THE LUMBRICIDAE IN THE HEBRIDES

T H E S I S

for the

Degree of Doctor of Philosophy

in the

University of Glasgow

by

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November, 1956

CONTAINS
PULLOUTS

THE LUMBRICIDAE IN THE HEBRIDES

Slightly amended in printing. C.M. Yonge

by

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The occurrence of seventeen species of Lumbricidae in the Hebrides is described. Endemicity, colonisation, and vectors are discussed. Field populations in Islay, Tiree, Coll, Gunna, Barra, North Uist, Harris, Shillay (Harris), Scarp (Harris), Scalpay (Harris), St. Kilda, and Lewis are studied; all, with the exception of some records from Barra, previously undescribed. The soil mantle of the outer fringe of islands from Islay to Lewis, with some exceptions, is a calcareous sand-peat complex. This complex forms an ecological gradient from soils of one particular character to those of the opposite character, usually along the line of the prevailing wind from shore dunes to inland moorland. The gradient is outlined biologically and chemically, and the distribution of the Lumbricidae within it, which was not known, is described. Significant differences are shown between communities in sandy and peaty soils; differences between communities in niches of open soil, in and under dung-pats, and under stones were also found to be significant in most species. These differences are described in the light of the findings of workers in other areas.

The species complex and the ecological distribution of the Lumbricidae at St. Kilda are described separately.

A detailed study of a field population of Lumbricidae in natural maritime soil has been carried out in Tiree, Argyll. Problems of earthworm sampling are discussed with particular reference to machair soils, and the two methods finally adopted are described. These are (1) a quadrat method with the use of a standard solution of potassium permanganate, and (2) a pit-fall trap method. The distribution of the population is outlined over the transition from sand (dune) to mature maritime soil (machair). The presence of dung-pats is seen to affect the distribution of some species more than others. Grazing greatly affects the distribution of some species, and the grazed and ungrazed grasslands on either side of a cattle fence were found to possess significantly different communities of lumbricids. The distribution in uniform soil was found to be heterogeneous, large variations in numbers occurring without apparent ecological change. This aspect is discussed in the light of work done in cultivated soils. Reproduction appears to be ~~at a maximum~~ greatest in winter and ~~at a minimum~~ least in summer. ~~as is~~ This is also true of abundance~~, the latter having~~ where there are secondary peaks in spring and autumn and a distinct trough in summer. The continuous reproduction throughout the winter in this maritime population, subjected to comparatively mild weather, is not paralleled by mainland or continental populations. Fluctuations in abundance of the maritime population are approximately similar to those of British mainland populations. Surface activity is ~~at a maximum~~ greatest in late autumn and late spring, with proportionately fewer unpigmented species moving on the surface than pigmented.

Laboratory experiments were carried out to investigate the reaction to certain natural soil media encountered in the Hebrides of four ecologically distinct species of Lumbricid, Allolobophora caliginosa Savigny and A. terrestris forma longa Ude (both acid-intolerant), Bimastus eiseni Levinsen (acid-tolerant), and Lumbricus rubellus Hoffmeister (ubiquitous). The soil media used were peat, calcareous sand, machair soil, cow-dung, horse-dung, soil or sand steeped in dung water, and soil or sand steeped in tap water. In these experiments a "choice" between two media was presented to each species separately in specially designed chambers. Before the experiments began the bias of the chambers in a state of "no choice" was carefully investigated, and compensations made to eliminate it. The occurrence of A. caliginosa, as shown by field survey, is fully supported by the experiment; that of A. terrestris forma longa is also supported, but the formation of intertwined clusters tended to obscure the result in some cases; those of B. eiseni and L. rubellus were not supported by all the experiments. Cow-dung appeared to be more attractive to Lumbricids than horse-dung.

Ann. Mag. Nat. Hist., 1956, (12), 9: 129-133. Proc. Roy. Soc. Edinb., in the press. Scot. Nat., in the press.

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ACKNOWLEDGEMENTS

This work was financed by a grant from the Nature Conservancy to the University of Glasgow during the years 1953 to 1956.

The work on the geographical and ecological distribution of the Lumbricidae in the Hebrides is original, but a few records by J.E. Forrest et al. (1936), and J.D. Robertson (Bertram, 1939) are included. The detailed study of a Lum:bricid population in a machair soil is original, and compa:risons are made with the work of A.C. Evans, W.J.McL. Guild, and J.E. Satchell in other soils at Rothamsted, the English Lake District, and in eastern Scotland. The work with the Lumbricidae in "choice" chambers is also original.

The author is indebted to Professor C.M. Yonge, C.B.E., F.R.S., for his interest and encouragement. Special thanks are due to Dr. J.D. Robertson who provided much helpful criticism. Thanks are also due to Mr. M.V. Brian, Mr. R.A. Crowson, Mr. A. Fraser, Dr. A.R. Hill, Dr. W. Russell Hunter, Mr. A. Macfadyen, Mr. D.A. Muir, and Dr. H.F. Steedman for stimulating discussion on various biological and technical points, and to Dr. R.A. Robb for statistical advice. The Marquis of Bute kindly gave permission on three occasions for visits to St. Kilda.

The/

The weather data were supplied by the Meteorological Office at Tiree.

During the course of the work in Tiree the author received much hospitality and kindness from Mr. and Mrs. Hector MacCallum and Miss M. Cameron, for which he expresses grateful thanks.

PAPER I

THE GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION OF THE LUMBRICIDAE IN THE HEBRIDES

PAPER I, SECTION A

GEOGRAPHICAL DISTRIBUTION

I. INTRODUCTION

The global distribution of the Lumbricidae is reviewed by Stephenson (1930), and the more precise distribution in the British Isles by Cernosvitov and Evans (1947). Such a phrase as "we now find them (the Lumbricidae) distributed over a considerable part of the British Isles", used by Cernosvitov and Evans in 1947, reflects to some extent the lack of precise knowledge of the widespread distribution in Britain. Some of the first Scottish records come from the Forth area (Evans, 1910). Guild (1948) describes the presence of 14 species in the Carse of Stirling, and later (Guild, 1951a, 1951b, 1952a) the distribution of 15 species in Scottish pastures (2 of which had not previously been recorded) from the Lothians, the Borders, and from a few sites in Perthshire, Argyll, and Ross-shire. Satchell (1955b) and Svendsen (unpublished) have recorded the occurrence of earthworms respectively in Lake District woodlands and a Northumberland moorland, close to the Scottish border.

The only Hebridean lumbricid records already published are 7 species from Barra, Outer Hebrides (Forrest *et al.*, 1936) and/

and 11 species found by J.D. Robertson in Canna (Bertram, 1938), making 13 different species in all. The distribution of the Lumbricidae in Hirta (Boyd, 1956, in press), the main island of St. Kilda, is described later in this paper. There, 9 species were recorded, 3 of which, all of the genus Dendrobaena, were not previously reported from Barra or Canna. This paper incorporates those records already mentioned with others obtained from 13 islands on the outer fringe, including 4 of the Inner Hebrides and 9 of the Outer Hebrides.

II. THE SPECIES COMPLEX

At present 27 species of earthworm have been identified from British soils. Of these, 25 are listed by Cernosvitov and Evans (1947), and the remaining 2 by Muldal (1952) and Satchell (1955a). So far 16 species have been reported from the Scottish mainland (Guild, 1951a), and 14 (excluding the disputed specimen Allolobophora (?) relicta Southern) have been recorded from Ireland (Southern, 1913; Cernosvitov and Evans, 1947). Other species are undoubtedly present, distributed locally. Here, 18 species are recorded from the Hebrides, Dendrobaena rubida and D. subrubicunda being considered as separate species. Two, Bimastus tenuis and D. subrubicunda, are not mentioned by Guild from the Scottish mainland/

mainland, and Allolobophora icterica, found in one locality near Stirling, has not so far been found in the Hebrides.

Large-scale collections have been made by transect methods over all major soil types such as shell-sand dunes, machair (a natural calcareous grassland described in greater detail in Section B of this paper), cultivated (enclosed) ground, grass-moor, and heather-moor (peat bog), with niches in dung-pats, under stones, in marsh, and in open soil being searched. These transects and casual collections were carried out in Islay, Tiree, Gunna, Coll, Barra, South Uist, Benbecula, North Uist, Harris, Shillay (Harris), Scalpay (Harris), Scarp (Harris), St. Kilda, and Lewis, and the precise sites are described in Section B, Appendix I of this paper.

Table 1 shows the complex for all the islands in which major collections were made, together with the Canna collection (Bertram, 1938). Tiree, where more collecting was done than elsewhere, has at least 16 species, and Shillay, the 113 acre island off Pabbay, Sound of Harris, which has never been inhabited, at least 4 species. The minor collections from South Uist and Benbecula show Allolobophora caliginosa, A. chlorotica, A. longa, B. tenuis, L. castaneus, and L. rubellus to be present in both islands.

No/

No sign of endemicism has so far been detected in Hebri-:dean earthworms. All species are widely distributed throughout the world and have been given the name _peregrine_ (Michaelsen, 1900) to distinguish them from the endemic. The immediate geological history of the Hebrides (Phemister, 1948; Charlesworth, 1955) suggests that during the Pleistocene and early Quarternary the whole area was blanketed by an ice-sheet, with the exception of a few ice-free _nunataks_. Heslop Harrison (1948) suggests that Pleistocene plants in the Hebrides survived the ice-ages on those nunataks, but Raven (1949) takes the view that such plants may have been introduced.

Earthworms cannot survive freezing, and although exceptional records have been obtained in Kolguev, Nova Zembla, and the north coast of Siberia (Stephenson, 1930), the probability of earthworms surviving the ice-ages in the Hebrides appears very small. Endemic species are found in southern Ireland and England which lay beyond the southern limit of ice transgression. Colonisation of soils in northern Britain probably followed closely the settlement of the ice-free land by man, since man is considered (Stephenson, 1930) to be the principal vector of earthworms. The distribution of such species as _Dendrobaena mammalis_, _Eisenia foetida_, _Lumbricus festivus_, and _Octolasium lacteum_ in the Hebrides suggests that colonisation may still be in progress.

Since/

Since the colonisation of the Hebrides by man, trading has been carried out directly with the mainland, Ireland, and probably Norway. There have also been strong inter-island trade connections. Heslop Harrison (1948), in his explanation of the presence of animals and plants with Irish affinities in the Western Isles of Scotland, overlooks the fact that strong connections existed in the days of sailing boats between the Inner Hebrides and Ireland. A member of the crew of the old sailing ship Mary Stewart, the remains of which are still to be seen in Scarinish harbour, Tiree, has described to the author the direct trade between the islands and Ireland in lime and farm produce. The shipment of potatoes, oats, animal fodder, livestock, implements, building materials, and in a few instances of soil to enhance gardens in the Outer Hebrides, have all played an important part in vectoring earthworms to the remotest Hebrides.

III. THE SPECIES

Allolobophora caliginosa Savigny.

A dominant species in all islands. Both forms *typica* and *trapezoides* A. Duges are often present in the same locality. It is abundant in machair and cultivated soils, present in grass-moor, but scarce in dunes, and absent from peat bogs. More numerous in the open soil than in dung-pats.

A. chlorotica/

A. chlorotica Savigny

Present, yet never abundant, in machair, cultivated ground, and grass-moor. Although common in islands south of the Sound of Harris, it is much less so in Harris and Lewis, no records having yet been obtained from there, or from St. Kilda. Common under stones.

A. terrestris forma longa Ude.

Patchy in distribution throughout the islands, and within each island. Reported from all the major islands searched, except Coll. Usually found in shell-sand loam, but colonises dune basins, and is found occasionally on grass-moor usually near derelict in-bye croftland. Not found in peat bogs.

Bimastus eiseni Levinsen.

A dominant species on moorland soils of all the major islands except perhaps Canna where it may have been overlooked. Not found at all in shell-sand, dunes or machair, but colonises peat cuttings. Aggregates in dung-pats.

B. tenuis Eisen.

Found to be most numerous in dunes and machair, and is common on cultivated ground and grass-moor, but not on heather-moor. Not reported from St. Kilda, but one was found in a peaty lazy-bed in Scalpay (Harris). More common in dung or under stones than in open soil.

Dendrobaena mammalis/

Dendrobaena mammalis Savigny.

Present in machair, cultivated ground, and grass-moor in Coll, Tiree, Barra, and North Uist, but not so far recorded from Harris, Lewis, or Canna. Never abundant, it colonises the niches in dung and under stones, and has not so far been taken from open soil.

D. octaedra Savigny.

A dominant species in all islands, but not so far recorded from Canna, though it is probably present there locally. Abundant in dung, in machair, cultivated soils, and moorland, it is also a successful colonist of shell-sand dunes and peat cuttings.

D. rubida Savigny - *D. subrubicunda* Eisen.

Both species, which are very closely related, are widely distributed from Islay to Lewis, occurring in small islands around the Harris coast and at St. Kilda. They are never dominant, but occur in dung-pats on all types of soil from shell-sand dunes to peat bogs.

Eiseni foetida Savigny.

This species has not been found to occur in natural field populations (Guild, 1951*a*), and its distribution in the Hebrides seems to confirm this. In Britain it occurs most abundantly in/

in middens, but though a few of those were searched in the Hebrides, no specimens were found. The only records come from a compost heap and garden soil in Canna.

E. rosea Savigny.

All specimens so far obtained are forma typica. A comparatively uncommon species in the islands where it occurs, found usually under stones on the grass-moor. It is common, however, in St. Kilda and Scalpay (Harris).

Eiseniella tetraedra forma typica Savigny.

A dominant species in marshes, but not common on well-drained or well-grazed ground. It has been found in rank ungrazed machair, in Tiree, well away from any marsh or water-course. It occurs in dung-pats on all marshes from the dunes to the peat bogs. Recorded in all the major collections.

Lumbricus castaneus Savigny.

Common on machair and cultivated soils, but scarcer in dunes and moorland, and not found in peat cuttings. Has been recorded almost everywhere, but so far only one specimen has been obtained from Islay.

L. festivus Savigny.

Found as a dominant in dung-pats in dunes and machair in Coll, but except for a few collected in dung on the grass-moor in/

in Tiree, the species has not been found elsewhere. The species, together with *O. lacteum*, clearly possesses a restric:ted geographical range in the Hebrides. Its distribution in the West Highlands and Inner Hebrides is unknown except for local occurrences in Coll and Tiree, but its complete absence from the ten islands searched in the Outer Hebrides seems to suggest that *L. festivus* has not yet colonised Hebridean soils on the scale of most other species. Guild (1951*a*) observes that this species is scarce and localised on the British mainland, and its sparse occurrence in the Hebrides stands out in contrast to the coincidental abundance and ubiquity of *L. rubellus*.

L. rubellus Hoffmeister.

A dominant species in all islands searched from Islay to Lewis, and in St. Kilda. It is found colonising both unstable dune and peat bog, and is abundant in machair, cultivated soils, and grass-moor. It is found in dung-pats, under stones, in open soils, and is present in tussocks of *Armeria maritima* on sea cliffs. It is not common in marshes.

L. terrestris Linnaeus.

An uncommon species in machair, cultivated ground, and grass-moor usually near present or ruined habitation. It is more common in open soils and under stones than in dung-pats.

Octolasium cyaneum/

Octolasium cyaneum Savigny.

Fairly common on machair, cultivated ground and grass-moor, but not in dunes or heather-moor. More common under stones than elsewhere. It has been recorded only once in the same locality as the related species *O. lacteum*, in Tiree, and then only by a single specimen of the latter.

O. lacteum Orley.

Local in distribution. Recorded from Tiree (one mature specimen), Barra, Scalpay (Harris), and Lewis. Most common under stones in peaty cultivated soils and under stones on the grass-moor.

PAPER I, SECTION B.

ECOLOGICAL DISTRIBUTION

I. INTRODUCTION

Evans and Guild (1947, 1948a, 1948b), Evans (1948), and Guild (1948) have examined populations of earthworms in agricultural fields at Rothamsted and in the Carse of Stirling, and show that different soil types and soils of different agricultural history possess different species complexes of earthworms, and that the complexes in acid natural pastures can be altered by agricultural treatment. Effects of ploughing on earthworms were studied, and also the casting and reproductive potential of important British species.

Guild (1951a, 1951b, 1952a) has described field populations in south-east Scotland giving species complexes, estimates of density, and the effects of acid soil conditions on earthworms. In upland pastures he found very high variability in both numbers and species complex over short distances, and also that earthworms are not uniformly distributed in agricultural fields (Guild, 1952b).

Neilsen (1951) found one species of earthworm in New Zealand highly correlated with the exchangeable calcium in the soil/

soil, but Satchell (1955*b*) found in experimental plots that differences between plot populations could be explained more by *pH* than by exchangeable calcium, and confirmed the effects of *pH* in natural populations. In a similar manner to Bornebusch (1930), Satchell classifies the species into "acid-tolerant", "ubiquitous", and "acid-intolerant". Aggregations probably similar to Guild's "sub-populations" (1952*b*), he thinks are the balance of the aggregating effects of reproduction and the randomising effects of mortality and dispersal.

Svendsen (*in lit.*) has studied the ecology of earthworms on a Pennine moorland. He describes the mode of aggregation in sheep dung, and by field experiment has shown that it is due not entirely to reproduction or the formation of "family" groups *in situ* as suggested by Satchell, but also to colonisation from outside the immediate area of the dung.

This paper deals with basic aspects of earthworm ecology and describes the soil system and part of the invertebrate fauna of the extreme north-west fringe of the British Isles (Fig. 1). Some insect groups have been surveyed by several other workers, and the general distribution, but not detailed ecology, of the land molluscs is known in the area (Roebuck, 1918; Forrest *et al.*, 1936), but the earthworms have been almost entirely neglected.

II. METHODS AND MATERIALS/

II. METHODS AND MATERIALS

(1) Survey Method

In order to arrive at a standard method of sampling which might be applied both to the insular populations as a whole, and also to the ecological subdivisions existing within those populations, it was essential that all possible soil niches should be investigated, and earthworms extracted for qualitative and quantitative determinations. This was done by a transect survey method which enables all, or practically all, soil niches present in the islands to be examined in the shortest possible time. Due to the soil gradient from shore sand to peat existing in most of the islands this transect method proved particularly suitable. While this method may not reveal the absolute species complex for each island, it closely approaches this, and is a means of investigating differences between the insular populations. Most islands present a full range in soils from sand to peat, but exceptions do exist in Tiree, where no extensive peat formations exist, and in Scalpay (Harris), where there is no calcareous sand.

Selection of transects (Appendix I) in each island with roughly similar topographical character and agricultural history, was very difficult. In the ideal case a "natural" transition or prisere (Tansley, 1939) would be chosen without interference from/

from cultivation or grazing, but this is never obtained. All parts are heavily grazed, and cultivation extends over most machairs with the grass-moors showing signs of derelict lazy-bed cultivation (Darling, 1945). Allowances were made to include all possible soil types and niches and to avoid bare rock, blowing sand, and open water where no earthworms normally exist.

Although adopting the usual procedure of sampling at regular intervals along a single line over fairly uniform ground in Tiree, the sampling was carried out in all other islands in distinct ecological zones straddling the transect line. All obvious soil niches within these zones, such as under stones, in dung-pats, in marsh, in woodland, and in moist open soil were searched. The ideal transition is hardly detectable over short distances, but sharp local changes do occur due to fencing, cultivation, and flooding, causing ecological discontinuity.

The ecological zones for sampling were selected on the basis of the vegetative succession (Tansley, 1939), and of whether or not the ground was enclosed. The vegetation of the area is briefly described in a community classification (Forrest et al., 1936; Darling, 1947; MacLeod, 1948) and as a flora (Heslop Harrison et al., undated; Kerr, 1954), but for the purposes of this work the following communities are used as labels for sampling zones.

(1)/

(1) Pure sand. The sandy shore above the level of high water ordinary spring tide colonised usually in fore-dunes by Agropyron junceum, Ammophila arenaria, and Carex arenaria.

(2) Very sandy soil. The sand dunes, known in the Hebrides as "bent-hills", colonised by Ammophila arenaria, Trifolium repens, T. procumbens, Plantago lanceolata, Galium verum, and Festuca rubra.

(3) Sandy loam. The sea-meadow or machair, possessing a complex sward which has been described elsewhere (see botanical references above). True machair is free from Ammophila arenaria, has never been tilled, and an "ecotone" (Tansley, 1939) exists between it and the dunes.

(4) Sandy loam grading to peaty loam. The cultivated ground (enclosed) which is acquired by tillage of the machair on the one hand and the grass-moor on the other. This includes usually the in-bye ground of crofts and yields crops of hay, oats, potatoes, turnips, and barley in that order of importance (Darling et al., 1955).

(5) "Mor" (Russell, 1950) soil. The grass-moor usually commences where the sandy drift meets the solid rock. The ground tends to slope steeply with many rock outcrops. Lochs, water-courses, and marshes frequently occur at the junction of the "light" and the "dark" soils. The vegetation consists of Molinia/

Molinia caerulea, Carex flava, Trichophorum caespitosum, Nardus stricta, and Eriophorum angustifolium. Calluna vulgaris and Erica tetralix are usually present also but are sub-dominant.

(6) Peat. The heather-moor usually on a raised, compara-:tively flat peat bog covered with luxuriant Calluna vulgaris and Erica tetralix.

(2) Soil Sampling

From each of those ecological zones a series of soil samples was taken for analysis in cores 10 to 15 centimetres deep according to the depth of the soil. Sampling stations were coincidental with those used for earthworm sampling. In dunes the soil changes rapidly over the parabolas from basin to crest, and in winter the rising water-table floods many basins. Similarly on the moorland soil conditions reflect the dampness patterns, and both here and in the dunes it was difficult to obtain samples which might be typical of the entire zone. These were taken, however, in localities where earthworms are readily available. On the machair and cultiva-:ted land soil conditions vary little by comparison.

In each zone three soil bags were filled with three samples in each, all taken from different sites. The samples were hand-sorted in the laboratory to remove as much as possible of the/

the plant material, and the three samples in each bag thoroughly mixed. From these three mixed samples, sub-samples were taken, and the following estimations made:

pH - by both colorimetric and electrometric (glass electrode) methods in each case.

$CaCO_3$ content - by the back titration method using dilute HCl and NaOH on samples of ignited soil.

Loss of weight on ignition (organic content) - by igniting soil dried at 110°C for 18 hours at 500°C which is below the temperature of dissociation of the $CaCO_3$.

(3) Earthworm Sampling

Guild (1951b, 1952a) discusses the problems of assessing earthworm populations in heterogeneous soils, and compares earthworm distribution with that of plants, pointing out that even on relatively uniform pasture fields the variation in species numbers in samples taken from individual fields frequently equals and sometimes exceeds $\pm$ 50 per cent of the mean. The soils of the dunes and the moorland are extremely heterogeneous, and wide variation also exists in the machair and cultivated soils.

Any sampling method capable of revealing the quantitative differences between ecological zones would therefore require to overcome the high variability of the ecosystem. This might/

might be partly accomplished by subdividing each zone into its own particular complex of communities (a difficult task since knowledge is scanty and the eye not sufficiently well-trained), by sub-sampling those communities to obtain as near an absolute measure of the biomass or numbers of earthworms per unit area, and summing to obtain a zonal estimate.

In all zones every niche which might be occupied by earth-:worms was searched, and earthworms extracted. By this means the species complex peculiar to each zone could be thoroughly investigated, and both qualitative and quantitative comparisons drawn. All extraction of earthworms was carried out in the field. The potassium permanganate solution method (Evans and Guild, 1947) was used where possible, but turfs were also dug and hand-sorted, dung-pats (cow and horse) broken up, and stones raised. No really efficient method of earthworm extraction has been described. The potassium permanganate solution method used alone is unsuitable for comparative studies on different earthworm populations (Svendsen, 1955), and the electrical method (Satchell, 1955c), although perhaps giving finer measure-:ments than the potassium permanganate solution method, is not suitable for remote field work.

When extracted, the earthworms were preserved in 4 per cent formalin, and taken to the laboratory for identification and counting/

counting. Identification was according to the key compiled by Cernosvitov and Evans (1947). Occasionally it was not possible to identify immature worms. These were allotted to the most closely related species according to the proportions of matures of each species present. Owing to taxonomic diffi-:culties B. tenuis, D. rubida, and D. subrubicunda were regarded as a complex in quantitative analysis.

III. THE SOIL HABITAT

(1) General Character

The soil mantle of the Hebrides is considered as being derived from three sources: (i) from the erosion of the country rocks, (ii) from materials taken from solution in the sea and subsequently cast up on the shore, and (iii) from organic material of both marine and terrestrial origin. (i) may be conveniently referred to as "erosion" derivatives, (ii) "marine" and (iii) "organic".

The area described here extends along the outer fringe of islands including Islay, Tiree, Coll, and the whole of the Outer Hebrides (Fig. 1). Through this arc of islands conside-:rable quantities of both erosion and marine derivatives have accumulated, been mixed, and have formed the basis for development/

development of the organic fraction. The erosion fraction comes from a comparatively uniform geological background of Lewisian gneiss, with major interruptions of Torridonian rocks in west Islay, and granite in Harris (Charlesworth, 1955; Phemister, 1948; Read, 1935). The marine fraction consists mainly of the finely divided hard parts of marine inverte:brates and algae.

Shore sand possessing this high marine fraction is known as shell-sand to distinguish it from silica and basalt sands which have mainly erosion derivatives. The shell content varies considerably both within each deposit and between de:posits. Within a single deposit at Durness (Darling et al., 1955) the range in $CaCO_3$ content was from 40 to 70 per cent, and considering the 18 analyses available for the fringing islands (Darling, 1955; Table II, and others by the author) the means for each deposit range from 38 to 86 per cent. In Islay, due to a large erosion fraction from the Torridonian, a low mean value for $CaCO_3$ is obtained, and a value of 40 per cent is obtained in Benbecula, while a few miles distant in North and South Uist the mean figures fall between 49 and 65 per cent.

The sand has accumulated on the western and southern aspects of the islands, while in the central, northern, and eastern/

eastern reaches much bare rock protrudes, and depressions are filled with glacial or raised beach deposits. Small islands such as those in the Sounds of Harris and Barra, together with north-pointing promontories such as the Eoligarry in Barra, Toe Head in Harris, and Lewis (Broad Bay) are exceptions having major accumulations on their eastern shores, while Tiree is almost completely encompassed by calcareous sandy beaches.

The general inference arises that the mineral base of the soil mantle has two major components so deposited as to cause a regional ecological gradient in the soil from a stratum of one particular character to that of the opposite character. Along the sandy shores occur the "light" soils of loose texture (Plate I), low physical stability, low organic content, high lime content, and high pH, while on the erosion soils exactly the opposite conditions prevail (Plate II). Soil character changes rapidly along transect lines at right angles to the sandy shore and usually in the direction of the prevailing wind. The transects from calcareous sand to peat described in this survey extend over distances of from 1 to 3 kilometres, but the transition can be accomplished in less than 100 metres in some sheltered north-facing bays such as those at the north tip of Coll. Between the two extremes occurs an ecotone upon which is evolved a gradient of soil types.

Soil is everywhere shallow. In a fairly uniform transition from/

from dunes to machair in Tiree, depth increases from 3 centi:metres in dune basins to 12 centimetres in the machair, in a horizontal distance of about 200 metres. In machair the soil depth does not usually exceed 15 centimetres, although it may be more than twice that in cultivation, and a sharp discon:tinuity normally exists between the soil and the sub-sand (Plate I). In places deep-rooting plants or an old over-blown soil gives a humus-rich layer, usually with fairly sharp demarcation, between 20 and 60 centimetres below the surface (Plate III). Fig. 2 shows the variation of moisture and organic content of the machair soil at Balinoe, Tiree in July, 1952, from the surface to the water-table. The "mor" soils of the moorland extend to a natural depth of between 30 and 40 centimetres when topped by a boulder clay, but are much shallower, sometimes only a root mat, over bare rock. Locally the depth is enhanced by lazy-bedding, where parallel trenches have been cut close together and thesoil heaped on the inter:vening ridges (Plate IV).

(2) Physical Stability (Faunistic Aspects)

Physical stability is the resultant of a force complex including weather, plant communities, animal activity, soil texture, water relations, and topography. It cannot be conveniently measured directly but is, nevertheless, a function of/

of other characteristics which can be accurately measured. It is the inverse of $CaCO_3$ content, since the $CaCO_3$ source (shore sand) lies at the lowest point of the stability gradient, and directly related to loss of weight on ignition since the peat lies at the highest point of that gradient.

Only aspects of soil mechanics which affect or are affected by animals, and particularly earthworms, lie within the scope of this work, and it is only possible to mention here a few of the macroscopic forms which play a major part in the disturbance of the soil. The vegetation is considered as the prime agent of sand fixation. An arbitrary line might be drawn through the machair parallel to the shore, dividing the unstable soils on the seaward side from the stable soils on the landward. The discussion on physical stability resolves itself into the fixation of wind-blown sand in dunes, the ultimate development of machair, and the damage to the fixation agency by animals.

The rabbit Oryctolagus cuniculus is by far the most impor-:tant wild animal in this connection. Having been introduced into the islands in the 18th and 19th centuries (Harvie-Brown and Buckley, 1888, 1892), the rabbit now occupies all the major islands with the exception of Tiree, where it became extinct in the middle of the 19th century. The situation in Tiree gives a fair standard for comparison to rabbit infested dunes and machair in other islands. At Machair Mhor, Coll, there is a fine/

fine example of how dune conditions are perpetuated on ground which would otherwise be free of Ammophila. Land of exactly similar character and situation at Balevoulin, Cornaigmore, and Balephetrish in Tiree, possesses well-developed machair. Rabbit damage is of two sorts; the burrowing causes blow-outs (Plate V), and the overgrazing eliminates important members of the sand-fixing plant community and weakens the root complex (Plate VI). The rapid spread of myxomatosis throughout the islands during 1954-55 has, however, reduced greatly the number of rabbits. All other wild vertebrates cause minor damage, but Mus norvegicus, Apodemus hebridensis, Microtus agrestis (Harvie-Brown and Buckley, 1898-92), and Sorex minuta are present locally and a new record of Erinaceus europaeus has recently been made by the author in sand dunes in Coll. Among the birds Tadorna tadorna (sheld-duck), and Riparia riparia (sand martin) make nesting burrows in sand dunes in both Outer and Inner Hebrides.

Extensive damage to dune vegetation is also wrought by cattle, sheep, and horses. Sheep and cattle cause damage by both body-rubbing against sandy scarps, and sheltering under those scarps in bad weather with excessive trampling (Plate VII). The total effect of domestic stock can be seen in Tiree where there is no rabbit damage to obscure the situation. Apart from the agency of grazing animals, however, man contributes directly/

directly by deliberate overgrazing by livestock, damage to the turf mat by vehicles, burying rubbish and dead farm stock in the dunes, and taking dune sand for building material. Children at play also cause much damage.

Earthworms play a great part in soil movement (Evans, 1948), probably more so than any other group of animals, but they do little to upset the physical stability of the soil. In the dunes and machair, the dominant species Allolobophora caliginosa, Bimastus tenuis, Dendrobaena octaedra, and Lumbricus rubellus, do not send up casts above the general level of the sward. The large casting species Allolobophora longa occurs occasionally in dunes and builds very sandy casts well above the general level of the sward. These quickly dry out, and become dispersed by the wind. In the machair A. longa and Octolasium cyaneum both build casts higher than the grazed sward, but these have a stickiness, and are washed down by the rain in situ.

Myrmica rubra and M. scabrinodis are abundant in the dunes and machair, where, in the absence of surface stones, they colonise dry cow-pats. The soil immediately under the cow-pat is excavated with the formation of tunnels and galleries causing damage to the root complex, and, on the drier and looser substrates, centres of instability. In Coll, Formica fusca has colonised outcrops of loose-textured shell-sandstone in/

in the dune basins. There, tunnel and gallery systems have been excavated on a grand scale. The ants may be seen transporting sand grains, and the excavations contribute greatly to the rapid break-down of the rock by wind action.

Throughout the entire area Geotrupes sterocorarius is found burrowing in all types of soil under dung-pats. It is particularly abundant in the dune and machair zones, and in the latter is responsible for the penetration of the 15 centi-:metre soil mat, and for sending to the surface considerable quantities of pure sand. It is the only invertebrate observed to do so on such a scale. Those sand heaps, usually on the fringe of a cow-pat, and sometimes as much as half the size of the pat itself, are quickly scattered by the wind.

(3) Soil Analysis

The distribution of earthworms within the wide range of soil conditions present in the Hebrides is the outline of a complete ecosystem, the frequency of the animals being a measure of the animal-environment interactions (Allee et al., 1949). Many factors are known to influence earthworm numbers, but Satchell (1955b) has shown that there is a high degree of correlation between these, pH, and available calcium. $CaCO_3$ content, pH, and loss of weight on ignition (organic content), which are correlated among themselves and also to moisture retaining/

retaining capacity are measured and later used as indicators of soil character. Table II shows the pH range between mean values of 8.6 in the shore sand to 4.4 in the peat moorland; Table III the range in $CaCO_3$ content from means of 65.5 per cent dry weight to 0.6 per cent at transect extremes; Table IV the same for loss of weight on ignition, means ranging from 1.7 per cent dry weight to 75.9 per cent.

IV. ECOLOGICAL DISTRIBUTION

(1) The Dune Community

The dune community is seen in Table V, there being a complex of 10 species (*B. tenuis*, *D. rubida*, and *D. subrubicunda* considered separately) with *L. rubellus*, *D. rubida-subrubicunda*, *L. castaneus*, and *B. tenuis* sharing dominance. These are the "pioneer" species existing in the unstable dune. Almost without exception *L. rubellus*, and in many cases the other three dominant species also, was found in thick *Ammophila* immediately above the shore sand. At no time were earthworms found in the unstable dune other than in dung-pats, and dung is undoubtedly the basis of colonisation. The population would appear to be clustered in or immediately under the dung-pats with practically no earthworms in the interspaces, except in moist basins where organic matter is more plentiful. The dung/

dung of cattle, horses, and to a lesser extent that of sheep, provides optimal or nearly optimal conditions for earthworms in an otherwise austere environment where both food and moisture are severely limited.

In Table V A. longa does not appear, although it occurs at the dune pH level of 8.2. This species was not obtained in sampling surveys in dunes but was observed casting among thinning Ammophila at Newton, North Uist. The casts and the soil were extremely sandy, and soil depth was about 5 centi-:metres. These earthworms were found casting in the dunes immediately landward to the shore rampart in September, 1955, only a month after the end of the drought. Eiseniella tetraedra, a species found usually in limnic situations, occurs in marshy basins. Having no obvious limnic migration route through the dunes, those earthworms appear to form more or less isolated communities.

In the Hebrides, except in the most severe conditions, only the upper 4 centimetres of the soil freeze hard in the winter, and then only for a few days. Summer drought, however, causes dune soils to dry out to a depth of 30 centimetres or more, and the compaction of the sub-sand prevents the movement of earth-:worms vertically. Lines of weakness in the tight sand do occur along the deep roots of Ammophila, and these may give access to more moist levels. Grant (1955) has shown, however, that/

that two common field species, A. caliginosa and E. foetida, can sustain a loss of 63.5 and 58.8 per cent respectively of their body weight before reaching their vital limits of desiccation.

The "family" group theory of aggregation (Satchell, 1955b) probably finds confirmation in the dune community, but provision almost certainly requires to be made for initial colonisation. So diffuse is the unstable dune community in the interspaces between the dung, that the chances of a pat being actually deposited on top of, or even near to, an earthworm are small. There is only negative evidence in support of this, since no earthworms have been found in the interspaces, but it is clear that, with the wholesale dispersion of dung by birds, flies, beetles, and the wind, surviving earthworms must migrate horizontally. The chances of dung being deposited on the same site within the lifetime of the youngest survivor are probably extremely small.

Evans and Guild (1948a) used L. rubellus, L. castaneus, and D. subrubicunda together with other 8 species in reproduction experiments, and found that those species named had the highest reproductive rates, apart from E. foetida which is not present in this area. They also found, using A. chlorotica, that moisture content of the soil greatly affected reproduction, and that below about 20 per cent of dry weight of soil it ceased altogether. Bullock, horse, and sheep droppings, they found, gave best feeding conditions for reproduction.

It appears that the colonisation of dunes by earthworms follows closely the dampness pattern, the population, as would be expected, being denser in the basins than on the slopes and crests. The successful colonists have a distinct preference for dung, both as an environment and as food, have a higher reproductive potential than others present, and are able to survive drought and predation in such numbers as to maintain the population.

(2) The Machair Community

The machair community is seen in Table VI, there being a complex of 15 species, L. rubellus, A. caliginosa, and D. octaedra sharing dominance. A. caliginosa is probably a more important species in machair soils than the figure of 22.8 per cent suggests, since it is found to prefer dung much less than other dominants, and is more difficult to collect in areas where the open soil cannot be sampled by the $KMnO_4$ solution method, due to lack of running water. The figure of 42.5 per cent obtained in Tiree (C), where sampling conditions are good, is probably more representative. From the percentages in these Tables, it is seen that the representative proportions of species in populations in different areas vary greatly, and that it is only by considering the areas cumulatively that a representative picture may be obtained.

No/

No really deep-burrowing species occur, but large casting species such as A. longa and O. cyaneum are sometimes present, though never dominant. The casts contain much more sand than the surrounding soil, due either to their concentrating the sand or taking it from the base of the soil mat. A. longa, however, is considered (Evans, 1948) to burrow only about 30 centimetres in English agricultural fields, and in the machair seldom goes deeper than soil base at about 15 centimetres.

The division between the soil mat and the sand below is a sharp ecological discontinuity (Plate VIII), and the main mass of the soil fauna, including earthworms, inhabits only the upper soil mat. This discontinuity, it may be argued, is created by an earthworm community able to live all year round in the surface layer without being forced down either by frost or drought. During a severe frost in February, 1955, only the upper 5 centimetres of the soil were frozen, and the earthworms were found to be active in the free 10 centimetres above the discontinuity. In July and August, 1955, when no fresh dung was being deposited in the area, after two months of drought the sward became scorched, and the soil very dry to a depth of about 8 centimetres. The remaining 7 centimetres immediately above the sand were slightly moist and there the earthworms lay curled and inactive.

Fig. 2 shows that across the soil-sand discontinuity environmental/

environmental factors controlling earthworm movement change sharply. The compaction of the sand is very tight; a spade going through the soil easily meets the sand with a sharp jolt as of striking a rock. No earthworms have been found in the sand immediately below the soil, and though dung was placed at intervals of 10 centimetres from the surface to the water-table, in this area with an organic layer between 30 and 45 centimetres, no earthworms were found below the 10 centimetre level. There is little doubt that one of the prime factors determining the soil depth in untilled sandy soils, such as machair, is the burrowing habit of the earthworms. The conspicuous absence of the deep-burrowing L. terrestris (Evans, 1948), a common Scottish field species (Guild, 1951a), from the machair soils is perhaps significant.

Eisenia rosea, a species abundant in Rothamsted soils (Satchell, 1955b) and a common field species in Scotland (Guild, 1951a), occurs only on one machair site, the warren (local name) Kilchoman, Islay. Ploughing is said to increase the proportions of this species (Evans and Guild, 1947) and to decrease others, but in Table VI E. rosea is not seen at all on soils cultivated from machair; the St. Kilda record is from derelict grass-moor cultivation. The occurrence of a species, however, not only depends on the acceptability of the habitat, but also on the chance of introduction to a geographically/

geographically isolated area. Perhaps the best illustration of this comes from the comparatively high proportion of L. festivus at the Machair Mhor, Coll, and its complete absence elsewhere.

(3) The Community in Cultivated Soils

Table VII shows the species complex on cultivated soils (including enclosed leys), and is roughly similar to that in machair soils (Table VI). Of the three machair dominants, A. caliginosa seems to have a similar status in cultivated soils, but D. octaedra and L. rubellus are less abundant, while L. castaneus is more numerous. L. festivus does not occur because cultivated ground was not included in the only transect in which this species was found. B. eiseni, absent in the dunes and machair, appears in Table VI, but it is found only in lazy-bed cultivation in Scalpay, Harris, and St. Kilda, a situation comparable to the grass-moor. B. tenuis, a species dominant in the dunes and also numerous in the machair, was found to be much less so on the cultivation and the moorland (Tables VIII and IX).

Ploughing and crop rotation on soils cultivated from machair (Darling et al., 1955) destroys the natural division between the soil mat and the sand, and results in increased depth with a much greater sand-mix. There is, however, no striking/

striking effect evident of this ecological change on the earthworm population.

At the Reef, Tiree, the airfield perimeter fence forms a sharp boundary between grazed machair with dung-pats, and machair which has not been grazed for about fifteen years without dung-pats. Before the construction of the airfield there was no such discontinuity, but now the fence separates two distinct earthworm populations. Under the deep rank vegetation (mostly Festuca rubra) within the airfield, B. tenuis and E. tetraedra were found to be more abundant than the other dominants found on grazed machair.

The airfield population has a different food supply, and is less affected by predatory birds mainly Sturnus vulgaris (starling), Vanellus vanellus (lapwing), Pluvialis apricaria (golden plover), and Larus spp. (gulls), which habitually search dung-pats for food. Sorex minuta is present in both areas and is perhaps more numerous in the long grass of the airfield, while the beetle community, particularly Nebria brevicollis, Pterostichus vulgaris, Carabus granulatus, and Staphylinus aeneocephalus, is much larger than on the short cropped grassland.

(4) The Grass-moor Community/

(4) The Grass-moor Community

Table VIII shows the species complex on the grass-moor. All species present on the machair except A. longa are found on the grass-moor and B. eiseni, not found in the machair, is abundant on the moorland. A. caliginosa appears to be less numerous, and the dominants are L. rubellus, D. octaedra, and B. eiseni. On the grass-moor (and to a lesser extent on the cultivated land) very many more stones are present at the soil surface than on the machair and dunes. Under these stones well-made earthworm burrows exist, and in the vicinity of derelict dwellings and sheep fanks such niches are plentiful. In such localities the earthworm population is found to be much denser than on the surrounding moorland (Boyd, 1956, in press, and Section C of this paper). Species such as L. terrestris and O. lacteum are found in the precincts of ruined crofts where the deeper and better drained soils favour deep-burrowing species. O. cyaneum is found in the same localities, but also under stones and in dung well away from signs of human habitation. E. tetraedra is found at Ness, Lewis, in cow-pats on old peat cuttings on grass-moor where there is much exposed peat and where conditions were similar to those normally found on the heather-moor (Table IX).

(5) The Heather-moor Community/

(5) The Heather-moor Community

Table IX shows the complex of 6 species found in the four heather-moors examined. Earthworms were collected in the immediate vicinity of dung, usually of sheep, or under turfs in peat cuttings. L. rubellus, D. octaedra, and B. eiseni, dominant on the grass-moor, are the main colonisers of the heather-moor. No deep-burrowing species are present, but it is obvious from the collections in the peat cuttings that those species are not entirely surface living, but do in fact inhabit the peat.

(6) Relationships between Earthworms and Soil Type

The occurrence of earthworms in the various communities already discussed is seen to be highly variable. The variation is due in part to sampling error, but much more so to the intrinsic disposition of a diverse fauna within a habitat of great variety (Plate IX). This variation together with the small number of samples makes regression analysis between earthworm abundance and environmental characteristics unprofitable. It is clear, however, that abundance of practically all species of earthworm in Hebridean soils is affected by changes in soil character of which pH, $CaCO_3$ content, and loss of weight on ignition are good indicators.

A/

A glance at Tables II - IV will show that pH, $CaCO_3$ content, and loss of weight on ignition are themselves corre:lated and outline the wide differences of character between the "light" or sandy soils of the dunes, machair, and culti:vated ground, and the "dark" or peaty soils of the grass- and heather-moor. Earthworm abundance expressed in absolute numbers and percentages of each species collected from the two types of soil are set forth in Table X. The classification of earthworms into "acid-tolerant" litter-dwelling species and "acid-intolerant" burrowing species made by Bornebusch (1930) and developed by Satchell (1955b), both of whom worked in woodland soils, again finds application. If the species living more abundantly on the moorland be considered as the "acid-tolerant" (pH of the soil, below 6), and those more abundant on the calcareous grassland as "acid-intolerant" (pH of the soil, above 6), the species complex, with the excep:tion of D. mammalis, L. terrestris, and O. cyaneum, can be thus divided. A. caliginosa, A. longa, E. tetraedra, L. castaneus, and L. rubellus are "acid-intolerant". A. chlorotica, B. eiseni, B. tenuis - D. rubida-subrubicunda complex, D. octaedra, E. rosea, L. festivus, and O. lacteum are "acid-tolerant". All the differences between abundance on the calcareous grassland and the moorland being significant (three exceptions mentioned above).

In/

In the cases of _A. chlorotica_, _A. longa_, _D. mammalis_, _E. rosea_, _L. festivus_, _L. terrestris_, _O. cyaneum_, and _O. lacteum_ comparatively small numbers were obtained, and the classifi-:cation of these species should be treated with some reserve. _A. caliginosa_, _B. eiseni_, _B. tenuis - D. rubida-subrubicunda_ complex, _D. octaedra_, _E. tetraedra_, _L. castaneus_, and _L. rubellus_ on the other hand appear in larger numbers and there is little doubt about the classification of these species. Some are clearly affected more than others. _A. caliginosa_ and _L. castaneus_ (both "acid-intolerant"), together with _B. eiseni_ and _D. octaedra_ (both "acid-tolerant"), show differences of the highest significance. Satchell (1955b) classifies _L. rubellus_ as "ubiquitous", and this species, together with the _B. tenuis - D. rubida-subrubicunda_ complex, is found fairly evenly distributed throughout the entire range of soil conditions from calcareous sand to peat; yet both have significant differences in abundance between "light" and "dark" soils. The term "ubiquitous" may apply more favourably to forest soils than to grassland soils, but is ambiguous. _A. caliginosa_, for example, is a distinctly "acid-intolerant" species, but it was found at low frequency in two of the four heather-moors examined (pH of the soil 4.3 - 4.9). It is, _in sensu stricto_, ubiquitous.

(7) Soil Niches/

(7) Soil Niches

While sampling earthworms in the various ecological zones it became obvious that the proportions of species present differed in different niches. From collections in exactly the same soil locality in Islay from dung-pats and under stones, 18 A. caliginosa, 31 D. subrubicunda, and 37 L. rubellus were found in the former, and in the latter 49, 7, and 23 respec:tively. Collections from dung-pats and open soil in exactly the same soil locality in Tiree show 277 A. caliginosa, 101 D. octaedra, 59 L. castaneus, and 448 L. rubellus in the dung-pats, and 439, 22, 1, and 52 respectively in the open soil. Dung-pat collections from marsh and from machàir 50 metres apart give 0 A. caliginosa, 71 E. tetraedra, and 0 L. rubellus in the former, and 19, 2, and 63 respectively in the latter. The differences in all cases are highly significant.

The dung-pat provides a randomly dispersed niche which over-rides the ecological zonation, and which is the basis of dune colonisation. Of the 10 dunes and machairs included in this survey all but 1 were grazed by cattle, and earthworm sampling in dung was mainly carried out in cow-pats old enough to be conveniently broken up with forceps. Cow-pat frequency varies according to the number of head per acre, and increases greatly around wind-breaks and water-holes. Table XI shows results of samples taken of 12 x 12 metre quadrats on dunes and machairs/

machairs at Balinoe, Barrapol, and the Reef, Tiree, in July, 1952, together with a satisfactory test for random distribution, the deviations being insignificant at the 5 per cent level and greater.

The detailed analysis of collections from different soil niches in 7 different localities - 2 in Islay, 1 in Tiree, 1 in Coll, 1 in North Uist, and 2 in Lewis: 4 from machair, and 3 from moorland - is set forth in Table XII, and Fig. 4.

Differences in the percentage constitution of all three communities - in open soil, in and under cow-pats, and under stones - are seen to be significant in only 2 species, 6 species in two out of three, 3 species in one out of three, and 4 species in none out of three. Of the three niches it is pos-:sible that open soil and under stones are more similar than each are separately to the dung-pat niche. Of the 15 species (counting B. tenuis - D. rubida-subrubicunda complex as a single species for the purpose), 10 show no significant diffe-:rence in numbers between open soil and under stones, while 8 show this between open soil and dung-pats, and 6 between under stones and dung-pats.

It is clear that A. caliginosa is most abundant in the open soil, and may be said to have a very distinct preference for the open soil, though still constituting a major part of the/

the communities under stones and in dung-pats. No other species possesses such a preference, with the possible exception of the B. tenuis - D. rubida-subrubicunda complex. The preferences of this complex, both for open soil and dung-pat, are equally strong but not significantly different. B. eiseni, D. octaedra, and L. rubellus possess a significantly stronger preference for dung-pats than for the other two niches, though all, with the exception of B. eiseni, are found there. The only instance of a distinct preference for under stones is A. chlorotica.

The niche preference of the sub-dominant species can be seen from the Table to be based on small numbers, and these should be treated with reserve.

V. SUMMARY

1. Past work on relationships between earthworms and the soil is briefly summarised.
2. A transect survey is described. In it earthworms were extracted from the soil by the potassium permanganate method, by digging, by searching dung-pats, and by raising stones at stations along a line from the shore sand to the moorland peat.
3. The general character of the soil habitat is outlined. The mineral base of the soil is derived from the erosion of/

of the country rocks, and from substances, mostly $CaCO_3$ taken from solution in the sea by organisms, and cast up on the islands as shell-sand. Calcareous sand and peat are so deposited that a major ecological gradient exists in the soil from the sand to the peat. The pH range of the soil is 8.6 to 4.4; that of $CaCO_3$ content, 65.5 to 0.6 per cent dry weight; and that of loss of weight on ignition, 1.7 to 75.9 per cent dry weight (mean values for extreme stations quoted in each case).

4. Faunistic aspects of physical stability of dune and machair soils are discussed. Stability is seen to be greatly affected by rabbits, domestic stock, direct human influence, and to a lesser extent by other small mammals, birds, earthworms, ants, and a species of beetle.

5. The ecological distribution of earthworms is discussed in zonal communities. The *B. tenuis - D. rubida-subrubicunda* complex, and *L. rubellus* are the dominant species in the dunes; *A. caliginosa* and *L. rubellus* in the machair; *A. caliginosa*, the *B. tenuis - D. rubida-subrubicunda* complex, *L. castaneus*, and *L. rubellus* in the cultivated soils; *A. caliginosa*, *B. eiseni*, *D. octaedra*, and *L. rubellus* in the grass-moor; and *B. eiseni*, *D. octaedra*, and *L. rubellus* in the heather-moor.

6. The large variation in earthworm numbers is discussed and the/

the comparative abundance of all species examined between "light" soils on the calcareous sand, and the "dark" soils on the peat. Significant differences were found in all cases except D. mammalis, L. terrestris, and O. cyaneum. Six species appear to be more abundant on the "light", and another six on the "dark" soils. A. caliginosa and L. castaneus are particularly more numerous on the "light", and B. eiseni and D. octaedra on the "dark".

7. Communities living in the three soil niches - open soil, in and under dung-pats, and under stones are examined and compared. Significant differences in abundance of each species are noted between niches in all cases except L. castaneus, L. festivus, O. cyaneum, and O. lacteum (due possibly to the low frequency in the last three cases). Differences are especially significant in the cases of A. caliginosa (which does not aggregate in dung), B. eiseni, D. octaedra, and L. rubellus (all three of which aggregate in dung). Niche preferences are discussed for all species.

APPENDIX I

List of Survey Areas

1. Islay. Transect from shore sand at Machir Bay over the raised beach at Kilchoman to the heights of Cnoc Dubh. June, 1954.

2. Tiree (A). Transect from shore sand at Traigh Shorobeadh, over machair at Balinoe Church, and across cultivated ground to heath. July, 1952.

3. Tiree (B). Transect from shore sand at Traigh a' Bheidhe west of Abhuinn Bheidhe, across dune and machair to the west shore of Loch a' Phuil. July, 1952.

4. Tiree (C). Transect from shore sand at Traigh Baugh across dunes and machair to ungrazed land lying within the airfield perimeter fence. March, 1954.

5. Gunna. Transect from shore sand to heath. May, 1954.

6. Coll. Transect from shore sand at Traigh Hogh across the Machair Mhor to heather-moor north of Acha. May, 1954.

7. Barra. Transect from shore sand at Allasdale through the small glen immediately south of Cuier, to the grass and heather-moor. April, 1954.

7a. South Uist. Collection from dunes and machair at Grogorry. November, 1953.

7b. Benbecula. Collection from dunes and machair at Creagorry. November, 1953.

8. North Uist. Transect from shore sand at Newton, across dunes, machair, and cultivated ground, through the small plantation at Newton House Hotel, and landward to mixed grass-heather moor. May, 1954.

9. Harris. Transect from shore sand at Traigh Luskentyre across dunes, machair, and cultivated ground on the west bank of the Scilebost River. October, 1954.

9a. Scarp, Harris. Collection from moorland dung-pats. September, 1954.

9b. Scalpay, Harris. Collection from lazy-beds and moorland. May, 1955.

9c. Hirta, St. Kilda. Collections from Village Bay and Gleann Mor. May, 1955.

10. Lewis. Transect from shore sand on the west shore below Eoropie, across machair and cultivated ground to grass-moor and peat cuttings on the east coast south of Port of Ness. July, 1954.

In all cases the shortest distance was chosen between the sand and the peat.

THE LUMBRICIDAE AT ST. KILDA

During visits to St. Kilda in July, 1952, May, 1955, with the kind permission of the Marquis of Bute, and June, 1956, the earthworm communities in the Village Bay and Gleann Mor areas of Hirta were closely examined, and notes made on those present on Dun and Boreray. A transect through the village area was carried out, the line of transect stretching from the wall above the storm beach, through the meadows, across the causeway at cottage No. 5, and from thence up over the perimeter wall through the walled enclosures in An Lag Bho'n Tuath to the steep slopes below the Gap (Fig. 5). Separate collections were made throughout the village area (Plate X), under stones and rotting wood, in disused middens, and by digging in the meadows. A similar collection was made in the area of the shielings in Gleann Mor (Plate XI), except that none was taken there from under rotting wood.

The only species of earthworm yet recorded for St. Kilda is Lumbricus rubellus Hoffmeister, but no mention is made of where the specimen was collected in the islands (Evans, 1906). Altogether nine species were successfully identified, and there is inconclusive evidence of a tenth. The list is as follows:

Allolobophora caliginosa/

Allolobophora caliginosa forma *typica* Savigny

Allolobophora caliginosa forma *trapezoides* A. Dugas

Bimastus eiseni Levinsen

Dendrobaena octaedra Savigny

Dendrobaena rubida Savigny

Dendrobaena subrubicunda Eisen

Eiseni rosea forma *typica* Savigny

Eiseniella tetraedra forma *typica* Savigny

Lumbricus castaneus Savigny

Lumbricus rubellus Hoffmeister

While sampling was being done in the walled enclosures in An Lag Bho'n Tuath a large dark red specimen, too large to be the typical form of *L. rubellus*, was found, and while digging in the village meadows three large dark red individuals were noticed, all of which escaped before final identification. This may mean, however, that *Lumbricus terrestris* L. is present at low frequency at Village Bay. No such specimens were noticed in Gleann Mor.

All the species recorded in this list have been previously found in the Outer Hebrides. The list for the entire Hebridean area, as far as it is known, contains 18 sepcies, 2 of which have been recorded only from the Inner Hebrides. All, except *D. subrubicunda*, have so far been recorded from the Scottish mainland (Guild, 1951a). The dominance of the species is also similar to that found elsewhere in the Hebrides, except for *E. rosea*/

E. rosea which has a much higher frequency in St. Kilda. A few mature specimens of this species have so far been recorded from Barra and Scalpay (Harris), and in Coll its frequency in a shore to moor transect was 1.1 per cent. The absence of cow-pats, especially on the moorland, must affect the distri:bution and numbers of such species as _L. rubellus_, _D. octaedra_, and _B. eiseni_, which are particularly fond of dung, and of all the other species generally. The withdrawal of cow and pony grazing probably caused a distinct change in the soil ecology of Hirta, which affected the earthworms greatly.

The history of the earthworm population of St. Kilda dates back not further than the end of the Quaternary glaciation, and is probably much more recent. During the peak of the Quater:nary glaciation St. Kilda appears to have escaped the main ice-sheet which covered the Hebrides, but supported small thin glaciers (Wager, 1953), and climatic conditions would severely limit the soil fauna. There are few natural vectors of earthworms to a place so isolated, and the population is probably a direct attribute of human colonisation within the last 2,000 years.

Although men have visited Soay, Boreray, and Dun (Fig. 5) regularly and have kept sheep there, the islands have not been permanently settled. Distinct signs of lazy-bed cultivation may be seen at the north-west end of Dun, and vague parallel ridges/

ridges not running along the contours on the southern slopes of Boreray may also be caused by lazy-bedding in the more distant past. No opportunity was obtained of examining at close quarters the grassland and soil of Soay, but various visits were made to Dun and Boreray, and searches for earth-:worms made.

During four visits to Dun considerable quantities of turf and stones were moved in search of nesting puffins Fratercula arctica, Manx shearwaters Procellaria puffinus, storm petrels Hydrobates pelagicus, and Leach's petrels Oceanodroma leucorrhoa, but no earthworms were found. During two visits to Boreray when turf and stones were moved for the same purpose as before, earthworms were readily obtainable. A. caliginosa forma typica, and B. eiseni were found together in the same place around the stone cells at Cleitean McPhaidein in turf riddled with puffin burrows, and in the locality of the faint signs of ancient lazy-beds. This is the only occasion on which A. caliginosa the "acid-intolerant" species, and B. eiseni the "acid-tolerant" species have been found abundant sharing exactly the same soil locality (they are both found in moorland soils (Tables VIII and IX), but not usually together). The situation is, however, extraordinary, the soil being very heavily manured by sea-birds.

There are two distinct communities within the isolated population in Hirta - one in the Village Bay area, and another in Gleann Mor. They are separated by the high central ridge of/

of Hirta from Mullach Mor to Mullach Sgar, the lowest point of which is the col of Am Blaid about 750 feet above sea-level. This ridge from the 200 to 300 feet contour upward on both sides possesses a shallow peaty soil mantle with much bare rock and talus, and supports mainly a Festuca ovina, Nardus stricta, Calluna vulgaris, Erica cinerea, Vaccinium myrtillus complex with a cotton-grass bog dominated by Eriophorum augustifolium on the high platform of Mullach Mor (Petch, 1933). The horizontal distance between the two communities is about three-quarters of a mile, and the actual distance by the col at Am Blaid, about 1 mile. The ridge is subject to a fairly high range in moisture conditions, and the manuring by sheep is too diffuse to cause the type of cluster distribution characteristic of cattle-grazed moors. Although perhaps assisted by the cloven hooves, fleece, and manuring of the large population of sheep (Boyd, 1953), communications between the two areas would appear to be very poor, but this was not always so. It was the custom of the St. Kildans to keep livestock at the Gleann Mor shielings and the accidental transference of earthworms and cocoons in fodder (damp hay, grass, potatoes, etc.) is highly probable. Turfs cut in the Gleann Mor area were used as fuel, and were probably a vehicle for transference in the opposite direction. Now uninhabited, however, there are no such facilities for earthworm movement in the island.

Table/

Table XIII shows the composition of the community at Village Bay in May, 1955, as far as it is known. From the two locali-:ties (i) the manse precincts, and (ii) the meadows and the village, it is seen that the community has approximately the same character throughout; the same species being present in about the same proportions. The frequencies involve mature worms only, and it should be added that two immatures taken at Village Bay were successfully identified as D. octaedra, and other two immatures not successfully identified had features similar to a mature D. rubida taken there in July, 1952.

Table XIV shows the composition of the Gleann Mor community with the mean frequencies of the Village Bay community for comparison. L. rubellus and A. caliginosa, the dominants at Village Bay, have a much lower frequency in Gleann Mor, and L. castaneus, a sub-dominant at Village Bay, is dominant in Gleann Mor. E. rosea and the D. rubida - D. subrubicunda complex are more common in Gleann Mor, and E. tetraedra together with B. eiseni found at Gleann Mor have not yet been recorded from Village Bay. Both are probably present in the latter, locally and at low frequency. Out of the 110 whole individuals collected in late July, 1952, only 22, or 20 per cent, were mature, i.e. possessing a clitellum and a tubercula pubertatis. In May, 1955, however, out of the 207 whole individuals examined

52.7/

52.7 per cent were found in this condition. This last figure is comparable with that obtained in Scalpay, Harris, a week earlier, where, in a somewhat similar population 49.2 per cent were found to be mature.

Throughout the transect sampling was carried out by the wet method (Evans and Guild, 1947), after which the soil and roots were separated by hand and the remaining worms extracted. Groups of three samples were taken - 1 square foot and to a spade's depth - at intervals of 100 feet. Table XV gives the data and shows clearly the change in density in passing from within the perimeter wall of the village to the moorland, and the increase in density within the walled enclosures in An Lag Bho'n Tuath to a level comparable to that existing within the village wall.

The soil within the perimeter wall tops a boulder clay and gravel deposit in the lower meadows (Wager, 1953), is deep, comparatively fine grained, and damp. Locally there are springs and seasonal streams which give rise to local dampness patterns. Around the village there are old middens, loose stones, rotting wood, and outcrops of rock all of which cause local variation in the soil habitat. On the hillside, where the meadow grasses become mixed with the moorland complex (Petch, 1933) the soil becomes shallow, course grained, and possesses a wide seasonal range in moisture content. Within the/

the sheep fanks in An Lag Bho'n Tuath, however, the soil regains depth, is of moderate grain, and has a range in moisture content much less than the surrounding moorland. The solid geology of the transect area shows granophyre at the drift base (Cockburn, 1935).

Of the two dominant species, A. caliginosa and L. rubellus, the former appeared to be present at varying frequencies in all the ecological zones, while the latter, abundant within the village wall and the walled enclosures was found only as a trace on the moorland. Had the moorland been grazed by cattle the frequency of L. rubellus there would have been greatly increased.

SUMMARY

1. Nine species of earthworm have been recorded from Hirta, St. Kilda, eight of which are new records for the island. All the species have been previously recorded from the Outer Hebrides, and from the British mainland. Comparisons are drawn with other Hebridean islands, and the history of the St. Kilda population is discussed.
2. Two nearly isolated communities within the Hirta population are described, and differences in the species complexes examined.

3./

3. A transect involving a group of three samples at twenty stations at intervals of 100 feet, along a line from the shore to the moor through the village meadows, is described. The density of the fauna is given for the various ecological zones.

TABLE I

The species complex of the Lumbricidae in the Hebrides incorporating all known records.

	Islay	Tiree	Gunna	Coll	Barra	North Uist	Harris	Shillay (Harris)	Scarp (Harris)	Scalpay (Harris)	St. Kilda (Hirta)	St. Kilda (Boreray)	Lewis	Canna
<u>A. caliginosa</u>	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<u>A. chlorotica</u>	x	x	x	x	x	x	-	-	-	-	-	-	-	-
*<u>A. longa</u>	x	x	-	-	x	x	x	-	x	-	-	-	x	x
<u>B. eiseni</u>	x	x	-	x	x	x	x	-	x	x	x	x	x	-
<u>B. tenuis</u>	x	x	x	x	x	x	x	x	-	x	-	-	x	x
<u>D. mammalis</u>	-	x	-	x	x	x	-	-	-	-	-	-	-	-
<u>D. octaedra</u>	x	x	x	x	x	x	-	x	x	x	x	-	x	-
<u>D. rubida</u>	x	x	x	x	x	x	x	x	x	x	x	-	x	-
<u>D. subrubicunda</u>	x	x	x	x	x	x	x	x	x	x	x	-	x	-
<u>E. foetida</u>	-	-	-	-	-	-	-	-	-	-	-	-	-	x
<u>E. rosea</u>	x	x	-	x	x	x	-	-	-	x	x	-	-	x
<u>E. tetraedra</u>	x	x	x	x	x	x	x	-	-	x	x	-	x	x
<u>L. castaneus</u>	x	x	x	x	x	x	x	-	-	-	x	-	x	x
<u>L. festivus</u>	-	x	-	x	-	-	-	-	-	-	-	-	-	-
<u>L. rubellus</u>	x	x	x	x	x	x	x	x	x	x	x	-	x	x
<u>L. terrestris</u>	x	x	-	x	x	x	-	-	-	-	-	-	x	x
<u>O. cyaneum</u>	x	x	-	x	-	-	x	-	-	-	-	-	-	x
<u>O. lacteum</u>	-	x	-	-	x	-	-	-	-	x	-	-	x	-

x = recorded

*<u>A. longa</u> = <u>A. terrestris</u> forma <u>longa</u> Ude

TABLE II

pH Measurements of soil
in the ten survey areas listed in Appendix I.

Zones	Survey Areas										Mean	St'd Dev'n
	1	2	3	4	5	6	7	8	9	10		
Shore	8.5	8.2	8.0	8.6	8.8	8.8	9.2	9.0	8.5	8.6	8.6	0.36
Dunes	8.2	8.0	7.6	8.2		7.9+ 8.5	8.5	8.8		8.4	8.2	0.35
Machair	8.0	7.2	7.4	7.7		7.7	8.0	8.6	8.4	7.7	7.9	0.45
Cultivated ground	. .	6.1					7.4 5.9+	7.8 7.6‡ 5.8‡		6.5	6.7	0.85
Grass-moor	4.7				5.9	5.7 5.1+	5.3	5.2	5.6		5.3	0.43
Heather-moor	4.3				4.4	4.3	4.3	4.9		4.1	4.4	0.27

+ = Marsh; ‡ = Wood

TABLE III

Percentage $CaCO_3$ per gram dry weight of soil in the ten survey areas listed in Appendix I.

Zones	Survey Areas													Mean	St'd Dev'n
	1	2	3	4	5	6	7	7a	7b	8	9	9a	10		
Shore	38.7	72.0	78.0	68.1	70.0	63.5	82.6	66.5	39.4	53.2	80.3	73.8	65.2	65.5	13.9
Dunes	35.5	63.0	74.7	67.8		56.1	81.3			49.1			56.6	60.0	15.1
Machair	1.9	56.1	65.4 6.0+	58.9 35.0+		31.4 5.0+	79.6			28.7	43.0		34.4	37.1	25.1
Cultivated ground		4.5					8.2+ 68.3			7.1 5.3‡				15.7	25.9
Grass-moor	0.4					0.4	1.7			1.4	0		1.4	0.9	0.7
Heather-moor	0.6				0.6	0	0.7			1.2	0		1.4	0.6	0.5

+ = marsh; ‡ = wood

TABLE IV

Percentage loss of weight on ignition per gram dry weight of soil in the ten survey areas listed in Appendix I.

Zones	Survey Areas										Mean	St'd Dev'n
	1	2	3	4	5	6	7	8	9	10		
Shore	0.9	2.0	3.0	1.8	2.4	2.4	2.0	1.6	0.2	0.2	1.7	0.94
Dunes	2.5	6.3	5.0	5.6		4.9	2.1	2.4		0.3	3.6	2.1
Machair	11.6	63.0+ 19.2	62.0+ 8.8	30.1+ 13.0		29.3+	2.4	7.2	0.7	7.5	21.2	21.47
Cultivated ground		12.9					28.1+ 7.4	21.5+ 8.3 13.6‡			15.3	8.0
Grass-moor	19.1					22.4	43.6	58.9	21.3		33.1	15.6
Heather-moor	75.6				85.6	90.5	90.7	43.8++		69.5	75.9	16.3

+ = marsh; ‡ = wood; ++ = very shallow

TABLE V

Specific constitution of duneland communities expressed in percentages of the total collection in each duneland surveyed.

Species	Survey Areas										Number of earthworms	Total percentage
	1	2	3	4	5	6	7	8	9	10		
A. caliginosa	-	3.5	11.4	4.8	-	-	-	-	-	-	21	1.92
A. chlorotica	-	-	-	-	-	2.1	-	-	-	-	7	0.64
B. tenuis	72.2	-	-	1.2	26.8	10.9	100	20.5	63.6	85.4	244	22.26
D. octaedra	1.4	-	2.8	1.2	13.4	14.2	-	9.6	-	-	72	6.57
D. rubida - subrubicunda	Numbers included under *B. tenuis*											
E. tetraedra	-	-	-	-	-	0.9	-	11.0	-	-	11	1.00
L. castaneus	-	5.0	1.4	13.3	4.9	5.3	-	5.5	-	-	57	5.20
L. festivus	-	-	-	-	-	14.7	-	-	-	-	50	4.56
L. rubellus	26.4	91.5	84.3	79.5	54.9	51.9	-	53.4	36.4	14.8	634	57.85
Number of earthworms	140	141	70	171	82	339	8	73	11	61	Total 1096	

TABLE VI

Specific constitution of machair communities expressed in percentages of the total collection in each machair surveyed.

Species	Survey Areas										Number of earthworms	Total percentage
	1	2	3	4	5	6	7	8	9+	10		
A. caliginosa	24.8	7.2	9.9	42.5	-	-	-	2.2	50.0	-	989	26.53
A. chlorotica	3.6	0.5	-	0.7	9.4	6.3	-	-	-	-	43	1.15
A. longa*	1.4	-	-	-	-	-	-	2.2	-	3.1	10	0.27
B. tenuis	12.2	-	-	8.7	1.6	-	37.2	19.6	30.2	18.7	276	7.40
D. mammalis	-	2.8	-	-	6.3	-	-	-	-	-	32	0.86
D. octaedra	0.8	1.4	5.8	10.7	3.2	63.8	51.2	15.2	-	-	295	7.91
D. rubida - subrubicunda	Numbers included under B. tenuis											
E. rosea	0.2	-	-	-	-	-	-	-	-	-	1	0.03
E. tetraedra	1.8	11.2	18.0	1.9	10.8	11.1	-	-	-	-	195	5.23
L. castaneus	0.2	6.2	1.7	3.7	9.4	-	-	6.5	-	39.1	162	4.35
L. festivus	-	-	-	-	-	12.5	-	-	-	-	10	0.27
L. rubellus	54.7	70.7	64.5	30.9	65.6	-	11.6	54.3	19.8	39.1	1699	45.57
L. terrestris	0.4	-	-	-	-	-	-	-	-	-	2	0.06
O. cyaneum	-	-	-	0.8	-	-	-	-	-	-	13	0.35
O. lacteum	-	-	-	0.1	-	-	-	-	-	-	1	0.03
Number of earthworms	501	939	172	1733	64	80	43	46	86	64	Total 3728	

*A. terrestris longa Ude   +No cow or horse dung on the machair

TABLE VII

Specific constitution of communities in cultivated soils expressed in percentages of the total collection in each cultivated area surveyed.

Species	Survey Areas							Number of earthworms	Total percentage
	2	7	8	9	9b+	9c‡	10		
A. caliginosa	6.7	36.4	10.2	6.3	34.1	29.5	-	210	16.89
A. chlorotica	-	7.6	0.2	-	-	-	-	10	0.80
_A. longa_*	-	2.5	3.9	4.7	-	-	-	30	2.41
B. eiseni	-	-	-	-	1.1	0.5	-	2	0.16
B. tenuis	-	6.8	47.6	11.0	1.1	6.3	21.6	328	26.39
D. mammalis	-	4.2	1.0	-	-	-	-	11	0.88
D. octaedra	1.7	0.8	1.6	4.7	14.2	0.9	28.6	39	3.14
D. rubida - subrubicunda	Numbers included under _B. tenuis_								
E. rosea	-	-	-	-	-	9.7	-	20	1.61
E. tetraedra	-	3.2	1.1	0.9	-	0.5	-	19	1.53
L. castaneus	9.2	5.1	14.6	28.1	-	15.9	42.8	170	13.68
L. rubellus	82.4	29.7	15.3	32.8	38.5	36.7	3.5	360	28.96
L. terrestris	-	1.2	4.5	-	-	-	3.5	30	2.41
O. cyaneum	-	-	-	1.5	-	-	-	1	0.08
O. lacteum	-	2.5	-	-	10.9	-	-	13	1.05
Number of earthworms	119	118	616	64	91	207	28	Total 1243	

+ = peaty lazy-beds; ‡ = derelict moorland cultivation

*_A. terrestris longa_ Ude

TABLE VIII

Specific constitution of grass-moor communities expressed in percentages of the total collection in each grass-moor surveyed.

Species	Survey Areas										Number of earthworms	Total percentage
	1	2	5	6	7	8	9	9a	9b	10		
A. caliginosa	10.4	2.3	4.5	15.5	32.1	1.0	-	7.8	8.7	12.6	164	12.56
A. chlorotica	0.3	4.6	5.0	3.5	7.1	-	-	-	-	-	26	1.99
B. eiseni	9.6	2.3	-	1.5	1.0	26.4	7.9	3.1	30.4	54.5	181	13.86
B. tenuis	10.5	8.8	-	5.0	7.1	9.9	31.6	21.9	4.3	7.7	118	9.03
D. mammalis	-	-	-	7.0	-	-	-	-	-	-	14	1.07
D. octaedra	27.8	20.7	61.9	19.5	3.3	20.6	10.5	20.3	18.5	7.7	246	18.84
D. rubida - subrubicunda	Numbers included under B. tenuis											
E. rosea	2.7	-	-	3.5	0.5	-	-	-	3.3	-	21	1.61
E. tetraedra	0.3	4.4	-	-	-	5.9	-	-	4.3	8.4	26	1.99
L. castaneus	-	8.8	-	1.5	0.5	-	-	-	-	-	12	0.92
L. festivus	-	-	-	6.0	-	-	-	-	-	-	12	0.92
L. rubellus	36.9	48.3	28.6	32.5	45.7	39.2	50.0	46.9	12.0	7.0	445	34.07
L. terrestris	1.3	-	-	3.0	-	-	-	-	-	-	11	0.84
O. cyaneum	0.3	-	-	1.5	-	-	-	-	-	-	5	0.38
O. lacteum	-	-	-	-	2.7	-	-	-	18.5	2.1	25	1.91
Number of earthworms	374	87	21	201	184	102	38	64	92	143	Total 1306	

TABLE IX

Specific constitution of heather-moor communities expressed in percentages of the total collections in each heather-moor surveyed.

Species	Survey Areas				Number of earthworms	Total percentage
	1	6	7	8		
A. caliginosa	-	-	9.1	4.7	3	2.86
B. eiseni	28.6	46.7	9.1	11.6	26	24.76
B. tenuis	-	6.7	18.2	-	4	3.81
D. octaedra	57.1	13.3	18.2	37.2	34	32.38
D. rubida - subrubicunda	Numbers included under B. tenuis					
L. rubellus	14.3	33.3	45.4	46.5	38	36.19
Number of earthworms	21	30	11	43	Total 105	

TABLE X

Distribution of species on "light" and "dark" soils.

Species	"light" (Machair and Cultivation) pH:8.5-6.0; $CaCO_3$:80%-7% Loss on Ignition: 1%-63%		"dark" (Grass- and Heather-moor) pH:6.0-4.1; $CaCO_3$:1.7%-0 Loss on Ignition:19%-90%		χ^2	Differen-:ces
	Actual Nos in total of 4971	Percen-:tage	Actual Nos in total of 1411	Percen-:tage		
A. caliginosa	1199	24.12	167	11.76	99.780	S
A. chlorotica	53	1.07	26	1.84	5.421	S
A. longa*	40	0.80	0	0	11.423	S
B. eiseni	2	0.04	207	14.67	740.312	S
B. tenuis - D. rubida - subrubicunda	604	12.15	122	8.65	13.383	S
D. mammalis	43	0.86	14	0.99	0.083	N/S
D. octaedra	334	6.72	280	19.84	216.988	S
E. rosea	21	0.42	21	1.49	17.397	S
E. tetraedra	214	4.30	26	1.84	18.431	S
L. castaneus	332	6.86	12	0.85	78.185	S
L. festivus	10	0.20	12	0.85	9.636	S
L. rubellus	2059	41.42	483	34.23	23.676	S
L. terrestris	32	0.64	11	0.77	0.147	N/S
O. cyaneum	14	0.28	5	0.35	0.027	N/S
O. lacteum	14	0.28	25	1.77	36.780	S

S = significant

N/S = not significant

*A. terrestris longa Ude

TABLE XI

Showing the dung-pat frequency in 12m x 12m quadrats in three dune - machair systems in Tiree.

Machair	Number of Quadrats 12m x 12m	Average Dung-pat Frequency	Standard Deviation	x^2	P
Balinoe	30	16	9	33.937	0.05
Barrapol	14	14	5.5	8.214	0.05
Reef	6	19	3	2.421	0.05

TABLE XII

Distribution of earthworms in three soil niches.

	A Open soil		B Cow-pats		C Under stones		Differences		
	Actual numbers	Percen-:tage	Actual numbers	Percen-:tage	Actual numbers	Percen-:tage	A-B	A-C	B-C
A. caliginosa	511	62.54	299	16.23	117	30.79	S	S	S
A. chlorotica	2	0.24	12	0.65	25	6.58	N/S	S	S
A. longa[+]	16	1.96	9	0.49	5	1.32	S	N/S	N/S
B. eiseni	0	0	97	5.27	1	0.26	S	N/S	S
B. tenuis - D. rubida - subrubicunda	72	8.81	203	11.02	25	6.85	N/S	N/S	S
D. mammalis	4	0.48	15	0.81	8	2.11	N/S	S	S
D. octaedra	31	3.79	227	12.32	15	3.95	S	N/S	S
E. rosea	0	0	6	0.32	12	3.16	N/S	S	S
E. tetraedra	0	0	12	0.65	1	0.26	S	N/S	N/S
L. castaneus	32	3.92	85	4.61	21	5.53	N/S	N/S	N/S
L. festivus	0	0	9	0.49	3	0.79	N/S	N/S	N/S
L. rubellus	119	14.56	854	46.36	130	34.21	S	S	S
L. terrestris	21	2.57	7	0.38	11	2.89	S	N/S	S
O. cyaneum	8	0.96	7	0.38	3	0.79	N/S	N/S	N/S
O. lacteum	1	0.12	0	0	3	0.79	N/S	N/S	N/S
Total	817	99.95	1842	99.98	380	100.28			

S = significant
N/S = not significant
[+]A. terrestris longa Ude

TABLE XIII

Composition of the Village Bay community.

Species	Percentage Frequencies		
	Manse Precincts	Meadows & Village	Average for Village area
A. caliginosa	36.2	32.1	34.6
D. octaedra	-	trace	trace
D. rubida	-	trace	trace
E. rosea	6.4	3.6	5.4
L. castaneus	17.0	14.3	16.0
L. rubellus	40.4	50.0	44.0

TABLE XIV

Comparison between the Gleann Mor and Village Bay communities.

Species	Percentage Frequencies	
	Precincts of Shielings	Average for Village area
A. caliginosa	14.7	34.6
B. eiseni	2.9	-
D. octaedra	2.9	trace
D. rubida D. subrubicunda	17.6	trace
E. rosea	11.8	5.4
E. tetraedra	2.9	-
L. castaneus	26.5	16.0
L. rubellus	20.6	44.0

TABLE XV

Village Bay transect.

Ecological zone	No. of samples	No. of groups	Range in group means gms/m^2 Min.	Max.	Average zonal weight gms/m^2
Village meadows	18	6	3.01	11.73	7.96
Between village and perimeter wall	15	5	2.04	16.46	10.22
Lower hill-slopes	15	5	-	5.57	2.47
Sheep fanks	6	2	7.42	16.24	11.94
Upper hill-slopes	6	2	0.12	4.63	2.37

Fig. 1.

Area of survey.

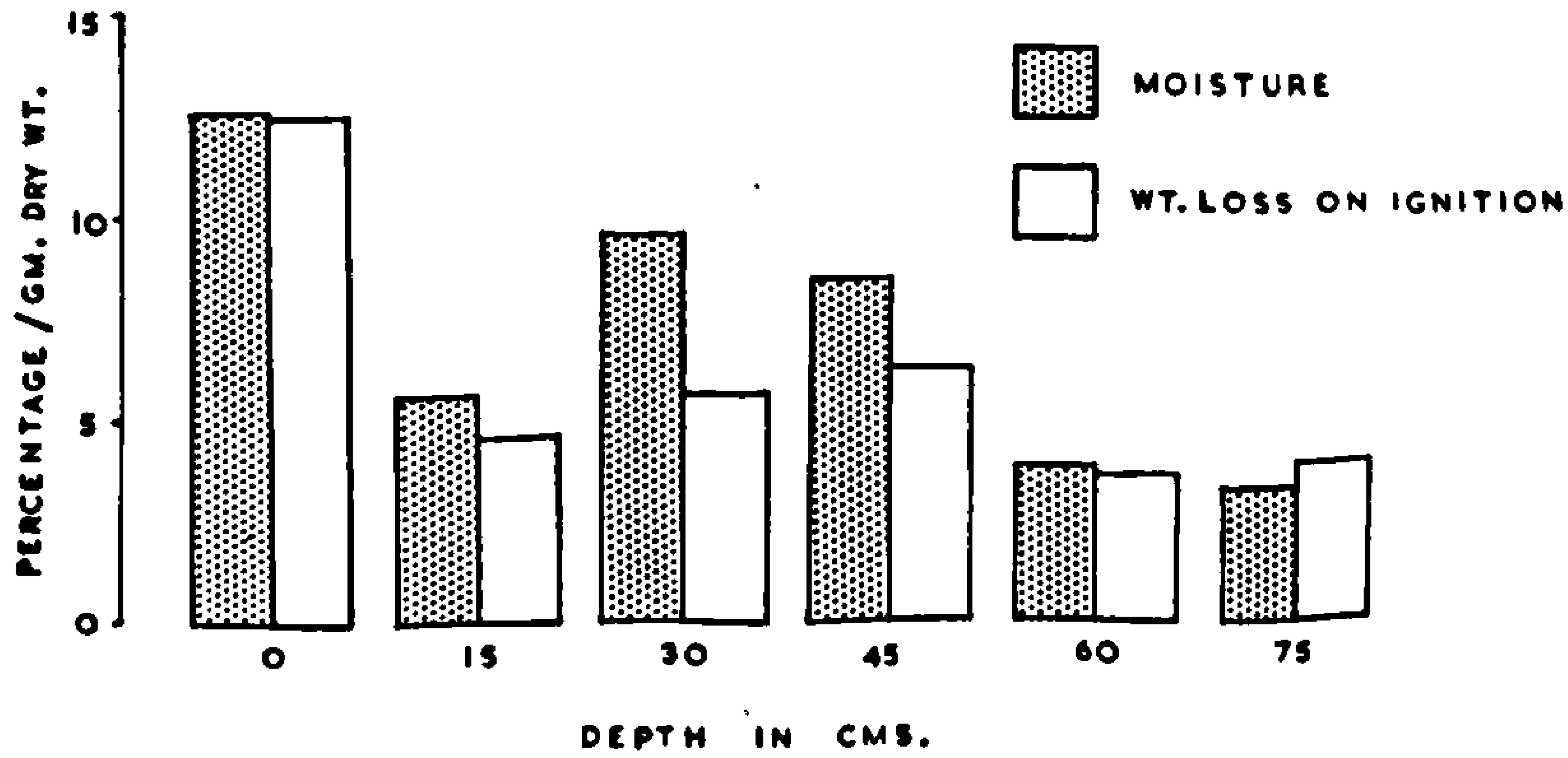
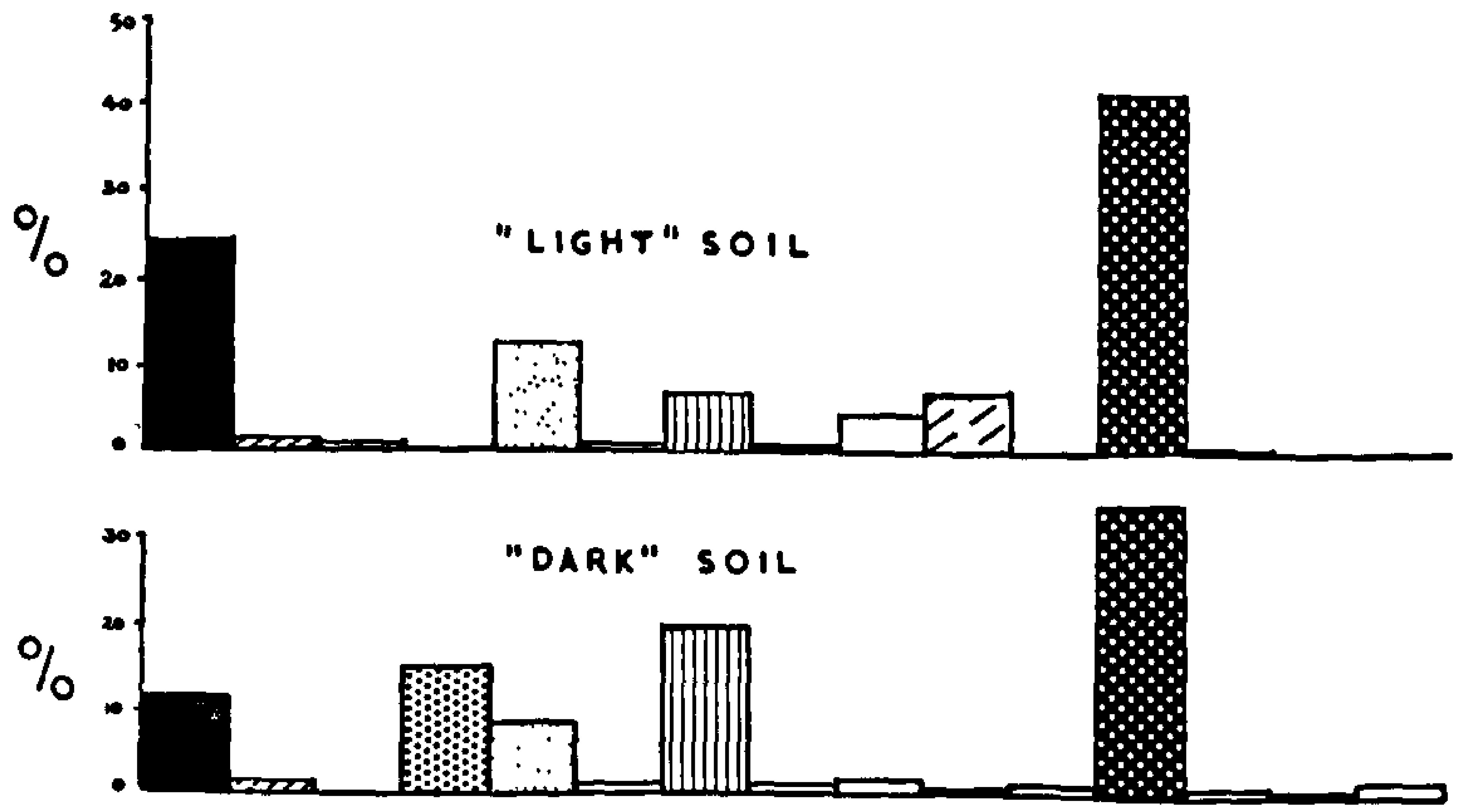


Fig. 2. Showing the variation of the moisture content and the loss of weight on ignition of machair soil at Balinoe, Tiree in July, 1952. The values are expressed as a percentage of the dry weight of soil.



Order of species from left to right.

A. caliginosa
A. chlorotica
A. longa
B. eiseni
B. tenuis - D. rubida-subrubicunda
D. mammalis
D. octaedra
E. rosea
E. tetraedra
L. castaneus
L. festivus
L. rubellus
L. terrestris
O. cyaneum
O. lacteum

Fig. 3. Showing the percentage constitution of the earthworm communities on "light" and "dark" soils in the Hebrides.

Order of species from left to right.

A. caliginosa
A. chlorotica
A. longa
B. eiseni
B. tenuis - D. rubida-subrubicunda
D. mammalis
D. octaedra
E. rosea
E. tetraedra
L. castaneus
L. festivus
L. rubellus
L. terrestris
O. cyaneum
O. lacteum

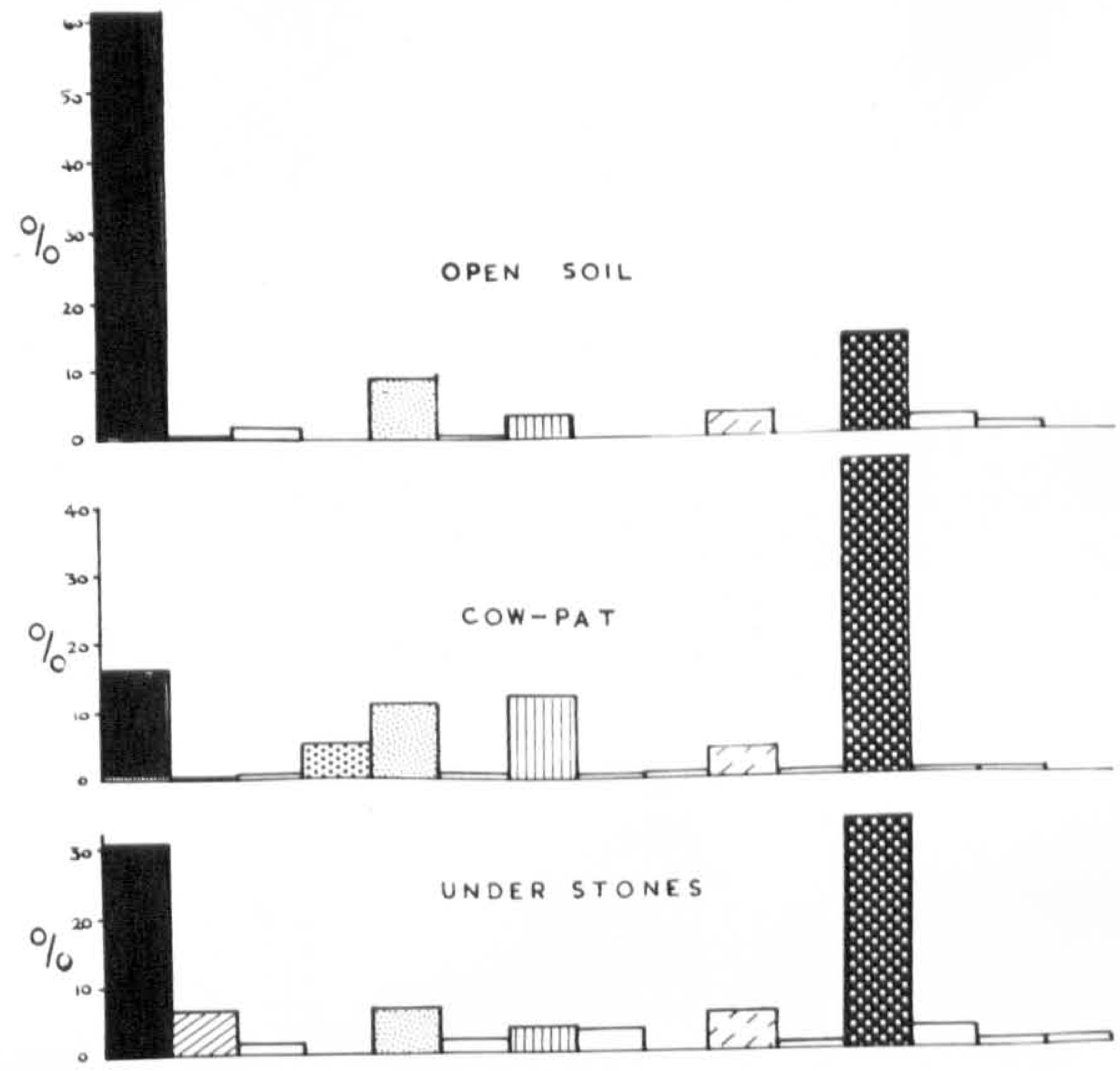


Fig. 4. Showing the percentage constitution of the earthworm communities in open soil, cow-pats, and under stones.

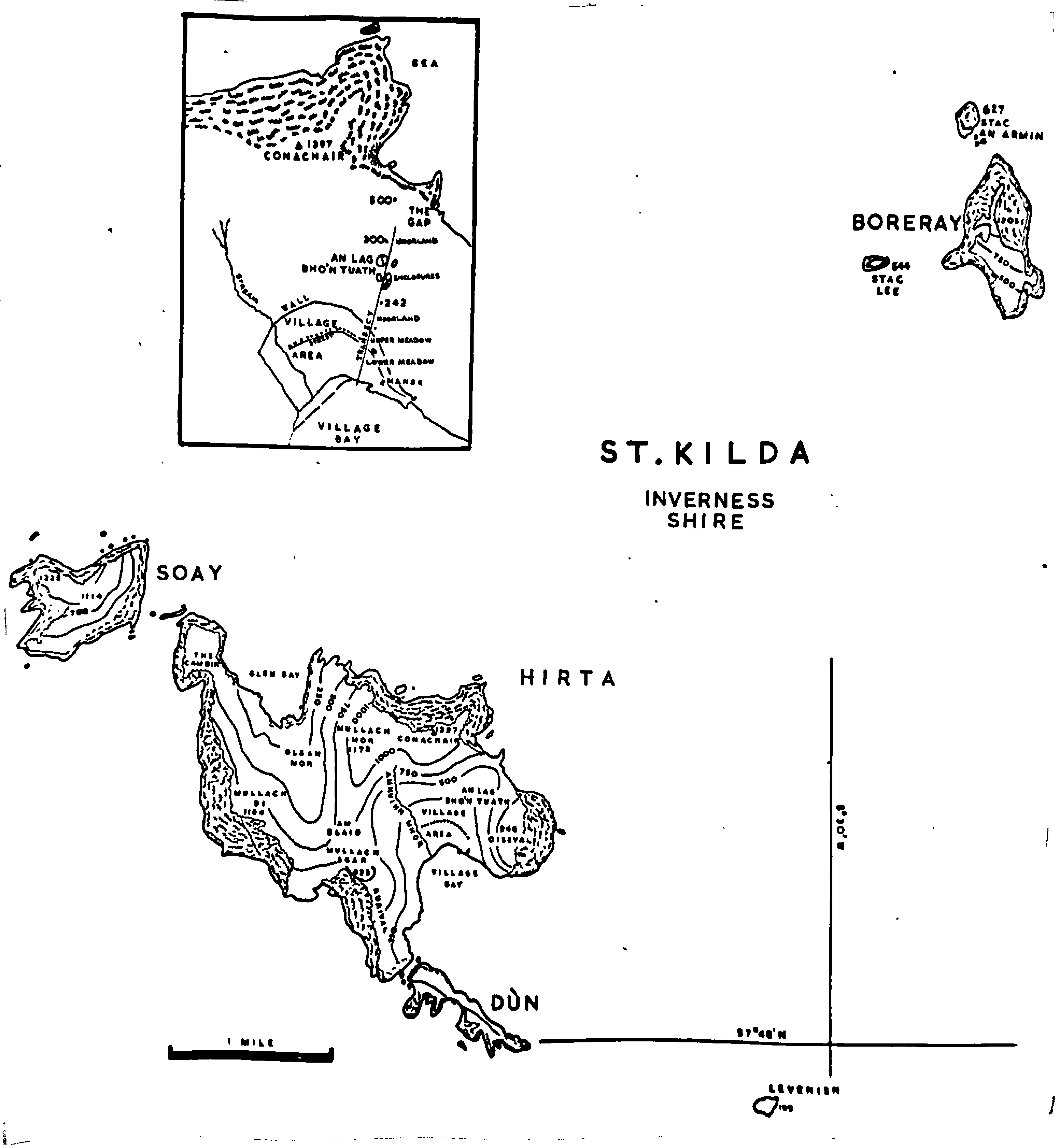


Fig. 5. A map of St. Kilda, showing inset the village area the transect line.

Plate I. "Light" loam forming a mat on top of shell-sand at the Reef machair, Tiree. A "marine" soil.

Plate II. "Dark" peaty soil forming a mat on top of boulder clay at Newton, North Uist. An "erosion" soil.

Plate III. A section through a dune-machair ecotone at Crossapoll, Tiree, showing the soil depth to about 150 centimetres. At a depth of 60 centimetres a prominent organic layer is seen, below which are seen finer organic bands.

(a)

(b)

<u>Plate IV</u>. (a) Lazy-beds being du~~n~~g in enclosed ground derived from machair at Allasdale, Barra, in 1954. Sea-weed has been applied in strips and covered with turf.

(b) Derelict lazy-beds on the grass-moor at Newton, North Uist. These are probably about 100 years old or over.

Plate V. Rabbit damage due to burrowing and subsequent blow-out by the wind on machair at Newton, North Uist. This is characteristic of all the major islands with the exception of Tiree.

(a)

(b)

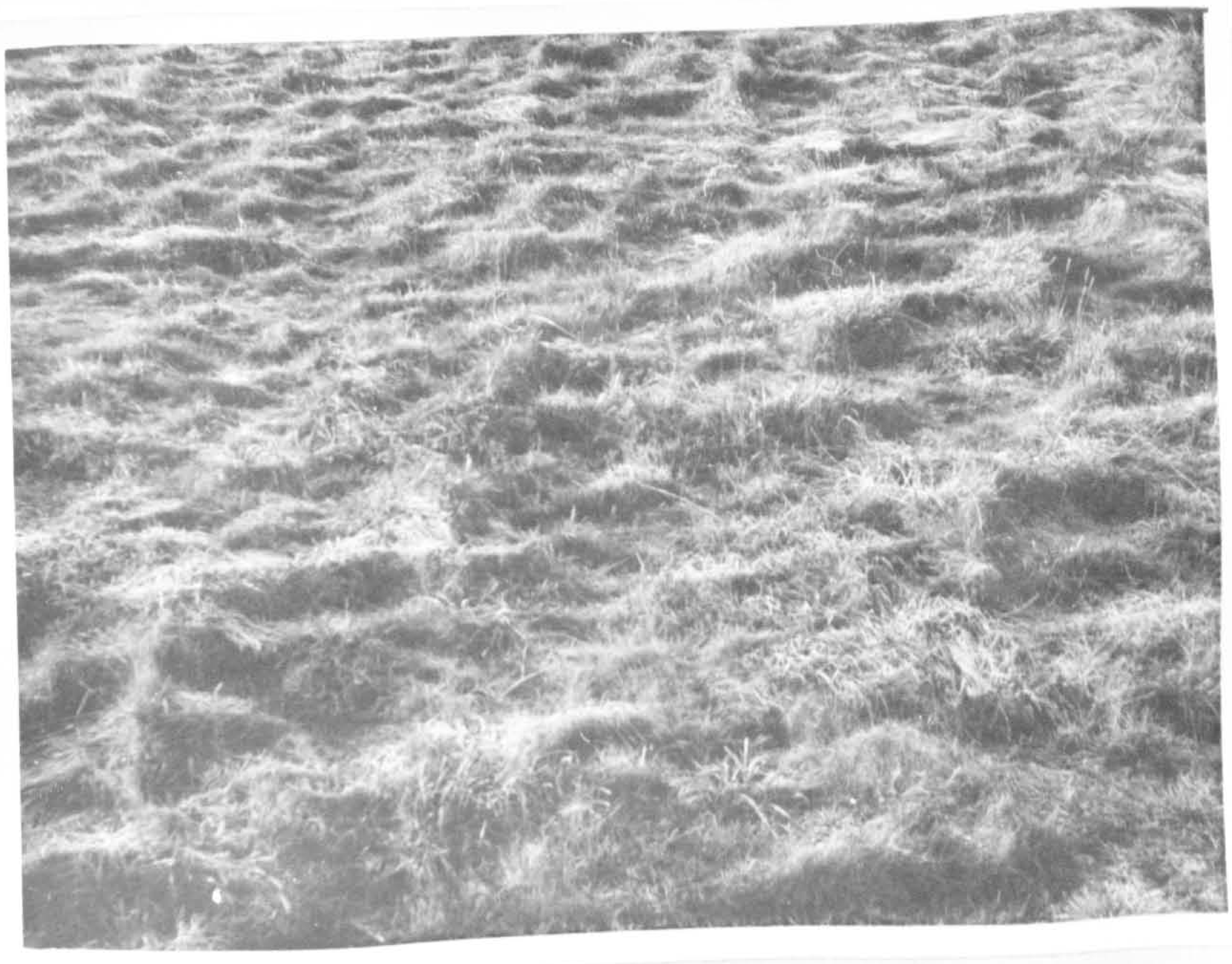


Plate VI. (a) Rabbit damage due to over-grazing on machair at Newton, North Uist. The grasses have given way to bryophytes, and the sandy soil shows through.

(b) A completely ungrazed tract of machair at the Reef, Tiree. The grasses are luxuriant and no soil is visible.

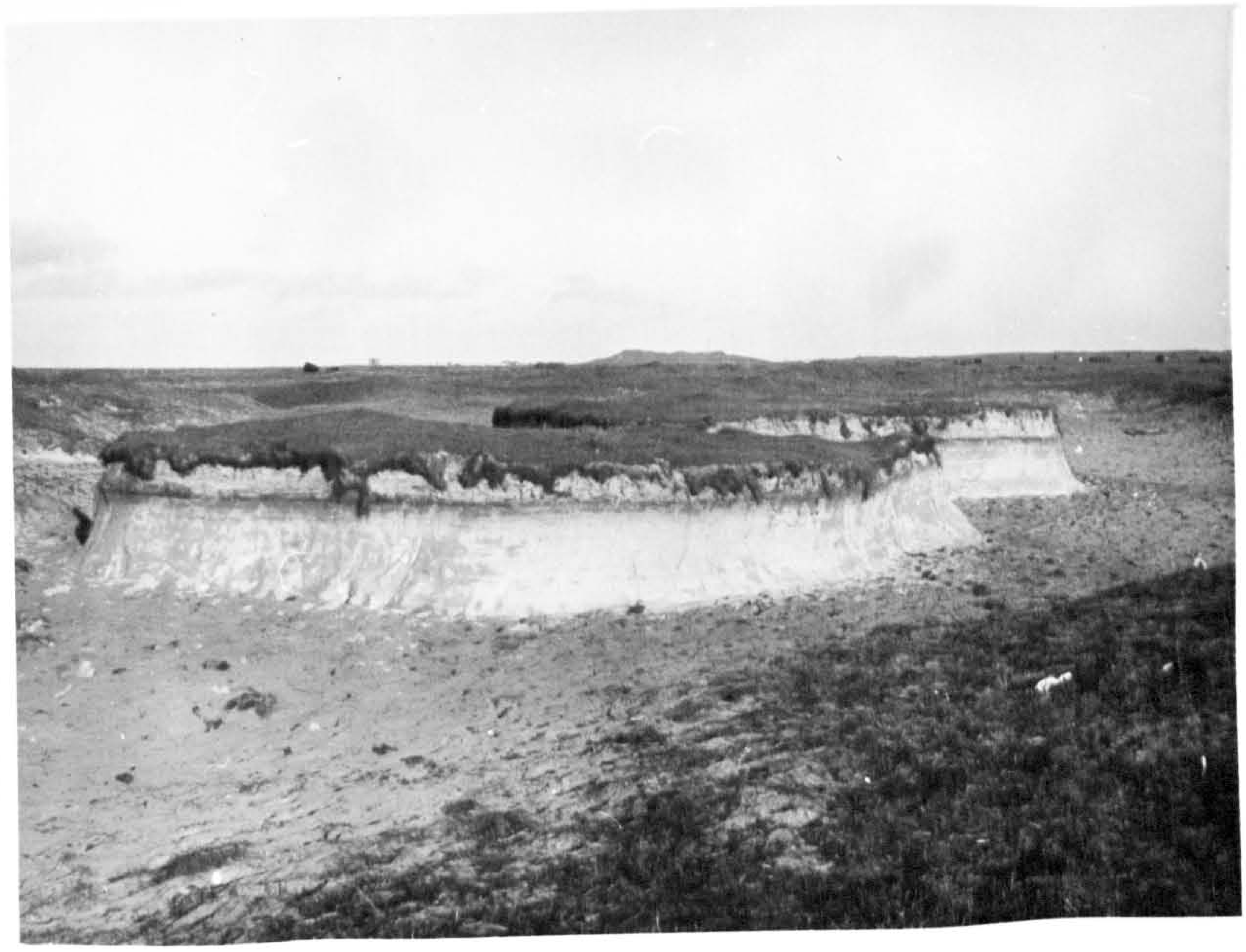


Plate VII. Cattle damage to a dune-machair soil at the Reef, Tiree. Isolated plateaux have been formed, and excessive rubbing and trampling prevent the re-establishment of the vegetation.

Plate VIII. The sharp discontinuity between soil and sub-sand is seen in this section of machair soil at the Reef, Tiree.

(a)

(b)

Plate IX. (a) Newton House, North Uist, viewed from the machair, and (b) the same viewed from the grass-moor, the pictures being taken near the extre-:mities of a transect line. These pictures show the diverse nature of the habitat. Behind the skyline in (a) heather-moor is to be found, and the sand dune can be seen in the background of (b).

Plate X. The village area, Hirta, St. Kilda, showing the derelict dwellings, meadows, and grass-moor. The manse and church are in the foreground.

Plate XI. Gleann Mor, Hirta, St. Kilda in cloud shadow with shielings beside the stream at the left-hand side.

PAPER II

A FIELD POPULATION OF EARTHWORMS IN MACHAIR SOIL AT THE REEF, TIREE, ARGYLL

PAPER II

A FIELD POPULATION OF EARTHWORMS IN MACHAIR SOIL AT THE REEF, TIREE, ARGYLL

I. INTRODUCTION

In Paper I the distribution of the Lumbricidae in the shell-sand - peat soil complex of the Hebrides is discussed in broad terms. Now the earthworm population in one locality is selected for detailed study. Sampling programmes involving four diffe:rent techniques were carried out to examine (1) the species complex and how it is affected (a) by the dune-machair ecotone, (b) by the presence of cow-dung, (c) by the presence of a fence separating permanently grazed and ungrazed grassland, and (d) by the mowing of ungrazed grassland; (2) the variation in num:bers of earthworms in a highly uniform habitat; (3) the annual reproductive cycle as shown by the proportion in the monthly collections of individuals possessing a clitellum; (4) seasonal abundance and surface activity. Complementary to the earthworm data are temperature and rainfall figures supplied by a Meteorological Office in the same locality.

Evans and Guild (1948b) discussed the life-cycles of some British earthworms including five species present in the popu:lation now under examination, and (1947) the seasonal activity of several species, including two present here, relating all with the temperature and moisture content of the soil. Guild (1952) examined the variation in numbers of earthworms in a Scottish agricultural field, and found that the population was not uniformly distributed.

II. MATERIALS AND METHODS

(1) The Survey Area

The dune-machair system chosen for detailed survey is shown in Fig. 1, and is situated on the south-east shore of the island of Tiree, Argyll. The site possesses a remarkably even transition - due partly to the absence of the rabbit Oryctolagus cuniculus - from duneland to mature grassland (Plate I). The mature grassland is flat, possessing no large-scale undulations, and broken only by a system of widely separated ditches (Plate II). The broad sections between the ditches have a uniform sward and what appears to be a highly uniform soil. The soil is a vegetable mould shell-sand mix of very fine grain, and forms a shallow mat on top of the sand. At no time has the ground been cultivated. Soil depth increases from 0 in the dune-crest to about 15 centimetres in a distance of about 250 metres, and transition from soil to sub-sand is sharp (Plate III).

The mature grassland is artificially divided into two distinct ecological compartments by the perimeter fence of the Tiree airport (Plate IV). Outside the fence the pastures are grazed by cattle and possess a short herbage, while inside the pastures have not been grazed for at least 15 years and are rank. Grazing takes place from December to May inclusive and is/

is usually intense, while during the summer and autumn the herbage cover is allowed to grow and the cow-pats degenerate. The sward composition on either side of the fence is noticeably different. The soil is darker and the particles have aggre:gated much more coarsely under the ungrazed swards. In certain areas the uniformity of the grazed swards is broken by the occurrence of moss hillocks about 30 centimetres in diameter (Plate V).

(2) Transect Method

The line of transect at right angles to the shore is shown in Fig. 2 extending from the shore-sand immediately under the dune escarpment to a point about 20 metres inside the airfield perimeter fence at its nearest point to the shore.

The sampling stations are as follows (Fig. 2), the extreme values for pH, $CaCO_3$ content, and loss of weight on ignition being quoted from five samples at each station in a brief soil survey carried out before earthworm sampling was undertaken (the soil analysis was carried out in exactly the same way as described in Paper I, Section B):

(i) The shore above the level of high water ordinary spring tide. pH: 8.6 to 8.7; $CaCO_3$ content: 65.0 to 69.5 per cent dry weight; loss of weight on ignition: 1.6 to 2.5 per cent dry/

dry weight; vegetation: fore-dune.

(ii) The dune-crest. pH: 8.3 to 8.4; $CaCO_3$ content: 63.2 to 72.8 per cent; loss of weight on ignition: 2.4 to 5.0 per cent; vegetation: thick Ammophila arenaria, sparse Festuca, Galium, Trifolium, and Plantago.

(iii) The dune-basin. pH: 7.9 to 8.0; $CaCO_3$ content: 66.3 to 68.8 per cent; loss of weight on ignition: 6.6 to 8.3 per cent; vegetation: thin A. arenaria, thin Festuca, Galium, Trifolium, and Plantago.

(iv) Dune-machair transition. pH: 7.7 to 7.8; $CaCO_3$ content: 58.0 to 63.7 per cent; loss of weight on ignition: 10.0 to 19.4 per cent; vegetation: sparse A. arenaria, thick Festuca, Galium, Trifolium, and Plantago.

(v) Machair (grazed). pH: 7.6 to 7.7; $CaCO_3$ content: 60.0 to 55.5 per cent; loss of weight on ignition; 11.9 to 14.4 per cent; vegetation: no A. arenaria, mature grassland.

(vi) Machair (ungrazed). pH: 7.7 to 7.8; $CaCO_3$ content: 20.2 to 58.6 per cent; loss of weight on ignition: 14.2 to 43.3 per cent; vegetation: rank Festuca, with Galium and Plantago.

In choosing a suitable sampling unit the following aspects had to be considered: (a) density of fauna, (b) the effect of bullock/

bullock droppings on the distribution, (c) the availability of a fresh water supply for the "wet" method of extraction of earthworms from the soil (Evans and Guild, 1947).

(a) Preliminary inspection by digging in the grazed and the ungrazed machair soils showed that the earthworm popula:tion was light. There were usually less than 5 individuals, and in many cases none, obtained from a turf approximately 20 x 20 x 15 centimetres conveniently taken up by the spade.

(b) In and under bullock droppings on the grazed machair earthworms were found to be numerous, there being usually more than 10 individuals taken from each pat, and in only a very few cases were no earthworms obtained. It was obvious that an easily accessible proportion of the earthworm population was centred in the dung-pats, and that until a number of those were sampled no accurate idea might be obtained of the species complex and its spatial distribution.

The dung-pat frequency was measured in 144 square metre (12 metres x 12 metres) quadrats, two being chosen randomly in stations (iii), (iv), and (v), and the following figures obtained:

15 17 19 19 20 24

Mean = 19; d.f. = 5; chi-square = 2.421

The/

The chances therefore of obtaining in 10 one square metre randomly cast quadrats - 10 being the maximum number which a single worker might hope to analyse at each station during a week-end visit - one or more randomly distributed dung-pats, would therefore be small. These chances are further reduced by the fact that pats less than a week old and more than 8 weeks old are not representative.

(c) The two methods of quadrat analysis are (a) digging and hand-sorting, and (b) the "wet" method (Evans and Guild, 1947), where a solution of $KMnO_4$ is applied to the soil surface. The availability of a freshwater supply at distances of 100 to 200 metres from the transect line placed a severe handicap on a single worker, since the recommended dose is 4½ litres of solution to 1 square metre of soil surface. Neither of those methods in themselves can be depended upon to give the absolute number of earthworms present, nor is this ideal likely to be obtained by applying both, viz. administering the solution, waiting 10 minutes in order that the maximum earthworm collection might be made, and then digging and hand-sorting to extract the remaining individuals. Experience suggests that the former operation tends to defeat the end of the latter, at least on the light, shallow soils of the machair, very few earthworms ever being obtained by digging and hand-sorting after potassium permanganate treatment.

The/

The following sampling method was finally adopted for the transect. 20 samples were taken at each station from 900 square centimetre (1 square foot) quadrats. 10 of those were taken in dung-pats (each pat not occupying more than the quadrat), the dung-pats being chosen randomly (the newest and the oldest excepted), and 10 randomly in the interspaces between dung-pats. The dung-pats were broken up with forceps. Half a litre of $KMnO_4$ solution (7 grammes $KMnO_4$ in 4½ litres) was applied to each quadrat, and thereafter the turf was raised with a spade and broken by hand. The problem of ob-:taining samples from dung-pats in the ungrazed swards was conveniently solved. Cattle had temporarily broken through the airfield fence on the transect line, and a few dung-pats had been deposited on the rank swards.

Svendsen (1955) has shown by analyses of variance that the "wet" method is unsuitable for comparative population studies with earthworms, and this is strongly endorsed by a practical comparison of its efficiency on smooth grazed swards, and on thick matted ungrazed swards. On the former the solution reached the soil in much greater quantities than in the latter where the grass had to be clipped over and some distance around the quadrat in order that the solution might penetrate to the soil, and that the earthworms could be observed emerging. This pre-dressing of the quadrat might have an appreciable effect/

effect in causing the earthworms to migrate from the scene before the solution could be applied.

The method proved effective in showing the changes which exist in the fraction of the population occupying dung-pats in the dune-machair system along the transect line from the shore-sand to the mature soil. The method proved ineffective, however, in showing the changes in the population as a whole, in that it failed to detect in detail the diffuse, yet no doubt much greater fraction, existing in the interspaces between the pats. Some of this fraction may be transient from spent dung-pats to the freshly laid, but evidence from Paper I shows it is improbable that bullock dung is equally attractive to, or favourable to the existence of, all species. It is therefore not safe to assume that those samples taken in dung-pats are random for the population as a whole, but only for the fraction actually living in the dung. A more elaborate method will be described below which effectively shows diffe:rences which do in fact exist between the fraction in dung and that out of dung.

(3) Monthly Sampling of a Machair Population

The site selected for this sampling programme was close to station (v) of the transect already described (Fig. 2, Plate IV). The grassland is very flat, evenly drained, evenly grazed/

grazed, and possesses a remarkably uniform sward and fine grained soil of depth 15 centimetres. The situation was indeed more than usually uniform over an area wide enough for monthly sampling to be done through a 12 month period without covering the same ground twice.

The points of faunal density, the effect of dung-pats, and the availability of fresh water for the "wet" method of sampling discussed above in connection with the transect method also apply here. No attempt at achieving absolute numbers was intended in this programme, only monthly comparisons of the same population by a standard method of sampling. The quadrat size selected was 1 square metre, and the "wet" method of extraction used, applying 9 litres (2 gallons) per square metre of $KMnO_4$ solution (14 grammes in 9 litres of water). A supply of fresh water was obtained about 50 metres from the sampling area. The same procedure was taken each month for 12 months. 20 samples were taken at random within the survey area on different ground each month, 10 not including a dung-pat within the quadrat, and 10 including a dung-pat.

(4) Monthly Pit-fall Trap Sampling

The site selected was close to stations (v) and (vi) of the transect already described, and also close to the area of monthly "wet" method sampling (Fig. 2). Pit-fall traps in the form/

form of 2 lb. jam-jars counter-sunk to the level of the soil surface were used to catch earthworms. Two batteries of these traps were set up about 50 metres apart, each battery containing 12 traps set in a grid, each trap at the corner of a 3 metre square. One battery was set on the grazed machair and the other battery on the ungrazed machair inside the airfield fence. The traps were not moved during the period of sampling. They were not baited, but a small quantity (approximately 10 cubic centimetres) of strong formalin (approximately 10%) was put in each trap. Strong formalin had to be used in order that the dilution by rain over the space of a month would not cause the decay of the catch. Controls were set up containing no formalin, but these were foul before they could be emptied, though it was clear that the catch differed little from those with formalin. The traps were cleared at approximately monthly intervals.

(5) Dung-pat Pattern Sampling

Within the airfield a strip of grass about 40 metres broad is mown on either side of the tarmac runway. The grass gives way abruptly to long unmown grass which occupies the interior of the airfield well away from the runways. None of this grassland is grazed. The mown ground is only slightly undulating and the sward is very uniform.

Patterns/

Patterns of dung-pats were set out on the mown and unmown swards to attract earthworms. These were in the form of lines and squares of carefully measured amounts of dung which was obtained from the grazed grassland on the other side of the airfield fence. Exactly the same amount of dung, two fillings of a tin of volume 400 cubic centimetres, was put in each pat, and the pat spread out to cover approximately the same area of ground, and to render it less noticeable to birds. The experiment was set up in December and continued till March, having stood exactly 3 months.

Pattern (i) has been called "very long line", the pats being placed at 2 metre intervals in a straight line, 24 in all, 12 on the mown ground, and 12 on the unmown. This pattern was used for species complex work only.

Pattern (ii) is known as "long line", the pats being placed at 1 metre intervals in a straight line, 16, all on the mown ground.

Pattern (iii) is known as "short line", the pats being placed at intervals of 25 centimetres in a straight line, 16, all on the mown ground.

Pattern (iv) is known as "large square", the pats being placed at intervals of 1 metre, 16 in a solid square.

Pattern/

Pattern (v) is known as "small square", the pats being placed at intervals of 25 centimetres, 16 in a solid square.

The distances between pats is the distance from the edge of one to the edge of the next, not between centres.

(6) Treatment of Earthworms

The earthworms were preserved in 4% formalin, and taken to the laboratory for identification and counting. Identification was according to the key compiled by Cernosvitov and Evans (1947). In a few cases immatures could not be identified to the species level and were allotted to the most closely related species according to the proportions of matures of each species present. The three species Bimastus tenuis, Dendrobaena rubida, and D. subrubicunda are combined in a complex. This was prompted by the difficulty experienced in definite identifi:cation of each species. A number of specimens of B. tenuis possessed a tubercula pubertatis, while the specimens of the two Dendrobaena species could not be convincingly separated. Dissection of the seminal vesicles served to separate the two genera, but not in some cases and did not clarify the situation. It was impossible to identify the immatures of these three species even to the genus level, and the uncertainties of the proportions of matures of each species made it impossible to allot these proportionately, with confidence, to each of the three species.

The/

The weighing of earthworms obtained in the transect was carried out on a beam-balance, each sample being carefully dried by hand with blotting paper before placing on the scale pan. Each sample was given identical treatment.

III. THE SPECIES COMPLEX

(1) Dune-Machair System

The transect method shows the changes which occur in the fraction of the population occupying dung-pats along a line from the shore sand to the mature grassland. In Table I, Fig. 3 the numbers of earthworms of each species obtained at each station are set forth.

No earthworms were found occupying the dung-pats which were found on the shore-sand below the dune escarpment. On the dune-crest (Fig. 2) 9 earthworms, all *Lumbricus rubellus*, were obtained from 10 dung-pats, and no earthworms were obtained in 10 samples taken in the interspaces between the dung-pats. In the dune basin numbers increased greatly, 91 earthworms being obtained from 10 dung-pats, and none in 10 samples in the interspaces. *L. rubellus* was dominant, with *Lumbricus castaneus*, and the *B. tenuis - D. rubida-subrubicunda* complex present in smaller numbers. 71 earthworms were obtained in 10 dung-pats, and none in the 10 interspace samples on/

on the ecotone, Allolobophora caliginosa and Dendrobaena octaedra being included in the species complex. In the machair, 99 were obtained from 10 dung-pats, and 9 from 10 interspace samples, the species complex showing a decrease in the numbers of L. rubellus, and an increase in the numbers of D. octaedra. In the ungrazed machair (airfield), 180 earth-:worms were obtained from the 10 dung-pats, and 8 from the 10 interspace samples. The species complex shows distinct differences from that found on the grazed machair, namely the fall from dominance of D. octaedra and L. rubellus, and the rise to dominance of the B. tenuis - D. rubida-subrubicunda complex and Eiseniella tetraedra.

Three distinct ecological zones are included in this transect (i) dunes, (ii) grazed machair, and (iii) ungrazed machair. Throughout the entire transect area the distribution of all species is heterogeneous, the only evidence for homo-:geneous distribution being that of A. caliginosa in stations (iv), (v), and (vi) (chi-square = 3.250). In Table II the differences between contiguous zones are shown, and in all cases except two, namely E. tetraedra between the dune basin and the grazed machair, and A. caliginosa between the grazed and ungrazed machair, the differences are significant (chi-square greater than 3.841).

It emerges that the character of the fraction of the earthworm/

earthworm population living in dung, and probably the population as a whole changes rapidly in passing from dunes to machair, and that the airfield fence constitutes a sharp ecological discontinuity. A. caliginosa, the B. tenuis - D. rubida-subrubicunda complex, and D. octaedra would appear to be numerous only in dung-pats on the mature soils, while in the case of L. castaneus and more particularly L. rubellus the opposite would seem to be the case. The proportionately low numbers of the last two species obtained in the ungrazed machair may be due to the absence of dung, while the proportionately high numbers of the B. tenuis - D. rubida-subrubicunda complex and E. tetraedra to the dampness under the rank sward and the rotting grass.

Table III shows the weights of earthworms obtained in the transect survey. The variation in weights of individual samples may not be due entirely to intrinsic distribution of the fauna but also the fact that the dung-pats from which each was taken were not exactly similar. The total weight of earthworms obtained at each station gives a truer basis for biomass comparisons between stations. Table III(a) shows an analysis of variance of the weights in stations. Stations (i) and (ii) are not included in the analysis because of the obvious heterogeneity existing there. The analysis shows F_0 less than $F_{0.05}$ and gives a satisfactory test for homogeneity. Actual numbers/

numbers of earthworms fluctuate in concert with total weights between stations from the dune to the machair (stations (iii) to (v)), but between the grazed and ungrazed machair (stations (v) and (vi)) the numbers of earthworms rise greatly with no corresponding rise in the biomass. This is due to the fall from dominance of larger species such as L. rubellus and the gain of smaller species, B. tenuis - D. rubida-subrubicunda complex and E. tetraedra.

The question now arises as to whether the changes which are evident in the fraction of the population living in dung-pats may be applied to the population as a whole. From Paper I it is seen that D. octaedra and L. rubellus were to be found much more abundantly in dung-pats than in open soil, and there can be little doubt that the numbers obtained in the case of these species reflect true changes in population constitution. The B. tenuis - D. rubida-subrubicunda complex and L. castaneus were seen in Paper I to be present in open soil, and in dung-pats in approximately equal strength, and thus the representa:tion of these species in dung-pats would also reflect true change in population constitution. E. tetraedra found only in damp situations is a special case and its change in status across the airfield fence also represents a true change in population constitution. A. caliginosa is seen to be more abundant in open soil than in dung-pats (Paper I), but constituted/

constituted as much as 16 per cent of all the earthworms collected in dung-pats. It is therefore very probable that the comparatively small numbers, 9, 11, and 4, obtained in stations (iii) to (vi) reflect a very much greater rise in numbers of this species through the population as a whole, and at the same time reflect a true change in population constitution. In considering the population as a whole the effects shown in Fig. 3 tend to exaggerate the changes occurring in species attracted by dung and to subdue the changes in those not attracted by dung.

(2) Monthly Sampling of a Machair Population

In Paper I the constitution of the machair community is given for a number of surveys made throughout the entire range of the shell-sand habitat in the Hebrides. On page 31 some doubt is cast upon the validity of the percentages obtained for _A. caliginosa_, _D. octaedra_, and _L.rubellus_ as being a measure of the intrinsic proportions of those species in machair soils.

In the sampling described in Paper I emphasis is laid on the fractions of the populations existing in dung-pats and under stones. Paper I, Fig. 4 shows that proportions of species vary greatly from niche to niche. Although samples were taken from the open soil and the niche under stones, to which it is closely related, it is improbable that enough of these/

these were taken to offset the over-all concentrating effect of the dung on D. octaedra and L. rubellus, and to bring out the diffusely scattered A. caliginosa in truly representative numbers. This refers only to machair and cultivated soils, since no earthworms were found in the interspaces between dung-pats in dunes, and in the dung-stone interspaces on the moorland the soil is acid and would restrict the distribution of A. caliginosa (Paper I, Fig. 3) (Satchell, 1955).

Tables IV and V, Fig. 7, show the sampling results for the detailed machair survey for the period November, 1954 to November, 1955. The differences in numbers of the various species are listed in Table VI. In the cases of A. caliginosa, A. chlorotica, D. octaedra, L. castaneus, and L. rubellus these are seen to be significant (chi-square greater than 3.841), and insignificant in the cases of the B. tenuis - D. rubida-subrubicunda complex, O. cyaneum, and O. lacteum. Comparing the distribution of A. caliginosa with that of D. octaedra and L. rubellus, it is clearly seen that the distribution of the former is affected by dung in a way contrary to the latter two species. Fig. 4 shows the same for 20 samples (10 including a dung-pat and 10 not including a dung-pat) for April and October, 1955, while Table VII shows the frequency of dung-pats in 144 square metre quadrats taken over the grazing season at bi-monthly intervals. As might be expected the frequency increases fairly uniformly throughout the season. Table VIII combines/

combines earthworm and dung-pat distribution. The mean values with and without dung are given for April and October, 1955, and the dung-pat frequency for the period April-May, 1955, is then used to divide the 144 square metre (12 metres x 12 metres) quadrat into 122 square metres without dung, and 22 square metres with dung. The dung-pat frequency in October, when the pats would be degenerate, would be approximately the same as that in April and May, none having been added in the intervening period.

By simple multiplication and addition a figure is obtained which is not intended in any way as an absolute number, but as an index for comparison of species strength. The figure might only apply to the highly uniform type of machair over which this sampling was done. It does not represent an ideal case, however, since the shape, size, and quality of the dung-pat, some of which may have been searched by birds, varies. Dung is, for instance, frequently deposited by a walking animal with a resultant shallow streak extending several yards, and presenting an entirely different niche from the pat deposi:ted by a stationary animal. It is clear, however, from the figures obtained towards the end of the grazing season (May), and towards the end of the non-grazing season (November) that <u>A. caliginosa</u> is much more numerous throughout the population of the grazed machair than <u>L. rubellus</u>, the suggested figure being six to seven times as great. It is much more numerous still than <u>D. octaedra</u>.

Grazing ceased on the Reef, machair, Tiree on May 27th, 1955 and re-commenced on 27th November, 1955. During this period the sward was allowed to grow, and no fresh dung was deposited, but observations were continued throughout the summer and autumn in order to detect, if possible, the decline of the influence of the dung-pats on the earthworm population.

From Tables IV and V giving numbers of earthworms obtained in sampling and also from Fig. 5 showing the temperature and rainfall figures for the period, it is seen that due to unusual heat and drought for several months the dung-pats dried out completely, the soil became dry to a depth of 8 centimetres, and no earthworms could be obtained by the "wet" method. The decline in numbers was therefore so sharp as to defeat attempts at tracing a fall-off in numbers with a decay of the dung-pats.

Comparisons between numbers of A. caliginosa, D. octaedra, and L. rubellus at the end of April, when the effect of the dung would be thought to be approaching a maximum and in mid-October when the effect would be approaching a minimum (Fig. 4), show significant differences. The difference in the distribution of the three species is shown symbolically in Fig. 4(a). The diffuse distribution of A. caliginosa is sustained both in April and October, while the cluster distribution in the dung-pats seen in the other two species in April appears to have broken down in October. The values adopted are the mean number per/

per square metre to the nearest whole number (Table VIII). The differences between the numbers of A. caliginosa obtained from 1 square metre with a dung-pat, and 1 square metre without, was not significant in April (chi-square = 0.806), but was significant in October (chi-square = 4.945). Those for D. octaedra were highly significant in April (chi-square = 26.133), and not significant in October (chi-square = 3.000). Those for L. rubellus were highly significant in April (chi-square = 63.000), and not significant in October (chi-square = 1.471).

The presence of dung-pats is seen to affect greatly the distribution of the earthworm population, all species probably being affected to a different degree. The dung-pat may be identified as the focus of an earthworm community distinct, yet primarily derived from, the background complex of the field population.

(3) Monthly Pit-Fall Trap Sampling

The results of the pit-fall survey are set forth in Tables IX and X and Fig. 8. Differences between grazed and ungrazed communities have been already discussed when dealing with stations (v) and (vi) of the transect. The differences in the pit-fall catches over the period 18th July, 1955 to 31st May, 1956 are listed in Table XI, and are seen to be significant in all cases except A. chlorotica and D. octaedra, not altogether similar to the differences seen in the dung-pat communities on the grazed and ungrazed land shown in Table II. Although the numbers obtained from the pit-fall traps were primarily meant to represent surface activity of the population, they may also throw light on the species complexes existing in the open soil on both the grazed and ungrazed land. Comparison of Figs 7(a) and 8(a) show a great similarity, the same complex having been arrived at by two different methods of estimation.

(4) Dung-pat Pattern Sampling

The results from the dung-pat pattern "very long line" are shown in Table XII, and Fig. 9. The earthwormsfrom the dung-pats of this pattern show differences in numbers obtained from dung-pats placed in mown and unmown ungrazed grassland. The differences are seen to be significant in all species except L. rubellus. It is perhaps worthy of note that L. rubellus, which is greatly influenced by the presence of dung, is uninfluenced by the height of the sward, while the B. tenuis - D. rubida-subrubicunda complex which is uninfluenced by the presence of dung is apparently influenced by mowing. E. tetraedra, as might be expected, is greatly influenced by mowing. It is also clear that although the presence of dung may favour D. octaedra, the species can live successfully in the complete absence of dung under the long swards of ungrazed grassland./

grassland. Comparisons between Figs 9(b) and 6(c) (which show the complexes obtained from collections in a similar habitat at sites about 50 metres apart) show similarities, but there is a much denser aggregation of D. octaedra apparent in 9(b).

(5) Species Spectra

Guild (1952b) has discussed the variation in earthworm populations in detail. Working in a comparatively uniform agricultural field he has shown that the sub-division of the population is finer than would be suggested from a superficial examination of the vegetation and the soil. An examination of the area surveyed in Tiree shows it to be an involved system of continuous and discontinuous variations, which might be conveniently broken up into different ecological compartments; compartments such as dunes, grazed machair, ungrazed machair, ungrazed mown machair, marsh (present in the locality but not sampled), dung-pats, and open soil all possessing distinctly different assemblages of earthworms. From samples taken within these compartments, however, the finer sub-division, outlined by Guild, can be detected but for that there is no obvious ecological explanation, though a "family" group theory has been put forward by Satchell (1955) (Paper I, page 30). The species complex in this and probably in all other field population of earthworms cannot be summarised in a single spectrum. A large/

large number of spectra are required, taken from all the recog-:nisably different compartments. At the same time it must be recognised that such spectra are merely the average qualitative and quantitative expression of a chequered distribution in which no two clusters are identical.

Figs 6, 7, 8, and 9 show the spectra which have been obtained for all the readily recognisable compartments of the soil habitat in the dune-machair system, except marsh. The spectra have been obtained by several different methods, and in some cases two different methods have been applied to the same compartment. Strong similarities have emerged between related spectra, but there are also distinct differences which perhaps can be attributed to failure of two methods to give comparable results.

This is seen in the case of comparing Fig. 6(b) with Fig. 7(b). The former figures were obtained from quadrats of 900 square centimetres covered almost entirely by dung, while the latter were obtained from quadrats of 1 square metre only a minor fraction of which were covered by dung. This perhaps explains the comparative dearth of A. caliginosa, a species not attracted by dung, in Fig. 6(b), and its comparative abundance in Fig. 7(b), where much open soil was included in the quadrat.

IV. SPATIAL VARIATION IN NUMBERS OVER UNIFORM GRASSLAND/

IV. SPATIAL VARIATION IN NUMBERS OVER UNIFORM GRASSLAND

When discussing the species spectra obtained in the various ecological compartments over which the machair population is spread, a finer sub-division existing within these compartments was mentioned for which there was no obvious ecological expla-:nation. An attempt is now made to describe the extent of these localised variations in numbers, in a highly uniform soil context.

The numbers obtained by the "wet" method of sampling of the open soil over a highly uniform tract of machair in months when earthworms were readily obtainable by that method are shown in Table XIII. Numbers obtained by this method from quadrats containing a dung-pat were not used. In these samples a certain amount of heterogeneity does in fact exist due to the variation in the nature of the dung-pats. In Table XIII(a) is seen the analysis of variance between months and dung-pat interspaces, and from the F values the distribution is seen to be just heterogeneous at the 5 per cent level. In this analysis the values of actual earthworm numbers in Table XIII, general value $\underline{x}$, are transformed to a more suitable form thus: $x' = (x + 0.357)^{\frac{1}{2}}$.

The numbers obtained in the two batteries of pit-fall traps set in uniform grazed and ungrazed machair are also used for/

for tests of homogeneous distribution. In this case only two plots, one 108 square metres and another 81 square metres, were used in which the traps remained in the same position for the period of the trapping. Each trap stood the same chance of catching the same number of earthworms, providing the fauna was uniformly distributed. The results are shown in Table XIV, and it is seen that in both batteries the catches are very heterogeneous. Fig. 10 shows the density pattern revealed by the battery on the grazed machair, each trap having been given a station number and the monthly catch at each station care-:fully logged. The closer the density lines the higher is the heterogeneity of population distribution. In this square of uniform machair there are two centres of high density due mainly to comparatively high aggregations of A. caliginosa. It proved difficult to make the lip of the traps flush with the grass in all cases due to the action of the wind and rain, but variation in the turf-lip contact of the traps would not account for the large variation in numbers of earthworms caught in each. It appears therefore that the variation in numbers between contiguous squares 9 square metres in area is great, and much more than could be expected by chance alone.

The numbers obtained in the dung-pat pattern survey are set forth in Table XV. Fortunately all the patterns had almost completely escaped the attention of birds, only one of the pats showing/

showing a few prod-holes. The sets of figures from the long line, the short line and the large square are homogeneous, while that from the small square is heterogeneous. Fig. 11 shows the density patterns for the large and the small squares. Careful note should be taken of the scale of each pattern, and of the intervals between the lines joining points of equal density. It is clear, however, that the type of variation occurring in the small square, which is a ninth of the size of the large square, will not readily be detected by the large square distribution. In such large grid patterns the "mesh" may be too large to detect finer density variations. Since the density in the small square can change from 3 (density units, derived from the actual number attracted by the dung) to 10 in a distance of 25 centimetres, such variation could occur within the grid spaces of the large square without being detected. It is apparent, however, from the numbers obtained on the long and short lines that considerable distances can be traversed without encountering such density variation as that seen in the small square.

The total numbers of earthworms obtained from the long and short lines and from the large square are not significantly different (chi-square = 4.300), but the differences between these three figures, 14, 19, and 27, and that for the small square, 102, is highly significant. The high numbers in the small/

small square were due to the presence of comparatively dense clusters of D. octaedra and E. tetraedra. This was due most probably to the fact that the square chanced to fall on an area where the density of these species was high. This is underlined by the fact that the B. tenuis - D. rubida-subrubicunda complex, which shares dominance with D. octaedra throughout the dung-pat patterns as a whole, is not particularly numerous in the small square.

V. REPRODUCTION

In a study of the life-cycles of British Lumbricidae, Evans and Guild (1948a) examined the reproductive cycle by measuring cocoon production in laboratory cultures. They showed that cocoon production differed greatly between species and seasons, and is greatly affected by the temperature and moisture content of the soil. In a complementary work on field populations, Evans and Guild (1948b) show seasonal trends in populations of immature, adolescent, and sexually mature earthworms. Such trends are adopted here to trace the annual reproductive cycle of the earthworm population in machair soil at the Reef, Tiree. The percentage of mature earthworms, i.e. earthworms possessing a clitellum, present in the monthly "wet" sampling of the machair population from November, 1954 to November, 1955, and also in the monthly catches from the pit-fall/

pit-fall traps set in the grazed and ungrazed machair from April, 1955 to May, 1956, are used for the purpose.

The annual cycles obtained by Evans and Guild from the cocoon counts are reproduced in Fig. 12*. Before comparing these cycles with those obtained by counts of mature worms in Tiree (Figs 13, 14), it must be emphasised that the two cycles, though comparing two closely related attributes, viz. numbers of cocoons with percentages of mature earthworms, do not compare the same attributes of the population; cocoon data were obtained from laboratory cultures with the temperature varying naturally, but with the moisture content always optimal, and the mature earthworm data were obtained from the sampling of a natural population in natural conditions.

From Fig. 12* it is seen that the species can be divided into those which have continuous production of cocoons through-:out the year following closely the soil temperature gradient, and those which have a reproductive pause during the summer. All the species, except A. longa and A. nocturna, including five found in this particular population in Tiree, are shown by Evans and Guild to have uninterrupted reproduction throughout the year in optimal moisture conditions. Later in the same paper (Evans and Guild, 1948a) the effects of soil moisture on cocoon/

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* Seen in Evans and Guild (1948b)

cocoon production were seen to be great. Although production was seen to differ between soils of different types, it clearly ceased completely between soil moistures of 15 and 20 per cent of the dry weight of the soil. Unfortunately no comparable graphs for the moisture content of the soil such as those for temperature are given by Evans and Guild, since moisture content was not measured as a natural variation over the space of a year, but was controlled in a replicated experiment, in which several moisture levels were maintained simultaneously for 43 days.

Fig. 13, Table XVI show the monthly percentages of mature earthworms obtained from the total monthly collections by the "wet" method. The over-all percentage is broken up to show those of A. caliginosa, L. rubellus, and all the other species considered cumulatively. Temperature and rainfall data are also shown.(Fig. 5).

The period of this sampling programme included the extra-:ordinarily dry spring and summer of 1955 when air temperatures remained normal and rainfall values from December, 1954 to August, 1955 inclusive, except June, were well below the normal. In contrast to the results of the cocoon counts by Evans and Guild, maximum reproduction appears to take place in the machair population during the winter, and not in summer, the peaks and troughs being reversed. The percentages of A. caliginosa, L. rubellus/

L. rubellus, and the other species considered cumulatively show similar tendencies. No result was obtained for February, 1955 because of hard frost prevailing at the time of sampling.

Evans and Guild (1948b) show, however, that the strength of a field population is lowest between May and August in the south of England, when numbers of sexually mature individuals are also at a minimum. It follows that the reproductive cycle of a field population is not similar to that shown by the cocoons produced by a laboratory culture at optimal moisture levels. The peak shown in Fig. 12 may not in fact exist in British field populations where reproduction is freely influenced by variation in soil moisture. It is probable that it does not exist in Tiree since there were no sexually mature individuals found in the grazed and few in the ungrazed swards in the dry season.

The peak occurred between November and January when the mean monthly air temperature ranged from 45.5 to 40.9°F, the seasonal trough, and the monthly rainfall ranged from 225 to 96 millimetres, the seasonal peak. In February the mean monthly temperature was 39.3°F and although the frost precluded sampling during that month it did not last for more than a few days, and at worst the soil was only frozen to a depth of 5 centimetres (extraordinary freezing in Tiree). The frozen crust was broken by a pick and below the earthworms were found to be plentiful/

plentiful and active, many matures being noted. Between April and May a distinct ecological threshold had been crossed, and the numbers of matures in the population had dropped almost to zero. Such a threshold is mentioned by Stephenson (1930) in the sudden disappearance of earthworms with clitella from a North American population subjected to a sudden spell of cold weather in autumn. In this case, however, there is no apparent temperature threshold, but a possible moisture one. Fig. 5 shows the temperature and rainfall figures for the period together with the mean monthly values for the period 1943-52. It will be seen that the rainfall values are much lower than normal for January-May, while the temperature values are normal. May is the normal seasonal trough for rainfall when the sandy grasslands are fairly dry.

Throughout the summer in question the weather remained abnormally dry, being extremely so through July and August. During this period no earthworms, neither mature nor immature, were obtained by the "wet" method. Digging showed the soil to be dry to a depth of 8 centimetres and that in the moist soil remaining above the sub-sand the earthworms were small and mostly curled in a tight ball. No earthworms were found bearing a clitellum.

A similar threshold would seem to be crossed in the opposite direction to that of April-May, between September and October. At/

At this time the rainfall figures rose greatly with a corres-:ponding increase in the number of clitellum-bearing earthworms in the population.

From the pit-fall trap catches (Table XVII, Fig. 14), the reproductive cycle obtained for the period April, 1955 to May, 1956 shows the same characteristics as those already described by the data from the monthly "wet" sampling programme. It may be argued that the proportion of matures in the total catch of earthworms in surface traps might not give a true reflection of the proportions in the total population. The fact that earth-:worms move on to the soil surface to copulate might be said to bias the samples in favour of the mature rather than giving an unbiased selection of both mature and immature animals. A glance at Figs 13 and 14, however, shows that this is not the case, the same distribution being obtained from two independent methods in the same soil locality, the grazed machair. The catch from the pit-fall traps would appear to give a fairly reliable estimate not only of the percentage of matures moving on the surface throughout the year, but also the percentage in the whole population.

In the case of the ungrazed machair (airfield) the pit-fall catches give a much less uniform annual build-up and decline, and, as has been brought out in other sections of the work, are noticeably different from the two histograms which have been obtained/

obtained for the grazed grassland on the other side of the perimeter fence. There is a fairly distinct trough from May-July, with a gradual build-up from August to a peak in November, and a decline through the winter and the spring to the May trough. The salient changes seen in the histograms on the grazed ground are evident from October-November and April-May, though the winter peak would seem to occur in advance of that on the grazed machair.

Perhaps the main difference between the two contemporaneous pit-fall collections is the comparatively large percentage of matures which were obtained on the ungrazed land in the height of the drought, when the community on the grazed land was in suspended animation. In August when the drought was intense 3 of the 10 earthworms caught were found to be mature in the ungrazed machair traps, while on the grazed machair no earth-:worms were caught. The soil of the ungrazed land, blanketed with the thick rank Festucatum is a much more moist habitat all year round than the grazed grassland. The presence of E. tetraedra in the ungrazed and its absence in the grazed is in agreement with this. Cernosvitov and Evans (1947) described the habitat of E. tetraedra as "amphibious, in moist soil, mostly covered with water or in purely aquatic habitats".

VI. ABUNDANCE AND ACTIVITY/

VI. ABUNDANCE AND ACTIVITY

Evans and Guild (1948b) estimated the abundance of five species of earthworm in agricultural fields in England. The sampling method used was the "wet" method, and the work might be thought unconvincing as a measure of the abundance of the earthworms present in the soil at any particular time, due to the criticism of the sampling method (Svendsen, 1955). The vertical movement in such old-established agricultural soils is probably great. Stephenson (1930) summarises information by Darwin and others about the depth to which earthworms penetrate in winter. It is generally accepted that they penetrate to deeper levels where the temperature is higher and more constant. It follows, therefore, that the deeper the bulk of the population goes in winter the less effective will become the "wet" method of sampling in giving a standard measure of abundance.

The descent of the main body of the population 10 centimetres or more might place an appreciable fraction beyond the influence of the permanganate solution. In Tiree the same method of extraction was employed, but in this case there was little or no vertical movement of earthworms throughout the year. The soil depth above the pure sub-sand is about 15 centimetres, and there is no evidence that earthworms do in fact penetrate the sub-sand which is very tightly compacted. In/

In winter there is seldom need for deep penetration since the soil freezes very infrequently, and then usually the upper 2 or 3 centimetres only, and in summer the sub-sand immediately under the soil is drier than the soil layer (Paper I, Fig. 2), and tends to be less favourable to earthworms. Comparisons of the findings of Evans and Guild with those now presented may help, however, to confirm the reliability of both.

Table XVIII, Fig. 15 show the data obtained from the "wet" method. No sampling was possible during the visit in February because of hard frost, but during that time earthworms were seen to be numerous and active immediately below the thin frozen layer. Fig. 15(b) shows a complementary survey carried out simultaneously on another machair in Tiree from January till June, 1955. Somewhat similar to the findings of Evans and Guild (1948b), the cycle of abundance of this population would appear to reach a peak in December declining gradually to a trough in June-August, with a secondary peak in April. During the summer in question a great proportion of the population on the grazed machair probably died in the drought. Few earth-:worms were obtained from June-August. This was not entirely due to the failure of the population in a state of suspended animation to respond to the chemical stimulus for digging showed that comparatively few were in fact present. In autumn, numbers rise to a secondary peak in September, but before rising to the primary winter peak there is a trough in November.

All/

All the features shown by Evans and Guild for most of the five species which they considered, are repeated in this work with small time variations. The reasons advanced by them in explanation involving predation, emergence from seasonal quiescence, the emergence from cocoons, and the effects of limiting moisture content of the soil, seem satisfactory when applied to this situation. Comparison of Figs 13 and 15 shows that seasonal abundance and percentage of matures in the popu-:lation are related in time.

The catch from the two batteries of pit-fall traps set in the grazed and ungrazed grassland is used to estimate the seasonal variation in surface activity of the respective commu-:nities. The data are set forth in Table XIX, Fig. 16. The two histograms are similar with two peaks, one in October-November and the other in April-May, between which occur exten-:ded troughs. The pattern appears closely related to rainfall, but not to temperature. In the case of the grazed machair the surface activity appears less related to the numbers of matures present in the population (Fig. 13) than is the case in the ungrazed machair where the primary peaks for surface activity and percentage of matures are coincidental. Surface activity does not appear closely related to seasonal abundance the primary abundance peak in December-January being missed in the surface activity figures.

Stephenson/

Stephenson (1930) in discussing the causes of death in earthworms mentions that daylight is intensely harmful due to effects of ultra-violet rays, and that even in dull weather they will be paralysed by two to three hours' exposure. The only occasions when earthworms were noticed moving on the surface in daylight on the Reef machair, Tiree, were during cool wet days, usually in fine drizzle. The species concerned were A. caliginosa and O. cyaneum, and there was a distinct difference in the behaviour of the two. The specimens of A. caliginosa were sluggish in movement, while O. cyaneum moved quickly as if errant. A visit was also made to the site on a wet night in December, 1955, when A. longa were abundant on the lawn of a neighbouring garden, and though a search was made over a wide area of grassland very few individuals were found. These belonged to the species A. caliginosa, B. tenuis, L. rubellus and O. cyaneum.

If it is the case that earthworms are highly sensitive to daylight it may be thought that the effects of daylight may be less intense with pigmented species than with unpigmented. To examine this possibility of proportionately more pigmented earthworms moving on the surface than unpigmented, the numbers of an unpigmented species (A. caliginosa), and of a pigmented species (L. rubellus) are compared. Table XX shows the numbers of the two species obtained (i) from the body of the soil/

soil (open soil) in one year's sampling by the "wet" method, and (ii) from the soil surface in one year's sampling by pit-fall traps. For every 100 of the unpigmented species present in the body of the soil there were 12 pigmented, but for every 100 unpigmented moving on the surface there were 42 pigmented. The difference is highly significant (chi-square = 47.150) and shows that more pigmented species are found moving on the surface than is their proportion in the soil to the unpigmented species. This, however, should not obscure the fact that unpigmented earthworms do in fact move on the surface in large numbers. Out of the 746 earthworms caught in the pit-fall traps while moving on the surface, 505 (67.7 per cent) were unpigmented, and 241 (32.3 per cent) were pigmented.

VII. SUMMARY

1. The survey area together with four sampling programmes are described. These programmes are: (i) a transect, (ii) monthly sampling of a machair population by the "wet" method over 12 months, (iii) monthly sampling of a machair population by monthly collections from pit-fall traps over 12 months, and (iv) dung-pat sampling from pats set out in square and line patterns.
2. The species complex of the dune-machair system is described. The habitat is subdivided into several distinct ecological compartments/

compartments, viz. dunes, grazed machair, ungrazed machair, ungrazed mown machair, and the effect of the presence or absence of dung-pats in the compartments examined. The species complex is summarised in a series of species spectra showing the differences existing between the commu:nities in different compartments, and the effect of dung-pats in each compartment.

3. Variation in the numbers of earthworms over uniform grass:land is investigated and found not to be homogeneous. Large variations in numbers are seen to occur over very short distances with no obvious environmental change.

4. Reproduction of the machair population is examined by means of the percentages of matures in the monthly collec:tions. It is seen to be at a maximum during the winter (which is mild in Tiree), and at a minimum in summer (when machair soils are comparatively dry).

5. The numbers in the population are greatest in mid-winter with secondary peaks in spring and autumn. There is a distinct trough in summer.

6. Surface activity of the population is at a maximum in late autumn and late spring. Although large numbers of unpigmented earthworms are found moving on the surface, there are proportionately fewer doing so than of pigmented species in the population.

TABLE I

Transect sampling, 20 samples at each station, 10 in dung-pats, and 10 in the dung-pat interspaces

Dung-pat Sampling						
Species	Number of earthworms in 10 samples					
	Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
A. caliginosa	0	0	0	8	11	4
B. tenuis – D. rubida – subrubicunda	0	0	1	1	13	119
D. octaedra	0	0	0	2	49	12
E. tetraedra	0	0	0	0	0	34
L. castaneus	0	0	18	5	0	4
L. rubellus	0	9	72	55	26	7
Total earthworms	0	9	91	71	99	180
Interspace sampling Number of earthworms in 10 samples						
A. caliginosa	0	0	0	0	6	0
B. tenuis – D. rubida – subrubicunda	0	0	0	0	0	4
D. octaedra	0	0	0	0	0	4
E. tetraedra	0	0	0	0	0	0
L. castaneus	0	0	0	0	0	0
L. rubellus	0	0	0	0	3	0
Total earthworms	0	0	0	0	9	8

TABLE II

Showing differences between main ecological compartments of the transect.

Species	Dune basin	Grazed machair	Difference	Grazed machair	Ungrazed machair	Difference
A. caliginosa	0	11	S	11	4	N/S
B. tenuis - D. rubida - subrubicunda	1	13	S	13	119	S
D. octaedra	0	49	S	49	12	S
E. tetraedra	0	0	N/S	0	34	S
L. castaneus	18	0	S	0	4	N/S
L. rubellus	72	26	S	26	7	S

S = significant (χ^2 greater than 3.841)

N/S = not significant (χ^2 less than 3.841)

TABLE III

Transect sampling. Wet weight in gms of earthworms in 20 samples at each station, 10 in dung-pats and 10 in the dung-pat interspaces

Dung-pat Sampling					
Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
0	2.437+	2.288	0.223	0.980	1.171
		2.088	1.334	0.920	0.923
		0.857	2.310	2.061	2.055
		0.789	0.096	0.269	1.630
		1.771	0.719	2.735	1.635
		1.910	0.653	2.013	1.720
		1.682	0.343	0.635	2.323
		2.545	2.075	0.629	0.368
		0.171	1.328	0.833	1.413
		0.632	0.600	2.433	1.560
0	2.437+	14.74+	9.68+	13.51+	14.80+
Interspace Sampling					
0	0	0	0	2.318+	0.488+

+ total weight of 10 samples

TABLE III (a)

Analysis of variance of weights of samples taken at stations (iii), (iv), (v) and (vi).

Variation due to	Degrees of freedom	Sum of squares	Mean square	F_0	$F_{0.05}$
Station	3	1.738	0.579	1.03	2.86
Residue	36	20.682	0.563		
Total	39	22.420		$F_0 < F_{0.05}$ (Homogeneity)	

TABLE IV

Open soil sampling 1954-55, showing number of earthworms obtained in monthly sampling by the 'wet' method

Species	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Totals
A. caliginosa	59	69	72	+	48	67	0	0	0	0	37	46	41	439
A. chlorotica	0	1	2	+	0	0	0	0	0	0	0	0	0	3
A. longa														
B. eiseni														
B. tenuis - D. rubida - subrubicunda	1	2	0	+	0	0	0	0	0	0	0	1	1	5
D. mammalis														
D. octaedra	6	2	4	+	0	1	0	0	0	4	1	0	4	22
E. rosea														
E. tetraedra														
L. castaneus	0	0	0	+	1	0	0	0	0	0	0	0		1
L. festivus														
L. rubellus	25	8	4	+	2	0	1	0	0	4	0	6	3	53
L. terrestris														
O. cyaneum	1	0	3	+	0	1	0	0	0	0	1	2		8
O. lacteum	0	0	0	+	0	0	0	0	0	0	0	0	1	1
Total earthworms	92	82	85	+	51	69	1	0	0	8	39	55	50	532

+no sampling because of frost

TABLE V

Dung-pat sampling 1954-55, showing number of earthworms obtained in monthly sampling by the 'wet' method.

Species	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Totals
A. caliginosa	‡	51	73	+	36	57	0	0	0	0	33	27	‡	277
A. chlorotica	‡	7	1	+	0	0	0	0	0	0	4	0	‡	12
A. longa														
B. eiseni														
B. tenuis - D. rubida - subrubicunda	‡	3	2	+	1	0	0	0	0	0	1	5	‡	12
D. mammalis														
D. octaedra	‡	6	10	+	18	29	17	0	0	2	16	3	‡	101
E. rosea														
E. tetraedra														
L. castaneus	‡	37	14	+	3	0	0	0	0	0	5	6	‡	65
L. festivus														
L. rubellus	‡	154	70	+	38	63	69	0	2	8	41	11	‡	456
L. terrestris														
O. cyaneum	‡	0	0	+	0	0	0	0	1	0	4	0	‡	5
O. lacteum	‡	0	0	+	0	0	0	0	0	0	0	0	‡	0
Total earthworms	‡	258	170	+	96	149	86	0	3	10	104	52	‡	928

+no sampling because of frost

‡dung-pat degenerate

TABLE VI

Showing difference between collections from open-soil and dung-pats.

Species	Open-soil	Dung-pat	Difference
A. caliginosa	439	277	S
A. chlorotica	3	12	S
B. tenuis - D. rubida - subrubicunda	5	12	N/S
D. octaedra	22	101	S
E. tetraedra	0	0	N/S
L. castaneus	1	65	S
L. rubellus	53	456	S
O. cyaneum	8	5	N/S
O. lacteum	1	0	N/S

S = significant

N/S = insignificant

TABLE VII

Dung-pat frequency on the Reef machair Tiree taken at bi-monthly intervals throughout the grazing period from December 1954 to May 1955 inclusive. Measured in 144 sq.m. quadrats

	December - January	February - March	April - May
	11	15	16
	15	20	16
	12	16	22
	14	18	27
	17	16	22
	19	15	24
	14	24	22
	14	16	19
	9	21	13
	11	28	19
		16	24
		17	26
			30
Mean	13.6	18.5	21.5
St'd Dev'n	2.99	4.05	4.81

Analysis of the sampling results for April and October, 1955 from 10 samples each 1 sq.m. in-:cluding dung-pats randomly distributed 22 per 144 sq.m., and 10 samples in the interspaces between dung.

		A. caliginosa		D. octaedra		L. rubellus	
		Dung 22 sq.m.	Op. soil 122 sq.m.	Dung 22 sq.m.	Op. soil 122 sq.m.	Dung 22 sq.m.	Op. soil 122 sq.m.
Mean no. per sq.m.	Apr. Oct.	5.7 2.7	6.7 4.6	2.9 0.3	0.1 0	6.3 1.1	0 0.6
No. per 144 sq.m.	Apr. Oct.	125.4 59.4	817.4 561.2	63.8 6.6	12.2 0	138.6 24.2	0 73.2
No. per 144 sq.m. quadrat	Apr. Oct.	942.8 620.6		76.0 6.6		138.6 97.4	
Ratio of totals Nos A. caliginosa / Nos L. rubellus	Apr. Oct.	6.802 6.372					

TABLE IX

Collections from pit-fall traps on grazed machair.

Dates 1955-56	28/3 -29/4	29/4 -18/6	18/6 -18/7	18/7 -18/8	18/8 -14/9	14/9 -15/10	15/10 -11/11	11/11 -14/12	14/12 -14/1	14/1 -12/3	12/3 -16/4	16/4 -31/5	Total earthworms
A. caliginosa	63	14	6		13	28	9	5	9	16	16	59	238
A. chlorotica								3			1	1	5
B. tenuis - D. rubida - subrubicunda										1			1
D. octaedra	3	1	2						2	3			11
E. tetraedra													
L. castaneus		2					4	4	2		1		13
L. rubellus	34	4	5	1	5	8		6	5	11	11	10	100
O. cyaneum	1	2			2	4	8	1		3		7	28
Total number of earthworms	101	23	13	1	20	40	21	19	18	34	29	77	396

TABLE X

Collections from pit-fall traps on ungrazed machair (airfield).

Dates 1955-56	29/4 -18/6	18/6 -18/7	18/7 -18/8	18/8 -14/9	14/9 -15/10	15/10 -11/11	11/11 -14/12	14/12 -14/1	14/1 -12/3	12/3 -16/4	16/4 -31/5	Total
A. caliginosa	3	7	1	5	6	3	1	2	-	5	26	59
A. chlorotica						1						1
B. tenuis - D. rubida - subrubicunda	1	1		2	6	22	5	3	8	3	3	54
D. octaedra	1				2	1	1	1	3			9
E. tetraedra		1		1	5	9	10	19	10	6	49	110
L. castaneus					2	8	3	8	3	1	1	26
L. rubellus	4	2		2	1	2	7	2		3	4	27
O. cyaneum	1	4	9	7	13	4	2	1	1		22	64
Totals of earthworms	10	15	10	17	35	50	29	36	25	18	105	350

TABLE XI

Showing differences between grazed and ungrazed ground, between 18-7-55 and 31-5-56.

Species	Grazed	Ungrazed	Differen-:ces
A. caliginosa	155	49	S
A. chlorotica	5	1	N/S
B. tenuis - *D. rubida* - *subrubicunda*	1	52	S
D. octaedra	5	8	N/S
E. tetraedra	0	109	S
L. castaneus	11	26	S
L. rubellus	57	21	S
O. cyaneum	25	59	S

S = significant
N/S = insignificant

TABLE XII

Differences in collections from "very long line", 24 dung-pats of equal size and quality on ungrazed machair, 12 from mown and 12 from unmown ground.

Species	Mown	Unmown	χ^2
A. caliginosa	-	-	-
A. chlorotica	-	-	-
B. tenuis - D. rubida - subrubicunda	106	77	4.596*
D. octaedra	50	111	23.112*
E. tetraedra	1	13	10.286*
L. castaneus	-	-	-
L. rubellus	18	15	0.073
O. cyaneum	-	-	-

*significant

TABLE XIII

Showing variation in number of earthworms obtained in sampling uniform machair each month by the 'wet' method. (Studied only in months when the collection was suffi-:ciently great.

	Nov. 1954	Dec.	Jan. 1955	March	April	Sept.	Oct.	Nov.
	7	13	8	4	14	5	6	4
	4	7	6	6	5	3	6	4
	12	7	12	4	3	5	2	6
	5	5	6	5	7	3	9	3
	8	5	16	5	6	2	4	5
	4	4	8	3	4	5	2	5
	6	13	9	4	14	3	13	5
	5	7	4	9	9	4	5	9
	4	16	11	6	2	5	7	2
	3	5	5	5	5	4	1	7
	7							
	3							
	11							
	4							
	9							
χ^2	18.319	19.463*	14.176	4.882	26.420*	2.766	21.545*	7.200

*significant (Heterogeneity)

TABLE XIII (a)

The analysis of variance of the data presented in TABLE XIII. If x = number of earthworms, the transformation to x' quoted in this table is $x' = \sqrt{(x + 0.375)}$.

December 1954	January	March	April	September	October	November 1955	Total
3.657	2.894	2.092	3.792	2.318	2.525	2.092	19.370
2.716	2.525	2.525	2.318	1.837	2.525	2.092	16.538
2.716	3.519	2.092	1.837	2.318	1.541	2.525	16.548
2.318	2.525	2.318	2.716	1.837	3.062	1.837	16.613
2.318	4.046	2.318	2.525	1.541	2.092	2.318	17.158
2.092	2.894	1.837	2.092	2.318	1.541	2.318	15.092
3.657	3.062	2.092	3.792	1.837	3.657	3.062	21.159
2.716	2.092	3.062	3.062	2.092	2.318	2.318	17.660
4.046	3.373	2.525	1.541	2.318	2.716	1.541	18.060
2.318	2.318	2.318	2.318	2.092	1.173	2.716	15.253
28.554	29.248	23.179	25.993	20.508	23.150	22.819	173.451

Variation due to	Degrees of freedom	Sums of squares	Mean square	F_0	$F_{0.05}$
Months	6	6.299	1.050	4.66	
Interspaces	9	4.367	0.485	2.15	2.05
Error	54	12.164	0.225		
Total	69	22.830	1.760	$F_0 > F_{0.05}$ (Heterogeneity)	

TABLE XIV

Showing the variation in numbers of earthworms caught by two batteries of pit-fall traps set respectively in uniform grazed and ungrazed machair. 12 traps are considered in the grazed grassland battery, and 9 traps in the ungrazed grassland battery.

Total No.	Grazed Grassland Battery	Total No.	Ungrazed Grassland Battery
1	21	A	24
2	39	B	37
3	46	C	32
4	47	D	24
5	30	E	37
6	33	F	51
7	31	G	25
8	35	H	32
9	14	K	22
10	44		
11	23		
12	28		
χ^2	35.795*		76.250*

*significant (Heterogeneity)

TABLE XV

Showing the variation in number of earthworms obtained from various patterns of 16 dung-pats of equal size and quality set in mown ungrazed machair.

Dung-pat No.	'Long-line'	'Short-line'	'Large square'	'Small square'
1	-	-	2	-
2	-	2	1	3
3	1	-	3	3
4	-	1	1	3
5	1	-	-	4
6	2	3	3	4
7	2	-	1	6
8	1	1	1	6
9	3	1	-	3
10	1	1	-	10
11	-	-	2	8
12	-	-	-	12
13	-	3	1	9
14	1	1	4	12
15	-	3	5	10
16	2	3	3	9
Total earth-:worms	14	19	27	102
χ^2	15.289	18.700	19.147	27.190*

*significant (Heterogeneity)

TABLE XVI

Percentages of matures in the monthly collections by the 'wet' method on uniform machair.

Species	Nov. 1955	Dec.	Jan. 1956	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
A. caliginosa	44.1	49.2	51.7	+	33.3	34.8	-	-	-	-	18.6	43.8
L. rubellus	36.0	50.6	43.2	+	42.5	41.3	2.9	-	-	-	3.3	35.3
Others	25.0	51.7	50.0	+	13.0	29.8	2.3	-	-	-	18.8	58.8
Total	40.2	49.7	46.2	+	32.7	32.6	2.3	-	-	-	14.0	44.9

+no collection due to frost

TABLE XVII

Percentages of matures in the monthly catches of the two batteries of pit-fall traps in the grazed and ungrazed grasslands.

Dates 1955-56	28/3 -29/4	29/4 -18/6	18/6 -18/7	18/7 -18/8	18/8 -14/9	14/9 -15/10	15/10 -11/11	11/11 -14/12	14/12 -14/1	14/1 -12/3	12/3 -16/4	16/4 -31/5
Collection on grazed land	53.5	27.3	-	-	-	2.5	33.3	36.8	61.1	47.1	44.8	14.3
Collection on ungrazed land	+	20.0	6.7	30.0	23.5	20.0	60.0	42.9	20.0	24.0	41.7	3.8

+no collection made

TABLE XVIII

Total number of earthworms obtained by the 'wet' method, showing monthly abundance.

Species	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Totals
A. caliginosa	59	120	145	+	84	124	0	0	0	0	70	73	41	716
A. chlorotica	0	8	3	+	0	0	0	0	0	0	4	0	0	15
A. longa														
B. eiseni														
B. tenuis – D. rubida – subrubicunda	1	5	2	+	1	0	0	0	0	0	1	6	1	17
D. mammalis														
D. octaedra	6	8	14	+	18	30	17	0	0	6	17	3	4	123
E. rosea														
E. tetraedra														
L. castaneus	0	37	14	+	4	0	0	0	0	0	5	6	0	66
L. festivus														
L. rubellus	25	162	74	+	40	63	70	0	2	12	41	17	3	508
L. terrestris														
O. cyaneum	1	0	3	+	0	1	0	0	1	0	5	2	0	13
O. lacteum	0	0	0	+	0	0	0	0	0	0	0	0	1	1
Total earthworms	92	340	255	+	147	218	87	0	3	18	143	107	50	1460

+no collection due to frost

TABLE XIX

Showing number trapped by pit-fall traps on the grazed and ungrazed land, these are interpreted as monthly measures of surface activity.

	April	May–June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.–Mar.	April	May
Days standing	32	50	30	31	27	31	27	33	31	58	35	45
Conversion factor to 30 days	1.1	1.7	1	1	0.9	1	0.9	1.1	1	1.9	1.2	1.5
Earthworms 'grazed'	101	22	13	1	20	40	21	19	18	34	29	77
Earthworms 'grazed' converted	91.8	12.9	13	1	22.2	40	23.3	17.3	18	17.9	24.2	51.3
Earthworms 'ungrazed'		10	15	10	17	35	50	28	35	25	18	105
Earthworms 'ungrazed' converted		5.9	15	10	18.9	35	55.6	25.5	35	13.2	15.0	70.0

TABLE XX

Number of pigmented and unpigmented species in soil and on soil surface.

	A. caliginosa UNPIGMENTED	*L. rubellus* PIGMENTED	% PIGMENTED	χ^2
In soil	439	53	12.1	47.150
At soil surface	238	100	42.0	

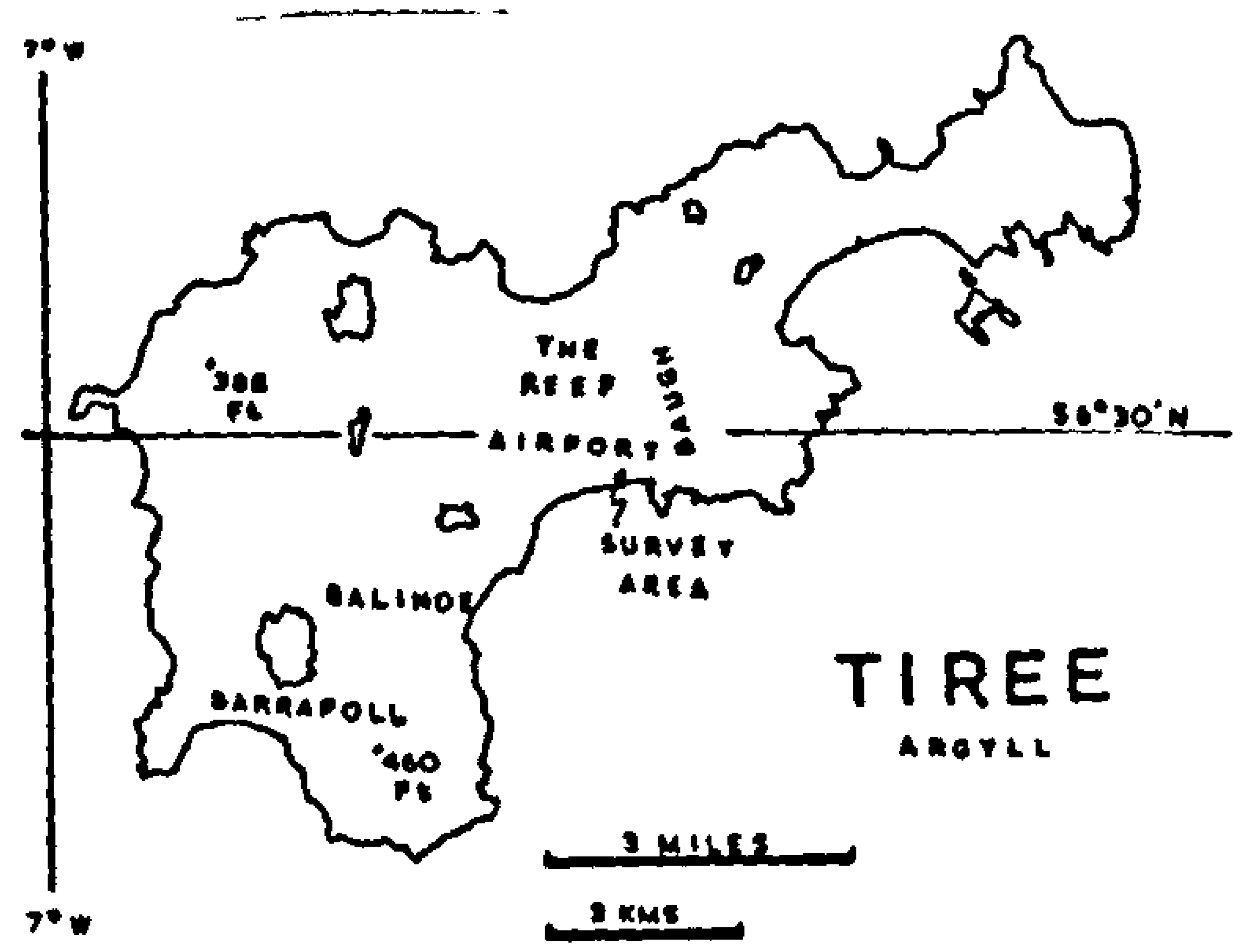


Fig. 1.

An outline map of Tiree showing the location of the survey area.

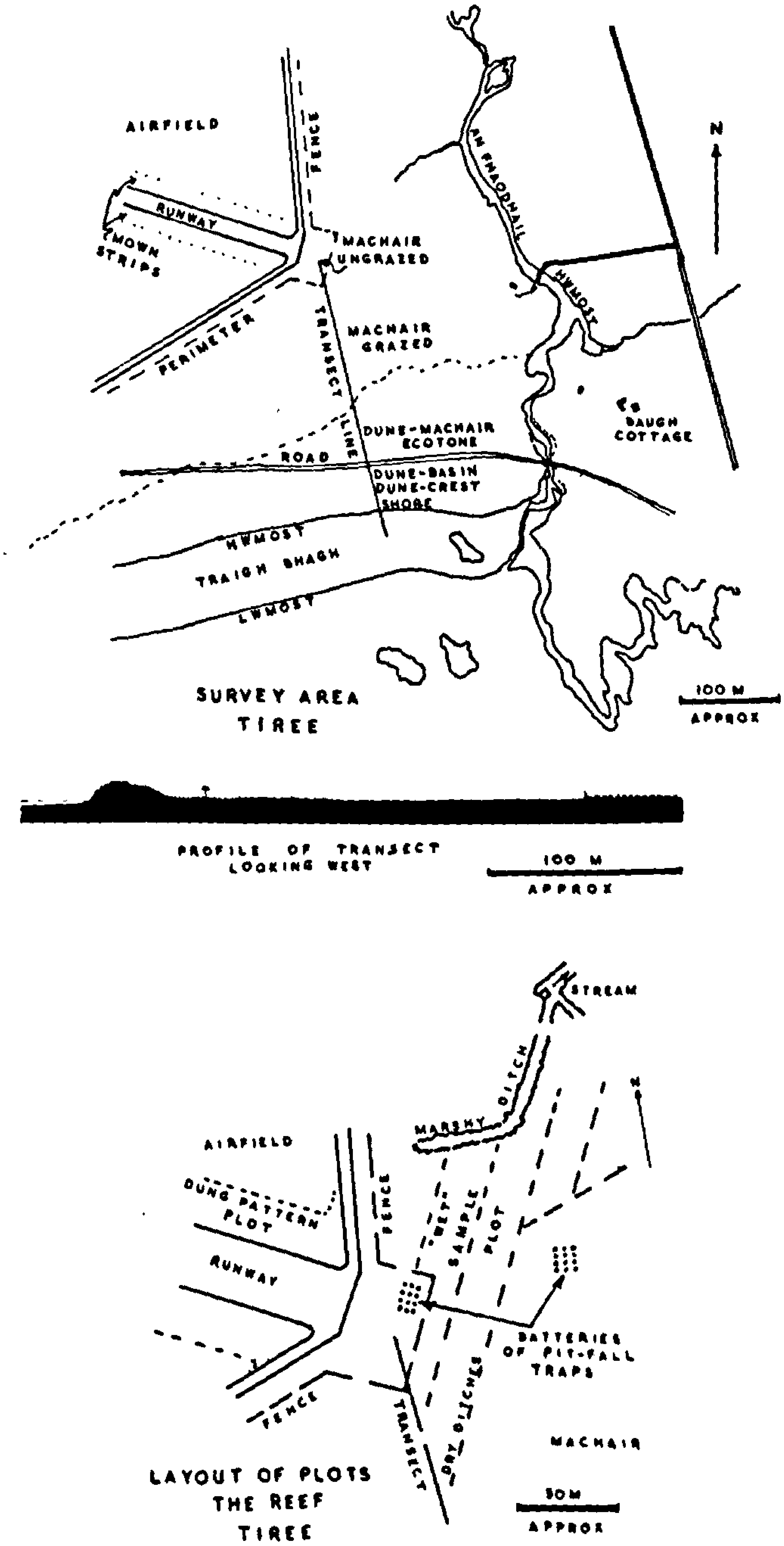


Fig. 2.

Showing in two outline maps the details of the transect area at Baugh, Tiree, and those of the expe-:rimental plots at the north end of the transect line.

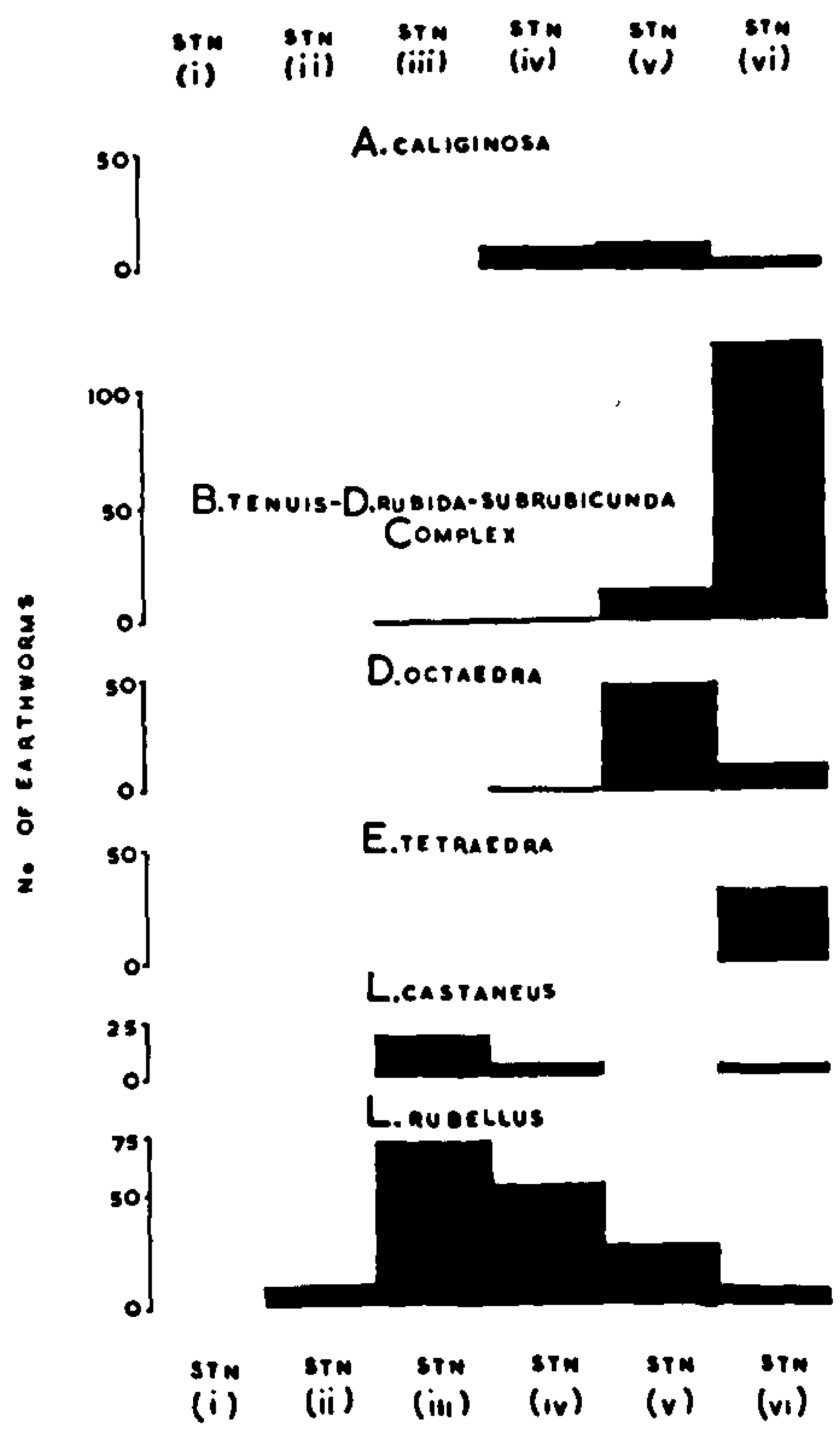


Fig. 3. Showing the numbers of earthworms obtained from 10 samples of dung-pats at each station of the transect at the Reef, Tiree, in March, 1954.

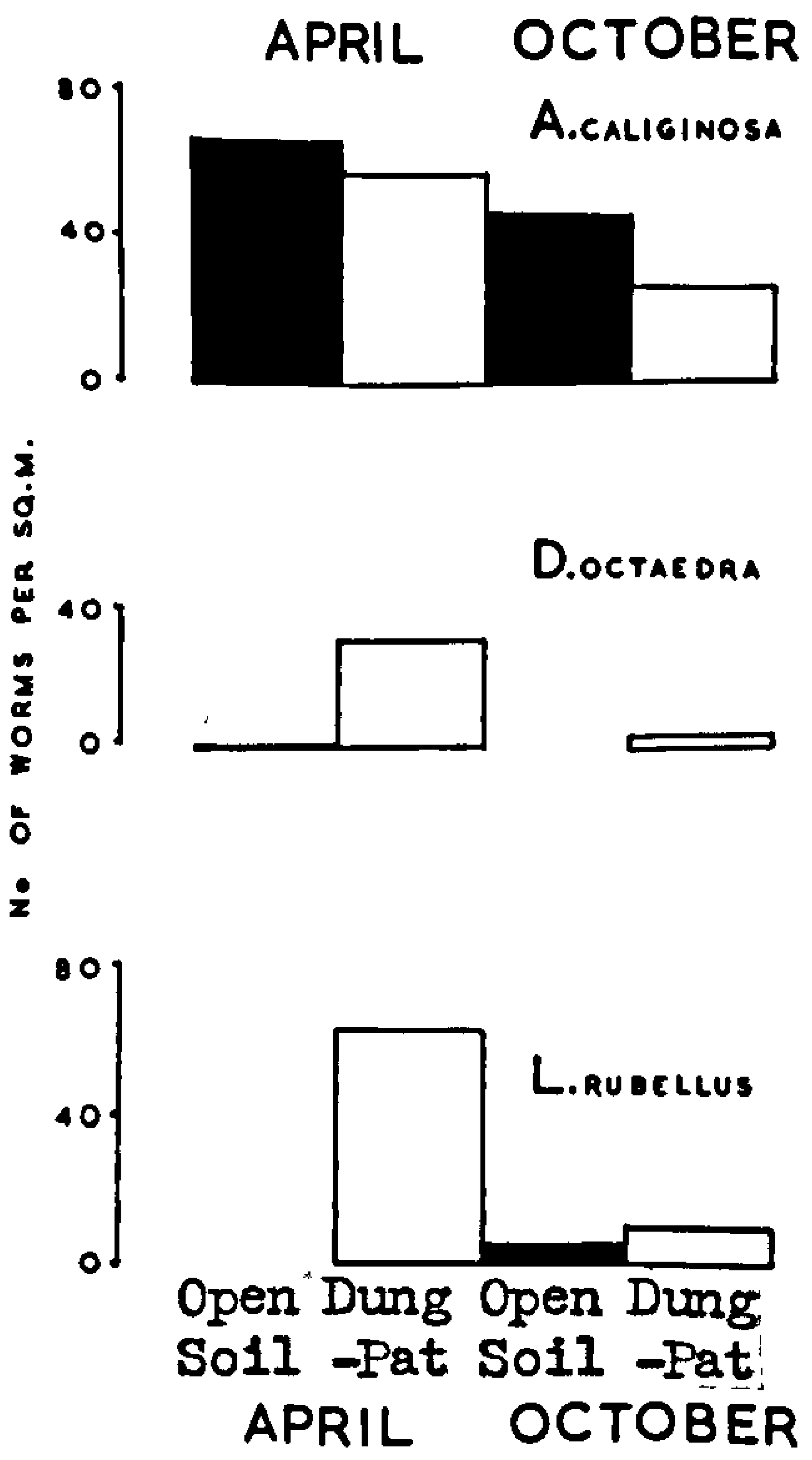


Fig. 4.

Number of three species of earthworm per square metre obtained from 20 samples (10 including a dung-pat, and 10 not including a dung-pat) in April, 1955, and the same for October, 1955, at the Reef machair, Tiree.

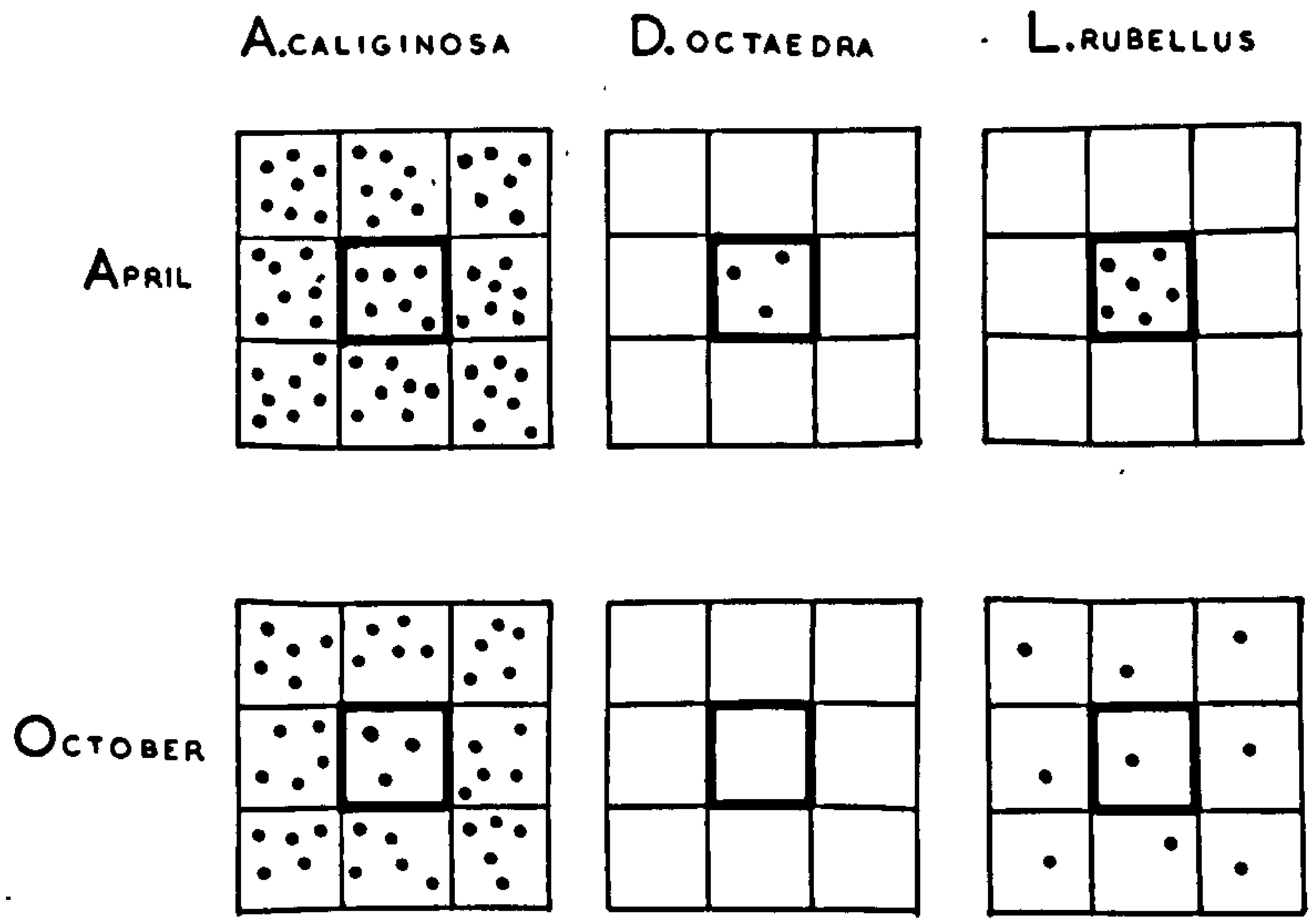
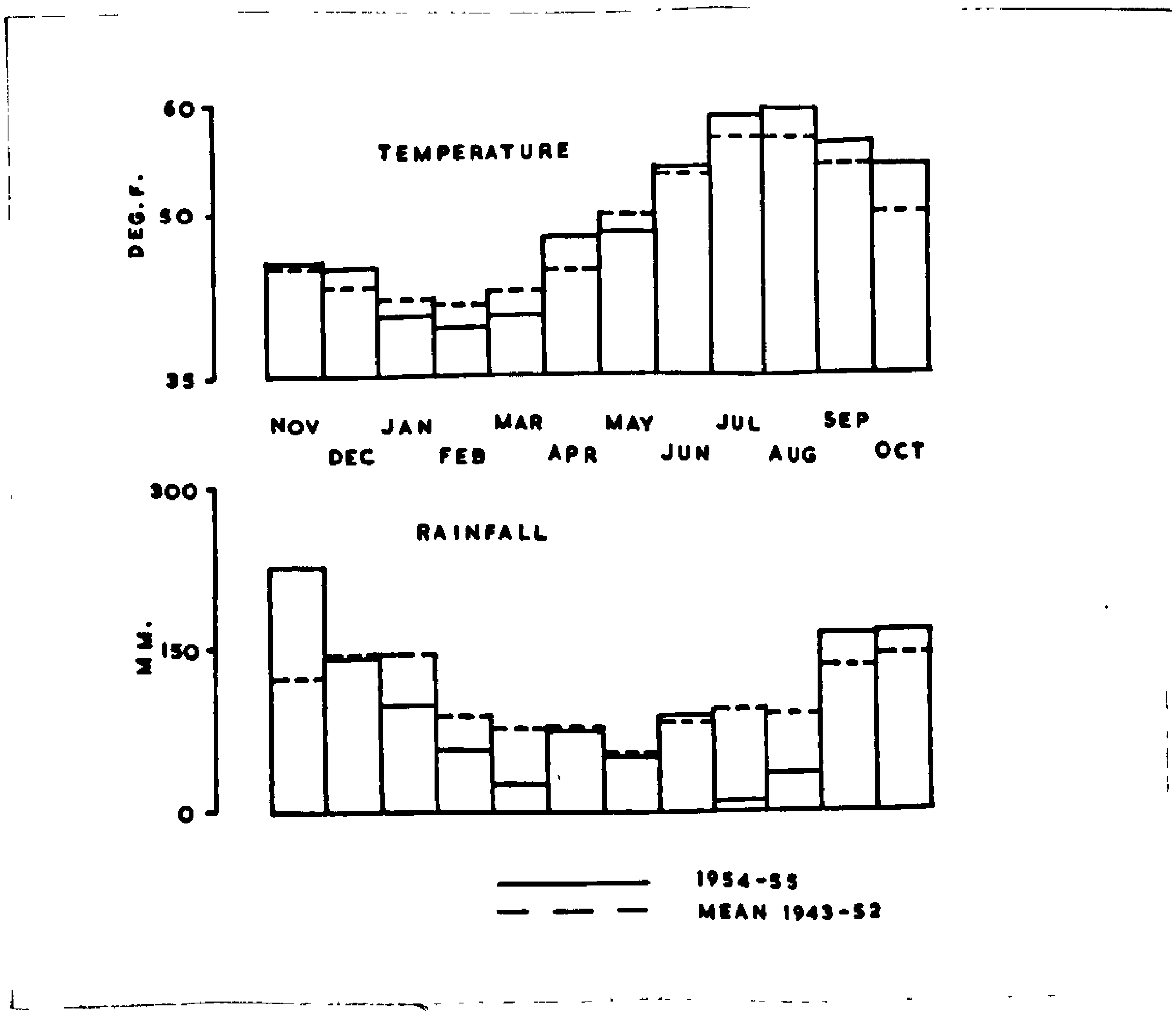
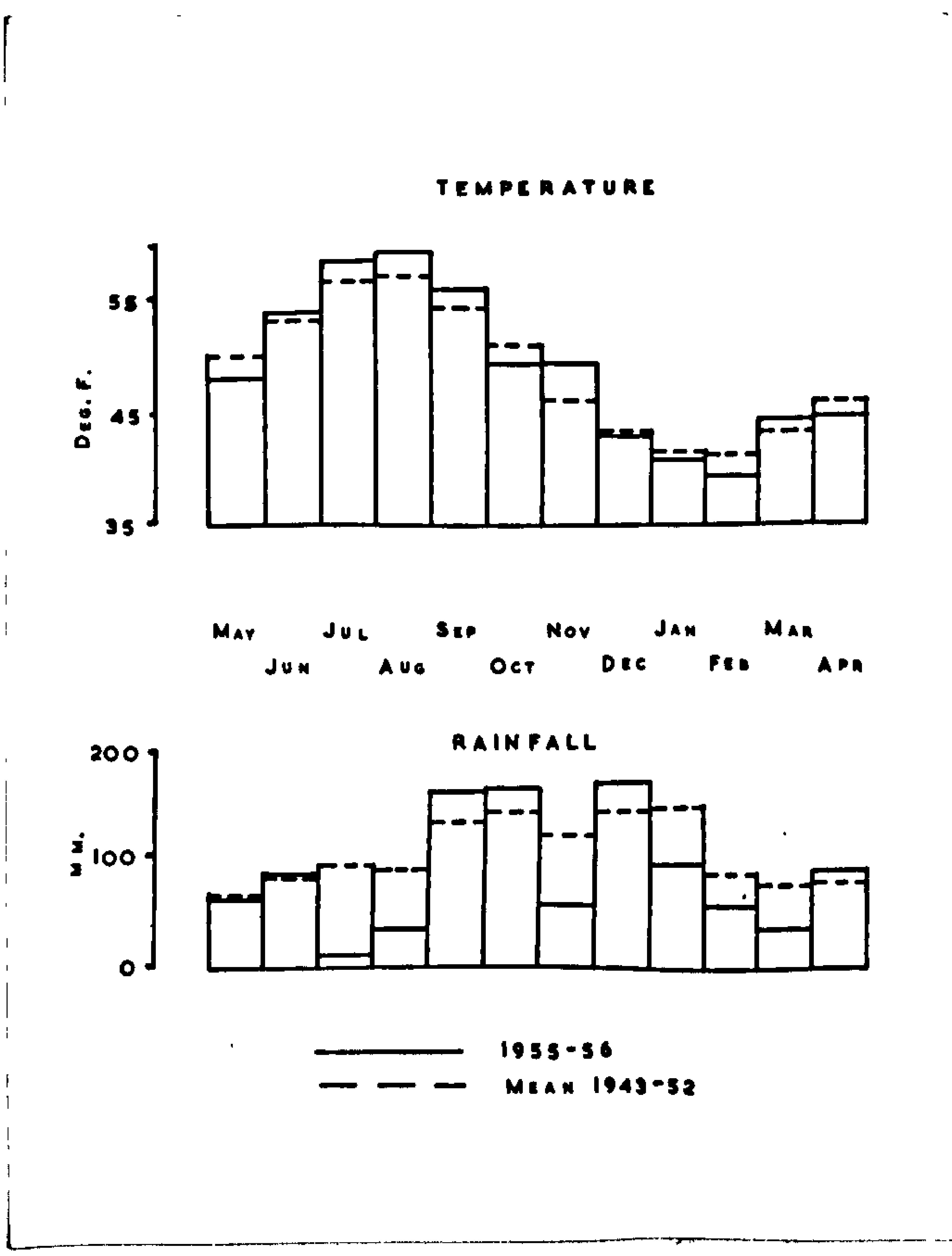


Fig. 4(a). A symbolical representation of the distribution of three species of earthworm in April and October. Each square in 1 square metre and each dot represent one earthworm. The heavy outlined square contains a degenerating dung-pat.





<u>Fig. 5</u>. Air temperature and rainfall data for the periods November-October, 1954-55 and May-April, 1955-56. Means for the period 1943-52 are also shown.

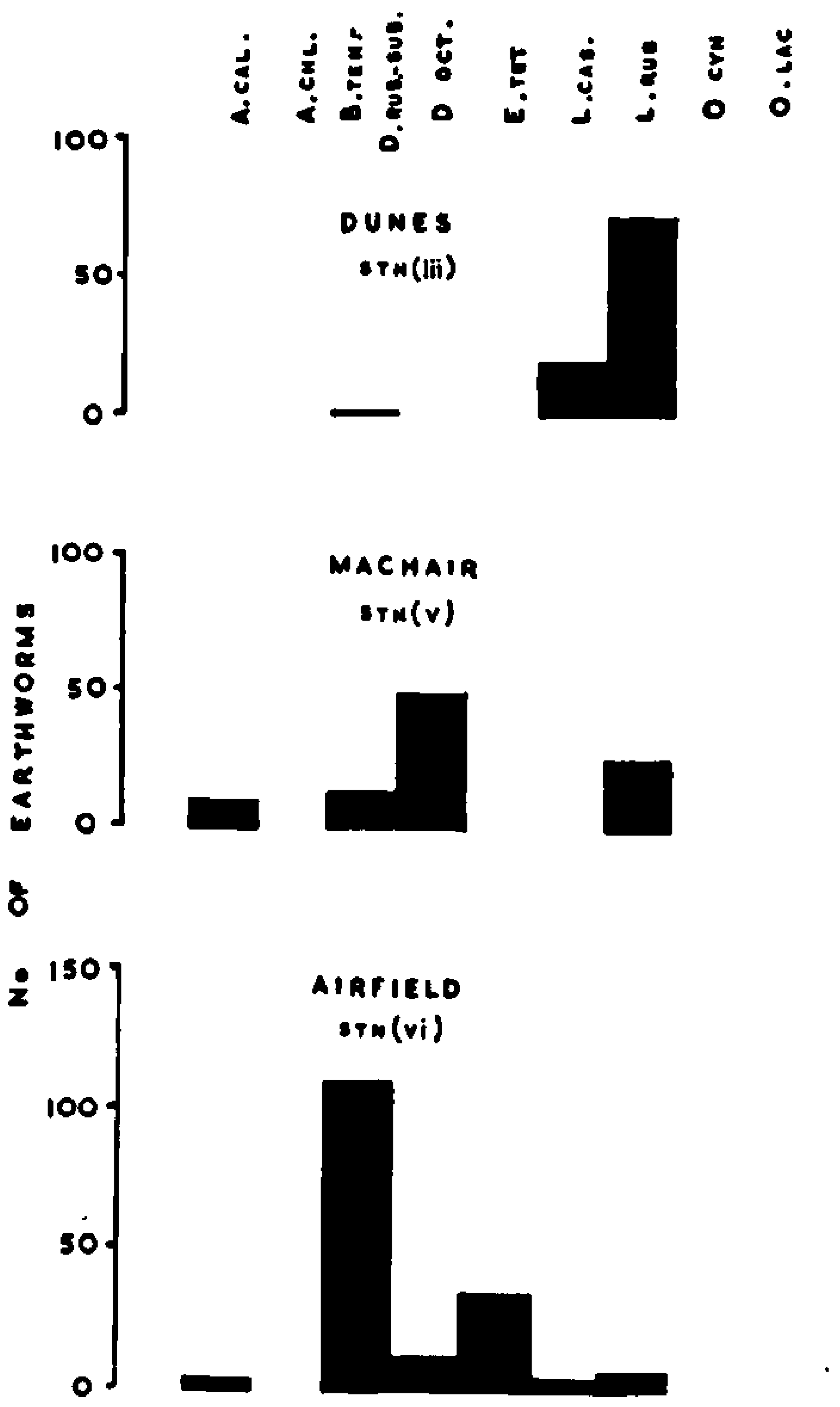
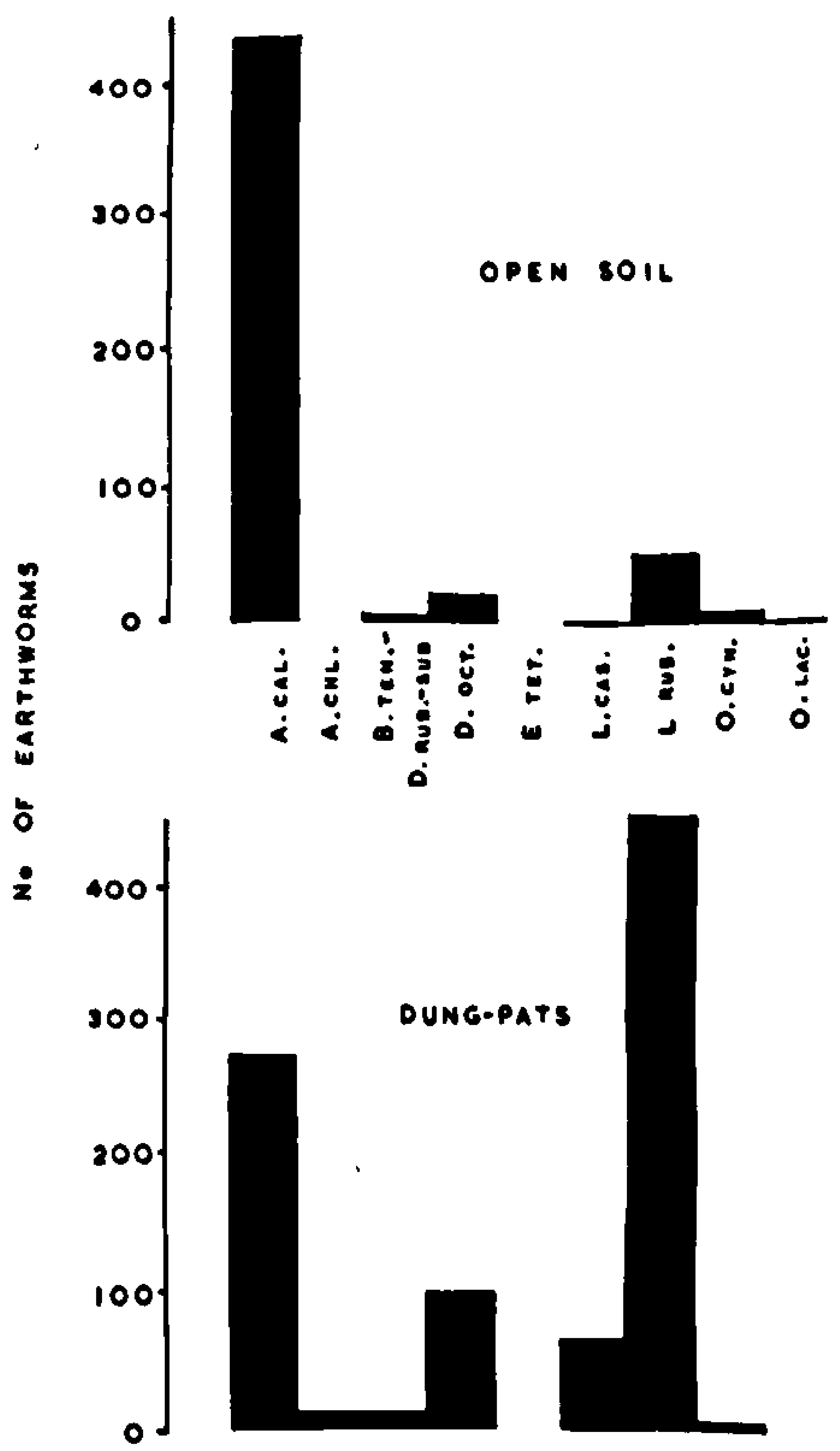


Fig. 6.

The species spectra for stations (iii), (v), and (vi) of the transect at the Reef, Tiree, showing numbers of earthworms obtained from 10 dung-pat samples at each station.



(a)

(b)

Fig. 7.

The species spectra obtained by monthly "wet" method on grazed machair, showing the numbers of earthworms obtained (a) from samples taken with no dung in the quadrat and (b) from samples with a dung-pat in the quadrat.

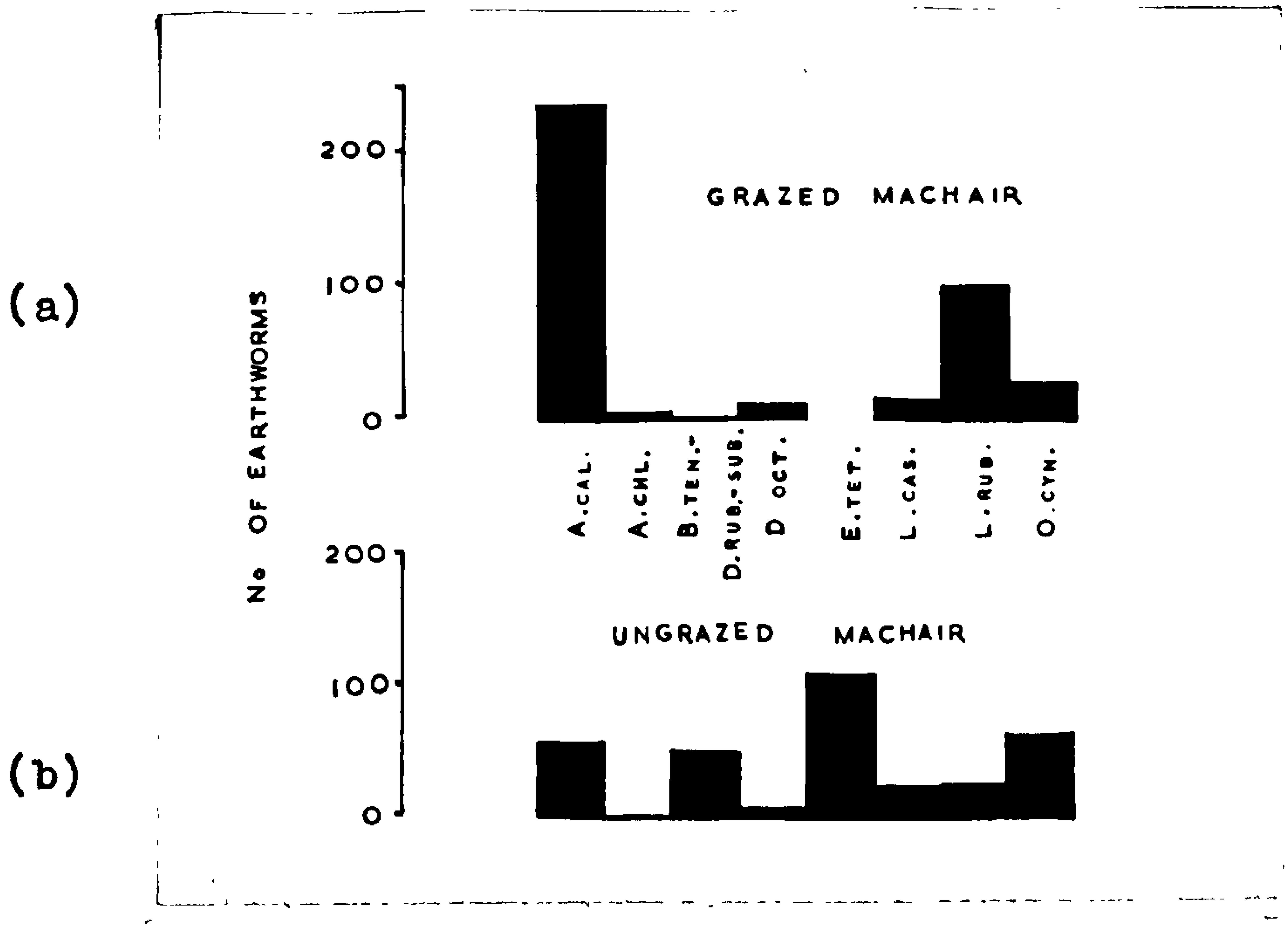


Fig. 8. The species spectra showing the total number of earthworms obtained on (a) grazed and (b) ungrazed machair from the monthly catches of the pit-fall traps over the space of 1 year.

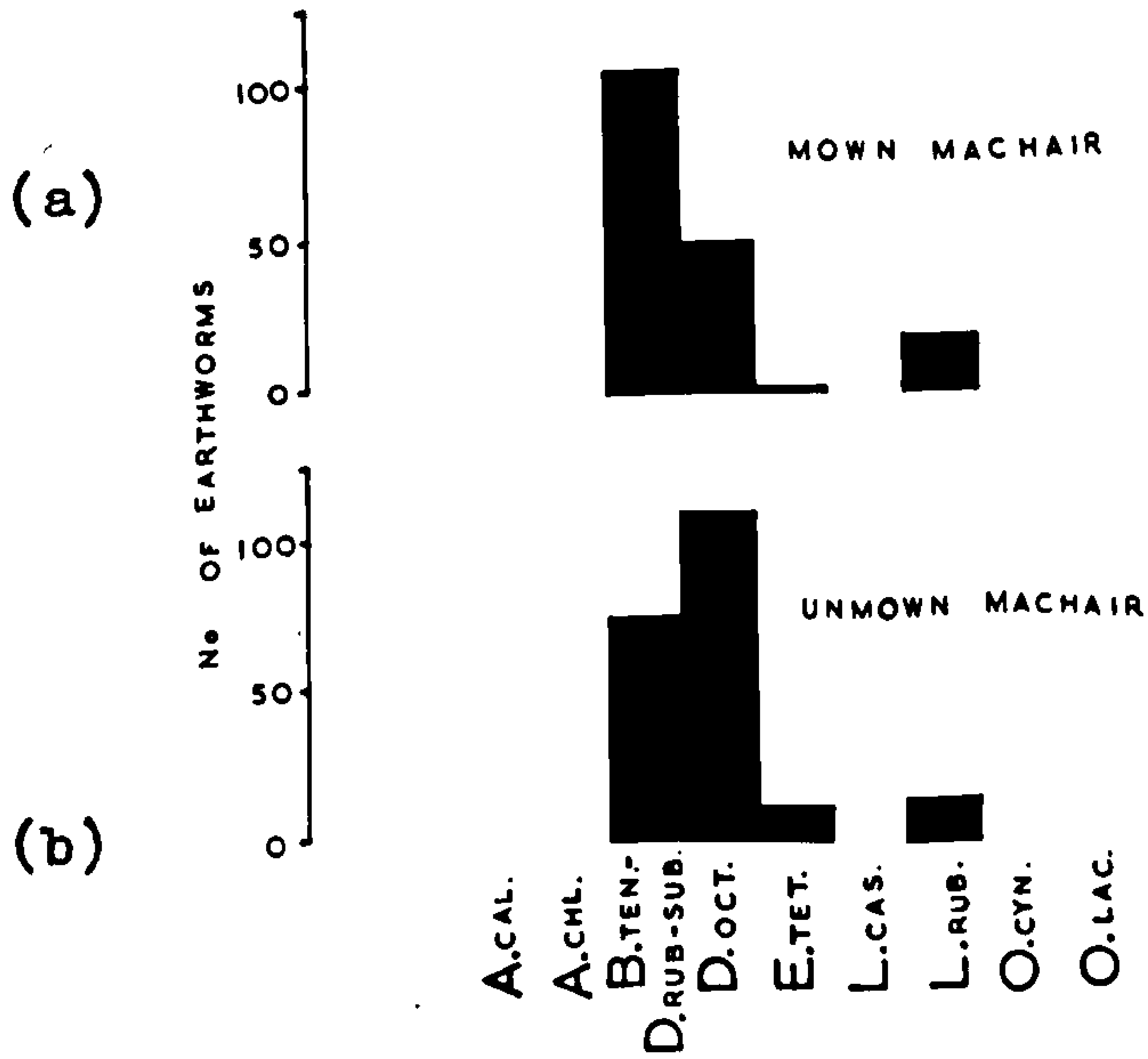
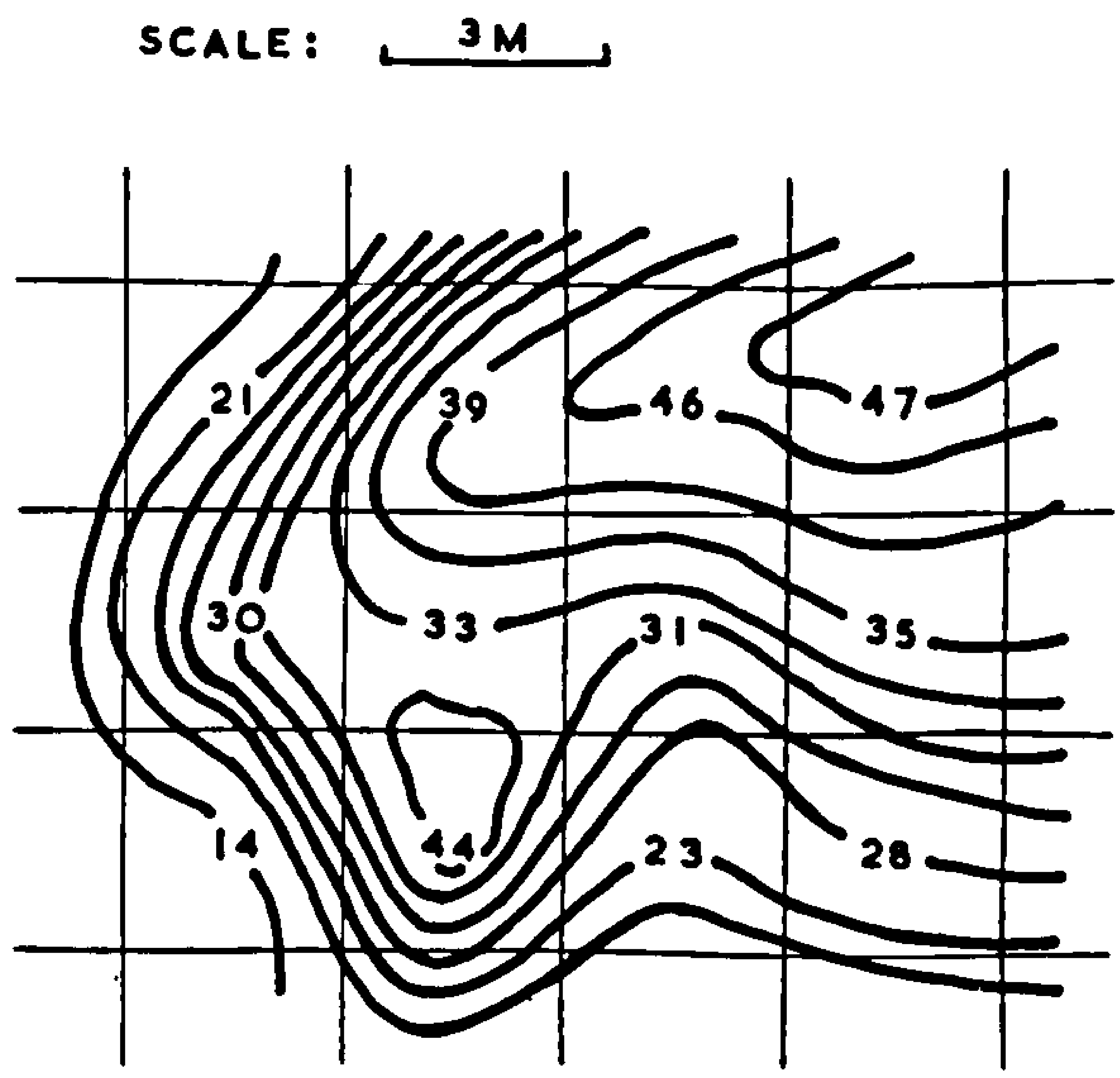


Fig. 9.

The species spectra showing the total number of earthworms obtained on mown and unmown machair (ungrazed), from (a) 12 dung-pats deposited in "very long line" on mown, and (b) 12 on unmown machair.



<u>Fig. 10</u>. The density pattern of earthworms on a uniform plot of machair ground as shown from the numbers of earthworms obtained by a battery of pit-fall traps each trap located on the position of the numbers in the centre of mesh of the grid. The lines join points of equal catch (density), interpolations being made between points of unequal catch (density).

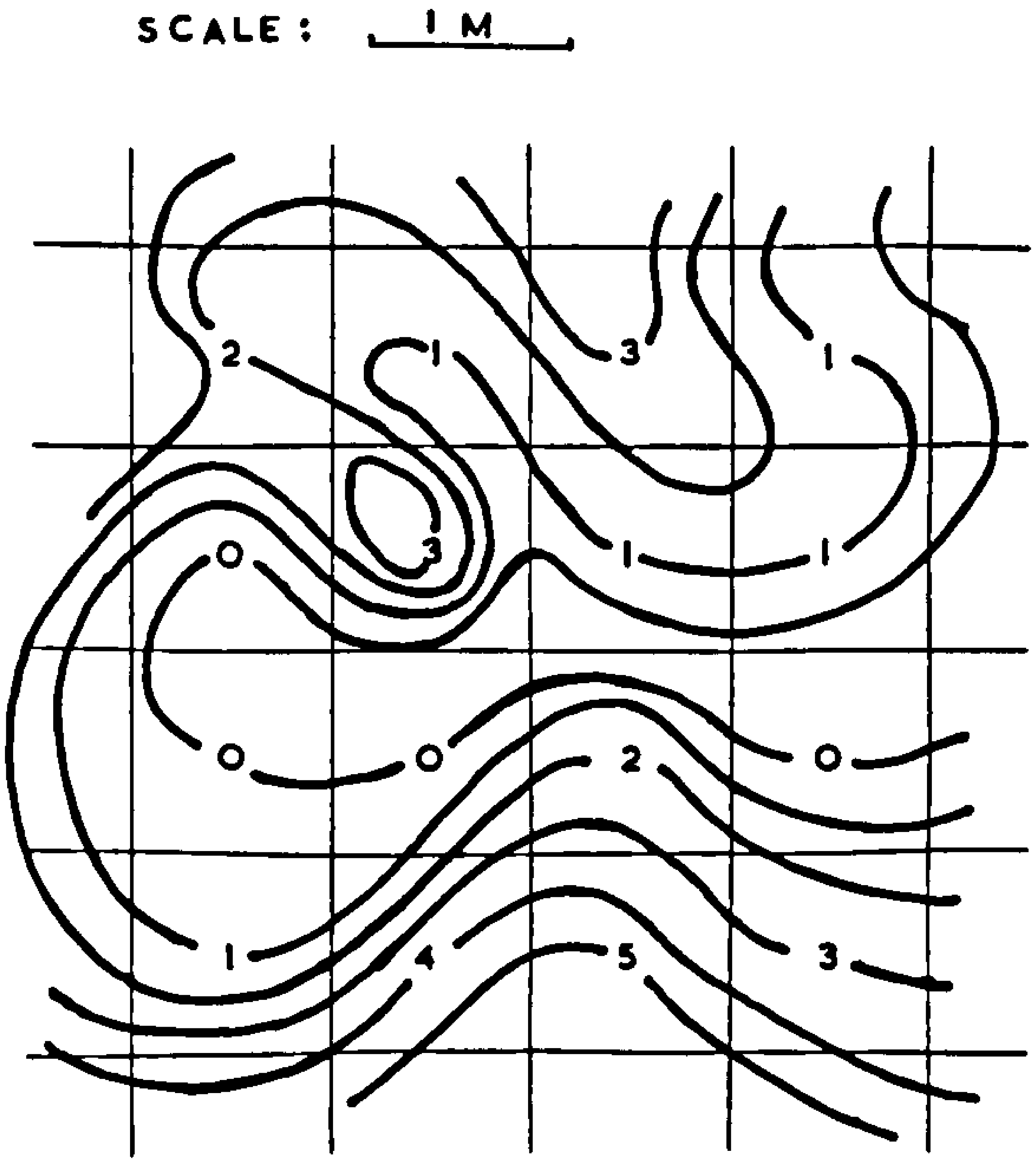


Fig. 11(a).

The density pattern of earthworms on a uniform plot of machair ground as shown by the numbers of earthworms taken simultaneously from 16 equal-sized dung-pats arranged in a grid with the centre of the pat in the position of the figures. Density lines as for Fig. 10.

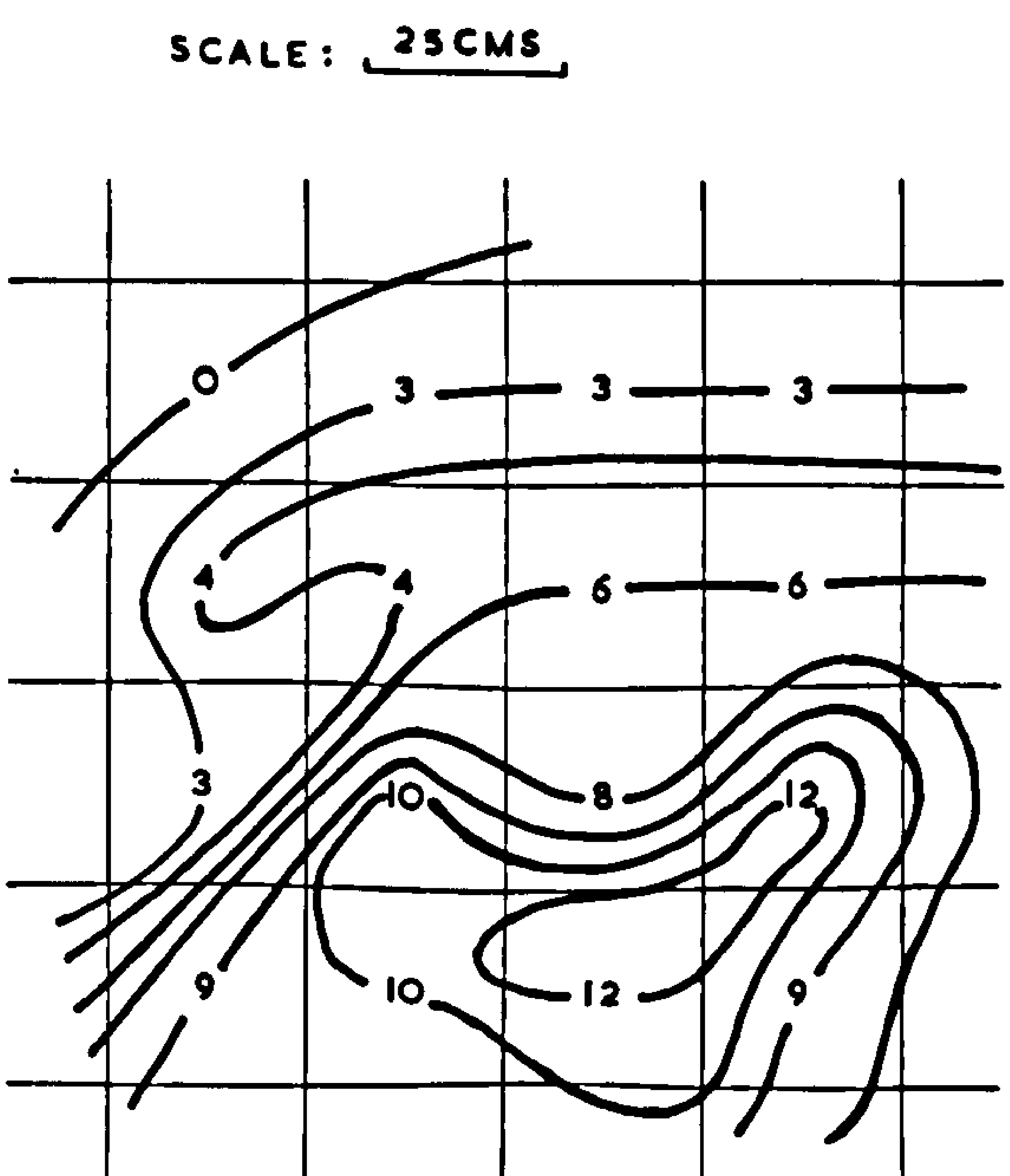
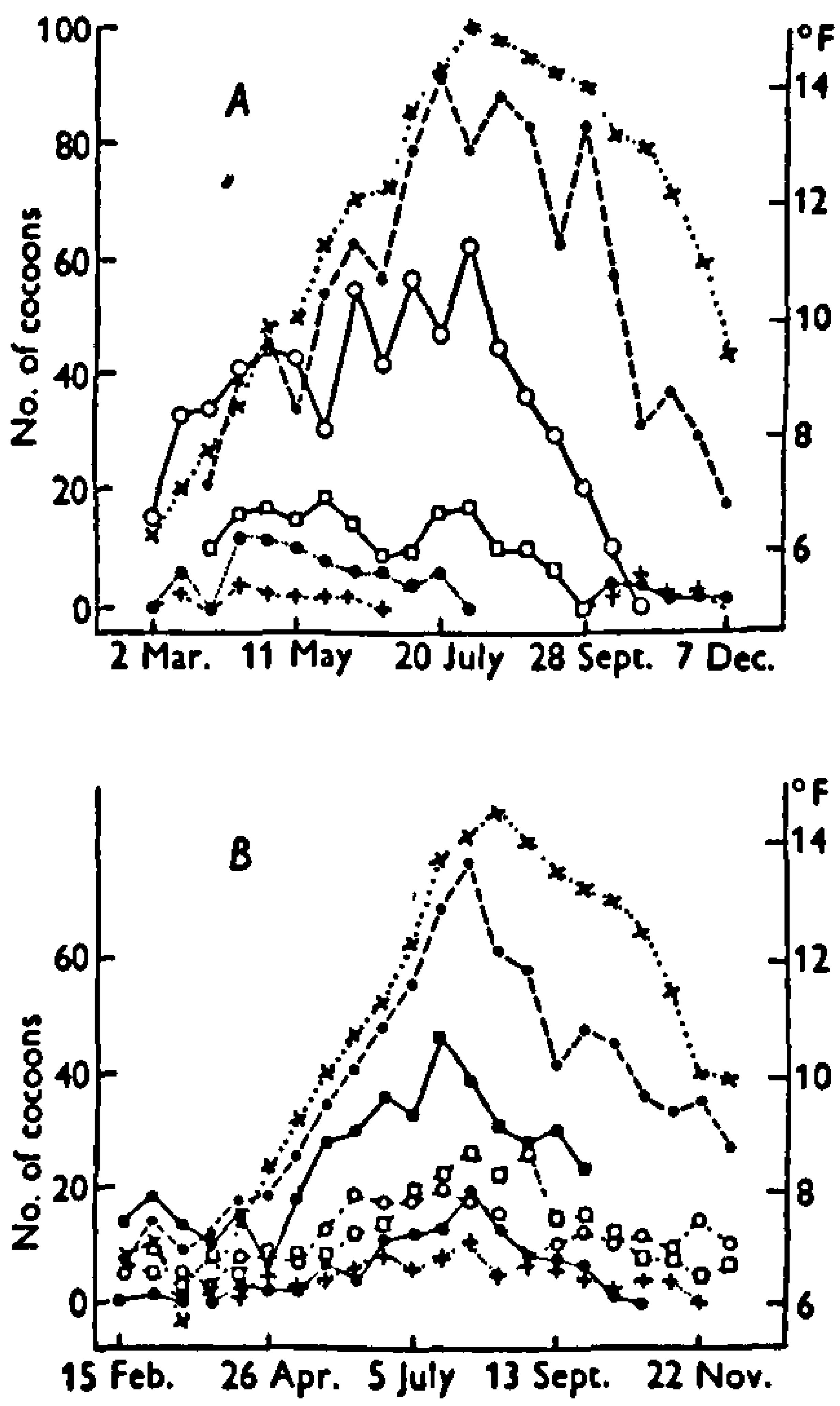


Fig. 11(b).

The density pattern of earthworms on a uniform plot of machair ground similar to that in 11(a) but on a quarter scale. Density lines as for Fig. 10.



Fortnightly production of cocoons by ten individuals of ten species of earthworms. ×···×, temperature; ●--●, *L. rubellus*; A: ○—○, *L. castaneus*; □—□, *D. mammalis*; ●···●, *A. longa*; +--+, *A. nocturna*. B: ■—■, *D. subrubicunda*; □-·-□, *A. caliginosa*; ○--○, *A. chlorotica*; ●—●, *E. foetida*; +···+, *E. rosea*.

Fig. 12. After Evans and Guild, 1948b.

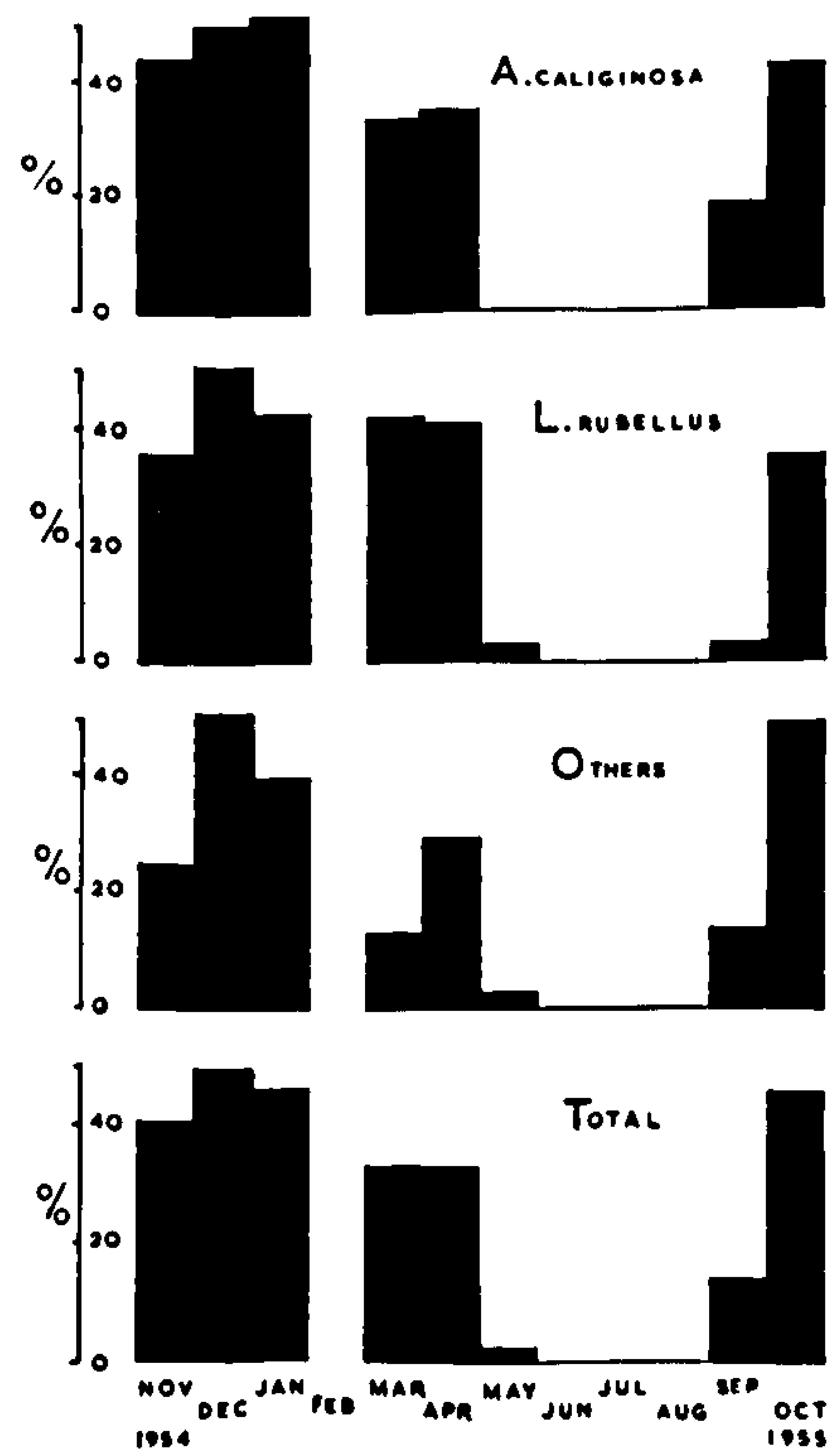


Fig. 13. Showing the percentage of mature earthworms in the monthly batches of samples taken between November, 1954, and October, 1955 by the "wet" method at the Reef, Tiree.

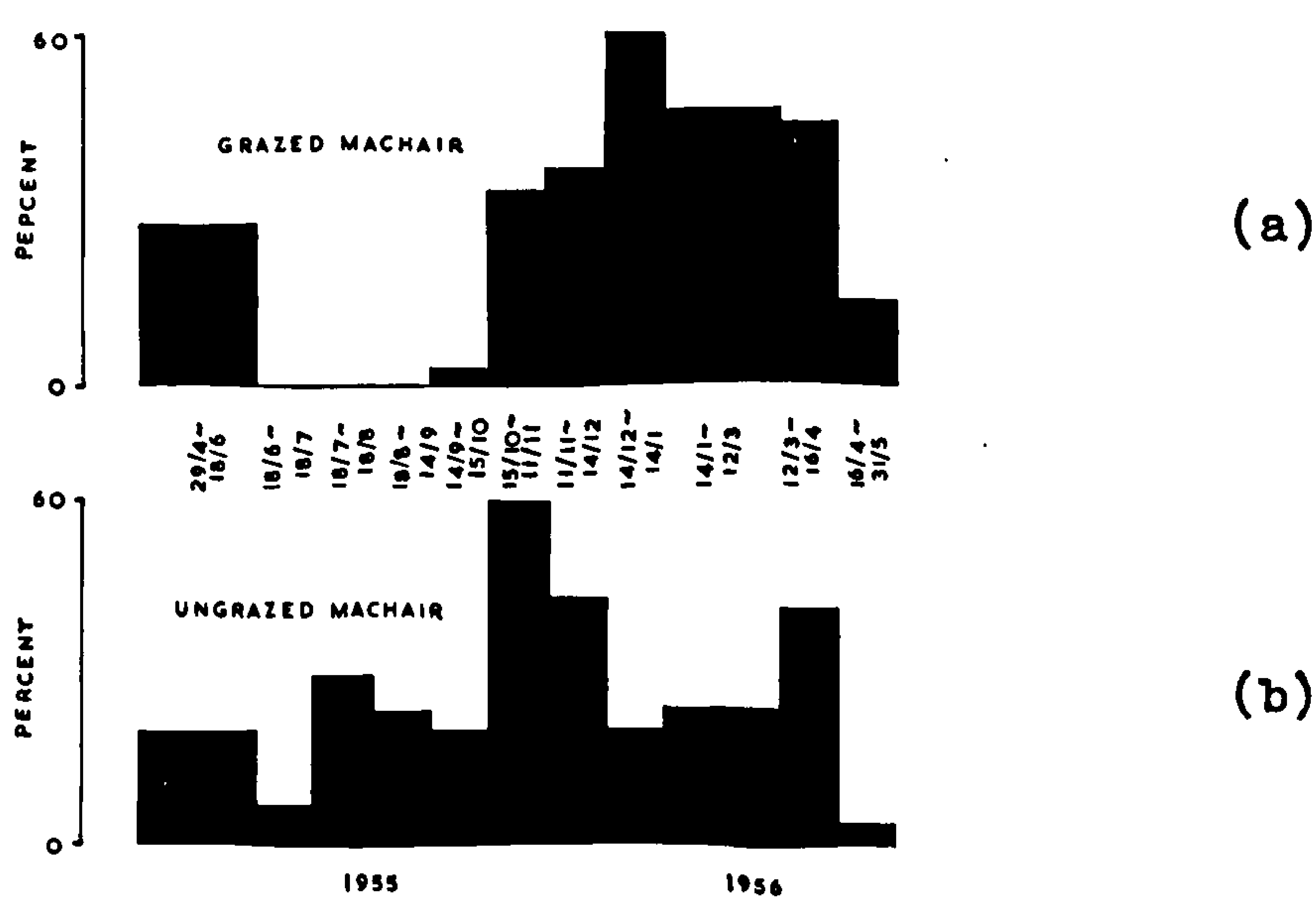


Fig. 14. Showing the percentage of mature earthworms in the total monthly catches of the pit-fall traps, between April, 1955 and November, 1956, at the Reef, Tiree.

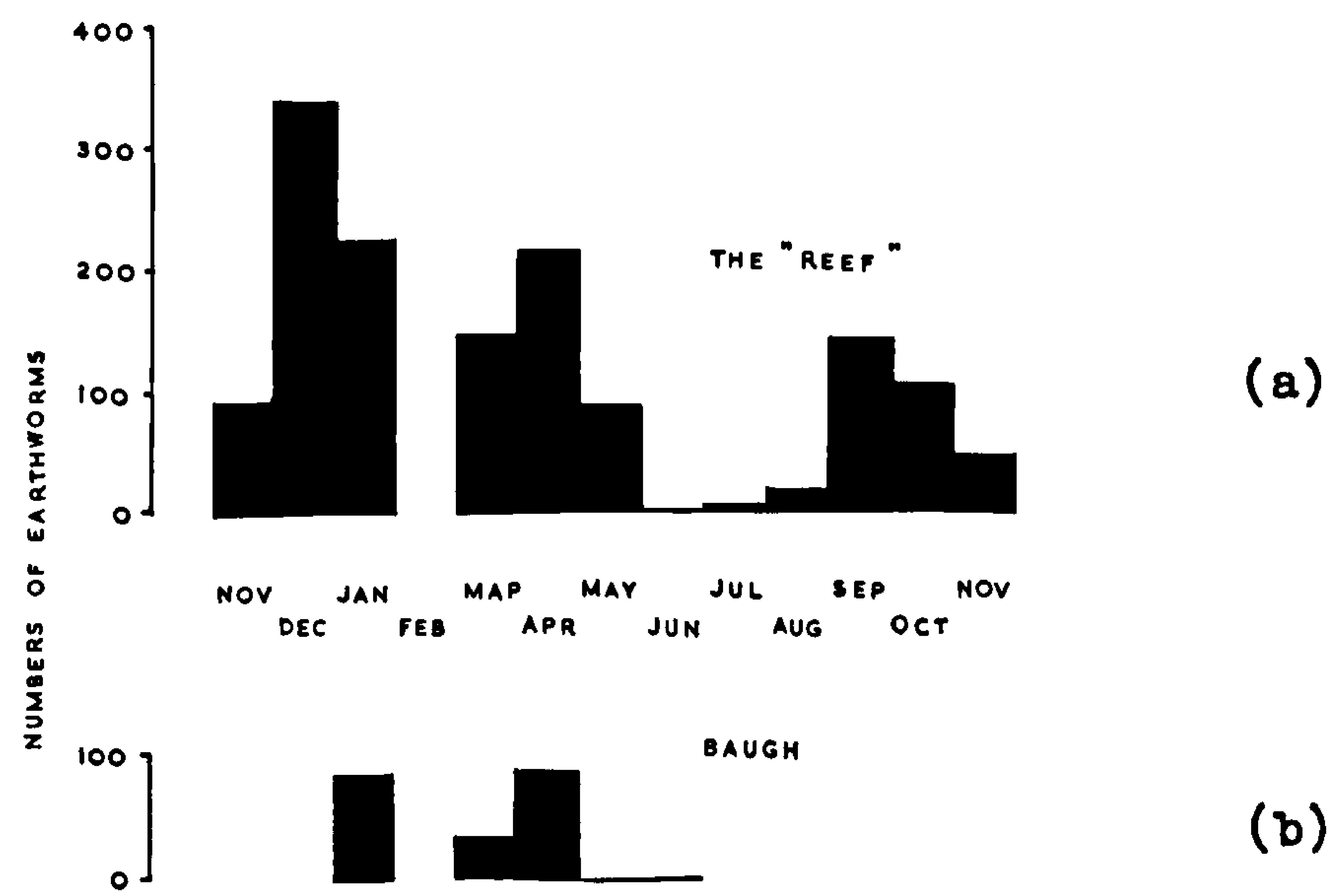


Fig. 15. Showing the total number of earth-:worms in each monthly batch of samples between November, 1954 and November, 1955 at the Reef, with some samples from Baugh, Tiree.

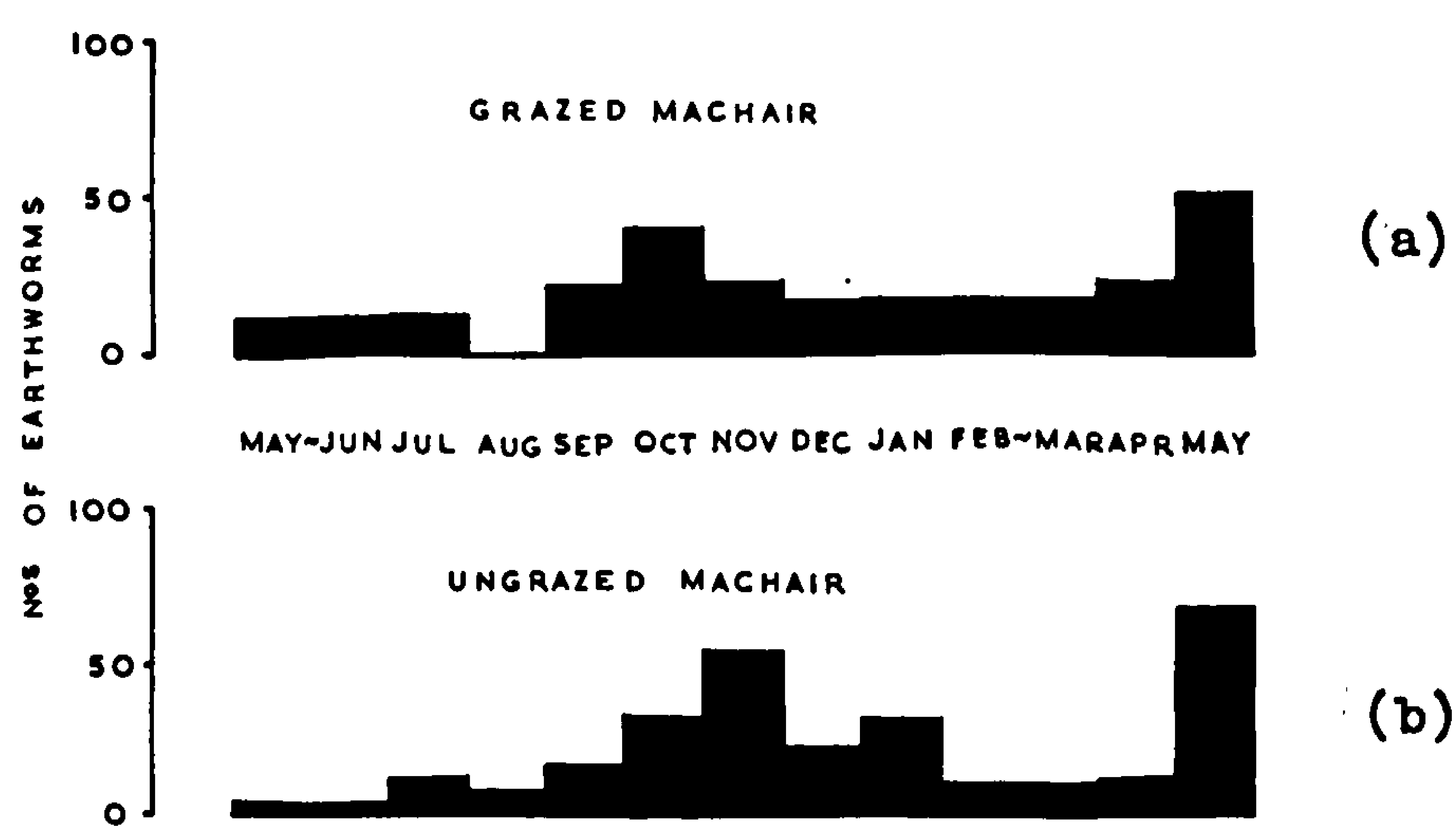


Fig. 16. Showing total numbers of earthworms in the total monthly catches of the pit-fall traps between May, 1955 and May, 1956, at the Reef, Tiree.

Plate I. The dune-machair ecotone at the Reef machair, Tiree. Slight undulations and sparse Ammophila are seen.

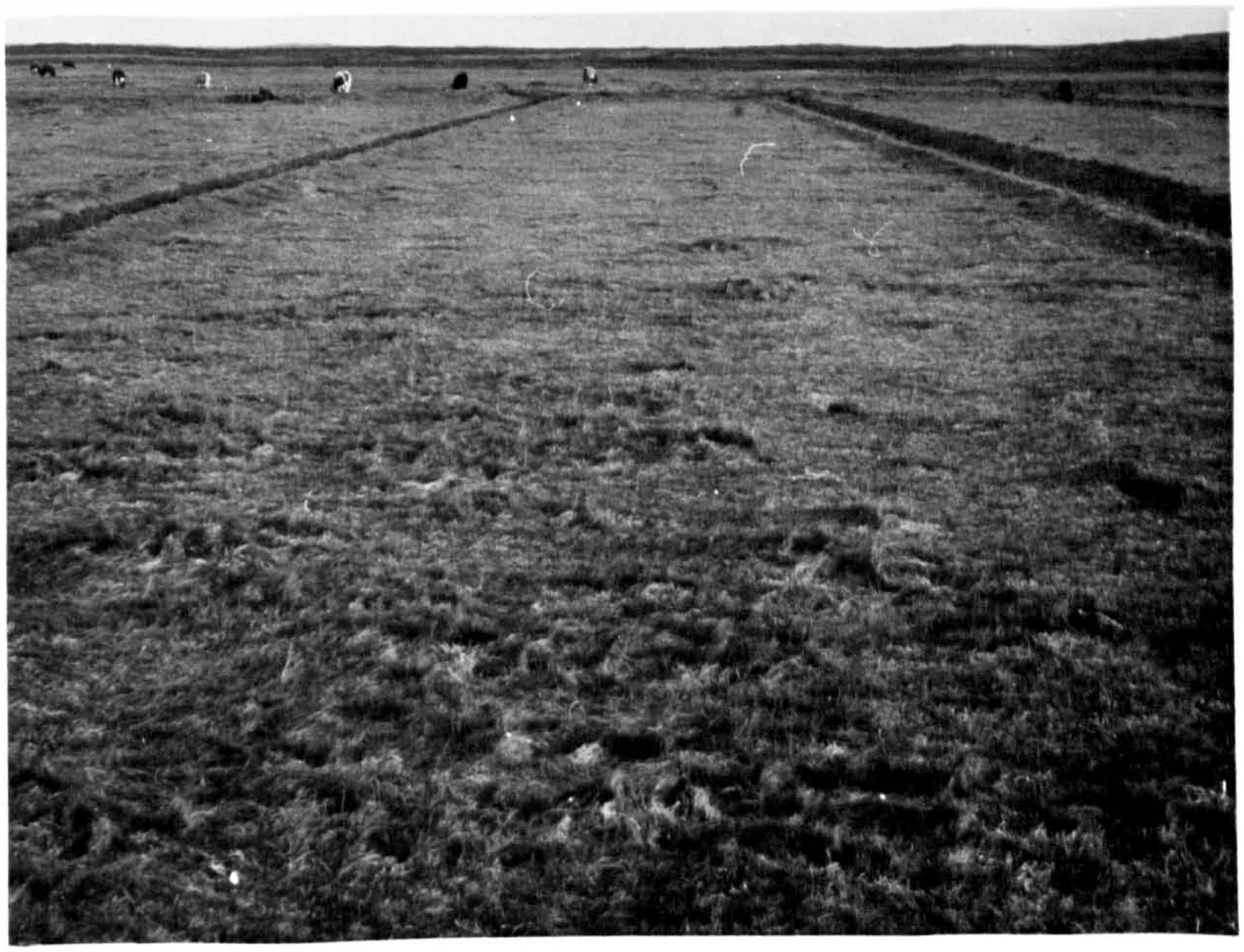


Plate II. The machair at the Reef, Tiree, showing the parallel ditches and the flat, fairly uniform sections.

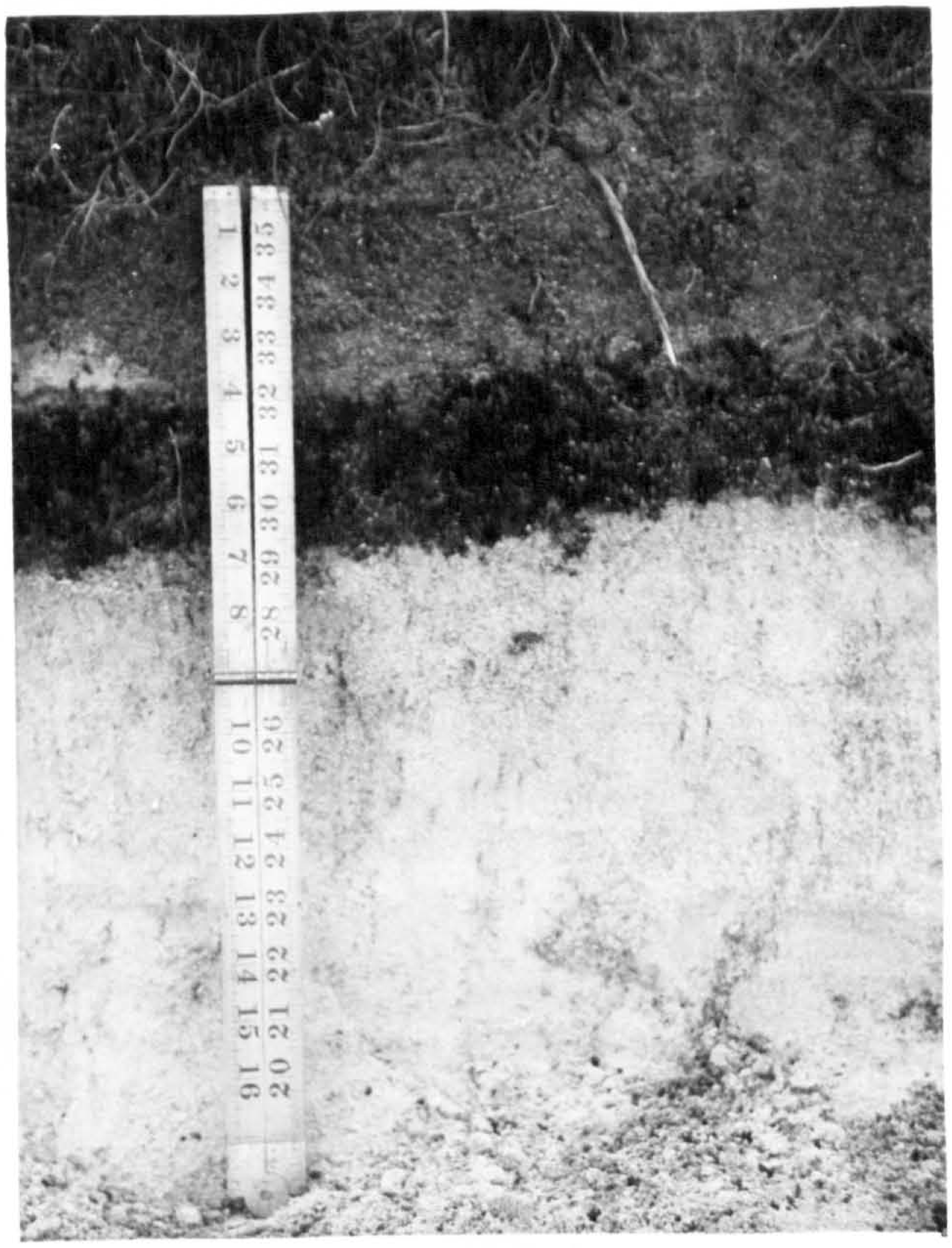


Plate III. This section of machair soil at the Reef, Tiree, was taken close to a ditch. The upper layer is light brown loam which has arisen from the sand thrown out from the ditch excavation; the dark brown middle layer in the original soil which was covered by the throw-out from the ditch and which has been slightly compressed; the base layer is shell-sand into which roots are seen to penetrate.

Plate IV. The interior of the airfield is seen in the foreground with cattle fence in the background. The swards are completely ungrazed.

Plate V. The Reef machair, Tiree, showing the moss hillocks.

PAPER III

SOME "CHOICE" EXPERIMENTS WITH EARTHWORMS

SOME "CHOICE" EXPERIMENTS WITH EARTHWORMS

I. INTRODUCTION

From recently published work on the distribution of earth-:worms in the field, and more particularly from the distribution of earthworms in the shell-sand - peat complex from the Hebrides, it is clear that all species are affected by the soil environ-:ment in a different way. Guild (1948, 1951a, 1951b, 1952a) has shown that earthworm communities differ in different types of soil, and Satchell (1955b) that the distribution of species is closely related to the various reactions to low pH, classifying the Lumbricidae into "acid-tolerant", "acid-intole-:rant", and "ubiquitous" species.

In Paper I it is seen that the "light" and "dark" soils which combine to form the Hebridean soil complex have distinct species complexes, the differences between numbers of practi-:cally all species being significant in the two soil types. In the same paper it is seen that different niches present in both soil types also possess particular species complexes, and that in a great number of the individual species, preferences are different. This is further endorsed by a detailed study of a dune-machair population in Paper II, where it is seen that the presence of grazing animals greatly affects the constitution and structure of a field population of earthworms.

Laboratory work on the sensitivity of earthworms to environmental/

environmental factors, principally pH and available calcium, is summarised by Satchell (1955b), who, employing a technique similar to that first used by Parker and Metcalf (1906) measured the sensitivity of five species of earthworm to pH. In this work the field distribution of four species, A. caliginosa and A. longa (both acid-intolerant), B. eiseni (acid-tolerant), and L. rubellus (ubiquitous) found commonly in the Hebrides is examined by a series of choice experiments. In these experi:ments simple choices of the principal media of the "light" and "dark" soils, viz. peat, calcareous sand, machair soil, cow-dung, and horse-dung are replicated. The numbers of the various species found in each media are subjected to a chi-square analysis, in which any value of chi-square greater than that at the 5 per cent probability level is said to give a significant expression of "choice", and any value less than that at the 5 per cent level, "no choice". The results of the experiments are then discussed in the light of what is known of the field distribution of the species concerned.

II. METHODS AND MATERIALS

(1) The Choice Chamber

The choice chamber is seen in Plate I, and was an adap:tation of a sectional terrarium designed to suit various types of/

of laboratory experiment with earthworms. The plaster of Paris tiles were set in a special mould, and designed to fit evenly on top of each other giving no space for earthworms to escape. The gauze mat on which the base tile rested required to be absolutely flat. The grooves, into which the front panel fitted, were vertical, with the panel cut exactly to size and fitting closely to the gauze at the base. The partition over which the choice existed was set exactly in the centre of the semi-circular chamber dividing it into two equal quadrants. The partition, representing a minimum of mechanical division between the soil media on either side, was perforated with large holes without jagged edges, and permitted freedom of movement to the earthworms between quadrants. The top was completely covered with a sheet of glass, and any escape routes were plugged with plasticine.

Such an elaborate chamber is, however, not necessary. Its use in this case was merely a convenient adaptation of the sectional terrarium. A worker interested in choice chamber work alone might conveniently use ordinary flower pots. The hole at the bottom is merely plugged with plasticine, the plug being raised slightly from the bottom to support the perforated partition which divides the circular chamber into two equal semi-circular ones. This type of chamber is seen in Plate II.

The/

The media were introduced into the chamber with the perfo:rated partition in place, taking care that each medium was entirely confined to one side of the partition. In the experi:ments using the same media treated with different waters, a narrow trench about 3 millimetres broad was made along one side of the partition. This trench was free of water and a complete separation, with no diffusion of chemical characteristics of the media across the partition, was thus assured.

(2) The Experimental Method

The idea underlying this series of experiments was the presentation of one alternative choice of natural materials of different ecological character to a species of earthworm, the field distribution of which was fairly well known. The four species, *A. caliginosa*, *A. longa*, *B. eiseni*, and *L. rubellus* were selected because of their field distribution as seen in Papers I and II, and also to cover the range of Satchell's classification of acid-tolerance. The natural materials used were initially the three successive stages in the transition from calcareous sand dunes to peat moorland, viz. shell-sand, machair soil, and peat, and in later experiments both bullock- and horse-dung were introduced separately into the choice complex.

The earthworms, all of which were mature, were brought from/

from the same locality at Baugh, Tiree (Paper II, Fig. 15). The specimens of A. longa were obtained from a machair situa:tion by stalking at night with an electric torch, while those of A. caliginosa and L. rubellus were obtained by raising old turfs which had been cut a year or two previously in the making of ditches on a grass moor, and those of B. eiseni from bullock droppings on a grass-heather moor. The specimens were brought to Glasgow by air, and were placed in terraria containing machair soil, peat, and bullock-dung.

All the materials except the peat were brought from Tiree. A search for pure peat in the locality proved unsuccessful and commercially supplied peat, guaranteed free of chemical ferti:lisers, was used. The water used in the experiments was Glasgow tap-water, pH 6.7 to 6.8. The sand was obtained from the upper shore immediately under the dune escarpment, and was steeped in running water for at least 24 hours to remove any salt. The soil was not allowed to dry out, retaining its natural texture throughout, and was obtained from the machair at station (v) of the transect described in Paper II. The bullock droppings were also brought from that site, and the horse droppings from a field at Baugh. All the dung was fairly fresh.

The horse-dung and cow-dung waters were obtained by steeping 250 cubic centimetres of moist dung in 2000 cubic centimetres/

centimetres of tap water for 24 hours, and then decanting. While decanting, care was taken to include in the decantation as little of the dung material as possible. The medium to which the dung water was applied was then steeped in it for a few hours before being placed in the choice chambers.

The experiments were carried out in an open air insectary on the roof of the Department of Zoology, Glasgow University in the spring (1955, 1956) and autumn (1955) when earthworm activity in the field is greatest, and were discontinued during the winter and summer when the temperature might have seriously affected the success of experiments carried out in the open air under a glass roof. The moisture content of the media placed in the chambers was kept moist but never waterlogged.

The battery of chambers was set up at noon and the earth:worms introduced, usually not more than 16 (10 in the case of A. longa) in each chamber. This precaution was taken to avoid the possibility of overcrowding, if all the earthworms introduced moved into the same quadrant and bias. The animals were carefully introduced to avoid bias. All were laid across the partition touching both media, half the number facing to one medium and the other half to the opposite medium. The earthworms were carefully handled with the fingers, and forceps were not used in order to avoid damage.

The/

The battery was allowed to stand for approximately 22 hours, about 10 hours of which were in darkness. Thereafter the chambers were dismantled. The top and front glasses were first removed, and then the tiles removed without disturbing the soil. The two quadrants of media were then separated by pushing them apart with the partition. Earthworms crossing the partition (under the surface) at the time of parting were allotted to the side of the partition (the medium) to which they finally held. At no time were there any earthworms moving on the surface at the time of parting of the media, and no case arose where an individual could not be definitely allotted to one of the two media in the replicate. The numbers and con-:dition of earthworms were noted in each experiment.

In all, 4,862 earthworms were introduced into the choice chambers, and 66 or 1.358 per cent escaped before the experi-:ments could be analysed.

(3) The Bias of the Choice Chamber

Before embarking upon the experiments it was necessary to test the bias of the chambers when set in the same position where they would be used in the experiments. The chambers were assembled in position and a replicated series of tests for "no choice" was carried out in exactly the same manner in which the subsequent experiments were to be executed. Instead of/

of presenting a "choice" over the partition, exactly the same media was presented on either side to the same species of earthworm. Throughout these tests for "no choice", A. caliginosa was used, and two media, machair soil and bullock droppings. 48 replicates using machair soil and 36 using bullock droppings were carried out.

The data for the experiments of "no choice" are set forth in Table I. Of the 840 individuals recovered, 408 were taken from the right compartment of the chambers, and 432 from the left compartment. The difference is insignificant (chi-square = 0.685). Only 5 out of the 84 replicates give significant chi-square tests. 3 of the summed chi-square (1 summed chi-square for each of the seven sets) are significant, 2 of them being only just so, and 2 of the 7 interaction chi-squares are significant, 1 of them being only just so. Though there is a certain amount of heterogeneity present in the data, there is nevertheless an over-all homogeneity when considered cumulatively, and a reasonable expression of "no choice".

The distribution of the results for the seven sets, and the over-all distribution of the 84 replicates around the "ideal no choice" 5:5 ratio are shown in Fig. 1. From these results the choice chambers set in this situation are seen to possess a slight bias to the left. Though this bias is insignificant it was minimised in the experiments by alternating the side of the chamber in which any one medium was placed. In a set of 12/

12 replicates presenting a "choice" of sand or peat, the sand would be placed in 6 on the right side of the partition, and in the other 6 on the left of the partition.

The cause of this bias is difficult to determine, but it may be due to the traverse of the sun across the chambers. The sun traversed from left to right, and when the chambers were dismantled, usually about 10 a.m., the left side was partly in shadow. There is no other immediate explanation.

III. THE CHOICE EXPERIMENTS

Except where stated all earthworms were recovered from the experiments in good condition.

(1) Between Peat (pH : 3.6 - 5.0) and Sand (pH : 8.6 - 8.7)

A. caliginosa (Acid-intolerant)

Table II shows the results of 16 replicates, 12 with 16 and 4 with 10 A. caliginosa in each. Of the 213 individuals recovered 31 were taken from the peat and 182 from the sand. The difference is highly significant. The range in chi-square for the replicates is 0 - 16, 4 out of the 16 showing no choice. The interaction chi-square is significant, but it is at the same time clear that A. caliginosa shows a strong preference for/

for shell-sand rather than for peat. The heterogeneity of the results may be caused by the behaviour of earthworms in an unfavourable environment, where, if present in numbers, they will aggregate in an intertwined cluster. In such clusters each individual contributes secretion for the common good, and renders the immediate environment more clement. Such inter-:twined clusters were found in 4 replicates of this set showing no choice. There is a distinct choice in favour of calcareous sand.

A. longa (Acid-intolerant)

Table III shows the results of 22 replicates with 10 A. longa in each. Of the 209 individuals recovered 81 were taken from the peat and 128 from the sand. The difference is significant. The range in chi-square for the replicates is 0 - 10, 13 out of the 22 showing no choice. The inter-:action chi-square is highly significant, and the result is obscure. A slight choice would seem to have been expressed in favour of the shell-sand, but in this case the heterogeneity caused by the intertwined clusters already described, is so intense as to withdraw confidence from the result of the experiment.

B. eiseni (Acid-intolerant)

Table IV shows the results of 10 replicates with 10 B. eiseni in each. Of the 100 individuals recovered, 28 were taken/

taken from the peat and 72 from the sand. The difference is highly significant. The range in chi-square for the replicates is 0 - 6.4, 6 out of 10 showing no choice. The interaction chi-square is just insignificant, and, with 2 exceptions, more B. eiseni were obtained from sand than from peat. There is a distinct choice in favour of sand.

L. rubellus (Ubiquitous)

Table V shows the results of 16 replicates, 12 with 16 and 4 with 10 individuals in each. Of the 231 individuals recovered, 96 were taken from the peat and 135 from the sand. The difference is significant. The range in chi-square for the replicates is 0 - 12.250, 8 out of the 16 showing no choice. The interaction chi-square is highly significant, and the result is obscure. The heterogeneity may again be due to both compartments being repellent, causing the intertwined cluster behaviour.

In all four species more earthworms were obtained from the calcareous sand than from the peat, the differences in each case being significant. The total number of earthworms of all species recovered from the experiment was 753, of which 236 (31.3 per cent) were taken from peat and 517 (68.7 per cent) from sand.

(2) Between Peat (pH : 3.6 - 5.0) and Machair Soil (pH : 7.5)/

(2) Between Peat (pH : 3.6 - 5.0) and Machair Soil (pH : 7.5)

A. caliginosa

Table VI shows the results of 12 replicates with 10 *A. caliginosa* in each. Of the 116 individuals recovered, 17 were taken from the peat and 99 from the soil. The difference is highly significant. The range in chi-square for the replicates is 0 - 10, 5 out of the 12 showing no choice. The interaction chi-square is insignificant, and in 11 out of 12 replicates more *A. caliginosa* were taken from machair soil than from peat. In one case equal numbers were taken. There is a distinct choice in favour of soil.

A. longa

Table VII shows the results of 21 replicates with 10 *A. longa* in each. Of the 210 individuals recovered, 32 were taken from the peat and 178 from the machair soil. The difference is highly significant. The range in chi-square for the replicates is 0.4 - 10.0, 9 out of the 21 showing no choice. The interaction chi-square is insignificant, and in all replicates more *A. longa* were taken from soil than from peat. There is a distinct choice in favour of soil.

B. eiseni

Table VIII shows the results of 10 replicates, with 10 *B. eiseni*/

B. eiseni in each. Of the 100 individuals recovered 39 were taken from the peat and 61 from the soil. The difference is only just significant. The range in chi-square for the replicates is 0.4 - 6.4, 1 out of the 10 showing no choice. The interaction chi-square is insignificant, and more *B. eiseni* were obtained from soil than from peat in 8 replicates out of 10. There seems to be a slight choice in favour of soil.

L. rubellus

Table IX shows the results of 12 replicates, with 10 *L. rubellus* in each. Of the 117 individuals recovered 21 were taken from the peat and 96 from the machair soil. The diffe-:rence is highly significant. The range in chi-square for the replicates is 0 - 10, 6 out of the 12 showing no choice. The interaction chi-square is insignificant. There is a distinct choice in favour of the machair soil.

In all four species of earthworm, more were obtained from the machair soil than from the peat, the differences in each case being significant. The total number of earthworms of all species recovered from the experiment was 543, of which 109 (20.1 per cent) were taken from the peat and 434 (79.9 per cent) from the soil.

(3) Between Calcareous Sand (pH : 8.6 - 8.7) and Machair Soil (pH : 7.5)

(3) Between Calcareous Sand (pH : 8.6 - 8.7) and Machair Soil (pH : 7.5)

A. caliginosa

Table X shows the results of 12 replicates, 9 with 10, 2 with 20, and 1 with 17 *A. caliginosa* introduced. Of the 145 individuals recovered, 37 were taken from the sand and 108 from the machair soil. The difference is significant. The range in chi-square for the replicates is 0.4 - 6.4, 7 out of the 12 showing no choice. The interaction chi-square is insignificant. There is a distinct choice in favour of machair soil.

A. longa

Table XI shows the results of 20 replicates, 11 with 10, 3 with 11, and 6 with 12 *A. longa* introduced. Of the 221 individuals recovered 41 were taken from the sand, and 180 from the machair soil. The difference is highly significant. The range in chi-square for the replicates is 0.091 - 12.000, 7 out of the 20 showing no choice. The interaction chi-square is significant, but more earthworms were taken from the soil than from the sand in all replicates. There is a distinct choice in favour of machair soil.

B. eiseni

Table XII shows the results of 10 replicates, with 10 *B. eiseni*

B. eiseni in each. Of the 99 individuals recovered, 2 were taken from the sand and 97 from the machair soil. The values of chi-square for the replicates are all above 3.841, and all show choice. The interaction chi-square is insignificant. There is a distinct choice in favour of machair soil.

L. rubellus

Table XIII shows the results of 12 replicates, 8 with 10, 2 with 20, 1 with 11, and 1 with 19 L. rubellus introduced. Of the 144 individuals recovered 40 were taken from the sand and 104 from the machair soil. The difference is highly significant. The range in chi-square for the replicates is 0.111 - 7.200 and 8 out of the 12 show no choice. The interaction chi-square is insignificant, and from all except 1 replicate more earthworms were taken from the soil than from the sand. There is a distinct choice in favour of soil.

In all four species more earthworms were taken from machair soil than from peat, the differences in each case being significant. The total number of all species recovered in this experiment was 609, of which 120 (19.7 per cent) were taken from the sand, and 489 (80.3 per cent) from the soil.

(4) Between Cow-Dung and Machair Soil

A. caliginosa/

A. caliginosa

Table XIV shows the results of 16 replicates, with 10 A. caliginosa in each. Of the 160 individuals recovered 39 were taken from the cow-dung and 121 from the machair soil. The difference is significant. The range in chi-square for the replicates is 0.4 - 10.0, and 12 out of the 16 show no choice. The interaction chi-square is insignificant, and in all replicates more were taken from the machair soil than from the cow-dung. There is a distinct choice in favour of machair soil.

A. longa

Table XV shows the results of 12 replicates, with 10 A. longa in each. Of the 120 individuals recovered 17 were taken from the cow-dung, and 103 from the machair soil. The difference is significant. The range in chi-square for the replicates is 1.6 - 10.0, and 4 out of 12 show no choice. The interaction chi-square is insignificant, and in all repli:cates more earthworms were taken from the soil than from the cow-dung. There is a distinct choice in favour of the soil.

B. eiseni

Table XVI shows the result of 10 replicates, 7 with 10, and 3 with 11 B. eiseni introduced. Of the 103 individuals recovered 64 were taken from the cow-dung, and 39 from the machair/

machair soil. The difference is significant. The range in chi-square for the replicates is 0 - 3.6 and consequently all replicates show no choice. The interaction chi-square is insignificant, with more being taken from cow-dung than from machair soil in seven cases, and in two cases equal numbers were obtained in both. There is a fairly distinct choice in favour of cow-dung.

L. rubellus

Table XVII shows the results of 20 replicates, with 10 L. rubellus in each. Of the 200 individuals recovered 50 were taken from the cow-dung and 150 from the machair soil. The difference is significant. The range in chi-square for the replicates is 0 - 10 and 17 out of 20 show no choice. The interaction chi-square is insignificant, and in 18 of the replicates more L. rubellus were taken from the soil than from the cow-dung, with equal numbers in the remaining 2. There is a distinct choice in favour of soil.

In three of the four species considered, more were taken from soil than from cow-dung, the exception being B. eiseni and the differences in all cases being significant. The total number of earthworms of all species recovered in this experiment was 538, of which 170 (31.6 per cent) were taken from the cow-dung and 413 (68.4 per cent) from the soil.

(5) Between Machair Soil and Horse-Dung/

(5) Between Machair Soil and Horse-Dung

A. caliginosa

Table XVIII shows the results of 12 replicates, with 10 *A. caliginosa* in each. Of the 120 individuals recovered 9 were taken from the horse-dung and 111 from the machair soil. The difference is highly significant. The range in chi-square for the replicates is 0.4 - 10.0 and 2 out of the 12 show no choice. The interaction chi-square is insignificant, and in all cases more earthworms were taken from the soil than from the horse-dung. There is a distinct choice in favour of soil. The few specimens found in the horse-dung were in much poorer condition than those found in the soil.

A. longa

Table XIX shows the results of 20 replicates, 17 with 10, and 3 with 12 *A. longa* introduced. Of the 204 individuals recovered 14 were taken from the horse-dung and 190 from the machair soil. The difference is highly significant. The range in chi-square for the replicates is 1.6 - 12.0, and 3 out of the 20 show no choice. The interaction chi-square is insignificant, and in all replicates more earthworms were taken from the soil than from the horse-dung. There is a distinct choice in favour of soil. Some of the specimens found in the horse-dung were dead, and all others were in very poor condition.

B. eiseni/

<u>B. eiseni</u>

No experiment carried out.

<u>L. rubellus</u>

Table XX shows the results of 10 replicates, 10 <u>L. rubellus</u> in each. Of the 100 individuals recovered, 6 were taken from the horse-dung and 94 from the machair soil. The difference is highly significant. The range in chi-square for the replicates is 3.6 - 10.0, and 1 out of the 10 shows no choice. The interaction chi-square is insignificant, and in all repli:cates more were taken from soil than from horse-dung. There is a distinct choice in favour of soil.

In all three species considered, more were taken from the machair soil than from the horse-dung, the differences in all cases being highly significant. The total number of earth:worms of all species recovered in this experiment was 424, of which 29 (6.8 per cent) were taken from the horse-dung, and 395 (93.2 per cent) from the machair soil.

(6) Between Cow-Dung and Horse-Dung

<u>B. eiseni</u>

Table XXI shows the results of 10 replicates, with 10 <u>B. eiseni</u> in each. Of the 100 individuals recovered, 36 were taken from the horse-dung and 64 from the cow-dung. The difference/

difference is significant. The range in chi-square for the replicates is 0 - 6.4, and 8 out of the 10 show no choice. The interaction chi-square is insignificant, and in only one case were more earthworms taken from the horse-dung than from the cow-dung. There is a fairly distinct choice in favour of cow-dung.

L. rubellus

Table XXII shows the results of 24 replicates, 21 with 10, and 3 with 11 L. rubellus in each. Of the 241 individuals recovered, 98 were taken from the horse-dung and 143 from the cow-dung. The difference is significant. The range in chi-square for the replicates is 0 - 6.4, and 23 out of the 24 show no choice. The interaction chi-square is insignificant, and out of the 24 replicates in 16 cases more were taken from the cow-dung, in 5 cases more from the horse-dung, and in 3 cases equal numbers from both. Though little choice is expressed by each replicate, a fairly distinct choice in favour of cow-dung is obtained when the totals are considered.

In the two species considered, more were taken from the cow-dung in both cases, and the differences were significant. The total number of earthworms recovered in this experiment was 341, of which 134 (39.9 per cent) were taken from the horse-dung, and 207 (60.1 per cent) were taken from the cow-dung.

(7) Between Cow-Dung and Peat/

(7) Between Cow-Dung and Peat

(Media of similar texture)

B. eiseni

Table XXIII shows the results of 10 replicates, with 10 B. eiseni in each. Of the 100 individuals recovered, 9 were taken from the peat and 91 from the cow-dung. The difference is highly significant. The range in chi-square for replicates is 3.6 - 10.0, and 3 out of the 10 show no choice. The interaction chi-square is insignificant, and in all cases more were taken from the cow-dung than from the peat. There is a distinct choice in favour of the cow-dung.

(8) Between Horse-Dung and Shell-Sand (Calcareous)

B. eiseni

Table XXIV shows the results of 10 replicates, with 10 B. eiseni in each. Of the 100 individuals recovered, 15 were taken from the sand and 85 from the horse-dung. The range in chi-square for the replicates is 0.4 - 10.0, and 3 out of the 10 show no choice. The interaction chi-square is insignificant, and in all replicates more were taken from the horse-dung than from the sand. There is a distinct choice in favour of horse-dung.

(9) Between Shell-Sand with Horse-Dung Water and Shell-Sand with Tap Water/

(9) Between Shell-Sand with Horse-Dung Water and Shell-Sand with Tap Water

A. longa

Table XXV shows the results of 18 replicates, with 10 A. longa in each. Of the 180 individuals recovered, 60 were taken from the horse-dung water and 120 from the tap water. The difference is significant. The range in chi-square for the replicates is 0 - 10.0, and 12 out of the 18 show no choice. The interaction chi-square is highly significant, though in 13 out of the 18 replicates more were taken from the tap water than from the horse-dung water. The result is again obscured by the formation of intertwined clusters, but there seems to be choice in favour of tap water.

(10) Between Machair Soil with Cow-Dung Water and Machair Soil with Tap Water

A. longa

Table XXVI shows the results of 18 replicates, 10 A. longa in each. Of the 179 individuals recovered, 84 were taken from the horse-dung water and 95 from the tap water. The difference is insignificant. The range in chi-square for the replicates is 0 - 6.4, and all but 2 show no choice. The interaction chi-square is highly significant, and in 10 cases more were taken from the tap water than from the horse-dung water. There is no convincing sign of choice.

(11) Between Shell-Sand with Cow-Dung Water and Shell-Sand with Tap Water

L. rubellus

Table XXVII shows the results of 15 replicates, 13 with 10, and 2 with 11 L. rubellus in each. Of the 144 individuals recovered, 71 were taken from the cow-dung water and 73 from the tap water. The difference is insignificant. There is no sign of choice.

IV. DISCUSSION OF EXPERIMENTS

The results of all the experiments carried out are summarised in percentage form in Table XXVIII.

(1) A. caliginosa (Acid-Intolerant)

In Paper I A. caliginosa is seen to constitute a significantly higher percentage of the earthworm population in the "light" sandy soils than in the "dark" peaty ones. This is confirmed by experiment. Significantly more were taken from the sand than from the peat. An alternative choice between the same type of machair soil and sand and peat shows the soil to be more attractive than the other two media, and that a significantly greater number was taken from the sand in the sand-soil experiment, than from the peat in the peat-soil experiment (chi-square = 4.836)

From/

From Papers I and II it is seen that a significantly smaller number of A. caliginosa was taken from the dung-pats than from the open soil. This is also confirmed by experiment. An alternative choice between machair soil and cow-dung and horse-dung shows the soil to be more attractive than the other two media, and that a significantly greater number was taken from the cow-dung in the cow-dung - soil experiment than was taken from the horse-dung in the horse-dung - soil experiment (chi-square = 18.132).

(2) A. longa (Acid-Intolerant)

In Paper I A. longa appears to be completely restricted to the "light" sandy soils, none being found in the "dark" peaty soils. Significantly more were taken from the sand than from the peat, and the difference may well have been greater than is registered in the experiment due to the formation of the intertwined clusters which have already been described as causing a possible alteration of the environment. Though the calcareous sand might be more attractive than the peat when they are presented together, an alternative choice between those two media and machair soil shows that the soil is more attractive than either, and that the numbers taken from peat and sand in the respective experiments were not significantly different.

In/

In Paper I *A. longa* is seen to occur only in small numbers in the samples taken, but constitutes a significantly higher percentage of the community living in the open soil than that in and under dung-pats. This is also confirmed by experiment. An alternative choice between machair soil and cow-dung or horse-dung shows that the soil is more attractive than either of the dung media, and that the numbers taken from the cow-dung in the cow-dung - soil experiment, and from the horse-dung in the horse-dung - soil experiment were insignificantly different.

Further experiments with *A. longa* using the same media on either side of the partition of the chamber, treated with different waters proved somewhat inconclusive due to formation of the intertwined clusters. It is, however, fairly obvious that the strong repellent effect shown by the horse-dung in the horse-dung - soil experiment is not shown in the case of soil treated with a solution decanted from the same horse-dung. In only one out of the three dung-water - tap water experiments were the differences of numbers of *A. longa* taken from each significant, and in that instance intertwined clusters were found.

(3) B. eiseni (Acid-Tolerant)

In Paper I *B. eiseni* is seen to be completely restricted to the "dark" peaty soils, none being found on the "light" sandy soils/

soils. This is not, however, confirmed by experiment. Significantly greater numbers were taken from the sand than from the peat. An alternative choice between the same machair soil on the one side and peat or sand on the other shows the soil more attractive than the other two media, and that a significantly greater number were taken from the peat in the peat-soil experiment than were taken from the sand in the sand-soil experiment. The results of the first experiment seem to contradict those of the other two considered together, which are more corroborative of its field distribution.

In Paper I B. eiseni is seen to aggregate in dung-pats, none being obtained from sampling in open soil, and few in the niche under stones. This is not confirmed by experiment, there being a significantly greater number taken from the soil than from the cow-dung in that particular experiment. Given the choice of cow-dung or horse-dung, significantly more were taken from the former than from the latter, and further experiment showed that in a choice between cow-dung and peat, one which exists in the natural habitat of B. eiseni, the species will aggregate in the dung. The choice between horse-dung and calcareous sand is not one likely to occur in nature as far as B. eiseni is concerned, but the experiment shows a distinct aggregation in the dung.

(4) L. rubellus (Ubiquitous)/

(4) L. rubellus (Ubiquitous)

In Paper I L. rubellus is seen to constitute a significantly greater percentage of the population in "light" sandy soils than in the "dark" peaty soils. This is confirmed by experiment. The results of the peat-sand experiment, though showing significantly greater numbers in the sand, were rather heterogeneous due to the formation of intertwined clusters. There is evidence, however, from the experiments in which an alternative choice was given between machair soil on the one side and peat or sand on the other that difference in numbers obtained from the peat-sand experiment gives a true expression of choice. There was a significantly greater number taken from the sand in the sand-soil experiment than from the peat in the peat-soil experiment (chi-square = 6.784).

In Papers I and II L. rubellus is seen to aggregate in dung-pats, a significantly greater percentage being present in the dung-pat community than in the open soil. This is not confirmed by experiment. An alternative choice of machair soil on the one side and cow-dung or horse-dung on the other shows the soil to be much more attractive than either of the dung media. There was a significantly greater number obtained from the cow-dung in the cow-dung - soil experiment than from the horse-dung in the horse-dung - soil experiment, and further experiment showed that in a choice between the two dung media, a/

a significantly greater number was taken from the cow-dung than from the horse-dung.

(5) General

The experiments can be divided into two sets (1) those dealing with earthworm distribution in the sand-soil - peat complex, and (2) those dealing with the influence which cow- and horse-dung have upon the distribution of earthworms within that complex.

The basic experiment of the first group is that between sand and peat. In this the results proved heterogeneous in some cases, due possibly to the fact that both the media presented a rigorous environment, one perhaps not so rigorous as the other. In all species more earthworms were obtained from the sand. This is in keeping with the distribution of the species in the field with the exception of B. eiseni. There is no obvious explanation of this discrepancy, and in this case the results were homogeneous. The experiment may have failed to give an accurate expression of the preference of the species for any of the two media, but further experiments would be required to confirm this.

The supporting experiments in which the two basic media of sand and peat are presented separately with machair soil confirm/

confirm the field distribution of all the species concerned, including _B. eiseni_. The preference expressed in the basic experiment is reiterated in the experiments between peat and soil, and between sand and soil, but in the case of _B. eiseni_ the combined expression of these two experiments is contrary to the basic experiment, and is in line with field distribution.

A comparison of the results obtained from the two "acid-intolerant" species _A. caliginosa_ and _A. longa_ shows them to be very similar. Allowance should be made in the case of the peat-sand choice by _A. longa_ in which a great deal of inter-:twined cluster behaviour rather obscured the true issue. In the two remaining experiments the results obtained from the two species are insignificantly different in both cases (in peat-soil the percentages are identical, in sand-soil chi-square = 2.536). The results obtained for _L. rubellus_, the so-called "ubiquitous" species are similar to those of _A. caliginosa_ and _A. longa_, and those obtained from _B. eiseni_ the "acid-tolerant" species are much different from the other three.

The basic experiment in the second group is that between cow-dung and horse-dung. In this the "acid-intolerant" species were omitted because of the death and the extremely poor con-:dition of these particular species in the horse-dung after a period of about 22 hours. Taking the cases of the other two species/

species it is seen that the reaction of each is similar with a significantly greater number being taken from the cow-dung.

The supporting experiments in which the two dung media are presented separately with machair soil confirm the field distribution of the four species in dung-pats only in the cases of A. caliginosa and A. longa. The field distribution of B. eiseni and L. rubellus in dung is not confirmed, although in nature B. eiseni is not present in machair soils and does not meet with such a choice. Another factor may, however, operate here where the earthworm actually lives in the soil under the dung-pat only visiting the pat to feed or to deposit cocoons.

In both these supporting experiments the premise brought out in the basic experiment, that cow-dung is more attractive to all species than horse-dung, is confirmed. In all the cases tested, significantly more were found inhabiting the cow-dung than the horse-dung. The texture of those two dung media was very different, the cow-dung being composed of finely divided particles, and the horse-dung of comparatively large sharp-ended strawy material. (No straw was added, the material was taken fresh from the field.) To test whether texture might be a limiting factor in this case, A. longa, a species violently affected by horse-dung, was presented with a choice of sand steeped in decanted horse-dung water, and sand steeped in tap water/

water; further to a choice of machair soil steeped in horse-dung water and machair soil steeped in tap water; and to sand with cow-dung water and sand with tap water. In one case the results were heterogeneous due to the intertwined cluster formation, but in this case all the earthworms were in good condition after the usual period of 22 hours, and in the other cases no significant difference was found between the effects of the dung-solutions and the tap water. This endorses the supposition that the sharp texture of the horse-dung may be a contributing factor to its not being colonised by certain species of earthworm. It may be, however, that this technique also serves to dilute toxic substances in the horse-dung.

<u>B. eiseni</u> is presented with the "choice" of peat or cow-dung which is close to that which occurs in nature, where the species is found abundant on cattle-grazed moorlands. This experiment supports a view that in conformity with field observations a great proportion of the <u>B. eiseni</u> population on peat moorlands grazed by cattle is situated in the dung-pats, and that the proportion not in dung-pats is transient between the spent and the newly laid. It is also clear that <u>B. eiseni</u> may live in the dung-pat rather than in the peat below.

In the dung experiments it will also be noticed that the results obtained from all species are roughly similar.

V. SUMMARY

1. The field distribution of four species of earthworm <u>A. caliginosa</u>, <u>A. longa</u> (both acid-intolerant), <u>B. eiseni</u> (acid-tolerant), and <u>L. rubellus</u> (ubiquitous) found commonly in the Hebrides, was examined in the laboratory by a series of "choice" experiments.

2. The "choice" chamber is described together with the experimental method. An effort was made to obtain as far as possible an unbiased result from the chamber. The bias of the chamber was examined in the position where the subsequent experiments were to take place, by seven sets of 12 replicates presenting "no choice". A slight bias to the left was found, and compensations made to eliminate it in the experiments.

3. The experiments carried out are listed on the Contents page of this paper.

4. The field distribution of <u>A. caliginosa</u> was confirmed by experiment; that of <u>A. longa</u> was confirmed, but the result tended to be obscure due to the formation of intertwined clusters by the earthworms; that of <u>B. eiseni</u> was not confirmed by all the experiments; that of <u>L. rubellus</u> was not confirmed by all the experiments. Cow-dung appeared to be more attractive to earthworms than horse-dung.

5. A general discussion is given of the results of the experiments and the field distribution. The basic experi-:ments are considered to be between calcareous sand and peat, and between cow-dung and horse-dung. All the others are considered as supplementary to one of the basic experiments.

TABLE I

Showing the results of control experiments to test bias of chambers. No choice was given to A. caliginosa using machair soil in sets 1-4 and cow-dung in sets 5-7.

Sets		REPLICATES												To- :tal	Sum of χ^2 d.f.=11	χ^2 Inter- :action d.f.=10
1	Left	7	6	5	5	3	4	5	5	6	6	5	6	63	5.2	4.9
	Right	3	4	5	5	7	6	5	5	4	4	5	4	57		
	χ^2 d.f.=1	1.6	0.4	0.0	0.0	1.6	0.4	0.0	0.0	0.4	0.4	0.0	0.4	0.3		
2	Left	6	5	8	7	4	5	4	7	6	6	5	4	67	9.2	7.6
	Right	4	5	2	3	6	5	6	3	4	4	5	6	53		
	χ^2 d.f.=1	0.4	0.0	3.6	1.6	0.4	0.0	0.4	1.6	0.4	0.4	0.0	0.4	1.6		
3	Left	2	5	9	7	9	5	3	5	5	5	7	6	68	22.0*	19.9*
	Right	8	5	1	3	1	5	7	5	5	5	3	4	52		
	χ^2 d.f.=1	3.6	0.4	6.4*	1.6	6.4*	0.0	1.6	0.0	0.0	0.0	1.6	0.4	2.1		
4	Left	6	5	5	6	4	5	6	6	6	4	5	5	63	2.8	2.5
	Right	4	5	5	4	6	5	4	4	4	6	5	5	57		
	χ^2 d.f.=1	0.4	0.0	0.0	0.4	0.4	0.0	0.4	0.4	0.4	0.4	0.0	0.0	0.3		
5	Left	5	7	4	2	1	8	6	1	7	3	5	5	54	25.2*	24.0*
	Right	5	3	6	8	9	2	4	9	3	7	5	5	66		
	χ^2 d.f.=1	0.0	1.6	0.0	3.6	6.4*	3.6	0.4	6.4*	1.6	1.6	0.0	0.0	1.2		
6	Left	6	7	6	6	8	6	6	5	3	3	6	5	67	10.8	9.2
	Right	4	3	4	4	2	4	4	5	7	7	4	5	53		
	χ^2 d.f.=1	0.4	1.6	0.4	0.4	3.6	0.4	0.4	0.0	1.6	1.6	0.4	0.0	1.6		
7	Left	6	3	7	6	2	0	4	3	4	6	4	5	50	20.8*	17.5
	Right	4	7	3	4	8	10	6	7	6	4	6	5	70		
	χ^2 d.f.=1	0.4	1.6	1.6	0.4	3.6	10.0*	0.4	1.6	0.4	0.4	0.4	0.0	3.3		

*significant at 0.05 probability level

TABLE II

Showing results of a single choice between peat and calcareous sand by <u>A. caliginosa</u> in 16 replicates.

Choice	REPLICATES (Number of Earthworms)																To-:tal	Sum of χ^2 d.f.=15	χ^2 Inter-:action d.f.=14
Peat	4	0	0	0	4	0	8	0	2	2	2	2	0	0	0	3	31	136.7*	29.7*
Sand	8	14	16	14	8	15	6	15	13	11	12	13	10	10	10	7	182		
χ^2 d.f.=1	1.3	14.0*	16.0*	14.0*	0.0	15.0*	0.3	15.0*	8.1*	6.2*	7.1*	8.1*	10.0*	10.0*	10.0*	1.6	107.0*		

*significant

Showing results of a single choice between peat and calcareous sand by *A. longa* in 22 replicates.

Choice	14 of 22 REPLICATES (Number of Earthworms)													
Peat	0	10	6	10	2	6	2	1	1	3	3	5	7	6
Sand	9	0	4	0	7	4	8	9	9	7	3	4	2	4
χ^2 d.f.=1	9.0*	10.0*	0.4	10.0*	2.8	4.0	3.6	6.4*	6.4*	1.6	0.0	0.1	2.8	0.4

Choice	8 of 22 REPLICATES (Number of Earthworms)								Totals	Sum of χ^2 d.f.=21	χ^2 Inter-:action d.f.=20
Peat	0	1	1	1	3	7	2	4	81	89.4*	78.8*
Sand	10	9	9	9	5	2	8	6	128		
χ^2 d.f.=1	10.0*	6.4*	6.4*	6.4*	0.5	2.8	3.6	0.4	10.6*		

*significant

TABLE IV

Showing results of a single choice between peat and calcareous sand by _B. eisen_i, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Peat	1	1	3	5	7	1	3	3	3	1	28		
Sand	9	9	7	5	3	9	7	7	7	9	72	33.6*	14.2
χ^2 d.f.=1	6.4*	6.4*	1.6	0.0	1.6	6.4*	1.6	1.6	1.6	6.4*	19.4*		

*significant

TABLE V

Showing results of a single choice between peat and calcareous sand by *L. rubellus*, in 16 replicates.

Choice	REPLICATES (Number of Earthworms)																To-:tal	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Peat	7	14	1	13	13	1	7	4	8	2	5	2	4	3	6	6	96	73.4*	66.8*
Sand	8	2	15	3	3	15	9	12	8	14	11	14	6	7	4	4	135		
χ^2 d.f.=1	0.1	9.0*	12.3*	6.3*	6.3*	12.3*	0.3	4.0*	0.0	9.0*	2.3	9.0*	0.4	1.6	0.4	0.4	6.6*		

*significant

TABLE VI

Showing results of a single choice between peat and machair soil by *A. caliginosa*, in 12 replicates.

Choice	REPLICATES (Number of Earthworms)												To- :tal	Sum of χ^2 d.f.=11	χ^2 Inter- :action d.f.=10
Peat	0	0	1	1	2	0	2	5	3	2	1	0	17	68.2*	10.3
Soil	10	10	9	9	7	10	8	5	7	6	8	10	99		
χ^2 d.f.=1	10.0*	10.0*	6.5*	6.5*	3.0	10.0*	3.6	0.0	1.6	2.0	5.4*	10.0*	58.0*		

*significant

TABLE VII

Showing results of a single choice between peat and machair soil by A. longa, in 21 repli-:cates.

Choice	15 of 21 REPLICATES (Number of Earthworms)														
Peat	0	0	3	3	3	0	2	0	1	3	4	4	1	2	1
Soil	10	10	7	7	7	10	8	10	9	7	6	6	9	8	9
χ^2 d.f.=1	10.0*	10.0*	1.6	1.6	1.6	10.0*	3.6	10.0*	6.4*	1.6	0.4	0.4	6.4*	3.6	6.4*

Choice	6 of 21 REPLICATES (Number of Earthworms)						Totals	Sum of χ^2 d.f.=20	χ^2 Inter-:action d.f.=19
Peat	0	1	1	3	0	0	32	117.8*	16.3
Soil	10	9	9	7	10	10	178		
χ^2 d.f.=1	10.0*	6.4*	6.4*	1.6	10.0*	10.0*	101.5*		

*significant

TABLE VIII

Showing the results of a single choice between peat and machair soil by B. eiseni, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Peat	6	3	4	3	3	1	4	4	4	7	39		
Soil	4	7	7	7	6	9	6	6	6	3	61	14.6	9.8
χ^2 d.f.=1	0.4	1.6	0.9	1.6	1.0	6.4*	0.4	0.4	0.4	1.6	4.9*		

*significant

TABLE IX

Showing the results of a single choice between peat and machair soil by <u>L. rubellus</u>, in 12 replicates.

Choice	REPLICATES (Number of Earthworms)												To-:tal	Sum of χ^2 d.f.=11	χ^2 Inter-:action d.f.=10
Peat	2	1	2	3	2	0	2	1	5	1	1	1	21	55.3*	7.2
Soil	8	9	7	7	8	10	8	8	5	9	8	9	96		
χ^2 d.f.=1	3.6	6.4*	2.8	1.6	3.6	10.0*	3.6	5.4*	0.0	6.4*	5.4*	6.4*	48.1*		

*significant

TABLE X

Showing the results of a single choice between calcareous sand and machair soil by *A. caliginosa*, in 12 replicates.

Choice	REPLICATES (Number of Earthworms)												Total	Sum of χ^2 d.f.=11	χ^2 Interaction d.f.=10
Sand	2	1	4	1	4	3	2	1	1	4	8	6	37		
Soil	8	8	6	9	6	7	8	9	8	13	12	14	108	41.1	11.9
χ^2 d.f.=1	3.6	5.4*	0.4	6.4*	0.4	1.6	3.6	6.4*	5.4*	4.8*	0.4	1.6	29.1*		

*significant

TABLE XI

Showing the results of a single choice between calcareous sand and machair soil by <u>A. longa</u>, in 20 replicates.

Choice	14 of 20 REPLICATES (Number of Earthworms)													
Sand	4	4	0	1	1	1	2	2	0	0	3	0	0	4
Soil	6	6	10	9	9	10	7	8	9	11	7	10	10	7
χ^2 d.f.=1	0.4	0.4	10.0*	6.4*	6.4*	7.4*	2.8	3.6	9.0*	11.0*	1.6	10.0*	10.0*	0.8

Choice	6 of 20 REPLICATES (Number of Earthworms)						Totals	Sum of χ^2 d.f.=19	χ^2 Inter-:action d.f.=18
Sand	0	2	0	1	2	5	41		
Soil	12	9	11	10	10	6	180	120.0*	32.6*
χ^2 d.f.=1	12.0*	4.5*	11.0*	7.4*	5.3*	0.1	187.4*		

*significant

TABLE XII

Showing the results of a single choice between calcareous sand and machair soil by *B. eiseni*, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Sand	0	0	0	0	0	0	1	0	0	1	2		
Soil	10	10	10	10	10	10	9	10	9	9	97	91.8*	0.6
χ^2 d.f.=1	10.0*	10.0*	10.0*	10.0*	10.0*	10.0*	6.4*	10.0*	9.0*	6.4*	91.2*		

*significant

TABLE XIII

Showing the results of a single choice between calcareous sand and machair soil by L. rubellus, in 12 replicates.

Choice	REPLICATES (Number of Earthworms)												To-:tal	Sum of χ^2 d.f.=11	χ^2 Inter-:action d.f.=10
Sand	5	3	3	3	3	3	1	1	2	5	4	7	40	35.7*	7.2
Soil	4	7	6	5	7	7	9	9	9	13	16	12	104		
χ^2 d.f.=1	0.1	1.6	1.0	0.5	1.6	1.6	6.4*	6.4*	4.5*	3.6	7.2*	1.3	28.4*		

*significant

TABLE XIV

Showing the results of a single choice between cow-dung and machair soil by A. caliginosa, in 16 replicates.

Choice	REPLICATES (Number of Earthworms)																To-:tal	Sum of χ^2 d.f.=15	χ^2 Inter-:action d.f.=14
Cow-dung	2	3	3	4	4	3	1	3	3	3	1	2	3	0	4	0	39		
Soil	8	7	7	6	6	7	9	7	7	7	9	8	7	10	6	10	121	54.4*	10.4
χ^2 d.f.=1	3.6	3.6	1.6	0.4	0.4	1.6	6.4*	1.6	1.6	1.6	6.4*	3.6	1.6	10.0*	0.4	10.0*	42.0*		

*significant

TABLE XV

Showing the results of a single choice between cow-dung and machair soil by *A. longa*, in 12 replicates.

Choice	REPLICATES (Number of Earthworms)												To-:tal	Sum of χ^2 d.f.=11	χ^2 Inter-:action d.f.=10
Cow-dung	1	4	1	2	1	0	0	3	0	3	1	1	17		
Soil	9	6	9	8	9	10	10	7	10	7	9	9	103	69.2*	7.6
χ^2 d.f.=1	6.4*	0.4*	6.4*	3.6	6.4*	10.0*	10.0*	1.6	10.0*	1.6	6.4*	6.4*	61.6*		

*significant

TABLE XVI

Showing the results of a single choice between cow-dung and machair soil by B. eiseni, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										To-:tal	χ^2 Totals d.f.=9	χ^2 Inter-:action d.f.=8
Cow-dung	5	5	7	7	5	7	6	7	8	7	64		
Soil	5	6	4	4	5	3	4	3	2	3	39	10.5	4.5
χ^2 d.f.=1	0.0	0.1	0.8	0.8	0.0	1.6	0.4	1.6	3.6	1.6	6.1*		

*significant

TABLE XVII

Showing the results of a single choice between cow-dung and machair soil by _L. rubellus_, in 20 replicates.

Choice	15 of 20 REPLICATES (Number of Earthworms)														
Cow-dung	0	2	2	2	3	3	1	2	5	5	4	4	2	3	1
Soil	10	8	8	8	7	7	9	8	5	5	6	6	8	7	9
χ^2 d.f.=1	10.0*	3.6	3.6	3.6	1.6	1.6	6.4*	3.6	0.0	0.0	0.4	0.4	3.6	1.6	6.4*

Choice	5 of 20 REPLICATES (Number of Earthworms)					Totals	Sum of χ^2 d.f.=19	χ^2 Inter-:action d.f.=18
Cow-dung	2	3	2	2	2	50	62.4*	12.4
Soil	8	7	8	8	8	150		
χ^2 d.f.=1	3.6	1.6	3.6	3.6	3.6	50.0*		

*significant

TABLE XVIII

Showing the results of a single choice between horse-dung and machair soil by <u>A. caliginosa</u>, in 12 replicates.

Choice	REPLICATES (Number of Earthworms)												To-:tal	Sum of χ^2 d.f.=11	χ^2 Inter-:action d.f.=10
Horse-dung	0	0	1	0	4	3	0	1	0	0	0	0	9		
Soil	10	10	9	10	6	7	10	9	10	10	10	10	111	94.8*	8.1
χ^2 d.f.=1	10.0*	10.0*	6.4*	10.0*	0.4	1.6	10.0*	6.4*	10.0*	10.0*	10.0*	10.0*	86.7*		

*significant

TABLE XIX

Showing the results of a single choice between horse-dung and machair soil by *A. longa*, in 20 replicates.

Choice	13 of 20 REPLICATES (Number of Earthworms)												
Horse-dung	2	0	2	1	0	0	1	0	1	3	1	0	0
Soil	8	10	8	9	9	10	9	10	9	7	8	10	10
χ^2 d.f.=1	3.6	10.0*	3.6	6.4*	9.0*	10.0*	6.4*	10.0*	6.4*	1.6	5.4*	10.0*	10.0*

Choice	7 of 20 REPLICATES (Number of Earthworms)							Totals	Sum of χ^2 d.f.=19	χ^2 Inter-:action d.f.=18
Horse-dung	0	0	0	2	1	0	0	14	158.1*	6.3
Soil	10	10	10	10	11	12	10	190		
χ^2 d.f.=1	10.0*	10.0*	10.0*	5.3*	8.3*	12.0*	10.0*	151.8*		

*significant

TABLE XX

Showing the results of a single choice between horse-dung and machair soil by L. rubellus, in 10 replicates.

Choice	R E P L I C A T E S (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Horse-dung	0	0	0	1	1	1	1	0	2	0	6		
Soil	10	10	10	9	9	9	9	10	8	10	94	158.1*	6.3
χ^2 d.f.=1	10.0*	10.0*	10.0*	6.4*	6.4*	6.4*	6.4*	10.0*	3.6	10.0*	77.4*		

*significant

TABLE XXI

Showing the results of a single choice between cow-dung and horse-dung by B. eiseni, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Cow-dung	5	6	7	6	6	4	5	7	9	9	64		
Horse-dung	5	4	3	4	4	6	5	3	1	1	36	17.6*	9.8
χ^2 d.f.=1	0.0	0.4	1.6	0.4	0.4	0.4	0.0	1.6	6.4*	6.4*	7.8*		

*significant

TABLE XXII

Showing the results of a single choice between cow-dung and horse-dung by L. rubellus, in 24 replicates.

Choice	17 of 24 REPLICATES (Number of Earthworms)																
Cow-dung	7	6	4	6	7	6	5	7	5	4	6	7	4	4	7	6	6
Horse-dung	3	4	5	4	3	4	5	2	5	6	5	3	6	6	3	5	4
χ^2 d.f.=1	1.6	0.4	0.1	0.4	1.6	0.4	0.0	2.8	0.0	0.4	0.1	1.6	0.4	0.4	1.6	0.1	0.4

Choice	7 of 24 REPLICATES (Number of Earthworms)							Totals	Sum of χ^2 d.f.=21	χ^2 Inter-:action d.f.=22
Cow-dung	6	4	5	6	9	8	8	143	26.8	18.4
Horse-dung	4	6	5	5	1	2	2	98		
χ^2 d.f.=1	0.4	0.4	0.0	0.1	6.4*	3.6	3.6	8.4*		

*significant

TABLE XXIII

Showing the results of a single choice between cow-dung and peat by _B. eiseni_, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter:action d.f.=8
Cow-dung	10	9	9	8	8	10	10	9	8	10	91		
Peat	0	1	1	2	2	0	0	1	2	0	9	70.0*	2.8
χ^2 d.f.=1	10.0*	6.4*	6.4*	3.6	3.6	10.0*	10.0*	6.4*	3.6	10.0*	67.2*		

*significant

TABLE XXIV

Showing the results of a single choice between horse-dung and sand by <u>B. eiseni</u>, in 10 replicates.

Choice	REPLICATES (Number of Earthworms)										Totals	Sum of χ^2 d.f.=9	χ^2 Inter-:action d.f.=8
Horse-dung	7	10	9	9	6	10	10	6	9	9	85		
Sand	3	0	1	1	4	0	0	4	1	1	15	58.0*	9.0
χ^2 d.f.=1	1.6	10.0*	6.4*	6.4*	0.4	10.0*	10.0*	0.4	6.4*	6.4*	49.0*		

*significant

TABLE XXV

Showing the results of a single choice between horse-dung water in sand and tap water in sand by <u>A. longa</u>, in 18 replicates.

Choice	REPLICATES (Number of Earthworms)																		To-:tal	Sum of χ^2 d.f.=17	χ^2 Inter-:action d.f.=16
Horse-dung water	4	1	7	4	1	1	2	0	1	3	5	4	4	5	6	1	8	3	60		
Tap water	6	9	3	6	9	9	8	10	9	7	5	6	6	5	4	9	2	7	120	56.0*	36.0*
χ^2 d.f.=1	0.4	6.4*	1.6	0.4	6.4*	6.4*	3.6	10.0*	6.4*	1.6	0.0	0.4	0.4	0.0	0.4	6.4*	3.6	1.6	20.0*		

*significant

TABLE XXVI

Showing the results of a single choice between horse-dung water in machair soil and tap water in machair soil by <u>A. longa</u>, in 18 replicates.

Choice	REPLICATES (Number of Earthworms)																		To-:tal	Sum of χ^2 d.f.=15	χ^2 Inter-:action d.f.=16
Horse-dung water	2	8	7	4	1	2	4	3	9	1	4	2	6	8	6	5	8	4	84		
Tap water	8	2	3	6	8	8	6	7	1	9	6	8	4	2	4	5	2	6	95	45.8*	45.2*
χ^2 d.f.=1	3.6	3.6	1.6	0.4	5.4*	3.6	0.4	1.6	6.4*	6.4*	0.4	3.6	0.5	3.6	0.4	0.0	3.6	0.4	0.7		

*significant

TABLE XXVII

Showing the results of a single choice between cow-dung water in sand, and tap water in sand by <u>L. rubellus</u>, in 15 replicates.

Choice	REPLICATES (Number of Earthworms)															To-:tal	Sum of χ^2 d.f.=14	χ^2 Inter-:action. d.f.=13
Cow-dung water	3	5	6	4	4	4	6	5	4	6	6	4	4	3	7	71		
Tap water	5	5	4	5	6	6	4	5	5	4	4	4	6	6	4	73	5.340	5.312
χ^2	0.5	0.0	0.4	0.1	0.4	0.4	0.4	0.0	0.1	0.4	0.4	0.0	0.4	1.0	0.8	0.0		

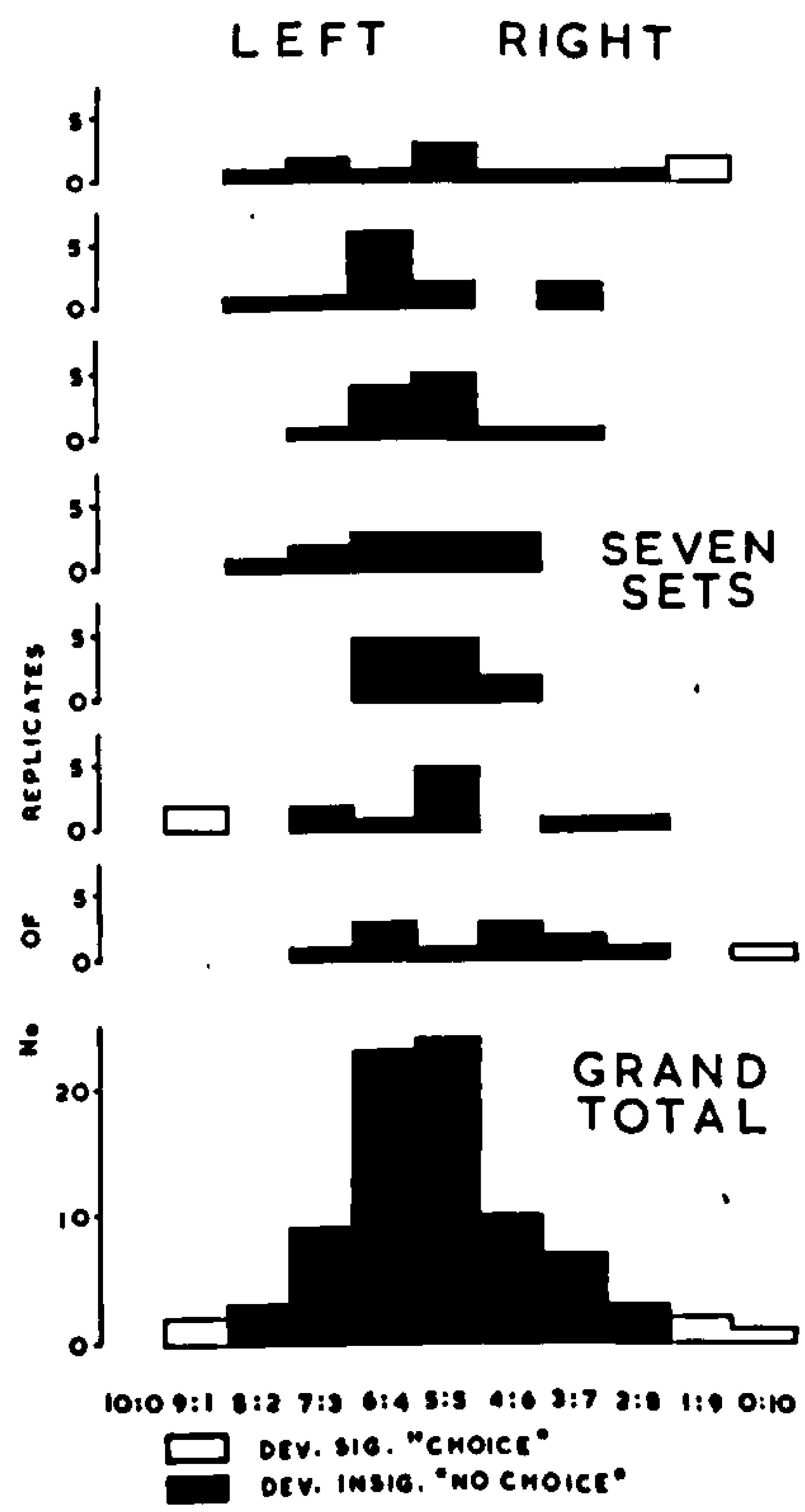
TABLE XXVIII

Showing the results of all choice experiments performed expressed in percentages of the total earthworms recovered from each experiment.

Species	EXPERIMENTS					
	Peat : Sand	Peat : Soil	Sand : Soil	Cow-dung : Soil	Horse-dung : Soil	Cow-dung : Horse-dung
A. caliginosa	15 : 85+	15 : 85	26 : 74	24 : 76	8 : 92	-
A. longa	39 : 61+	15 : 85	19 : 81+	14 : 86	7 : 93	-
B. eiseni	28 : 72	39 : 61	2 : 98	38 : 62	-	64 : 36
L. rubellus	42 : 58+	18 : 82	28 : 72	25 : 75	6 : 94	59 : 41
Total	31 : 69	20 : 80	20 : 80	30 : 70	7 : 93	61 : 39

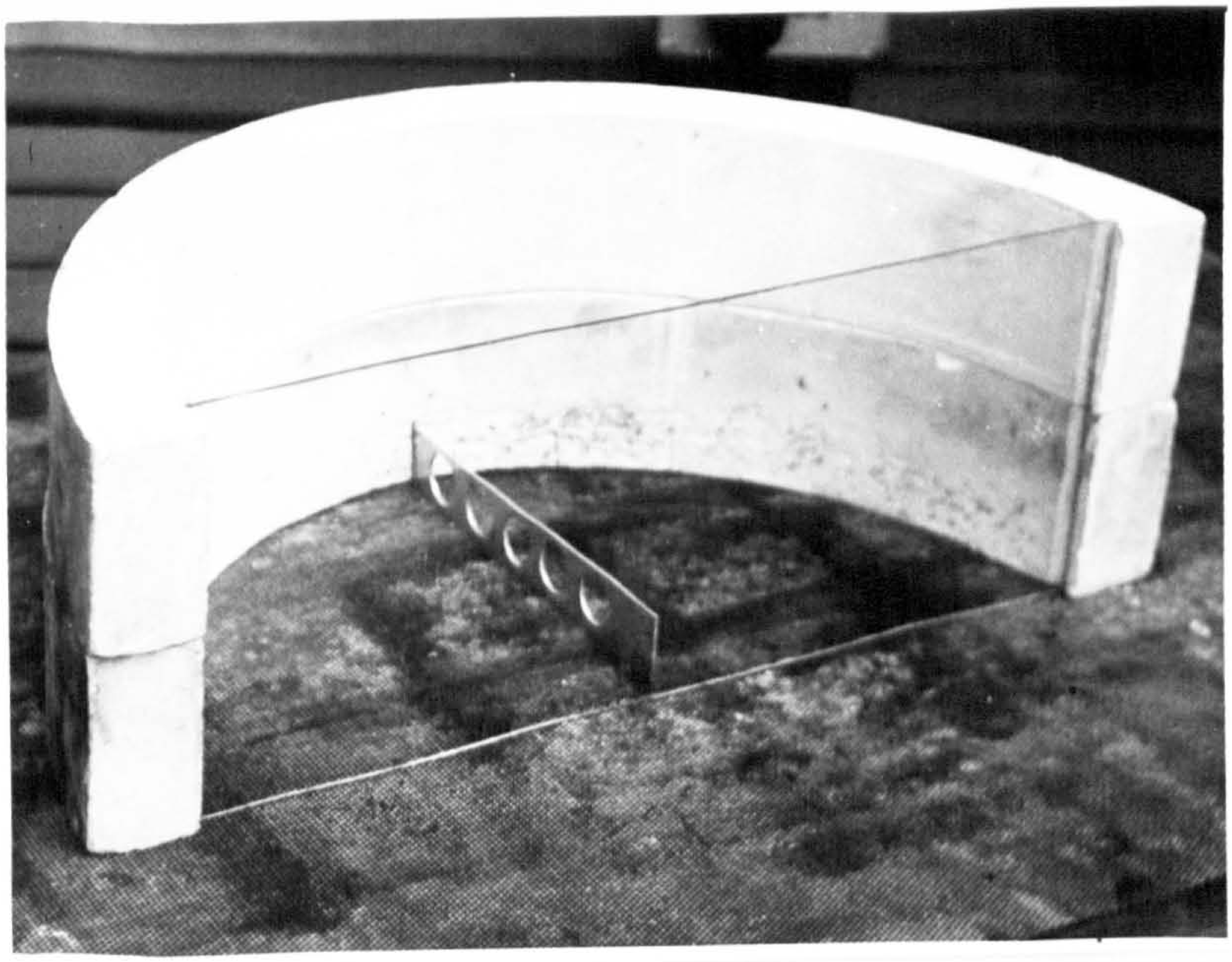
	Cow-dung : Peat	Horse-dung : Sand	Horse-dung water : Tap water In sand	Horse-dung water : Tap water In soil	Cow-dung water : Tap water In sand
A. caliginosa	-	-	-	-	-
A. longa	-	-	33 : 67+	47 : 53+	51 : 49
B. eiseni	91 : 9	85 : 15	-	-	-
L. rubellus	-	-	-	-	-
Total	91 : 9	85 : 15	33 : 67	47 : 53	51 : 49

+significant Heterogenity

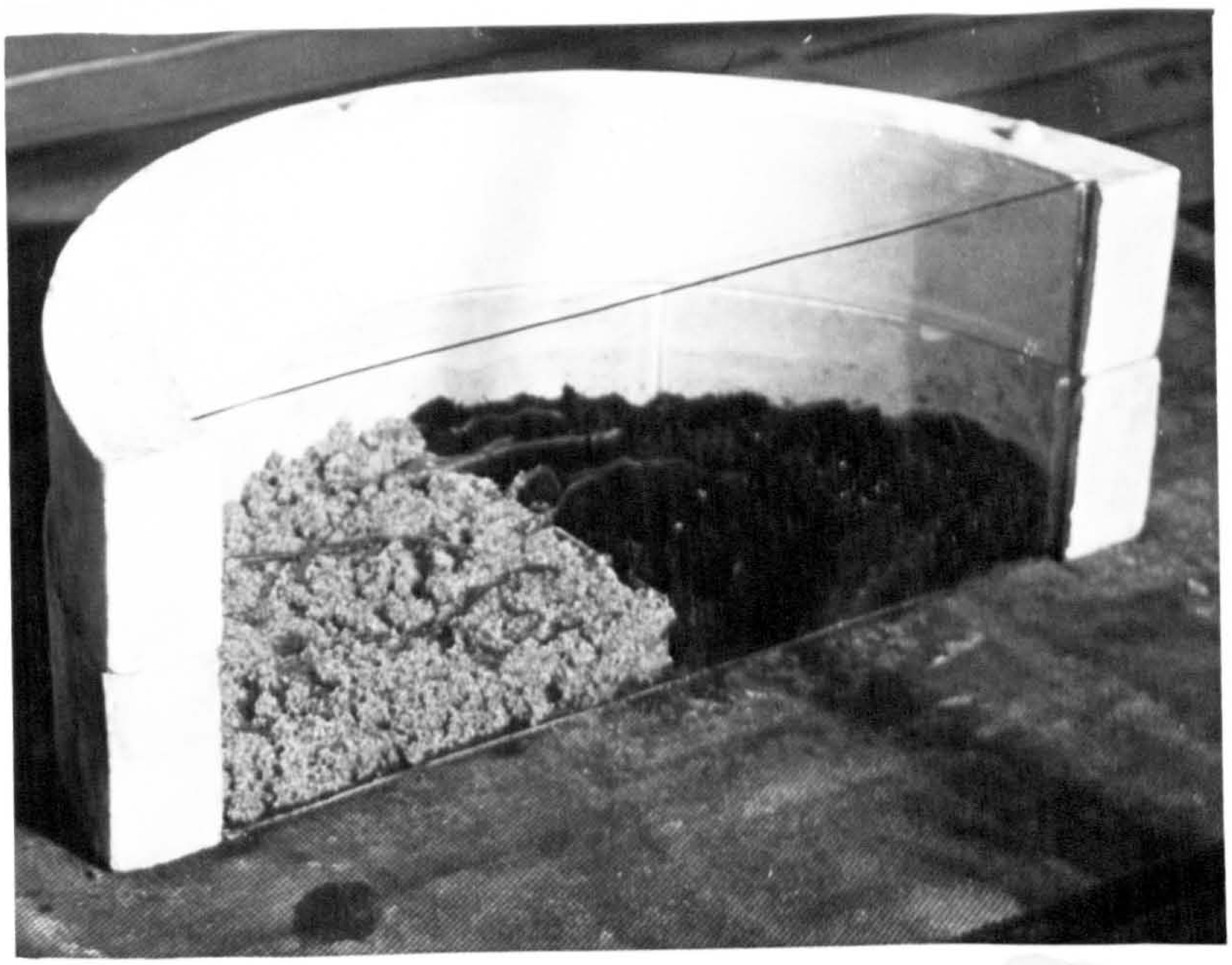


<u>Fig. 1</u>. The distribution of the seven sets of 12 replicates on either side of the 5:5 ratio which is the "ideal" of "no choice". The distribution of the total of 84 replicates is also shown.

(a)

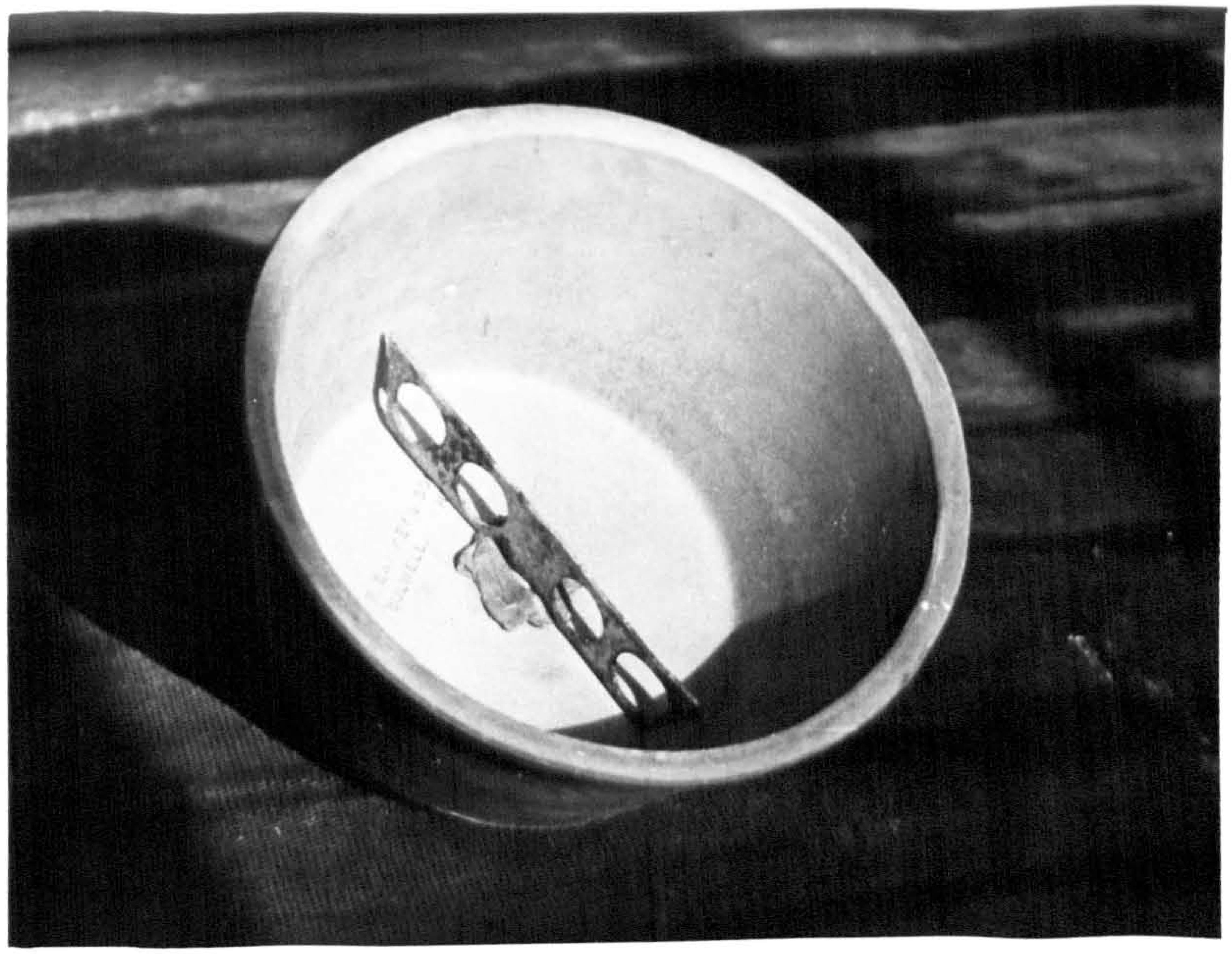


(b)



<u>Plate I</u>. The choice chamber (a) empty, (b) charged.

(a)



(b)

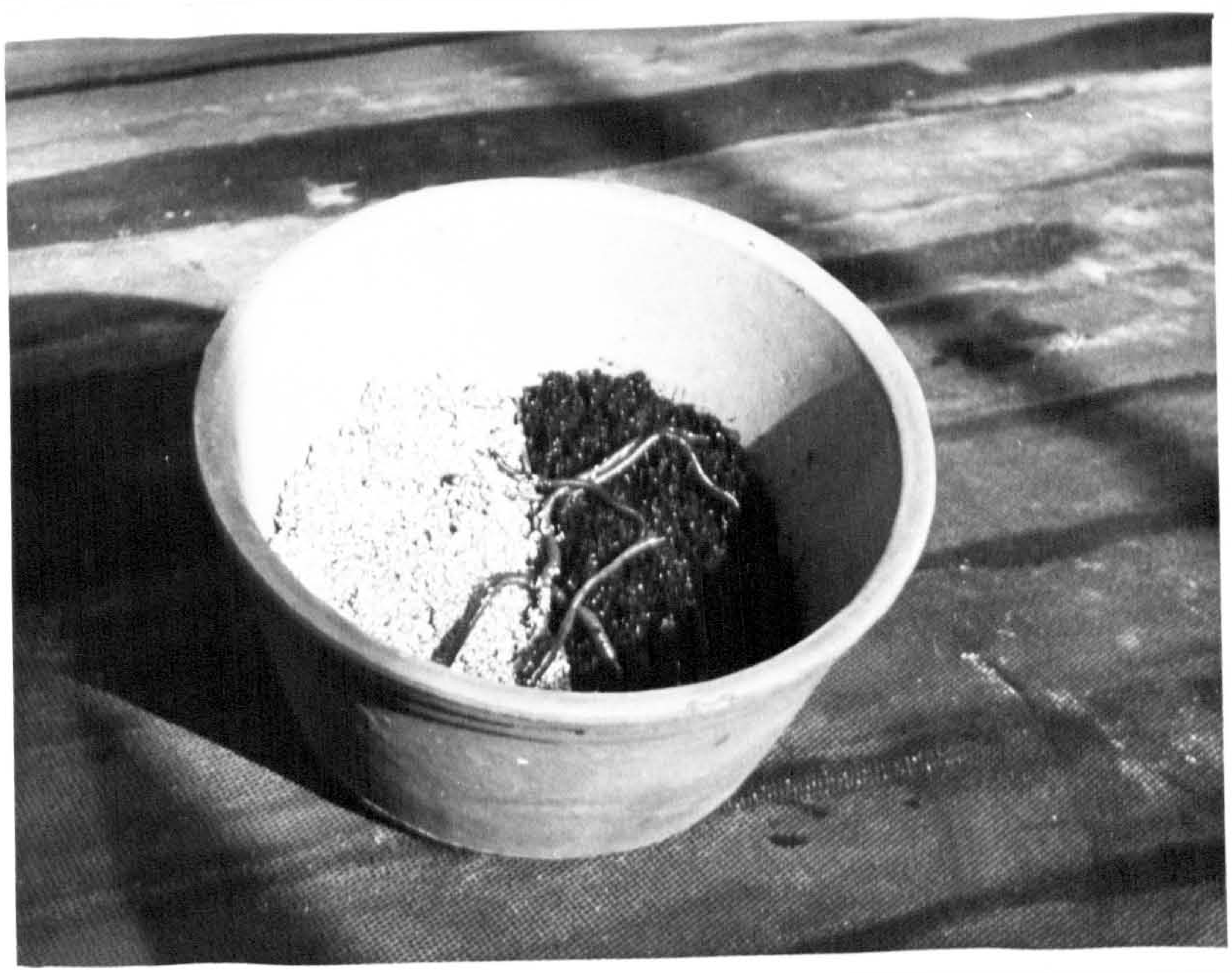


Plate II. A choice chamber made from a flower pot (a) empty, (b) charged.

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