number of moles is considered particularly in relation to their food supply. It was shown in the results that the population of 90 moles in Boghall glen at the beginning of the reproductive season rose to 138 after the juveniles

were weaned and that the increase in population numbers could have been higher if the population had not been disturbed by trapping. Larkin (1948) obtained similar results. There seems to be an intimate relationship between the reproductive cycle of moles and the abundance of their food. It was shown in the results that earthworms were most active and abundant from April to early June. Tipulid larvae were about full-grown in April and they were abundant in the soil and prominent in the diet of moles from April to July which may fulfil the food demands of moles during pregnancy and lactation, and for a short period after the juveniles are weaned. This probably also applies to other insect larvae which were very prominent in the food of moles in May to July 1969. When the populations of invertebrates are declining in summer, moles are also resolving a stable density with their habitats. Most juveniles are expelled from the populations during this period as shown in these investigations and also by Larkin (1948). When the balance between habitat, food and mole populations is finally reached in early winter, the favourable areas will be supporting the maximum or near-maximum number of moles and excess moles (mainly juveniles) would have been dispersed to the margins of occupied areas or to areas that were previously unoccupied. Moles in areas where food is abundant will have small home ranges and a high population density as on Section A, and moles in unfavourable areas with poor food supply will have relatively larger home ranges and a low population density as on Section B in Boghall glen. Moles in

shallow soils with poor food supply<sup>as</sup> in Section B made extensive shallow tunnels while moles in the relatively deeper soil with abundant food supply in Section A made mainly deeper tunnels and many mole-hills. It was shown that the earthworm species in Section B were all shallow-working 'non-burrowers' while those in Section A included deep-burrowers, shallow burrowers and 'non-burrowers'. It appears that the types of tunnels made by moles in any particular habitat depends directly on the soil depth and soil conditions and indirectly on the distribution and abundance of the moles' food supply.

In the present investigations invertebrates formed the only food eaten by moles. No major preferences for any food items were noted and the composition of the diet reflected mainly the distribution and the abundance of the moles' food in the soil. This confirmed the views of Kruishtal (1934). It was also suggested that the size of prey and the relative activity of the different prey species might be of some importance in their selection for food by moles. Large size might make a prey species easy for moles to locate while a very mobile prey might on one hand be able to escape capture and on the other might fall more often into tunnels. Earthworm cocoons were found in fresh mole-hills and relative to their abundance in the soil they were poorly represented in the stomachs of adults and entirely absent from those of juveniles in June. It is possible that cocoons are not a favourite item of the diet of moles. If the sense of smell is important in the location of food by moles, it was possible that cocoons were ignored by moles because

cocoons did not impart a strong smell. On the other hand, if vibrations in the soil caused by movements or activity of prey are important factors in the location of food, it could be understood why cocoons, which are not mobile, are ignored by moles. The relatively small size of most cocoons might also make them difficult to locate. No significant monthly differences were observed in the percentage weight of earthworms in the stomach contents from March to August 1969, which suggested that during this period the relative weight of earthworms in the diet was not significantly influenced by changes in soil conditions and earthworm activity in this particular locality. Significant differences ( $P = 0.05$ ) were observed in the percentage weight of earthworms in the diet of moles from different localities in the preliminary investigations but only slight differences were observed in this respect in the main investigations. The relative weight of earthworms in the diet in a particular locality may depend on the distribution and abundance of earthworms in that locality. The importance of insect larvae in the diet appeared to increase from January, and in May to July insect larvae contributed relatively more weight to the diet than earthworms, but after this period their importance in the diet declined again. The relative importance of insects in the diet was very much related to their ecology and life cycles and the period of maximum consumption of insect larvae coincided with the peak in body size and abundance of Tipulid larvae.

The food consumption was not significantly influenced by the seasonal changes in soil conditions and the abundance of prey.

There were no significant monthly differences in the weight of stomach contents as a percentage of body weight with or without the weight of stomach contents indicating that the food consumption was directly related to the body weight in all months. These results are similar to those of Godfrey and Crowcroft (1960) and Skoczen (1966). The analysis of body weight was made with and without the weight of stomach contents. This was attempted by Folitarek (1932) who compared the body weight of males and females with and without the weight of stomach contents. The body weight without the weight of stomach contents represents the starving weight and is a basic measurement of the living tissues of the animals. It was found that subtracting the weight of stomach contents from the body weight altered the trends in body weight and weight of stomach contents as a percentage of the body weight in adult females. The results indicated that it was better to take the weight of stomach contents into account when considering seasonal trends in body weight and weight of stomach contents as a percentage of the body weight. This is particularly important in comparative studies since the weight of stomach contents might vary from nothing to 14 g. (or from nothing to 12.4% and 16.1% of the starving weight in males and females respectively). The body weight and the weight of stomach contents were not significantly influenced by local habitat conditions particularly in moles collected in the same month from different pastures but the qualitative composition of the diet varied slightly in each locality indicating that the composition of the diet in each locality probably depended on the relative availability of the moles' potential food in the locality.

The qualitative composition of the diet was found to be basically similar in the sexes and in adults and juveniles. The weight of stomach contents, and the weight of undigested food in the stomachs were approximately equal in the sexes in all months and on average. The weight of full stomach (stomach contents + empty stomach) was, however, significantly higher in males than in females, on average and in moles collected in January 1970. The discrepancy between the results of analysis of weight of stomach contents and the weight of full stomach was due to the effect of the weight of empty stomach which was significantly higher in males than in females. This shows that the weight of empty stomachs must be taken into account when comparative analysis of the food consumption of moles (particularly males and females) are made. The weight of empty stomach may constitute between less than 10% to more than 90% of the weight of full stomach of a dead mole and serious errors might arise in analysis based on the weight of full stomachs. There were no significant monthly differences in the food consumption of males between March and July but the food consumption of females was significantly higher in May than in March. The weight of stomach contents as a percentage of the body weight (with or without the weight of stomach contents) was approximately equal in all months in males but in females the weight of stomach contents as a percentage of the body weight without the weight of stomach contents was significantly higher in May than in March and July and in June than in July. The relatively higher food consumption by females particularly in May but also in June was probably related to the necessity for lactating females to consume

much food. Males were significantly heavier than females both as adults and as juveniles. Adults were heavier than juveniles in June but partly because of a slight decrease in the body weight of adults at the end of the reproductive season and also because of a slight increase in the body weight of juveniles from June to July, there was no significant difference in the body weights of adults and juveniles in July although juveniles were still sexually immature in July. The food consumption, and the weight of stomach contents as a percentage of body weight were approximately equal in adults and juveniles.

When captive moles were fed on an excess of earthworms males ate between 73-75% of their body weights, and females ate between 84-89% of their body weights daily. These figures are higher than those obtained by Hawkins and Jewell (1962) and by Mellanby (1967) but they are within the ranges of those obtained by Skoczen (1957) and those estimated by Godfrey and Crowcroft (1960). Godfrey and Crowcroft (1960) based their estimation of food consumption on the weight of full stomachs. The weight of stomach contents of moles caught in traps would depend on the length of time the mole has spent on feeding activities and the quantity of food the mole could get before it was trapped. The low weight of stomach contents of some trapped moles probably indicated merely that they were caught before they had eaten sufficient food or that the stomach contents were at an advanced stage of digestion particularly in moles that were not freed from traps for a long time in warm periods. The analysis of the weight of stomach contents therefore is a good indication of the seasonal

and sexual differences in food consumption but would not give an indication of the actual food consumption except in cases where the stomach was full or approximately full at the time of analysis. The food consumption of captive moles in these investigations represented the amount of food the moles would eat in the presence of excess food. The food consumption of two moles captured in April and fed in captivity is compared here with those of the heaviest stomachs of dead moles obtained in the same period, using a method of calculation similar to that of Godfrey and Crowcroft (1960). The heaviest male stomach in April 1969 was 14.0 which represented a daily food consumption of 84 gm. on the assumption that a mole feeds six times in a day. The mole weighed 113 g. (without the weight of stomach contents) and the percentage food consumption per unit of body weight would be 74.3%. This compared favourably with the figure of 75% obtained on a mole captured in April 1969. The heaviest female stomach in April 1969 was 11.4 g. representing a maximum daily food consumption of 68.4 gm. The mole weighed 70.6 g. (without the weight of stomach contents) and the percentage food consumption per unit of body weight would be equal to 96.9% which compared favourably with the value of 89% obtained for a female captured in April. The figures obtained on the food consumption of captive moles did not appear to be very much different from the values calculated for wild moles. Captive conditions are, however, very artificial and the results of the food consumption of captive moles may not be a completely accurate picture of what happens in the field. It is very likely that the minimum biomass necessary for the existence of wild moles

would be lower than those obtained in these results owing to the difficulties of obtaining food particularly in the less favourable habitats like arable lands and rough hill grazings.

Captive moles stored earthworms from mid-September to the end of November and they always ate their stores unless they were provided with fresh food. The time when wild moles laid their stores was not definitely known but no stores were found in fortresses dissected on 15/10/68 which indicated that the stores were laid after this time. Earthworms collected from fortresses on 28/2/69 had healed injuries which suggested that they were stored much earlier. Moles probably laid their stores from after mid-October till early January. The species composition of earthworms populations in the fortresses agreed with the species composition of earthworms populations in the local soils which suggested that the moles gathered their foods in the immediate vicinities of their homes. This is contrary to the opinion expressed by Popov and Falkenshtein (1939) on the relationship between the homes and the feeding grounds of moles. It was also shown that moles have preferences for storing L. terrestris and O. cyaneum whenever these were present which confirmed the views of Evans (1948a). Observations made on mole activity at the probable time when stores were laid indicated that moles obtained their stores mainly by digging in mild periods in late autumn and early winter. This is contrary to the opinion of MacDougal (1942) but similar to that of Skoczen (1961a).

The methods of analysis of the body weight and feeding habits of moles adopted here indicate how the data collected on these

subjects could be dealt with. The results of analysis of the data on trapped moles agreed with laboratory observations and the general laws of food consumption in mammals. All moles in the main habitat studied in these investigations were killed between March and August so that broad annual generalisations could not be made. The broad similarity of the results to those of previous workers suggests that the only significant annual fluctuations in body weight and food consumption take place during the reproductive season and that at any particular time the composition of the diet of moles in a given habitat is an index of the relative distribution and abundance of the moles' food in the habitat at the given time.

The methods by which moles obtain their food can now be further explained using the results of the present work. Moles can obtain food by three methods: gathering invertebrates that fall into the tunnels, searching (digging) in the walls of existing tunnels or digging new tunnels, and searching above the surface of the soil. These methods have all been mentioned by previous workers (Folitarek 1932; Godfrey and Crowcroft 1960; Mellanby 1966, 1967, 1968) but the relative importance of each method has not been assessed. It was shown in the present investigations and also by Godfrey (1955) that digging and feeding may take place together. The findings of plant materials and adult insects in stomach contents suggest that moles sometimes explore the surface of the soil for food. It is suggested that when the soil is frozen in winter the mole's food will be composed of invertebrates that fall into the tunnels, those obtained during limited surface activities, and those obtained by

digging in the walls of existing tunnels. The fresh soil thrown over or forced under old mole-hills at this time is evidence of moles' diggings in existing tunnels. If the food obtained by these methods is not sufficient, the mole digs a new tunnel and this probably explains why a few fresh mole-hills are sometimes found in frozen soils. Earthworms from stores will probably serve as supplementary food in these circumstances though it has not been suggested that moles deliberately store them for this purpose. In dry periods in summer, moles probably obtain their food by a combination of all the methods mentioned above. At this time real shortage of food may be caused by dry, hard soils which make digging difficult for moles and as shown by Gerard (1960) earthworms may also be killed by soil desiccation. Moles migrate into moist soils or dig deeper tunnels to obtain food. Surface activities in search of food at such times have also been reported (Adams 1903; MacDougal 1942).

In the spring the soil is moist and invertebrates are abundant. Moles probably obtain most of their food at this time by digging shallow tunnels and raised ridges with no through passages under them. There is a direct relationship between the depths of these tunnels, the vertical distribution and abundance of invertebrates in the soil and the composition of food in mole stomachs. Thus, the peak in earthworm activity and populations in 1969 was in May but in that month, insect larvae were more prominent in the diet than earthworms and usually only small earthworms were found in stomachs. This suggests that the shallow tunnels and the raised ridges with no tunnels under them were mainly designed to capture

insect larvae and small earthworms living in the surface layers of the soil. Moles probably obtain food in the autumn mainly by digging but also by gathering invertebrates that fall into the tunnels. At the end of autumn, migrating moles are establishing permanent homes and resident moles are enlarging old homes. Earthworms are also active and abundant in the soil. The extensive diggings make an excess of earthworms available to moles and this is probably the source of earthworms stored in the fortresses. It is possible that the majority of large earthworms obtained in tunnels and during diggings are stored while the majority of the smaller ones are eaten immediately and this may be one of the reasons why small earthworms occur in relatively low numbers in stores.

More detailed investigations, covering all seasons, will be needed on the vertical distribution of invertebrates and moles before a final conclusion can be made on the relationship between the distribution of mole tunnels and that of invertebrates. The available evidence at the moment suggests that at all seasons in the year, there is a direct relationship between the depth and the extent of mole tunnels and the vertical distribution and abundance of invertebrates; this relationship is reflected in the seasonal composition of the moles' diet.

The population densities of moles in Boghall glen were determined by killing all the moles (complete 'trapping-out') and the population numbers were expressed as the highest densities. Elton (1933) showed that population numbers could be given as lowest density (number per area of country including habitats that are

unsuitable for the species) economic density (number per area of suitable habitats including places not utilized by the species), and highest density (number per actual area of space occupied by the species). Since moles show some preferences in their choice of habitats, it will be best to quote their population numbers in various habitats as the highest densities. In this way population estimates given by different workers could be compared.

Some methods were tried here to find out how population numbers could be determined without killing the moles. The failure of live-trapping was probably due mainly to the fact that moles avoided such traps and partly to the fact that enough time was not devoted to the trials. The design of one of the live-traps used was based on the one on which Rudge (1966) claimed 31% success (% of capture in total number of visits to traps). Moles either blocked the entrances to traps or tunnelled beneath or along the sides of traps. This avoiding action was not peculiar to traps but it probably showed that the inefficiency of the traps was mainly due to their structural deficiencies or cumbersomeness. Such avoiding actions could also be seen in tunnels as moles normally make tunnels over, beneath or along the sides of obstacles such as big stones. Since the assumptions of the "marking-and-recapture" ("Lincoln index") method of population estimate are not necessarily true for moles (moles are mainly solitary), it will be necessary to capture all moles in an area to determine their numbers. This was done in a studies of a small population on Leip field. The use of efficient live-traps will, however, make the social relationship of moles

(particularly with regards to the number of moles using a tunnel) easier to study.

It was found that increase in the number of moles and the number of mole-hills were directly correlated and that there was a high correlation ( $r = 0.995$ ) between the number of moles and the number of mole-hills in similar soil types. This confirmed the results of Kruishtal (1934). The correlation between the number of moles and of mole-hills was low ( $r = 0.841$ ) in a large area with diverse soil types. Thus, with similar soil types the number of mole-hills can be used to give a reliable estimate of the number of moles. In practice the reliability of the estimate may be improved and the number of moles killed reduced if isolated small colonies are chosen for trapping to determine the number of mole-hills made by a mole.

It was shown that the number of fortresses, and the number of nests that could be located from surface evidences were not reliable indices of the numbers of moles which confirmed the findings of Burton (1950) and Godfrey and Crowcroft (1960). It was found that when all existing mole-hills and surface tunnels were flattened on a field, the number of areas with fresh diggings found on the field on the second day was a reliable indication of the number of moles. It was also shown that less reliable results were obtained when the number of areas with fresh diggings were counted on the third day. The areas used in the present investigations were probably small but the results indicated that the number of moles could be counted fairly accurately without killing the moles

especially in spring and autumn when moles were digging actively. The possible errors in this method are not greater than those that could arise in estimates based on trapping-out of populations (Godfrey and Crowcroft 1960) or of compartments (Larkin 1948; Mellanby 1966). The main advantage of this method is that it can be used to study the local, seasonal and annual variations in numbers for which there are no reliable records at the moment.

Many cases of multiple catches of moles in a tunnel were recorded in the present investigations. A number of previous workers have also reported multiple catches (MacDougal 1942; Larkin 1948; Stein 1950; Mellanby 1966). Multiple catches from March to July are probably due to sexual activity. Multiple catches in March involved single females and many males but in April and May more than one female was involved. Adults and juveniles of both sexes were trapped in the same tunnels from June to mid-July. Multiple catches at other times were in tunnels which probably served as interconnecting routes between fields or different parts of the same field and as Godfrey and Crowcroft (1960) pointed out the use of such tunnels by more than one mole is not inconsistent with territorial behaviour. All the evidence obtained in the present investigations confirmed the views of Godfrey and Crowcroft (1960) that usually moles are solitary. Only single moles were caught in freshly dug tunnels which showed the exclusive ownership of such tunnels. The capture of more than one mole in a tunnel within 48 hours was recorded in 12 instances and these involved mainly females in May and adults and juveniles in June and July. The capture of more than

one mole in a tunnel at an interval of more than 48 hours was recorded in 35 instances. These showed that the tunnels of dead moles were usually not occupied immediately after their death.

It is not definitely known how a mole prevents other moles from intruding into its territory or how a mole knows the limits of its territory in an area where tunnel systems are joined. It is suggested that a system of constant marking, probably by excretion, at each period of activity might make a mole aware of the limits of its territory and keep other moles away from that territory. The effects of these markings will be most intense in the nests and in freshly dug tunnels which are used frequently and will be least in old tunnels which are visited less frequently. The markings will also have to be physically defended if the occasion arises and this probably gives rise to quarrels (Godfrey 1957a).

Tunnels of dead moles will lack both markings and defence and will be acquired easily by other moles. Burt (1943) pointed out that when an animal is in a trap it is unable to defend its territory. Burt's argument explains multiple catches but it does not explain why most juveniles are expelled from their parents homes in summer, or the expulsion of a mole from its home by an invading mole all of which were observed in the present investigations. It was described earlier how an adult mole expelled a juvenile mole when their tunnel systems joined, both receiving lacerated chests. Two moles kept in a large cage with separate nest chambers fought fiercely using the front paws to scratch the underside of the other's body. These observations suggest that moles are usually

solitary, and are aggressive in the presence of other moles except in the reproductive season during mating and rearing of the young when most multiple catches were obtained. The results obtained from the studies of a small population of moles on Leip field support the views of Larkin (1948) and Godfrey and Crowcroft (1960) that territorial behaviour is important in stabilizing the numbers of moles in a population.

The age of moles was determined by measuring the length of teeth; this method avoids errors of personal judgement inherent in the methods employed by all previous workers (Larkin 1948; Stein 1950; Deparma 1954, Godfrey in Godfrey and Crowcroft 1960; Skoczen 1966). The precautions suggested by Deparma were found to be unnecessary.

The age structure of a population was found to depend on the history of the population particularly on migrations, and on disturbances such as trapping. This confirmed the results of Larkin (1948) and Skoczen (1966). Another factor which was considered to be of some importance is the severity of the weather in summer and autumn. A very dry summer and autumn are likely to influence the death of a large number of juveniles either by exposing them to predators or by causing starvation when the moles cannot dig into the soil to obtain enough food. The effect of trapping on the age structure of the population was shown in Boghall glen where the percentage number of juveniles was comparatively low (35.6%). Here the trapping was started in March which meant that all females trapped in March and the pregnant females trapped in April, May and June did not produce babies. Also some juveniles probably died

because the parents were killed before the juveniles were weaned. The percentage of juveniles in a partially recolonized area (Leip field) was 85.7% which agreed with the findings of Larkin (1948).

There was a slight indication that males may live longer than females but generally there were no significant sexual differences in the age distribution. The maximum life span of the mole was found to be 4 years and moles of this age group constituted only 1.7% of the total populations. This confirmed the results of Deparma (1954), and Skoczen (1966) but not those of Larkin (1948) and Stein (1950).

The various causes of death in moles are generally well known but there are no quantitative data about their relative importance in the population dynamics. The results of the present investigations indicate that the natural mortality is very low. Moles aged three-and-half to four years constituted only 1.7% of the population and the death of these moles is not likely to play any significant part in the control of population numbers. If it is accepted that each female produces four juveniles (Adams, 1903, and others) and the sex ratio is 1:1 (present results, Larkin, 1948, and others) the estimated death rate in an undisturbed population in which all moles live to be four years old will be 1.2%. (The age structure of such a population starting with 2 moles, in 4 years, will be 108 juveniles, 36 one year old, 12 two years old, 4 three years old and 2 four years old). This theoretical natural mortality will decrease as the life span increases. However, it is generally agreed (Stein 1950; Godfrey and Crowcroft 1960) that various other mortality factors check any explosive increases in the number of moles, and the normal life span is rarely attained.

According to Deparma (1964) three-quarters of juveniles die in their first year. The relative importance of high juvenile mortality in different populations has not been assessed but it seems that it will be highest in habitats already supporting the maximum or near-maximum number of moles since <sup>the</sup>majority of juveniles will be dispersed from such habitats. Further investigations will be needed on this phenomenon and also relative to the fact that in over-populated areas the number of embryos may be reduced or possibly old females may not reproduce.

Movements of moles in June to early January was reported in the present investigations. These movements are an annual event related to the dispersal of juveniles and their selection of new homes. It was shown that some of these movements were made above the soil surface ("jump-spreading"). It seemed very likely that these annual movements always lead to a high wastage of juveniles, as predators have been reported to kill many moles at such periods (Southern 1954; Skoczen 1962). Juveniles caught by predators were probably mainly those which were exposed because of the dead vegetation and could not dig down because of the hardness of dry soils in summer.

Mortality factors which are independent of population numbers have also been reported (Adams 1903; Elton 1931; Larkin 1948). Seasonal migrations involving slight shifts of ranges from dry soils to damp soils in summer and from flooded soils to relatively drier soils in winter and autumn were reported in the present investigations. The moles usually returned to their original homes

when the soil conditions became favourable again. However, it was shown that the seasonal migrations of mole colonies from exposed habitats in response to severe drought and soil desiccation may not lead to the survival of the migrants. Six moles were ringed in Leip field in mid-August 1969 but only one of seven moles trapped on the field in January 1970 had a ring. It was suggested that the other five marked moles were killed during the drought which occurred at the end of August and early September and in October 1969. The new generation of moles on the field in January 1970 probably emigrated from adjacent better protected habitats.

A final synthesis of the results of these investigations indicates that the factors controlling the population density of moles are mainly factors which appear to be acting in a density dependent manner. The density dependent controlling factors are food supply which is directly related to habitat conditions and intra-specific strifes arising out of the solitary and aggressive habits of moles. It appears that in the favourable habitats with abundant food supply, the population density will be regulated mainly by intra-specific strifes since food is present in theoretically unlimited amounts. But in the unfavourable habitats, it appears that food supply will be the main factor controlling the population density. In such habitats it is likely that because of the poor food supply moles will have to search over large areas and each mole will of necessity have a large home <sup>range</sup> before it can get enough food so that food supply will limit the population numbers possibly before intra-specific factors could set in. Predation is also

another density dependent factor with probably an important role in reducing the numbers of moles particularly in the summer months during dispersal and migrations, and possibly in very adverse winters when moles might be forced to go above the surface. However, the number of moles involved in migrations will depend on the food level in the habitat and on whether the habitat is supporting the maximum number of moles already and partly on the density independent factors of weather and soil conditions. In extremely unfavourable weather as in very dry summers and very cold winters, density independent factors might, indirectly, be responsible for the death of a large number of moles. The action of weather is described as indirect because the death of moles during severe weather is probably caused directly by shortage of food or by exposure to predators. Moles may be killed by sudden adverse changes in their habitat conditions like flooding and cultivation but such deaths are better regarded as temporary fluctuations in numbers and not permanent control of population numbers.

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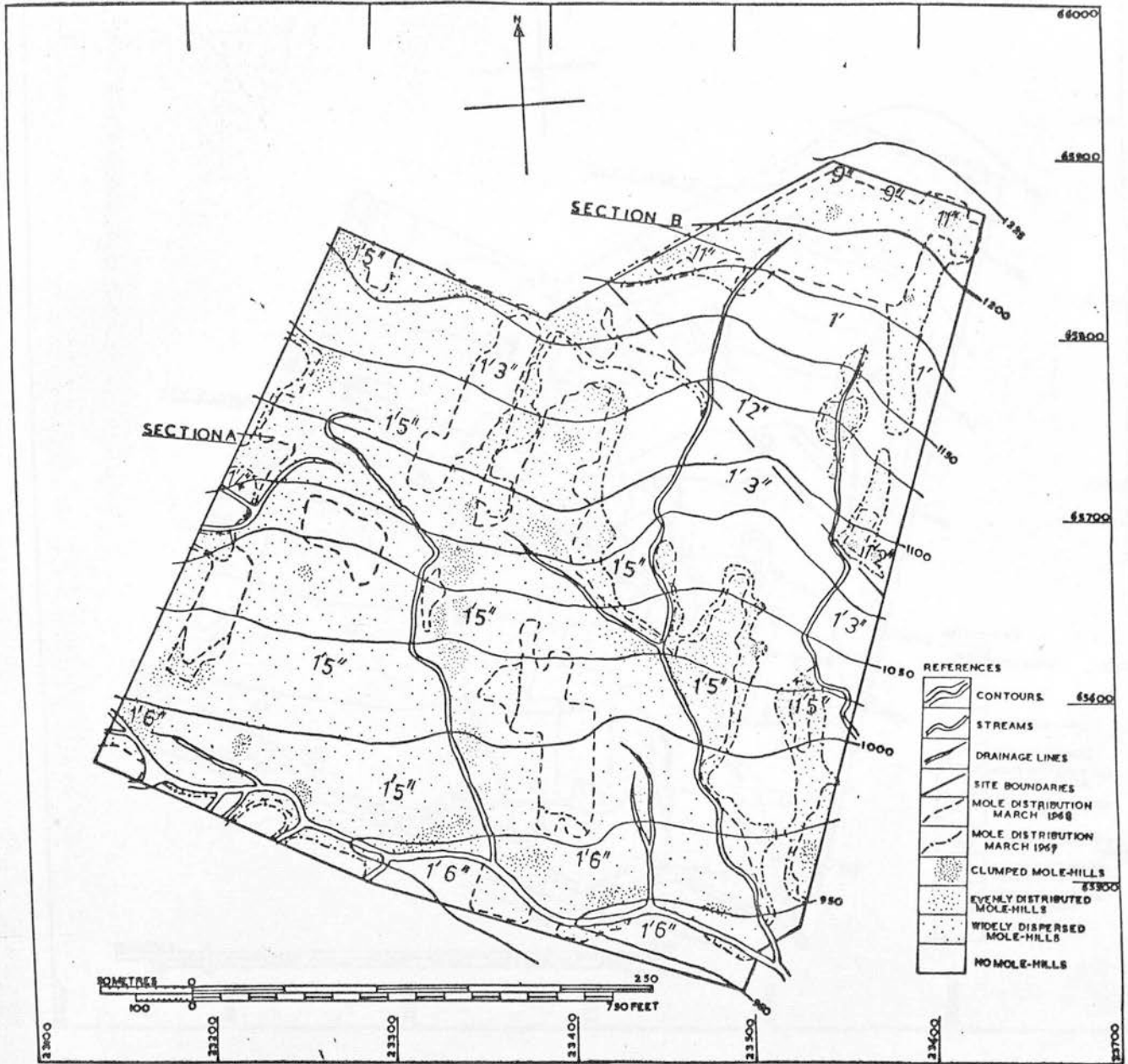
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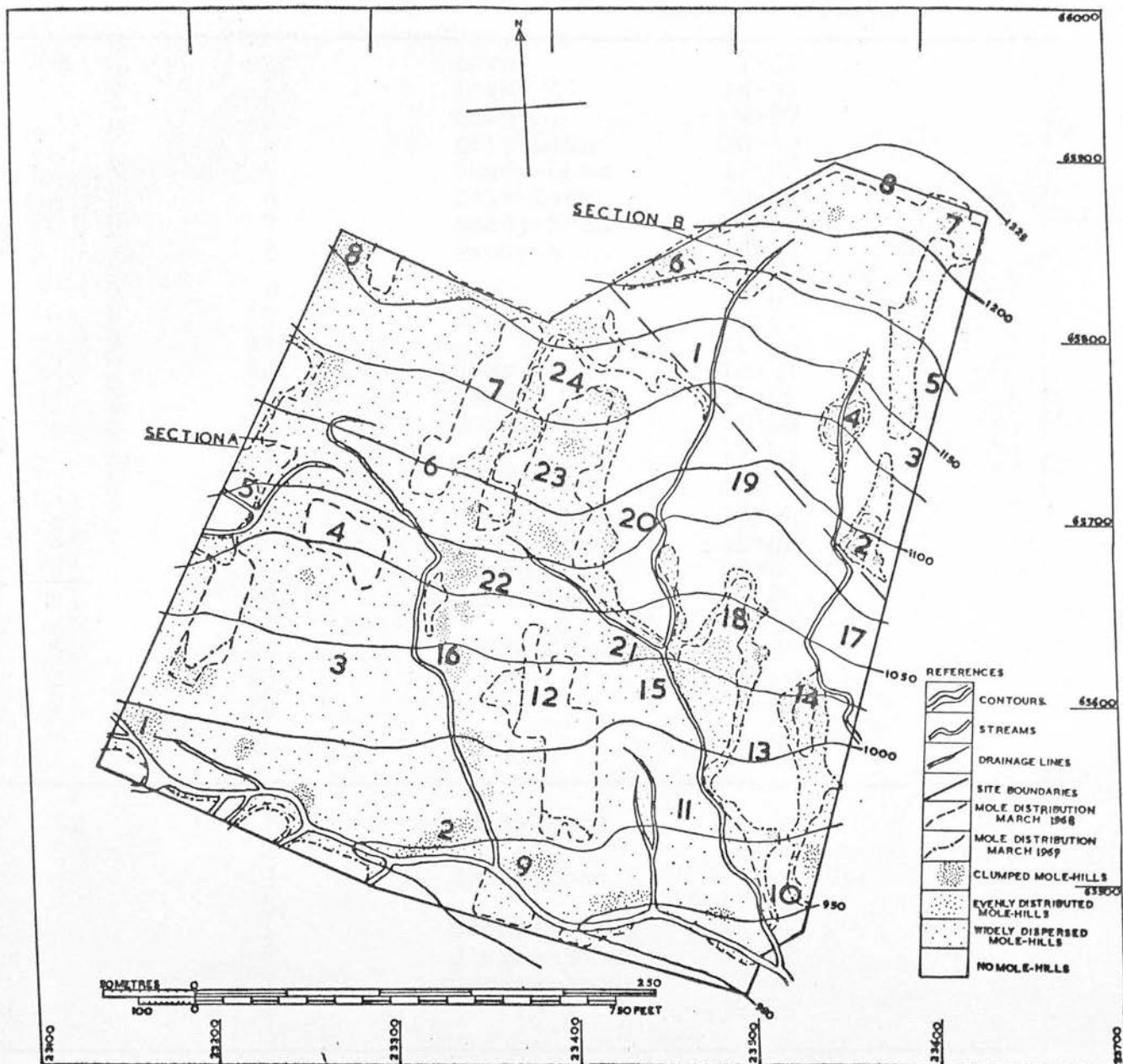
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Appendix 2. Soil depth at Boghall glan.

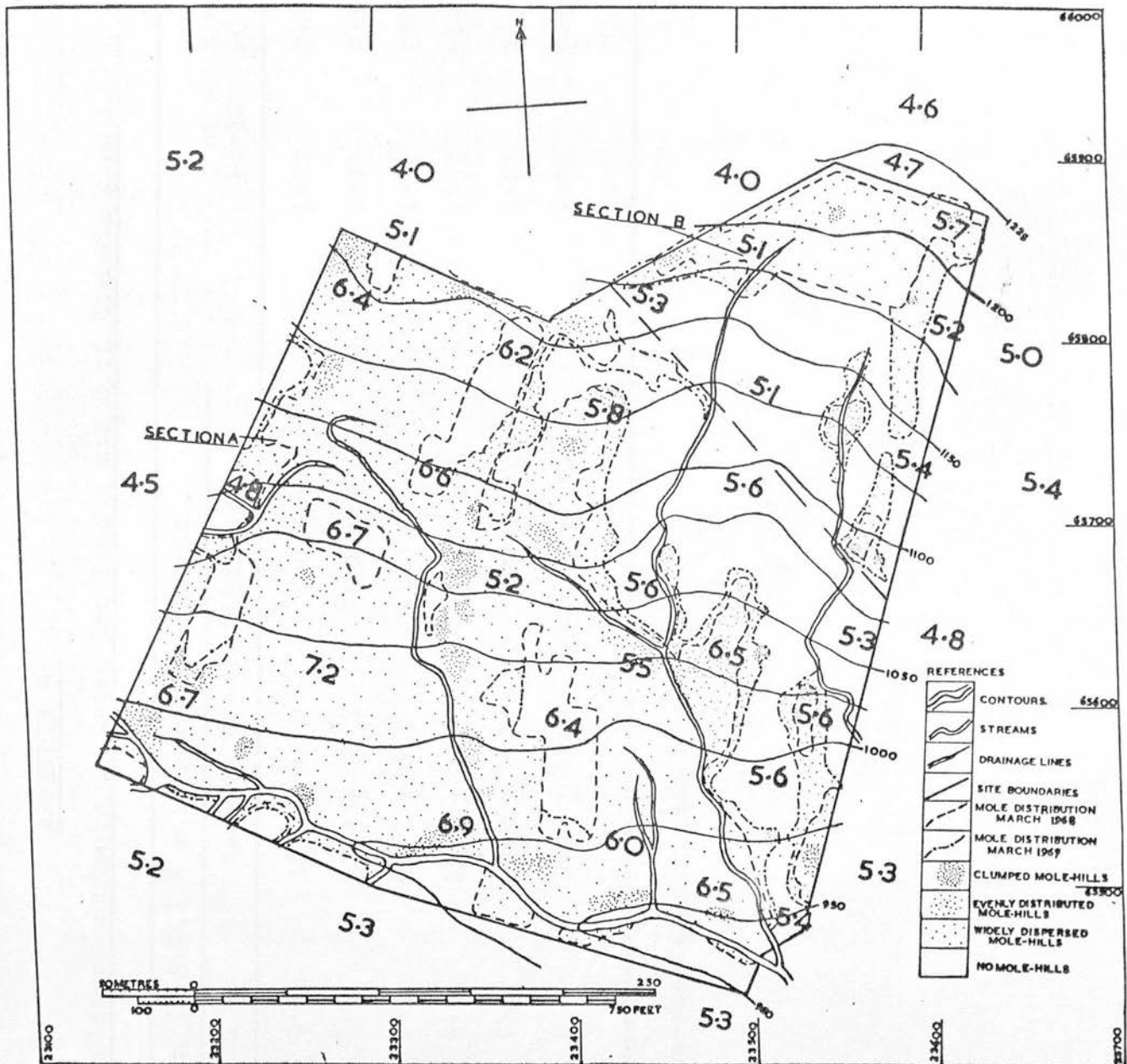


APPENDIX 3a. Sites where samples were taken for the investigations of soil texture and for measurements of the percentage organic matter contents (Results in Appendix 3b).

APPENDIX 3bTexture and Organic matter contents of soils at Boghall glen.

Section	Sample Number	Soil texture	Percentage organic matter contents
A	1	Loam	7.07
	2	Loam	15.31
	3	Loam	9.07
	4	Silt-Loam	10.52
	5	Sandy-Loam	12.28
	6	Silt-Loam	10.02
	7	Sandy-Loam	13.02
	8	Sandy-Loam	12.41
	9	Loam	10.44
	10	Sandy-Loam	13.64
	11	-	10.86
	12	Loam	12.91
	13	Loam	15.06
	14	Sandy-Loam	10.60
	15	-	15.03
	16	Sandy-Loam	11.93
	17	Sandy-Loam	11.94
	18	Sandy-Loam	12.44
	19	Sandy-Loam	20.86
	20	Sandy-Loam	10.84
	21	-	9.31
	22	Sandy-Loam	12.90
	23	Loam	15.70
	24	-	12.87
	25	Loam	22.92
B	1	Sandy-Loam	24.36
	2	-	10.66
	3	Sandy-Loam	-
	4	-	17.54
	5	Sandy-Loam	16.22
	6	Coarse-Sand	45.07
	7	Coarse-Sand	17.76
	8	-	32.44

Ref. Appendix 3a for sites of sampling.



APPENDIX 4. Soil pH in Boghall glen and its environs.

APPENDIX 5

Percentage soil moisture contents in areas Sections A and B of Boghall glen

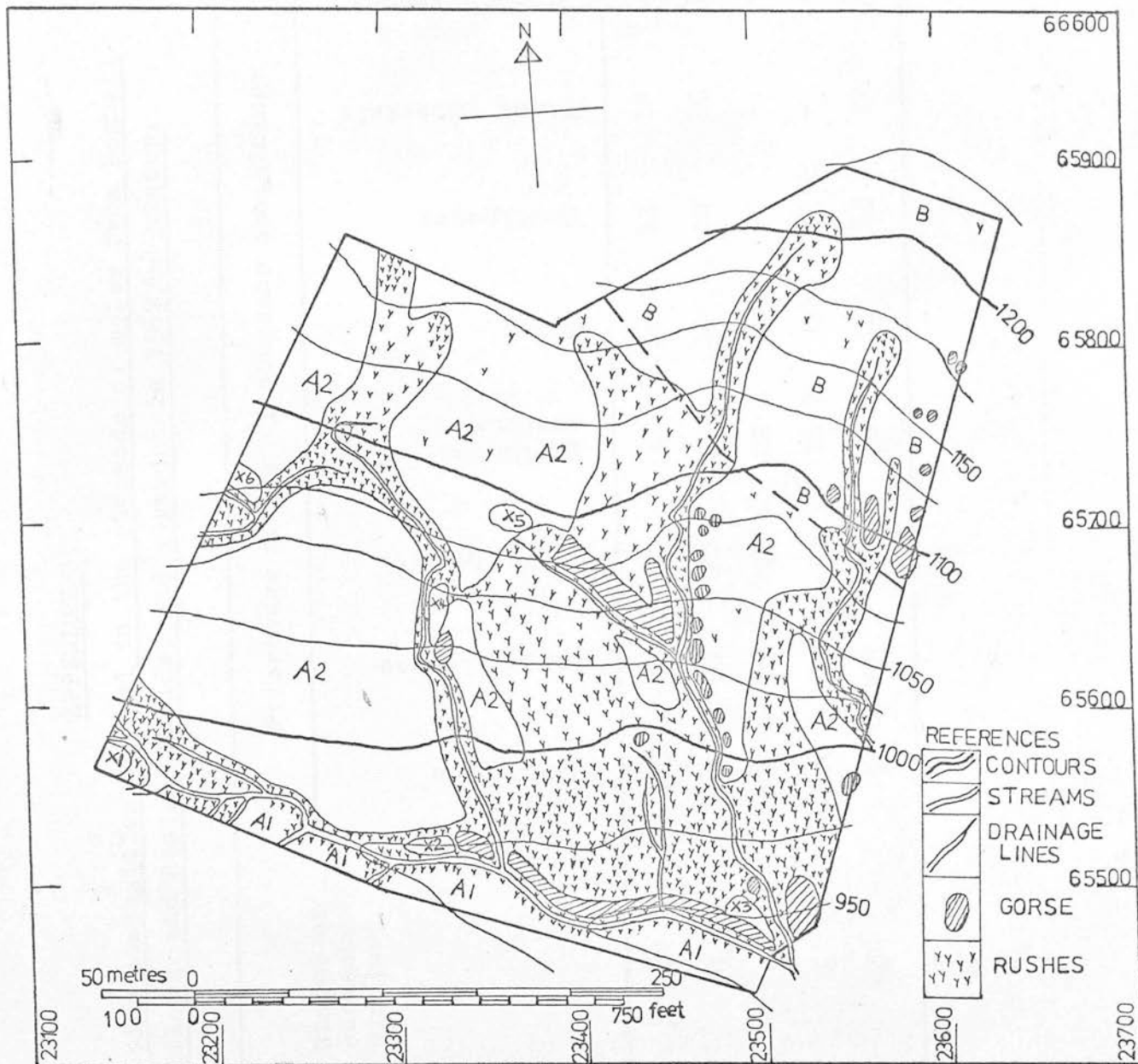
Date of Sampling	Mean ( $\pm$ S.E.) % soil moisture content		Difference	t	t at P0.10	t at P0.05
	Section A	Section B				
6/8/68	31.1 $\pm$ 9.8	38.1 $\pm$ 12.0	7.0 $\pm$ 6.6	1.1	1.70	2.04
29/1/69	33.2 $\pm$ 6.6	43.3 $\pm$ 10.1	10.1 $\pm$ 3.3	3.1	1.71	2.06*
12/3/69	36.5 $\pm$ 7.7	48.3 $\pm$ 8.4	11.8 $\pm$ 5.4	2.2	1.72	2.07*
1/4/69	35.1 $\pm$ 6.9	44.1 $\pm$ 11.5	9.0 $\pm$ 4.5	2.0	1.71	2.07
8/4/69	33.0 $\pm$ 5.0	38.9 $\pm$ 1.2	5.9 $\pm$ 3.6	1.6	1.81	2.23
11/6/69	31.3 $\pm$ 5.1	39.8 $\pm$ 10.4	8.5 $\pm$ 7.1	1.2	1.71	2.07

\* Difference significant at P0.05

APPENDIX 6aList of Plants at Boghall Glen

Brown Bent-grass (Agrostis canina), Common Bent-grass (Agrostis tenuis), Sweet Vernal grass (Anthoxanthum odoratum), Crested Dog's tail (Cynosurus cristatus), Cock's foot (Dactylis glomerata), Tufted Hair-grass (Deschampsia caespitosa), Wavy hair-grass (Deschampsia flexuosa), Sheep's fescue (Festuca ovina) Creeping fescue (Festuca rubra), Yorkshire fog (Holcus lanatus), Perennial Rye-grass (Lolium perenne), Moore mat grass (Nardus stricta), Timothy (Phleum pratense), Annual meadow grass (Poa annua), Smooth-stalked meadow-grass (Poa pratensis), Rough-stalked meadow-grass (Poa trivialis), Common sedge (Carex nigra), Carnation Grass (Carex panicea).

White clover (Trifolium repens), Bluebell (Campanula rotundifolia), Daisy (Bellis perennis), Cuckoo flower (Cardamine pratensis), Thistle (Carduus sp.), Common Mouse-ear Chickweed (Cerastium vulgatum), Horsetail (Equisetum sp.), Heath Bedstraw (Galium saxite), Ragged Robin (Lychnis flos-cuculi), Early forget-me-not (Myosotis hispida), Erect potentilla (Potentilla erecta), Creeping Buttercup (Ranunculus repens), Common Dandelion (Taraxacum officinale), Stinging Nettle (Urtica dioica), field Speedwell (Veronica agrestis), Bilberry (Vaccinium myrtillus) Rush (Juncus sp.), field Woodrush (Luzula campestris), Gorse (Ulex europaeus), Mosses (Polytrichum commune and Rhytidiadelphus squarrosus).



APPENDIX 6b. Distribution of Rushes (Juncus sp.) and Gorse (Ulex europaeus) at Boghall glen.

APPENDIX 7

Qualitative composition of food in the stomachs of moles from Boghall Farm, Bilston and Roslene Fields, and a garden in 1967/68 winter.

Site	Number of stomachs examined	Percentage number of stomachs containing:							
		Earthworms	Insect Larvae	Adult Insects	Earthworm cocoons	Slugs	Gentipedes	Plant Materials	Stomach stones
Boghall Farm	25	100	84	20	36	16	12	12	-
Bilston Field	10	90	50	20	40	10	10	20	10
Roslene Field	9	66.7	55.6	11.1	22.2	-	-	-	-
Garden	6	100	50	33.3	16.7	33.3	82.2	-	-
All sites	50	92	68	20	32	14	18	10	2

## APPENDIX 8

## Species composition of earthworms at Boghall glen

Number of samples	Date	Section	Adults										Immatures				Adults and Immatures			
			1 A. caliginosa	2 A. chlorotica	3 D. rubida	4 D. octaedra	5 E. rosea	6 L. castaneus	7 L. festivus	8 L. rubellus	9 L. terrestris	10 O. cyaneum	11 A. caliginosa E. rosea and O. cyaneum	12 A. chlorotica	13 Lumbricus sp.	14 Dendrobaena sp.	15 A. caliginosa E. rosea and O. cyaneum	16 A. chlorotica	17 Lumbricus sp.	18 Dendrobaena sp.
30	13/4/68	A	236	23	1	15	6	3	-	142	-	8			919					
10		B	-	-	6	6	2	-	-	64	-	-			347					
9	26/4/68	A	117	21	-	-	10	-	-	55	-	1	319	29	274	-	447	50	329	-
3		B	-	-	-	-	4	-	-	22	-	-	-	-	168	-	-	-	194	-
9	6/5/68	A	66	17	-	3	7	1	2	52	-	1	129	8	145	-	203	25	200	3
3		B	-	-	-	1	4	4	-	11	-	-	-	-	77	-	-	-	92	3
30	17/5/68	A	235	9	1	1	10	14	9	208	-	8	332	12	599	-	585	21	830	2
10		B	-	-	1	-	4	4	-	52	-	-	-	-	169	-	-	-	225	1
9	27/5/68	A	156	5	-	8	13	2	8	124	2	7	165	4	218	-	341	9	354	8
3		B	-	-	-	-	2	2	-	24	-	-	-	-	78	-	-	-	104	-
9	10/6/69	A	2	2	-	5	2	-	1	21	-	1	5	2	28	-	10	4	50	5
3		B	-	-	-	1	-	-	-	14	-	-	-	-	20	-	-	-	34	1
9	24/6/68	A	1	-	2	1	1	1	4	49	6	1	6	-	89	-	9	-	149	3
3		B	-	-	1	1	-	-	-	15	-	-	-	-	62	-	-	-	77	2
30	4/7/68	A	61	19	-	-	7	7	-	268	1	-	71	44	294	-	139	63	570	-
10		B	-	-	-	3	4	4	-	70	-	-	-	-	125	2	-	-	199	5
9	11/7/68	A	12	1	-	-	1	1	3	110	1	-	27	3	102	-	40	4	217	-
3		B	-	-	-	-	4	4	-	25	-	-	-	-	51	-	-	-	80	-
9	23/7/68	A	73	18	-	2	5	-	5	142	1	-	66	5	131	-	144	23	279	2
3		B	-	-	-	1	-	-	-	24	-	-	-	-	57	-	-	-	81	1
9	5/8/68	A	5	1	-	1	1	1	2	66	2	-	7	2	36	-	13	3	107	1
3		B	-	-	-	1	3	3	-	20	-	-	-	-	15	-	-	-	38	1
9	20/8/68	A	44	6	7	-	-	-	1	113	1	-	45	1	67	-	89	7	182	7
3		B	-	-	3	2	-	-	-	26	-	-	-	-	16	-	-	-	42	5
30	31/8/68	A	269	53	17	13	18	4	1	340	2	6	227	27	192	9	520	80	539	39
10		B	-	-	17	3	-	-	-	66	-	-	-	-	48	44	-	-	114	64
9	16/9/68	A	119	18	12	4	5	1	-	132	2	1	77	5	75	6	202	23	210	22
3		B	-	-	6	4	-	-	-	19	-	-	-	-	24	-	-	-	43	10
9	30/9/68	A	113	4	52	6	2	1	6	182	1	3	69	3	119	10	187	7	309	68
3		B	-	-	5	2	-	2	-	16	-	-	-	-	13	1	-	-	31	8

[Contd.]

## APPENDIX 8 (contd.)

	Date		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
30	6/10/68	A	507	17	61	8	21	9	3	501	5	4	468	6	375	7	1000	23	893	76
10		B	-	-	11	1		-	-	38	-	-	-	-	38	5	-	-	76	17
9	14/10/68	A	86	6	14	3	4	6	-	102	-	1	77	1	119	9	168	7	227	26
3		B	-	-	13	6		4	-	39	-	-	-	-	57	5	-	-	100	24
9	28/10/68	A	151	17	29	1	6	-	1	123	2	1	153	4	197	7	311	21	323	37
3		B	-	-	6	-		-	-	13	-	-	-	-	37	2	-	-	50	8
30	5/11/68	A	238	5	19	2	4	6	1	243	4	8	367	4	167	4	617	9	421	25
10		B	-	-	26	4		-	-	29	-	-	-	-	31	6	-	-	60	36
30	11/11/68	A	67	2	4	4	2	4	1	89	1	1	68	1	86	-	138	3	181	8
10		B	-	-	11	-		-	-	10	-	-	-	-	16	15	-	-	26	16
9	25/11/68	A	60	4	26	2	3	6	-	86	1	3	58	2	144	10	124	6	237	38
3		B	-	-	1	2		1	-	10	-	-	-	-	22	3	-	-	33	6
9	4/12/68	A	263	24	26	5	16	8	3	326	3	9	390	13	385	3	678	37	725	34
3		B	-	-	11	3		2	-	15	-	-	-	-	28	10	-	-	45	24
30	9/12/68	A	42	3	4	3	-	1	-	58	1	1	53	3	70	3	96	6	130	10
10		B	-	-	3	1		-	-	24	-	-	-	-	17	3	-	-	41	7
9	12/1/68	A	40	2	1	-	5	2	1	67	1	7	66	-	71	2	118	2	142	3
3		B	-	-	11	-		-	-	6	-	-	-	-	2	-	-	-	8	1
20	26/1/69	A	164	26	13	1	6	2	-	82	-	5	186	8	100	-	361	34	184	4
6		B	-	-	8	-		-	-	28	-	-	-	-	24	1	-	-	52	9
20	7/3/69	A	7	2	-	-	-	-	-	19	1	3	14	1	26	-	24	3	46	-
6		B	-	-	-	-	-	-	-	5	-	-	-	-	3	-	-	-	8	-
20	27/3/69	A	31	2	2	1	1	1	-	11	-	7	55	1	16	1	94	3	28	4
6		B	-	-	-	-	-	-	-	6	-	-	-	-	1	-	-	-	7	-
9	8/4/69	A	55	4	1	3	8	1	1	20	2	5	81	3	27	1	149	7	51	5
3		B	-	-	-	-	-	-	-	3	-	-	-	-	1	-	-	-	4	-
20	23/4/69	A	199	13	12	33	9	-	-	97	3	11	331	15	123	9	550	28	223	54
6		B	-	-	6	1	-	-	-	6	-	-	-	-	6	3	-	-	12	10
20	13/5/69	A	388	42	9	10	33	1	2	103	8	24	611	37	196	3	1056	79	310	22
6		B	-	-	5	1		-	-	13	-	-	-	-	27	11	-	-	40	17
20	9/6/69	A	155	20	10	36	29	1	1	68	3	22	354	2	110	15	560	22	183	61
6		B	-	-	3	1	-	-	-	15	-	-	-	-	25	10	-	-	40	14

## APPENDIX 9

Earthworm sampling at Boghall glen

Date of Sampling	Sample number	Number and weight (in g) of earthworms from each sample (1 yd. <sup>2</sup> )							
		Section A						Section B	
		Column 1		Column 2		Column 3		No.	Wt.
		No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
	1	2	3	4	5	6	7	8	
13.4.68	1	30	13.7	50	10.0	26	11.2	116	41.0
	2	101	48.5	30	99.6	5	1.2	7	3.8
	3	97	39.5	38	19.2	86	32.7	1	0.2
	4	27	8.4	52	15.3	33	12.3	71	30.0
	5	24	8.4	31	12.5	8	6.2	24	8.3
	6	78	37.3	31	8.9	14	7.6	29	8.3
	7	27	3.8	75	24.8	113	49.6	28	9.7
	8	50	18.6	48	18.8	82	34.4	8	31.7
	9	59	26.2	46	18.2	11	7.4	117	39.8
	10	12	7.5	27	10.3	21	9.8	25	6.7
26.4.68	1	59	15.8	103	24.2	159	42.3	26	5.7
	2	118	49.9	108	26.6	72	29.6	80	16.7
	3	16	8.2	141	55.1	50	12.5	88	16.8
6.5.68	1	38	14.0	48	14.6	56	15.3	31	10.2
	2	76	20.0	74	22.4	58	15.7	55	10.5
	3	9	3.4	37	9.8	33	10.5	11	1.3
17.5.68	1	43	17.1	67	15.5	14	8.6	16	10.5
	2	66	27.8	94	30.0	38	14.2	31	14.7
	3	13	4.6	44	15.5	50	14.4	2	0.7
	4	35	13.4	22	8.2	5	3.8	17	6.8
	5	42	22.1	76	19.8	16	7.6	25	9.1
	6	8	4.7	61	24.7	90	30.8	2	0.9
	7	31	10.6	38	10.3	14	7.1	11	4.3
	8	57	19.3	174	56.1	65	23.2	41	17.2
	9	27	12.0	141	49.1	11	4.2	12	5.6
	10	18	5.5	45	15.2	25	13.2	77	22.8
27.5.68	1	97	31.2	114	43.0	107	33.4	15	7.5
	2	74	26.1	141	47.5	19	12.0	36	11.6
	3	52	30.0	73	28.5	39	19.3	55	16.4
10.6.68	1	0	0	3	1.8	6	2.9	10	6.5
	2	3	1.7	21	8.3	3	2.0	17	6.9
	3	21	6.0	5	1.9	6	3.6	9	3.5

## Appendix 9 (Contd.)

Date of Sampling	Sample Number	Section A						Section B	
		Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8
24.6.68	1	36	25.0	17	10.5	16	5.2	16	4.6
	2	13	5.1	18	7.6	17	9.6	32	8.1
	3	17	4.6	24	10.5	12	6.8	32	8.3
4.7.68	1	21	6.5	16	4.4	13	7.8	28	12.3
	2	33	11.2	9	2.8	0	0	12	5.9
	3	44	9.0	14	5.1	49	16.0	18	9.0
	4	26	10.5	43	16.7	34	9.8	8	1.2
	5	64	24.0	0	0	15	7.7	4	1.1
	6	0	0	36	13.3	33	13.4	25	10.5
	7	93	20.8	32	15.0	30	10.7	23	7.8
	8	24	10.8	20	6.0	9	3.9	21	8.9
	9	17	7.2	26	9.5	18	10.8	57	17.0
	10	26	12.8	21	11.0	6	4.1	8	2.9
11.7.68	1	17	8.8	34	11.2	31	8.7	22	10.8
	2	34	16.5	43	13.4	33	11.6	18	7.1
	3	20	11.5	34	16.2	14	6.5	41	11.2
23.7.68	1	62	25.2	101	34.9	60	21.4	20	13.9
	2	73	38.0	44	15.8	30	15.7	7	3.0
	3	30	17.8	21	15.3	23	14.7	59	17.5
5.8.68	1	16	14.8	17	6.5	1	0.3	1	0.7
	2	11	6.5	31	15.4	10	4.0	29	12.2
	3	16	9.0	16	8.3	6	2.9	9	4.0
20.8.68	1	28	16.3	27	14.0	43	16.2	19	10.0
	2	23	10.4	65	24.2	35	17.0	2	0.8
	3	27	14.0	15	10.4	20	10.0	28	11.5
31.8.68	1	70	22.5	29	4.8	7	2.5	15	4.0
	2	29	11.0	44	13.2	18	7.1	35	10.5
	3	53	13.0	49	13.0	18	7.1	25	12.0
	4	60	27.0	14	7.9	34	12.2	3	2.0
	5	106	34.0	51	17.7	32	21.0	20	4.5
	6	27	13.0	37	12.0	35	10.8	19	5.0
	7	11	3.0	60	21.3	24	7.6	9	3.5
	8	20	8.5	75	33.7	8	5.7	13	4.5
	9	58	29.5	132	41.0	13	7.5	39	10.5
	10	10	4.0	40	14.4	11	6.0	3	2.0
16.9.68	1	65	29.0	84	26.5	95	35.5	16	5.0
	2	42	20.0	49	19.5	34	18.0	17	5.0
	3	20	11.0	29	6.5	29	9.5	30	10.0

## Appendix 9 (Contd.)

Date of Sampling	Sample Number	Section A				Column 3		Section B	
		Column 1 1	Column 2 2	Column 3 3	Column 4 4	Column 5 5	Column 6 6	Column 7 7	Column 8 8
30.9.68	1	43	19.5	78	29.5	67	25.0	9	6.0
	2	44	19.0	79	24.0	66	34.0	9	2.5
	3	9	4.5	77	29.0	84	20.5	25	9.5
6.10.68	1	62	22.0	79	32.5	36	10.0	10	6.0
	2	78	24.0	86	36.0	75	28.0	0	0
	3	119	53.0	67	31.5	127	31.0	11	3.0
	4	53	22.5	42	16.0	29	11.6	5	2.5
	5	49	17.0	20	11.0	113	25.0	7	4.0
	6	77	26.5	38	13.0	32	12.6	10	5.4
	7	9	3.5	0	0	9	3.0	7	1.5
	8	92	29.5	122	38.5	150	48.4	4	1.6
	9	27	13.5	46	15.5	70	27.5	31	12.0
	10	83	38.0	134	38.0	62	23.5	14	4.6
14.10.68	1	47	14.6	73	28.0	49	16.5	13	3.5
	2	52	25.0	70	17.5	70	33.0	21	10.5
	3	4	2.5	49	10.0	14	3.5	90	27.0
28.10.68	1	67	28.0	108	42.0	138	30.0	34	6.5
	2	59	26.0	136	42.0	40	10.0	11	6.0
	3	5	1.2	47	10.5	84	20.5	21	5.0
5.11.68	1	47	16.5	51	14.0	4	2.0	16	6.0
	2	41	13.0	25	5.4	52	11.5	17	9.0
	3	34	8.5	13	4.5	3	1.0	16	6.0
	4	42	20.5	38	13.0	2	1.8	1	0.6
	5	23	8.2	21	12.5	31	10.0	2	1.2
	6	31	11.0	33	15.5	36	17.2	9	2.0
	7	4	3.2	154	43.5	35	15.5	21	4.2
	8	33	9.0	52	19.0	11	4.0	8	2.0
	9	78	21.0	70	23.0	11	3.0	13	4.0
	10	34	9.0	39	13.0	13	4.0	4	1.0
11.11.68	1	25	12.5	42	12.0	90	21.0	15	2.5
	2	42	10.0	47	18.5	48	26.0	19	7.0
	3	10	4.0	10	4.0	16	3.0	8	2.0
25.11.68	1	37	18.5	65	20.0	37	10.0	19	10.0
	2	26	10.2	40	13.2	63	25.0	7	2.0
	3	6	3.2	49	11.0	78	21.0	17	4.0

## Appendix 9 (Contd.)

Date of Sampling	Sample Number	Column 1		Section A Column 2		Column 3		Section B	
		1	2	3	4	5	6	7	8
4.12.68	1	136	48.0	40	6.4	10	3.1	8	4.7
	2	108	37.0	52	24.5	123	38.7	7	1.2
	3	6	2.0	6	2.0	50	19.0	0	0
	4	68	27.0	41	10.5	24	14.4	1	1.5
	5	42	19.5	50	15.0	84	28.5	0	0
	6	7	4.2	89	28.6	10	4.7	13	1.5
	7	34	14.5	50	14.5	27	8.7	18	6.0
	8	16	6.0	69	25.7	18	7.0	2	1.0
	9	19	8.6	121	38.0	81	41.5	1	0.3
	10	21	12.5	27	10.5	43	18.5	21	6.5
9.12.68	1	42	16.5	17	8.0	48	10.0	22	11.7
	2	16	6.0	36	9.1	41	18.0	0	0
	3	2	1.5	35	10.0	4	2.0	27	7.5
12.1.69	1	13	4.2	13	3.0	8	2.7	1	0.6
	2	19	11.2	14	4.6	26	7.2	0	0
	3	20	6.5	8	3.0	3	1.4	7	3.5
	4	3	2.0	24	12.0	27	7.7	2	2.7
	5	8	3.2	13	4.0	4	2.0	0	0
	6	0	0	16	5.5	22	11.5	2	0.7
	7	5	2.8						
	8	16	6.0						
26.1.69	1	35	8.5	31	8.0	5	1.2	1	1.2
	2	21	5.7	5	3.3	72	16.0	27	13.0
	3	76	15.0	4	2.0	3	1.2	8	4.1
	4	44	11.0	35	10.0	70	15.0	0	0
	5	13	8.5	19	4.0	5	2.2	14	5.3
	6	11	5.2	55	19.0	47	15.0	14	3.3
	7	9	3.4						
	8	30	11.5						
7.3.69	1	0	0	4	1.5	5	1.5	3	2.0
	2	3	0.5	1	0.4	0	0	0	0
	3	17	12.0	5	3.0	4	1.4	0	0
	4	2	0.5	3	3.0	8	4.0	4	2.5
	5	1	0.8	2	0.5	0	0	0	0
	6	4	0.8	1	0.2	4	3.0	1	0.8
	7	2	0.7						
	8	7	2.0						

## Appendix 9 (Contd.)

Date of Sampling	Sample Number	Section A						Section B	
		Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	7	8
27.3.69	1	26	8.7	16	3.5	1	0.1	1	0.1
	2	15	8.5	0	0	4	07.	2	2.7
	3	8	5.2	4	1.2	1	0.1	0	0
	4	6	2.4	4	1.5	1	0.5	0	0
	5	5	2.0	4	0.8	6	0.8	1	0.9
	6	0	0	14	3.6	2	0.8	3	2.7
	7	4	1.5						
	8	7	2.9						
8.4.69	1	20	12.5	71	15.9	17	3.3	2	1.3
	2	15	2.8	39	10.7	26	7.3	0	0
	3	1	0.4	19	5.4	4	2.9	2	1.6
23.4.69	1	66	24.0	58	18.0	16	4.5	9	4.0
	2	73	17.5	1	1.1	54	9.2	1	0.2
	3	42	8.8	17	9.0	5	2.7	0	0
	4	18	4.0	127	29.0	4	4.0	1	1.0
	5	1	1.1	52	14.4	50	11.0	10	2.2
	6	25	4.4	153	29.5	69	23.0	3	1.0
	7	0	0						
	8	22	4.8						
13.5.69	1	88	35.0	29	12.2	33	17.0	28	10.0
	2	197	47.2	4	3.0	190	38.2	0	0
	3	108	38.8	41	18.5	5	3.6	0	0
	4	85	24.0	85	24.0	19	12.0	4	2.0
	5	27	12.2	144	51.6	106	30.7	37	10.0
	6	13	4.0	126	29.5	50	21.2	3	2.0
	7	26	11.0						
	8	99	28.7						
9.6.69	1	23	14.0	89	28.0	26	14.0	12	7.0
	2	60	17.0	5	3.0	114	27.0	2	1.0
	3	18	6.0	31	11.0	8	5.0	3	0.5
	4	27	8.0	80	27.0	5	5.5	1	0.2
	5	2	1.0	69	23.5	88	28.5	28	9.5
	6	37	5.5	26	8.0	82	35.5	12	5.0
	7	10	5.0						
	8	22	7.0						

## APPENDIX 10

Population density of earthworms in Section A and Section B of  
Boghall glen

	Date of Sampling	Mean ( $\pm$ S.E.) population density in thousands per acre			t	t at PO.05
		Section A	Section B	Difference		
1	13/4/68	168.9 $\pm$ 8.2	119.5 $\pm$ 11.6	49.4 $\pm$ 5.8	8.52	2.03
2	26/4/68	370.3 $\pm$ 4.5	256.5 $\pm$ 3.6	113.8 $\pm$ 5.8	19.62	2.23
3	6/5/68	183.0 $\pm$ 5.6	126.3 $\pm$ 3.9	56.7 $\pm$ 5.8	9.78	2.23
4	17/5/68	132.6 $\pm$ 4.9	73.6 $\pm$ 7.9	59.0 $\pm$ 5.8	10.17	2.03
5	27/5/68	333.0 $\pm$ 3.8	148.1 $\pm$ 3.1	184.9 $\pm$ 5.4	34.24	2.23
6	10/6/68	22.7 $\pm$ 6.5	56.1 $\pm$ 8.7	33.4 $\pm$ 5.8	5.76	2.23
7	24/6/68	89.5 $\pm$ 2.0	116.6 $\pm$ 8.7	27.1 $\pm$ 5.3	5.11	2.23
8	4/7/68	75.0 $\pm$ 6.2	81.3 $\pm$ 4.6	6.3 $\pm$ 5.2	1.21	2.03
9	11/7/68	126.3 $\pm$ 1.6	126.3 $\pm$ 7.7	0 $\pm$ 5.1	0	2.23
10	23/7/68	214.4 $\pm$ 3.3	99.2 $\pm$ 7.7	115.2 $\pm$ 6.3	18.29	2.23
11	5/8/68	50.3 $\pm$ 5.4	36.8 $\pm$ 10.2	13.5 $\pm$ 14.3	0.94	2.23
12	20/8/68	137.0 $\pm$ 2.3	56.1 $\pm$ 13.1	80.9 $\pm$ 6.8	11.90	2.23
13	31/8/68	149.1 $\pm$ 5.1	66.8 $\pm$ 6.3	82.3 $\pm$ 7.3	11.27	2.03
14	16/9/68	214.4 $\pm$ 5.0	99.2 $\pm$ 1.7	115.2 $\pm$ 7.7	14.96	2.23
15	30/9/68	250.2 $\pm$ 4.3	61.0 $\pm$ 5.5	189.2 $\pm$ 9.3	20.34	2.23
16	6/10/68	203.3 $\pm$ 9.5	34.4 $\pm$ 6.4	168.9 $\pm$ 7.7	21.94	2.23
17	14/10/68	178.1 $\pm$ 6.7	137.0 $\pm$ 9.6	41.1 $\pm$ 13.2	3.11	2.23
18	28/10/68	271.0 $\pm$ 6.6	92.0 $\pm$ 2.2	179.0 $\pm$ 9.7	18.45	2.23
19	5/11/68	120.5 $\pm$ 7.0	39.2 $\pm$ 15.0	54.2 $\pm$ 7.7	7.04	2.03
20	11/11/68	140.8 $\pm$ 5.0	66.3 $\pm$ 1.6	77.5 $\pm$ 7.7	9.68	2.23
21	25/11/68	178.1 $\pm$ 5.0	66.3 $\pm$ 2.7	111.8 $\pm$ 8.7	12.85	2.23
22	4/12/68	161.7 $\pm$ 6.8	17.9 $\pm$ 9.6	143.8 $\pm$ 5.5	26.15	2.03
23	9/12/68	94.4 $\pm$ 7.7	36.8 $\pm$ 17.9	57.6 $\pm$ 18.4	3.13	2.23
24	12/1/69	48.4 $\pm$ 5.8	5.8 $\pm$ 5.3	42.6 $\pm$ 5.3	10.88	2.06
25	26/1/69	76.5 $\pm$ 8.2	27.1 $\pm$ 10.2	49.4 $\pm$ 5.3	9.32	2.06
26	7/3/69	12.6 $\pm$ 5.5	3.9 $\pm$ 4.6	8.7 $\pm$ 5.4	1.61	2.06
27	27/3/69	19.8 $\pm$ 6.8	4.8 $\pm$ 3.4	15.0 $\pm$ 5.3	2.83	2.06
28	8/4/69	76.0 $\pm$ 8.7	5.8 $\pm$ 1.5	70.2 $\pm$ 11.1	6.32	2.23
29	23/4/69	102.1 $\pm$ 15.1	11.6 $\pm$ 6.8	90.5 $\pm$ 36.8	2.46	2.06
30	13/5/69	227.0 $\pm$ 8.7	21.3 $\pm$ 16.0	205.7 $\pm$ 6.8	30.25	2.06
31	9/6/69	130.2 $\pm$ 8.2	29.5 $\pm$ 7.7	100.7 $\pm$ 5.8	17.36	2.06
1-31	13/4/68- 9/6/69	112.8 $\pm$ 10.6	42.6 $\pm$ 11.6	70.2 $\pm$ 5.6	12.54	1.96

## APPENDIX 11

Biomass of Earthworms in areas Sections A and B of Boghall glen

	Date of Sampling	Biomass of earthworms (in Kg. per acre) at P0.05 confidence limit	
		Section A	Section B
1	13/4/68	82.5 - 118.1	69.3 - 104.5
2	26/4/68	109.3 - 174.9	31.2 - 95.4*
3	6/5/68	34.8 - 100.4	3.4 - 67.6
4	17/5/68	64.2 - 99.8	27.2 - 62.4*
5	27/5/68	102.0 - 167.6	25.2 - 89.4*
6	10/6/68	0 - 47.9	0 - 59.3
7	24/6/68	12.6 - 78.2	1.8 - 66.0
8	4/7/68	27.5 - 63.1	19.5 - 54.7
9	11/7/68	23.3 - 88.9	14.8 - 79.0
10	23/7/68	74.1 - 139.7	23.4 - 87.6
11	5/8/68	3.6 - 69.2	0 - 59.3
12	20/8/68	34.8 - 104.0	3.9 - 68.1*
13	31/8/68	51.9 - 87.5	10.7 - 45.9*
14	16/9/68	61.6 - 127.2	0.1 - 64.4*
15	30/9/68	77.5 - 143.5	0 - 61.1*
16	6/10/68	95.5 - 131.1	2.1 - 37.3*
17	14/10/68	48.2 - 113.8	34.1 - 98.3
18	28/10/68	80.3 - 145.9	0 - 60.3*
19	5/11/68	39.2 - 74.8	0 - 35.0*
20	11/11/68	26.9 - 92.5	0 - 50.6
21	25/11/68	38.3 - 103.9	6.3 - 57.9
22	4/12/68	63.2 - 98.8	0 - 28.6*
23	9/12/68	10.8 - 76.4	0 - 63.1
24	12/1/69	2.3 - 46.3	0 - 28.8
25	26/1/69	18.1 - 62.1	0 - 44.4
26	7/3/69	0 - 30.7	0 - 27.0
27	27/3/69	0 - 32.8	0 - 27.9
28	8/4/69	0.1 - 65.7	0 - 27.4
29	23/4/69	31.2 - 74.2	0 - 29.5*
30	13/5/69	89.0 - 133.9	0 - 42.1*
31	9/6/69	45.6 - 89.6	0 - 41.4*
1 - 31	13/4/68-9/6/69	61.0 - 74.4	22.9 - 37.1*

\* Differences significant at P0.05

## APPENDIX 12

Population densities of invertebrates at Boghall glen in June 1968

Invertebrates		Population density (No. per yd. <sup>2</sup> )		
		Section A	Section B	Sections A & B
1	All earthworms	185.0	29.5	157.0
2	A. caliginosa	40.0	-	33.0
3	A. chlorotica	5.0	-	4.2
4	D. octaedra	2.5	-	2.1
5	D. rubida	1.9	-	1.6
6	E. rosea	5.0	-	4.2
7	L. castaneus	-	-	-
8	L. rubellus	12.5	2.9	10.9
9	O. cyaneum	3.8	-	3.1
10	A. caliginosa	71.2	-	60.3
11	A. chlorotica	8.8	-	7.3
12	Dendrobaena sp.	-	-	-
13	Lumbricus sp.	30.6	26.5	30.2
14	O. cyaneum	-	-	-
15	A. caliginosa	111.3	-	93.6
16	A. chlorotica	13.8	-	11.4
17	E. rosea	5.0	-	3.6
18	Dendrobaena sp.	5.6	-	4.2
19	Lumbricus sp.	43.8	29.4	41.1
20	O. cyaneum	3.8	-	3.1
21	Earthworm cocoons	319.4	200.3	301.1
22	All insect larvae	35.6	61.9	40.6
23	Formicidae	-	-	-
24	Noctuidae	-	-	-
25	Carabidae	-	-	-
26	Curculionidae	-	-	-
27	Elateridae	5.0	47.1	12.5
28	Scarabaeidae	-	-	-
29	Bibionidae	-	-	-
30	Dolichopodidae	-	-	-
31	Empididae	-	-	-
32	Muscidae	11.3	8.8	10.9
33	Rhagionidae	-	-	-
34	Tipulidae	13.1	5.9	17.2
35	Insect pupae	4.4	2.9	4.2
36	Adult insects	4.4	5.9	4.7
37	Arion fasciatus	2.5	2.9	3.1
38	Agrolimax reticulatus	0.6	-	-

## APPENDIX 13

## Population densities of invertebrates at Boghall glen in May 1969

Invertebrates		Population density (No. per yd <sup>2</sup> )				
		Section A	Section B	Sections A & B		
1	All earthworms	241.3	32.4	206.4		
2	A. caliginosa	28.8	-	23.9		
3	A. chlorotica	10.6	-	8.8		
4	D. octaedra	3.1	-	2.6		
5	D. rubida	3.1	-	2.6		
6	E. rosea	1.9	-	1.6		
7	L. castaneus	0.6	-	0.5		
8	L. rubellus	2.5	-	2.1		
9	O. lacteum	4.4	-	3.6		
10	Earthworms (Lumbricidae)	Immatures	A. caliginosa	138.8	-	115.4
11			A. chlorotica	23.8	-	19.8
12			Dendrobaena sp.	3.1	17.7	5.7
13			Lumbricus sp.	19.4	14.7	18.7
14		O. lacteum	1.3	-	1.0	
15	Earthworms	Adults and Immatures	A. caliginosa	167.5	-	139.4
16			A. chlorotica	34.4	-	28.6
17			E. rosea	1.9	-	1.6
18			Dendrobaena sp.	9.4	17.7	10.9
19			Lumbricus sp.	22.5	14.7	21.3
20		O. lacteum	5.6	-	4.7	
21	Earthworm cocoons	433.8	197.4	482.0		
22	All insect larvae	256.9	344.7	274.6		
23	Formicidae	6.9	-	5.7		
24	Noctuidae	0.6	2.9	1.0		
25	Carabidae	5.0	11.8	6.2		
26	Curculionidae	0.6	-	0.5		
27	Elateridae	13.1	41.2	18.2		
28	Scarabaeidae	0.6	-	0.5		
29	Bibionidae	136.3	209.2	150.3		
30	Dolichopodidae	23.1	35.4	25.5		
31	Empididae	6.3	8.8	6.8		
32	Muscidae	5.6	17.7	7.8		
33	Rhagionidae	1.9	5.9	2.6		
34	Tipulidae	56.9	11.8	49.4		
35	Insect pupae	10.6	-	8.8		
36	Adult insects	1.9	-	1.6		
37	Slugs	Arion fasciatus	2.5	-	) 4.7	
38		Agrolimax reticulatus	3.1	-		

## APPENDICES 14 and 15

Comparison of the population densities of invertebrates in  
Section A and Section B of Boghall glen

(i) June 1968

Appendix 14

Invertebrates	Mean (+ S.E.) population density (in Nos. per 4" x 7" soil core)			t
	Section A	Section B	Difference	
All invertebrates	5.4±1.99	2.3±2.29	3.1±0.94	3.30*
Earthworms	1.82±1.70	0.26±0.75	1.56±0.35	4.46*
Earthworm cocoons	3.21±4.24	1.46±2.00	1.75±0.65	2.69*
Insect larvae	0.35±0.76	0.60±0.97	0.25±0.22	1.14
Elaterid larvae	0.04±0.26	0.43±0.85	0.39±0.17	2.29*

(ii) May 1969

Appendix 15

Invertebrates	Mean (+ S.E.) population density (in Nos. per 4" x 7" soil core)			t
	Section A	Section B	Difference	
All invertebrates	10.1±15.6	5.5±1.7	4.6±3.3	1.39
Earthworms	2.33±2.4	0.3±0.8	2.02±0.4	4.30*
Earthworm cocoons	5.2±6.4	1.9±4.4	3.3±1.42	2.32*
Insect larvae	2.5±14.1	3.3±8.7	0.8±3.16	0.25
Elaterid larvae	0.2±0.5	0.4±0.5	0.27±0.15	1.80

\* Differences significant (t at P0.05 = 1.96)

APPENDIX 16Seasonal trend in the weight of testis of male moles

## (a) Adults

Month	Mean ( $\pm$ S.E.) weight of testis (in mg.)
March	783 $\pm$ 106
April	434 $\pm$ 119
May	321 $\pm$ 47
June	203 $\pm$ 49
July	170 $\pm$ 28

Differences between months in testis weight of adults

Months	Mean ( $\pm$ S.E.) difference in testis weight (in mg.)	t	t at P0.05
March and April	349 $\pm$ 74	4.75	2.07*
March and May	462 $\pm$ 42	10.90	2.07*
March and June	580 $\pm$ 52	11.15	2.13*
March and July	613 $\pm$ 93	6.57	2.31*
April and May	113 $\pm$ 48	2.35	2.04*
April and June	231 $\pm$ 48	4.81	2.15*
April and July	264 $\pm$ 95	2.76	2.11*
May and June	118 $\pm$ 25	4.82	2.06*
May and July	151 $\pm$ 42	3.56	2.12*
June and July	33 $\pm$ 46	0.72	2.26

\* Differences significant (P = 0.05)

## (b) Differences between Adults and Juveniles in June and July

Month	Adults	Juveniles	Difference	t	t at P0.01
June	203 $\pm$ 49	49 $\pm$ 6	154 $\pm$ 25	6.2	2.87*
July	170 $\pm$ 28	44 $\pm$ 31	126 $\pm$ 32	3.9	2.98*

\* Differences highly significant (P = 0.01)

## APPENDIX 17

Seasonal trend in the weight of the reproductive tract (uteri + ovaries) in female moles

## (a) Adults

Month	Mean ( $\pm$ S.E.) weight of reproductive tract (in mg.)
April	760 $\pm$ 170
May	491 $\pm$ 327
June	210 $\pm$ 46
July	236 $\pm$ 96

## Differences between months in weight of reproductive tract

Month	Mean ( $\pm$ S.E.) difference in weight of reproductive tract (in mg.)	t	t at P0.05
April and May	269 $\pm$ 207	1.30	2.16
April and June	550 $\pm$ 101	5.45	2.16*
April and July	524 $\pm$ 130	4.03	2.26*
May and June	281 $\pm$ 157	1.79	2.2
May and July	255 $\pm$ 231	1.10	2.16
June and July	26 $\pm$ 66	0.40	2.16

## (b) Differences between adults and juveniles in June and July

Month	Mean ( $\pm$ S.E.) weight of reproductive tract (in mg.)			t	t at P0.05
	Adults	Juveniles	Difference		
June	210 $\pm$ 46	48 $\pm$ 9	161 $\pm$ 49	3.28	2.15*
July	236 $\pm$ 96	78 $\pm$ 28	158 $\pm$ 76	3.29	2.62*
August	-	113 $\pm$ 59	-		

\* Differences significant at P0.05

## APPENDIX 18

Species composition of earthworms in 5 mole fortresses at  
Boghall glen on 28.2.69.

Species of earthworms	Number and percentage number of each species in each fortress									
	Fortress 1		Fortress 2		Fortress 3		Fortress 4		Fortress 5	
	Total number	Percentage number	Total number	Percentage number	Total number	Percentage number	Total number	Percentage number	Total number	Percentage number
<i>A. caliginosa</i>	17	33.3	106	88.3	34	97.1	11	100	102	95.4
<i>A. chlorotica</i>	1	2.0								
<i>D. rubida</i>					1	2.9				
<i>E. rosea</i>			2	1.7						
<i>L. castaneus</i>			1	0.8						
<i>L. rubellus</i>			3	2.5					4	3.7
<i>L. terrestris</i>	22	43.1								
<i>O. cyaneum</i>	11	21.6	8	6.7					2	1.9
All species	51		120		35	11			108	

## APPENDIX 19

Record of mole trapping experiment at Boghall glen during March to August 1969

		The diet of the mole (X = occurrence)																										
Month	Sex	Body weight (in g)	Weight of stomach and food (in g)	Weight of empty stomach (in g)	Weight of earthworms (in g)	Weight of insect larvae (in g)	Number of adult insects	Number of earthworm cocoons	Weight of slugs (in g)	Number of centipedes	Weight of stomach stones (in g)	All earthworms	Number or occurrence of each family of insect larvae													Number of Slugs		'Age' of moles
													Formicidae	Noctuidae	Carabidae	Elateridae	Bibionidae	Dolichopodidae	Empididae	Muscidae	Rhagionidae	Tipulidae	Arion fasciatus	Agrolimax Reticulatus	Plant materials			
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27		
Jan	F	Killed in a live-mole trapping trial																									Adult	
Mar	M	103.0	8.7	1.0	2.72	0.27	-	5	0.20		0.36	X				2	54	1	1	1	2	6	-	2	X			
"	M	89.0	2.1	0.9	-	0.46	-	-				X					X					X	1					
"	M	96.0	6.0	1.4	1.06	-	-	1	0.27			X								2								
"	M	96.5	7.5	1.1	2.72	-	-	-		1		X		X														
"	F	70.0	2.5	0.9	0.20	0.32	1					X										X						
"	F	65.4	2.9	0.8	0.14	0.33	1					X																
"	M	106.5	9.3	1.4	4.24	1.18	-	-				X																
"	M	116.0	12.7	1.5	6.84	0.45	1	1				X			2	1												
"	M	118.0	12.2	1.0	1.79	3.06	-	-	0.15		0.84	X				2								1	1	1	X	
"	M	104.0	8.7	-	-	-	-	-				X																
Apr	F	82.0	12.3	0.9	4.37	1.51	-	-			0.22	X				3	X											
"	F	79.0	3.5	1.0	0.50	0.35	-	2				X			1	1												
"	F	97.0	2.2	1.1	-	0.16	-	-				X			1						2	X						
"	M	127.0	15.2	1.2	5.8	0.61	-	-				X				1	2	4				21						
"	M	102.5	2.2	0.9	-	0.30	-	-				X		X				X										
"	M	103.5	11.6	1.0	4.77	0.37	-	-				X						1				6						
"	M	104.5	7.1	0.8	1.14	0.76	-	-	0.10		0.19	X			1							18		1	X			
"	M	98.5	2.1	1.0	-	0.17	-	-				X						X				X						
"	M	108.5	14.1	1.1	6.62	0.22	-	1				X					X					X						
"	M	101.5	5.6	1.1	0.76	0.49	-	-				X					8	3	2		3	6						
"	F	80.0	Trapped alive and kept in captivity																									
"	M	104.5	9.6	1.0	2.27	0.14	-	-				X					1	4	1		1	1						
"	M	105.0	5.6	0.7	0.34	0.96	-	-				X			1	1	4	4			1	16						
"	F	83.0	1.8	0.8	-	-	-	-	0.10	(Died after 3 days in captivity)																X		
"	F	92.5	5.9	1.2	1.83	0.03	-	-				X				3	3											
"	M	105.5	5.4	0.9	0.37	0.63	-	-				X		X	X		4	4				X						
"	M	100.0	3.6	1.1	-	0.11	1	1				X					X											
"	M	95.0	3.9	1.0	0.17	0.32	-	-				X		2	2		9					3						
"	M	Captured alive and kept in captivity																										
"	M	105.0	4.6	1.2	0.11	0.28	-	-				X					X	X				X						

## Appendix 19 (Contd.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Apr	F	90.0	2.6	1.1	0.28	0.06							X			1						1					Adult
"	F	76.5	6.5	0.9	1.18	1.00							X				1	3				5	X				"
"	M	113.5	7.4	1.2	1.50	0.73			1				X		2	4	2			2		2	7				"
"	F	84.5	7.6	1.1	1.61	0.69							X			1	1	1				5	X				"
"	M	100.0	5.2	0.9	0.13	1.20		1			1		X				X	327					X				"
"	M	Captured alive and kept in captivity																									
May	M	103.0	5.8	1.2	0.60	0.52							X				X		X	X			X				"
"	M	108.0	8.5	1.0	1.55	0.36							X		X	2			3	1			3				"
"	M	114.5	6.5	1.1	1.22	0.62		1					X			2	4	129		1		3	3				"
"	M	102.0	6.0	0.9	1.86	0.38							X		X				2				5				"
"	M	115.5	7.8	1.1	1.92	0.60							X				X	47		X			X				"
"	M	122.0	5.1	0.9	0.61	0.92							X		X	2	2	98		2			6				"
"	M	110.5	2.2	1.0	-	0.04							X						2				1				"
"	M	106.5	3.6	0.8	0.15	0.30							X			2	5		6	1			2				"
"	M	129.0	8.6	1.2	1.20	0.83							X		3	3	1		1				7				"
"	M	119.0	7.6	0.9	1.12	0.21				0.06			X			5							6		2		"
"	F	94.0	5.5	0.7	0.50	0.34					0.09		X			1	2		X				6			X	"
"	F	86.0	4.8	1.0	0.45	0.24							X			1			X	X			X				"
"	M	125.0	11.0	0.9	2.37	1.15					0.04		X			X	X		X	X		X	X			X	"
"	M	120.0	3.6	1.0	-	0.36			1				X			1						2	8			X	"
"	F	100.0	9.7	1.0	0.81	0.73						0.22	X				1		6	2		2	X				"
"	F	86.0	5.3	1.3	-	0.67						0.06	X			1			5				X				"
"	M	117.0	6.5	1.0	0.98	1.07							X				X		X	X			X				"
"	M	121.0	8.0	1.3	0.74	1.36							X				1						X				"
"	M	103.0	4.3	1.1	-	0.86							X				1						X				"
"	M	110.0	7.0	0.9	0.68	1.72							X					3	2				X				"
"	F	94.0	7.7	1.0	0.62	0.82							X						5				X				"
"	M	112.0	7.2	1.3	1.74	0.76							X			3	1						10				"
"	F	104.5	8.6	1.2	0.58	0.56							X		X		1						7				"
"	F	102.5	11.0	1.4	0.94	1.81							X						X				X				"
"	F	97.5	8.6	1.3	0.93	1.63				0.02		0.06	X			1			8	1		3	X	-	1		"
"	M	117.0	8.3	1.2	1.43	0.94						0.25	X		1								X			X	"
"	F	102.0	7.8	1.4	0.16	1.26							X			1							X				"
"	F	85.0	4.7	1.0	-	0.94			1			0.05	X		1					2			X				"
June	F	94.0	6.2	0.9	-	0.98							X		X		1		7				X				"
"	M	116.0	8.6	1.1	1.64	1.55		1		0.34			X	X	1		1	89	1			1	X	-	1	X	"
"	F	61.0	4.0	0.8	0.09	0.44							X									1	8			X	Juvenile
"	F	69.5	3.8	0.4	-	0.51							X										X				"
"	F	106.0	9.7	1.2	1.08	0.57				0.03			X										7	1	-		Adult
"	F	99.0	6.9	1.0	1.91	0.19				0.07			X		1	1	1							-	1		"
"	F	107.0	9.7	1.0	0.44	1.99							X		1			11					22				"
"	F	82.5	9.0	0.4	1.27	0.36		1					X				1						7				Juvenile
"	F	100.0	7.3	0.6	0.46	0.08							X										2				Adult
"	M	83.0	10.9	0.6	0.65	0.46							X			4							10				Juvenile
"	F	58.0	2.1	0.5	-	0.51							X										1				"
"	F	87.0	3.2	0.9	-	0.43							X										6				Adult
"	F	97.0	8.9	0.9	1.65	0.13							X										3				"

[Contd.]

## Appendix 19 (Contd.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
June	M	118.0	9.8	0.8	1.83	0.47				0.14		-	X			3							9	1		X	Adult
"	M	110.0	5.8	1.0	0.42	1.02							X			6							9				"
"	M	111.0	7.0	0.9	-	1.82							X				1		1	1			X				Juvenile
"	M	92.0	7.5	1.5	0.96	1.49							X							1			X				"
"	F	63.0	5.0	0.6	0.48	0.09							X			5							X				"
"	M	75.5	3.8	0.6	-	0.95							X										X				"
"	F	69.5	5.4	0.6	0.66	-							X										X				"
"	M	101.5	10.5	1.2	1.73	1.80							X			1							X				"
"	M	86.0	8.3	0.7	1.11	0.66							X										X				"
"	M	81.0	2.8	0.8	0.30	-							X										X				"
"	F	65.0	2.9	0.6	-	0.48							X										X				"
"	M	109.0	6.6	0.8	0.35	0.60							X		1	8							4				Adult
"	M	116.5	6.6	1.1	0.46	-							X										1				"
"	F	79.0	3.1	0.7	0.26	-							X								1						"
"	M	105.0	6.4	0.9	0.28	0.41							X		2	2	1						1				"
"	M	100.0	4.1	1.0	-	0.71							X		1	2							13				"
"	M	104.0	7.8	1.0	1.14	0.92							X			5							14				"
"	M	99.0	4.7	1.1	0.55	0.48							X			1					2		4				"
"	F	83.0	4.5	1.0	0.52	0.34			1				X			1							5				"
"	M	85.0	4.4	0.8	-	2.00							X				1						X				Juvenile
"	F	67.0	4.3	0.5	0.84	0.14		1		0.02		0.04	X		1	8							-	1	-	X	"
"	F	63.0	4.5	0.5	0.34	0.13							X			1							1				"
"	F	86.0	4.3	1.0	-	1.19							X			1							11				Adult
"	M	95.0	4.4	1.0	-	1.47							X										X				Juvenile
"	F	76.0	9.4	0.9	2.28	1.15							X			5							12				"
"	M	88.5	2.0	1.0	-	-							X										1				"
"	M	96.5	7.3	0.9	0.10	1.91							X			2							X				Juvenile
July	F	82.0	5.5	0.8	0.91	0.14							X			1							X				"
"	F	68.5	1.7	0.9	-	-							X										X				"
"	F	73.0	3.7	0.7	-	0.57							X				2						X				Adult
"	M	100.0	5.2	1.0	0.88	0.43							X		5		1		1				1				"
"	M	98.0	Captured alive and kept in captivity																								Juvenile
"	M	88.0	6.1	0.8	0.04	0.45							X		1	2							X				"
"	M	85.0	6.0	1.0	-	2.08							X				1						X				"
"	M	87.0	10.3	0.8	1.35	2.15		1					X			3							X				"
"	M	89.0	6.2	0.8	0.29	1.35				0.06		0.08	X		X		1						X				"
"	M	98.0	2.6	1.0	-	0.46							X				1						X				Adult
"	M	90.0	6.5	0.9	-	1.25						0.22	X		X											X	Juvenile
"	M	87.0	4.6	0.8	-	0.80							X			1							X				"
"	M	90.5	4.1	0.7	-	0.93							X				1			X	X		4				"
"	M	106.0	6.7	1.1	0.66	1.15							X			1	1						X				"
"	F	92.0	4.9	0.8	0.59	0.07							X			2							1				Adult
"	F	82.0	3.4	0.8	-	0.79			1				X			1							9				"
"	M	81.0	4.7	0.8	-	0.90							X										X				Juvenile
"	F	71.0	7.2	0.6	0.30	1.01			1				X		X	X							X				"
"	M	84.0	5.4	0.9	-	1.26							X										X				"

[Contd.]

## Appendix 19 (contd.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
July	F	79.0	5.6	0.8	0.63	0.85							X			X	X		X				X				Juvenile
"	M	100.0	5.8	0.8	0.76	-							X														"
"	F	76.0	3.8	0.8	0.10	0.12							X		1		1						1				"
"	M	98.0	12.6	0.7	2.02	1.13							X			1	1		1				13				"
"	F	74.0	4.9	0.7	0.45	0.11							X			X	X						X				"
"	F	92.0	2.7	0.9	0.09	-							X										1				Adult
"	F	79.0	6.8	0.8	0.22	1.05							X		X								6				Juvenile
"	M	95.5	6.3	0.8	0.10	1.00							X				X						X				"
"	F	76.0	7.7	0.7	0.81	0.84							X			X	X						X				"
"	M	87.0	3.5	0.8	0.60	0.16							X		1								2				"
Aug	F	81.0	2.4	0.6	-	0.09							X										1				"
"	F	80.0	6.2	0.6	1.77	-							X		X												"
"	F	70.0	2.2	0.6	0.05	-							X										X				"
"	M	96.0	8.9	0.7	2.61	0.35							X		X								5				"

## APPENDIX 20

Invertebrates found in the stomach contents of moles at  
Boghall glen

Phylum	Class	Order	Family	Genus and Species	
Annelida	Chaetopoda	Oligochaeta	Lumbricidae	Allolobophora caliginosa	
				Allolobophora chlorotica	
				Dendrobaena octaedra	
				Dendrobaena rubida	
				Lumbricus rubellus	
				Lumbricus sp.	
Mollusca	Gastropoda	Pulmonata	Arionidae	Arion fasciatus	
			Limacidae	Agrolimax reticulatus	
Arthropoda	Myriapoda		Geophilidae	[Undetermined]	
		Insecta	Lepidoptera	Noctuidae	[Undetermined]
			Coleoptera	Carabidae*	"
				Elateridae	"
			Hymenoptera	Formicidae(?)	"
			Diptera	Bibionidae	"
				Dolichopodidae	"
				Empididae	"
				Muscidae	"
				Rhagionidae	"
				Tipulidae	"

\* Adults and larvae otherwise all other insects refer to the larval stages.

## APPENDIX 21

## Monthly variation in the qualitative composition of the food of moles at Boghall glen

Percentage number of stomachs containing																			
Families of insect larvae																			
Month	Number of stomachs examined	Earthworms (Lumbricidae)	All insect larvae	Formicidae	Noctuidae	Carabidae	Elatерidae	Bibionidae	Dolichopodidae	Empididae	Muscidae	Rhagionidae	Tipulidae	Adult insects	Earthworm cocoons	Slugs	Centipedes (Geophilidae)	Plant Materials	Stomach stones
March	9	88.9	100	-	11.1	11.1	33.3	44.4	11.1	11.1	22.2	11.1	88.9	33.3	33.3	33.3	11.1	22.2	22.2
April	22	86.4	100		18.2	50	50	59.2	27.3	18.2	-	31.8	72.7	9.1	18.2	4.5	4.5	9.1	9.1
May	28	100	100		28.8	50.4	54.0	14.4	64.8	50.4	-	18.0	100	3.6	7.2	7.2	-	10.8	25.0
June	40	85.0	97.5	2.5	17.5	50.0	20.0	5.0	7.5	5.0	5.0	5.0	90.0	7.5	2.5	12.5	-	7.5	5.0
July	28	90.0	93.6		28.8	39.6	46.8	0	21.6	3.6	0	0	86.4	3.6	7.2	3.6	-	7.2	7.2
August	4	100.0	100.0	-	50.0	-	-	-	-	-	-	-	75.0	-	-	-	-	-	-
March to August	131	90.0	97.7	0.8	23.7	43.5	38.2	17.5	25.9	16.8	3.1	3.1	11.4	88.5	7.6	9.2	1.5	9.2	11.4

APPENDIX 22Monthly percentage weight of earthworms in the stomach contents  
of moles at Boghall glen

Month	Mean (+ S.E.) percentage weight of earthworms in the stomach contents
March	51.3 ± 13.8
April	54.6 ± 7.9
May	42.4 ± 6.8
June	45.6 ± 5.4
July	37.6 ± 6.7
August	77.5 ± 19.8

Monthly differences in the percentage weight of earthworms in the diet

Months	Mean (+ S.E.) Difference in the percentage weight of earthworms	t
March and April	3.3 ± 15.7	0.21
March and May	8.9 ± 15.2	0.59
March and June	5.7 ± 14.6	0.39
March and July	13.7 ± 15.1	0.91
March and August	14.8 ± 24.0	0.62
April and May	12.2 ± 10.4	1.17
April and June	9.0 ± 9.6	0.84
April and July	17.0 ± 10.3	1.65
April and August	21.9 ± 21.3	1.03
May and June	3.2 ± 8.7	0.37
May and July	4.8 ± 9.5	0.51
May and August	35.1 ± 20.6	1.70
June and July	8.0 ± 8.6	0.93
June and August	31.9 ± 20.6	1.55
July and August	39.9 ± 20.9	1.91

Differences not significant in any month (t at P0.05 = 1.980)

## APPENDIX 23

Record of mole trapping on Leip field and environs, Fulford field and Bilston field in January 1970

Site	Sex	Body weight (in g)	Stomach weight (in g)	Weight of earthworms (in g)	Weight of insect larvae (in g)	Number of adult insects	Number of earthworm cocoons	Weight of slugs (in g)	Number of centipedes	Number of each food item in stomach contents (X = occurrence)																	
										Species of earthworms							Families of insect larvae										
										All earthworms	A. caliginosa	A. chlorotica	A. longa	Lumbricus sp.	L. terrestris	Dendrobaena sp.	O. cyaneum	Noctuidae	Carabidae	Elateridae	Bibionidae	Dolichopodidae	Empididae	Tipulidae	Slugs	Plant materials	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
Leip	M	95.5	4.6	0.62	0.06		1	0.05		2	-	-	-	-	2	-	-	1	1								1
"	F	65.0	3.7	1.14	0.05	1	-			5	-	2	-	3	-	-	-			3				1			
"	M	93.2	5.4	1.56	0.05		1			3	X	3	-	X	-	-	-			3				1			
"	M	100.4	6.0	1.66			-			X	X	X	-	X	-	-	-										
"	M	97.0	9.6	4.81			1			6	2	-	2	-	2	-	-			2					1		
"	M	90.0	7.0	2.98	0.03		-			4	-	-	3	-	1	-	-			2							
"	F	71.0	5.5	1.87			1	1	1	1	-	-	-	-	1	-	-										
Leip's environs	F	71.0	4.6	0.47	0.01		-	-	-	1	-	-	-	1	-	-	-			1					1		
"	F	78.0	5.9	2.07			2	-	2	3	3	-	-	-	-	-	-							1			
"	F	68.6	3.7	1.10			1	-	-	2	2	-	-	-	-	-	-			1							
Fulford	M	104.0	7.3	2.86			3	-	-	4	2	-	2	-	-	-	-		1						2		
"	M	85.0	5.4	1.88			-	-	-	1	-	-	1	-	-	-	-							2			
Leip's environs	M	81.0	5.2	1.12	0.64	-	-	-	2	3	2	-	-	1	-	-	-	2	-	5				2	1		
Fulford	F	73.0	4.7	1.49	-	-	2	-	-	1	-	-	-	-	1	-	-							1			
"	F	78.0	8.6	3.82	0.01	-	-	-	-	X	X	-	X	X	-	-	-			1				1			
"	M	98.0	5.1	0.26	0.07	-	-	-	-	X	X	X	-	-	-	-	-	1			1						
"	M	90.0	4.2	0.96	-	-	2	-	-	3	-	-	2	1	-	-	-										
"	M	89.0	1.6	-	-	-	1	-	-	X	-	-	-	-	-	-	-										
"	M	96.0	7.8	3.53	0.42	-	2	-	-	8	-	-	4	-	-	2	-	2		1				2			
"	M	91.0	5.7	1.05	0.09	-	8	-	-	X	-	-	-	-	-	-	-	1		1							
"	M	87.5	4.6	0.37	0.22	-	2	-	-	X	-	-	-	-	-	-	-	1		1				2			
"	M	96.8	12.0	6.49		-	1	-	-	6	-	-	6	-	-	-	-			1						2	1
"	M	81.0	7.5	3.41	0.16	-	4	-	-	6	-	-	3	1	-	-	1		2					4	2		
"	F	66.0	2.0	-	0.11	-	2	-	-	X	-	-	-	-	-	-	-		1	1						1	

[Contd.]

## Appendix 23 (contd.)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Fulford	M	100.0	12.4	6.05	0.05	-	3	-	-	-	8	-	1	6	1	-	-	-	1	-	-	-	-	4	-	-	-
"	M	94.0	6.0	1.74	0.04	-	2	-	-	-	2	-	-	1	-	1	-	-	-	-	2	-	-	-	1	-	-
"	M	94.6	7.2	4.19	0.15	-	1	-	-	-	4	-	-	3	-	-	-	1	1	-	-	-	-	2	2	-	-
Leip's environs	M	110.0	5.8	1.40	0.25	1	1	-	-	-	4	3	-	1	-	-	-	-	-	-	1	-	-	-	3	-	-
Fulford	F	71.0	5.3	2.04	0.02	-	-	0.09	-	-	3	-	-	1	-	1	1	-	-	-	2	-	-	2	-	1	-
"	F	68.0	4.3	1.71	0.01	-	3	-	-	-	4	-	-	1	2	1	-	-	-	-	1	-	-	1	-	-	-
"	M	103.0	3.7	0.87	0.05	-	1	-	-	-	1	-	-	1	-	-	-	-	-	-	1	-	-	2	-	-	-
"	F	70.0	3.5	0.86	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
"	M	91.0	4.3	1.62	0.03	-	-	-	-	-	4	-	2	2	-	-	-	-	-	-	-	-	-	5	-	-	-
Bilston field	F	81.0	9.3	5.24	-	-	1	-	-	-	8	4	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-
"	M	100.6	5.5	0.86	0.09	-	2	-	-	-	X	X	-	-	X	-	-	-	-	-	3	3	-	-	2	-	-
"	F	75.0	3.1	0.71	0.44	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	189	-	-	-	1	-	-
"	M	98.0	8.2	4.02	-	-	-	-	-	-	7	2	-	3	-	-	2	-	-	-	-	-	-	-	-	-	-
"	F	75.0	7.7	3.66	-	-	-	-	-	-	7	1	2	3	-	-	1	-	-	-	-	-	-	-	-	-	-
"	M	94.0	8.8	3.89	-	-	-	-	-	-	7	3	1	3	-	-	-	-	-	-	-	-	-	-	-	-	X
"	M	103.0	9.8	4.29	-	-	2	-	-	-	4	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-
"	F	72.0	4.8	1.20	-	-	1	-	-	-	X	-	-	X	X	-	-	-	-	-	-	-	1	1	1	1	-
"	F	72.8	5.5	2.55	-	-	-	-	-	-	2	-	-	1	-	1	-	-	-	-	1	-	-	-	-	-	X
"	F	61.0	3.9	1.27	-	-	1	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-
"	M	91.2	8.6	4.53	0.03	-	1	-	-	-	4	-	-	3	-	1	-	-	-	-	-	-	-	2	-	-	-
"	M	80.0	2.8	0.10	-	-	1	-	-	2	X	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
"	F	69.0	5.7	2.5	0.03	-	3	-	-	-	2	-	-	2	-	-	-	-	-	-	-	-	1	4	-	-	X

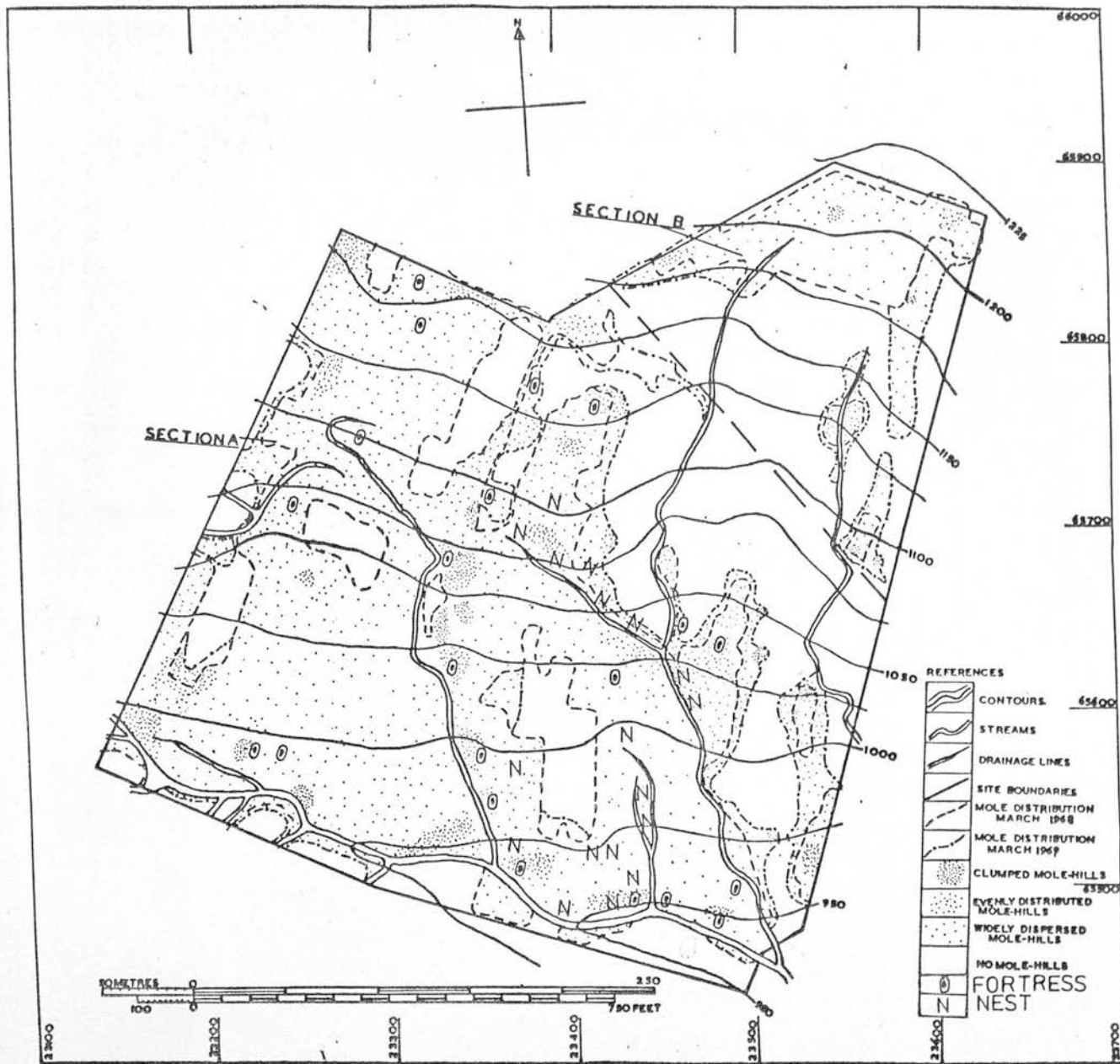
## APPENDIX 24

Daily food consumption of captive moles

Weeks	Days	Daily food consumption (in g.)			
		1st Mole	2nd Mole	3rd Mole	4th Mole
1	1	105.0	92	81	93
	2	103.0	90	85	85
	3	98.0	90	85	82
	4	91.0	80	73	100
	5	82.0	80	90	75
	6	78.0	80	90	90
	7	80.0	80	95	100
2	8	94.0	80	100	96
	9	93.0	80	82	84
	10	73.0	80	69	71
	11	78.0	75	86	100
	12	69.0	68	100	80
	13	65.0	70	84	73
	14	68.0	65	76	76
3	15	69.0	61	67	76
	16	71.0	61	74	62
	17	75.0	63	78	54
	18	80.0	60	50	67
	19	77.0	68	84	64
	20	81.0	64	50	75
	21	80.0	60	55	70
4	22	80.0	60	60	65
	23	79.0	60	60	76
	24	80.0	57	70	63
	25	80.0	56	75	57
	26	80.0	62	90	60
	27	80.0	62	77	70
	28	95.0	63	90	80
5	29	90.0	65	67	75
	30	90.0	65	75	67
	31	40.0	65	75	76
	32	90.0	60	65	71
	33	90.0	60	85	66
	34	90.0	71	90	62
	35	90.0	70	74	56

Appendix 24 (contd.)

Weeks	Days	Daily food consumption (in g.)			
		1st Mole	2nd Mole	3rd Mole	4th Mole
6	36	90.0	70	80	56
	37	59.0	69	83	61
	38	66.0	60	75	63
	39	90.0	65	57	75
	40	80.0	65	79	73
	41	80.0	70	62	70
	42	90.0	70	70	71
7	43	80.0	70	80	65
	44	82.0	66	85	75
	45	80.0	64	68	68
	46	72.0	66	35	64
	47	75.0	69	46	65
	48	85.0	60	85	72
	49	86.0	60	78	68
8	50	75.0	60	66	65
	51	71.0	60	65	66
	52	81.0	64	66	78
	53	80.0	65	70	71
	54	80.0	68	68	64
	55	90.0	68	68	73
	56	90.0	70	66	80
9	57	83.0	65	70	66
	58	67.0	60	71	86
	59	75.0	55	65	71
	60	75.0	60	75	75
	61	80.0	68	80	80
	62	77.0	68	80	80
	63	75.0	60	73	77
10	64	76.0	60	71	80
	65	70.0	62	67	76
	66	74.0	65	75	80
	67	71.0	65	75	64
	68	76.0	65	80	73
	69	84.0	70	85	85
	70	75.0	70	80	75



Appendix 25. Distribution of fortresses and nests at Boghall Glen.

APPENDIX 26Number of moles and number of mole-hills at Boghall glen

## A - Similar habitats (similar soils and soil conditions)

Number of moles	Number of mole-hills
1	91
2	171
3	360
6	804
14	3,806
16	3,541
21	4,712

## B - Dissimilar habitats (different soil types and soil conditions)

Number of moles	Number of mole-hills
1	197
1	309
1	91
2	171
3	360
4	155
4	170
6	804
14	722
14	3,806
16	3,541
21	4,712

## APPENDIX 27

Measurements of the left second upper molar tooth and the weight of skulls of moles from Boghall glen

Length of tooth (in micrometer units = X 0.86 mm)					Weight of skull (in g)
a	b	c	d	mean a b c d	
2.6	1.7	3.1	2.2	2.40	0.47
2.7	1.7	3.1	2.2	2.43	0.46
2.7	1.7	3.4	2.3	2.53	0.42
2.3	1.5	2.9	2.1	2.20	0.54
2.5	1.8	3.2	2.2	2.45	0.43
2.4	1.6	3.2	2.3	2.38	0.53
2.7	1.7	3.3	2.3	2.55	0.43
2.8	1.7	3.3	2.5	2.58	0.47
2.7	1.8	3.1	2.1	2.43	0.46
2.7	1.7	3.3	2.5	2.55	0.46
2.7	1.7	3.3	2.2	2.48	0.49
2.7	1.8	3.3	2.5	2.58	0.45
2.5	1.8	3.2	2.2	2.43	0.47
2.7	1.8	3.2	2.3	2.50	-
2.7	1.6	3.3	2.4	2.50	0.41
2.6	1.6	3.2	2.3	2.43	0.46
2.7	1.6	3.2	2.2	2.43	-
2.6	1.6	3.3	2.2	2.43	0.43
2.6	1.8	3.2	2.2	2.45	0.43
2.6	1.7	3.0	2.1	2.35	0.43
2.6	1.7	3.2	2.2	2.43	0.34
2.4	1.8	3.1	2.2	2.38	0.45
2.6	1.7	3.1	2.3	2.45	-
2.6	1.7	3.2	2.2	2.43	-
2.5	1.7	3.1	2.1	2.35	-
1.7	1.1	2.9	1.9	1.90	-
2.1	1.5	2.9	2.0	2.13	0.57
2.0	1.5	2.7	1.9	2.03	-

[Contd.]

## Appendix 27 (contd.)

Length of tooth (in micrometer units = $\times 0.86$ mm)					Weight of skull (in g)
a	b	c	d	mean a b c d	
2.2	1.0	2.8	1.9	1.98	0.51
1.9	1.2	2.9	2.0	2.00	0.54
2.2	0.7	2.8	1.8	1.88	0.50
2.0	0.8	2.8	1.8	1.85	0.50
2.2	1.0	2.9	1.6	1.93	0.49
2.0	1.3	2.7	1.9	1.98	0.54
2.0	1.1	2.5	1.8	1.85	0.48
2.2	1.4	2.8	1.9	2.08	0.54
2.0	0.8	2.7	1.8	1.83	0.51
2.0	1.1	2.2	1.7	1.75	0.47
2.4	1.5	3.2	1.6	2.18	0.60
1.9	1.2	2.2	1.7	1.75	0.64
2.0	1.1	3.1	1.9	2.03	0.67
2.3	0.9	3.0	1.8	2.00	0.62
2.1	0.9	3.0	1.8	1.95	0.59
2.3	1.2	3.1	2.1	2.18	0.62
2.4	1.3	3.0	2.0	2.18	0.63
2.4	1.3	3.0	1.6	2.08	0.57
2.6	1.4	3.3	1.8	2.28	0.56
1.9	1.2	2.2	1.7	1.75	0.66
2.6	1.6	3.0	2.2	2.35	0.43
2.5	1.4	3.0	2.0	2.23	0.56
2.4	1.1	2.9	2.1	2.13	0.66
2.5	1.1	3.1	2.0	2.18	0.55
2.2	1.3	2.7	1.7	1.98	0.65
2.3	1.3	2.9	2.0	2.13	0.64
2.3	1.2	3.0	2.0	2.13	0.61
2.3	0.9	3.1	2.2	2.13	0.51
2.4	1.1	2.9	2.1	2.13	0.50
2.5	1.8	3.2	2.2	2.43	0.48
2.7	1.6	3.4	2.4	2.53	0.52

[Contd.]

Appendix 27 (contd.)

Length of tooth (in micrometer units = X 0.86 mm)					Weight of skull (in g)
a	b	c	d	mean	a b c d
2.6	1.6	3.3	2.2	2.43	0.57
2.6	1.7	3.2	2.2	2.43	0.50
2.5	1.8	3.1	2.3	2.43	0.47
2.8	1.6	3.4	2.2	2.50	0.49
2.7	1.7	3.2	2.3	2.48	0.56
2.6	1.8	3.2	2.2	2.45	0.41
2.7	1.6	3.3	2.2	2.45	0.44
2.5	1.7	3.0	2.1	2.33	0.40
2.2	1.7	2.8	2.1	2.20	0.44
2.7	1.7	3.2	2.2	2.45	0.42
2.5	1.5	3.2	2.2	2.35	0.50
2.5	1.2	3.1	2.1	2.23	0.60
2.3	1.1	3.1	2.0	2.13	0.67
2.5	1.2	3.1	2.1	2.23	0.58
2.5	1.4	2.9	2.1	2.23	0.63
2.4	1.1	3.2	2.2	2.23	0.68
2.1	0.7	3.1	2.1	2.00	0.74
2.0	1.0	2.7	1.5	1.80	0.66
2.5	0.7	3.2	2.1	2.13	0.63
2.2	1.2	2.9	1.9	2.05	0.72
2.0	0.7	2.7	1.8	1.80	0.48
2.6	1.4	3.2	2.1	2.33	0.47
1.9	0.9	2.4	1.5	1.68	0.49
2.3	1.0	3.0	2.0	2.08	0.53
2.2	0.9	2.7	1.9	1.93	0.55
2.3	1.2	1.9	2.0	1.85	0.47
1.5	0.7	1.8	1.6	1.40	0.55
2.3	1.5	3.0	2.0	2.20	0.54
2.4	1.2	3.2	2.1	2.23	0.61
2.2	0.7	2.9	1.9	1.93	0.56
2.2	0.9	3.0	1.9	2.00	0.60

[Contd.]

## Appendix 27 (contd.)

Length of tooth (in micrometer units = X 0.86 mm)					Weight of skull (in g)
a	b	c	d	mean	
2.2	1.2	3.4	2.1	2.23	0.52
2.0	1.5	2.8	2.0	2.08	0.58
2.2	1.0	3.0	1.9	2.03	0.55
1.9	0.8	2.5	1.6	1.70	-
2.3	1.1	2.8	1.8	2.00	-
2.3	1.5	3.1	1.9	2.20	-
2.4	1.4	3.1	2.0	2.23	0.58
2.3	1.4	2.6	1.7	2.00	0.63
2.3	1.0	3.0	2.0	2.08	0.64
2.6	1.3	3.2	2.2	2.33	0.59
2.4	1.1	3.1	2.1	2.18	0.57
2.4	1.0	3.1	2.0	2.13	0.56
2.4	1.5	3.0	2.0	2.23	0.63
2.1	1.2	2.5	1.9	1.93	0.54
2.4	1.1	3.0	2.0	2.13	0.64
2.3	1.3	3.1	2.0	2.18	0.61
2.6	1.3	3.2	2.2	2.33	0.59
1.9	0.9	2.5	1.5	1.70	0.60
2.6	1.2	3.3	2.1	2.30	0.62
2.3	1.4	2.8	2.0	2.13	0.47
2.0	1.3	2.8	2.0	2.03	0.49
2.3	1.1	3.0	2.0	2.10	0.54
2.3	1.1	2.9	1.9	2.05	0.51
2.5	1.3	2.8	1.8	2.10	-
2.2	1.0	3.1	2.0	2.08	-

## APPENDIX 28

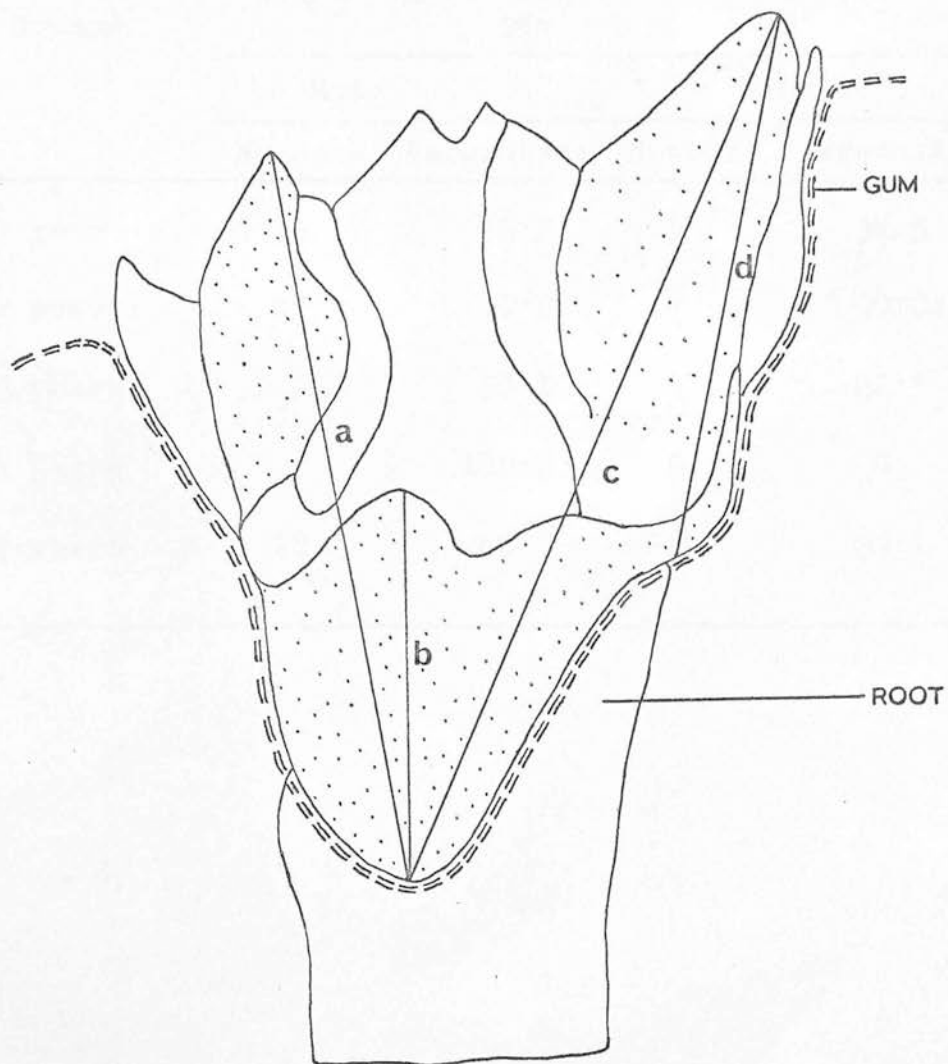
Measurements of the second upper molar teeth and the weight of skull of moles from Leip field and environs, Fulford field and Bilston field (January 1970)

Site	Sex	Tooth length (in micrometer units; 1 micrometer unit = 0.86 mm)								Mean tooth length	Weight of skull (in g)
		Left tooth				Right tooth					
		a	b	c	d	a	b	c	d		
Leip	M	2.3	1.0	3.0	1.8	2.3	1.0	3.0	1.8	2.03	0.64
"	F	2.3	1.3	3.0	1.9	2.3	1.3	3.0	1.9	2.13	0.47
"	M	2.5	1.4	3.2	2.1	2.6	1.4	3.2	2.1	2.31	0.60
"	M	2.4	1.3	3.0	2.0	2.3	1.4	2.9	2.1	2.18	0.66
"	M	2.4	1.5	2.9	2.2	2.3	1.5	3.0	2.2	2.25	0.66
"	M	2.4	1.1	3.0	2.0	2.4	1.1	3.1	1.9	2.13	0.55
"	F	2.2	1.3	2.9	2.1	2.4	1.1	2.9	2.2	2.14	0.44
Leip's environs	F	2.4	1.3	3.1	2.0	2.5	1.4	2.8	1.6	2.14	0.48
"	F	2.4	1.4	3.0	2.1	2.5	1.4	3.0	2.1	2.25	0.47
"	F	2.3	1.1	2.8	1.8	2.2	1.0	2.7	1.8	1.97	0.51
"	M	2.1	1.5	2.8	1.9	2.3	1.1	3.0	2.0	2.09	0.61
"	M	1.9	0.7	2.5	2.1	1.9	0.8	2.5	2.0	1.80	0.70
Fulford	M	2.4	1.4	3.1	2.1	2.5	1.3	3.1	2.1	2.25	0.66
"	M	2.4	1.3	3.0	2.0	2.4	1.2	3.0	2.0	2.17	0.60
"	F	2.1	0.7	2.8	1.6	2.1	0.8	2.7	1.6	1.80	0.57
"	F	2.2	1.0	2.8	1.8	2.3	1.0	2.8	1.8	1.99	0.51
"	M	2.0	1.1	2.8	1.8	2.0	1.1	2.8	1.8	1.93	0.64
"	M	2.6	1.5	3.1	2.2	2.6	1.4	2.9	2.1	2.30	0.60
"	M	2.5	1.4	3.1	2.1	2.5	1.3	2.8	1.7	2.18	0.61
"	M	2.4	1.0	3.0	1.9	2.4	1.0	3.0	1.9	2.08	0.63
"	M	2.5	1.1	3.1	2.0	2.4	1.1	3.1	2.0	2.17	0.58
"	M	2.2	0.7	2.1	1.0	2.3	0.9	2.9	1.7	1.77	0.59
"	M	2.5	1.1	3.0	2.0	2.4	1.1	2.9	2.0	2.13	0.64
"	M	2.2	1.0	2.8	1.8	2.2	1.0	2.8	1.8	1.95	0.55

[Contd.]

## Appendix 28 (contd.)

Site	Sex	Tooth length (in micrometer units; 1 micrometer unit = 0.86 mm)								Mean tooth length	Weight of skull (in g)
		Left tooth				Right tooth					
		a	b	c	d	a	b	c	d		
Fulford	F	1.9	1.0	2.8	1.8	2.2	1.0	2.7	1.8	1.91	0.49
"	M	1.8	0.4	2.4	1.2	1.9	0.4	2.3	1.2	1.45	0.63
"	M	2.3	1.2	3.1	1.9	2.4	1.3	2.9	2.0	2.14	0.56
"	M	2.3	1.0	2.9	1.8	2.3	1.0	2.9	1.8	2.00	0.61
"	F	2.2	1.2	3.0	2.0	2.2	1.2	3.0	2.0	2.10	0.44
"	F	2.2	1.0	2.8	1.8	2.2	1.1	2.7	1.8	1.95	0.48
"	M	2.5	1.5	3.0	2.1	2.6	1.4	3.0	2.1	2.27	0.63
"	F	2.3	1.1	2.9	1.8	2.2	1.2	3.0	1.7	2.03	0.50
"	M	1.2	0.1	2.2	1.3	1.5	0.3	2.1	1.1	1.23	0.64
Bilston	F	2.3	1.5	2.8	2.0	2.5	1.3	3.1	2.1	2.23	0.52
"	M	2.4	1.3	3.0	2.0	2.5	1.2	3.1	2.2	2.21	0.66
"	F	2.0	0.8	2.7	1.6	2.0	1.0	2.5	1.6	1.78	0.50
"	M	2.4	1.5	3.1	2.2	2.6	1.4	3.2	2.2	2.38	0.56
"	F	2.4	1.1	3.0	2.0	2.5	1.3	2.9	2.0	2.15	0.50
"	M	2.4	1.4	3.0	2.0	2.6	1.1	2.9	1.8	2.15	0.62
"	M	2.5	1.3	3.2	2.0	2.6	1.2	3.2	2.1	2.31	0.63
"	F	2.5	1.3	3.1	2.1	2.5	1.3	3.1	2.1	2.25	0.50
"	F	2.4	1.0	3.0	2.0	2.3	1.2	2.9	2.0	2.10	0.50
"	F	2.1	0.9	2.5	1.6	2.1	0.9	2.6	1.6	1.79	0.47
"	M	2.1	0.9	2.9	1.8	2.2	0.9	2.9	1.8	1.95	0.58
"	M	2.0	0.7	2.7	1.7	2.0	0.8	2.6	1.7	1.78	0.56
"	F	2.1	0.8	2.6	1.6	2.0	0.9	2.6	1.6	1.78	0.46



APPENDIX 29.

Left second upper molar of a juvenile mole  
(X 50) showing method of tooth measurements.

APPENDIX 30Age distribution in male and female moles

Age Groups	Sex			
	Male		Female	
	Numbers	Percentage	Numbers	Percentage
0 - 1 year	15	65.2	8	34.5
1 - 2 years	7	50.0	7	50.0
2 - 3 years	4	57.1	3	42.9
3 - 4 years	2	100.0	0	0
0 - 4 years	28	60.9	18	39.1

APPENDIX 31Dimensions of mole tunnels on Leip field

Sex and 'age' of moles	Depth of tunnel below soil surface (soil surface to tunnel floor)	Height of tunnel	Width of tunnel
Adult male (No. C <sub>1</sub> )	4 in.	2½ in.	2¾ in.
Adult male (No. 7)	3½ in.	2½ in.	2½ in.
Adult male (No. 3)	3½ in.	2½ in.	2½ in.
Adult female (No. 4)	3 in.	2 in.	2 in.
Adult female (No. 5)	3½ in.	2¼ in.	2 in.
Juvenile male (No. 6)	3 in.	2 in.	1¾ in.
Juvenile male (No. 6)	2½ in.	2 in.	1¾ in.
Juvenile male (No. 2)	3 in.	2 in.	2 in.
Juvenile male (No. 1)	2 in.	1½ in.	2 in.

## APPENDIX 32

Sex Ratio in Moles

Sites	Period of trapping	Total Number of moles	Number of Males	Number of Females	Sex Ratio ( : )	$X^2$
1. Boghall glen						
(a) Adults	March to August 1969	90	54	36	1.5:1	3.60
(b) Juveniles		48	27	21	1.29:1	0.75
(c) Adults and Juveniles		138	81	57	1.42:1	4.18*
2. Leip field	July 1969	10	6	4	1.5:1	0.40
3. Leip field and environs	January 1970	12	7	5	1.4:1	0.33
4. Fulford field	January 1970	21	15	6	2.5:1	3.86*
5. Leip field and environs and Fulford field	January 1970	33	22	11	2:1	3.78
6. Bilston field	January 1970	13	6	7	0.86:1	0.08
7. All sites		194	115	79	1.46:1	6.68*

\* Sex ratio significantly different from 1:1 ratio ( $X^2_{[1]}$  at  $P=0.05 = 3.841$ ).