Studies on the burrow systems of apodemus sylvaticus and clethrionomys glareolus in Houghall Wood Durham

Brooks, P.M.

STUDIES ON THE BURROW SYSTEMS OF APODEMUS SYLVATICUS AND CLETHRIONOMYS GLAREOLUS IN HOUGHALL WOOD, DURHAM

P.M. BROOKS, B.Sc. HONS. (LONDON)
UNIVERSITY OF DURHAM
ENGLAND.

1968-69.

DISSERTATION SUBMITTED AS PART OF THE REQUIREMENTS
FOR THE DEGREE OF M.Sc. ECOLOGY.

TABLE OF CONTENTS

CHAPTER 1 : INTRODUCTION

1.1. AIM OF STUDY.

The aim of this study is to establish the characteristics of the burrows of Apodemus sylvaticus (field mouse) and Clethrionomys glareolus (bank vole). The population ecology of these rodents has been extensively investigated, but their underground systems have been largely neglected.

1.2. REVIEW OF LITERATURE.

The terms relating to burrow systems have not been standardised. They are used in this review of literature in the sense they are used in the original texts. The definitions of the terms used by the author in the remainder of the present study are given in section 1.3.

The review of literature serves as a summary of the previous work on burrow systems. Therefore certain aspects such as burrow micro-climate and the effects of burrows on the soil are dealt with in the review, but are not included in the programme for this study.

Apodemus sylvaticus is mainly a woodland species and its abundance in this woodland is unaffected by the degree of ground cover (Ashby 1967). Barrett-Hamilton (1910) stated that some burrows made by this species are constructed solely for the purpose of breeding; but that deeper and more permanent burrows, often with food stores, may be used during the winter. Barrett-Hamilton (1910) also reported that such food stores may be shared by a number of mice, and that fourteen or fifteen individuals may be found in one burrow. Bolam (1912) stated that adult Apodemus may live in pairs and that the young may reside with the parents at least until they become sexually mature.

The nest, as reported by Walker (1964) and others, is normally located in a chamber at the end of a burrow and is constructed of finely-shredded grass and leaves. Brown (1966) stated for both Apodemus and Clethrionomys, that an individual may use from four to five home sites at any one time, all of which are visited at regular intervals and cleaned out. Brown (1966) also stated that burrows may be vacated for a period and be re-occupied by a later generation. Ashby (1967), working in Houghall Wood, Durham, found some evidence that Apodemus tends to avoid the wetter areas of this wood. It had previously been reported that areas of heavy clay are avoided (Elton et al. 1931), and although Crawley (1965) found Apodemus occupying parts of Castle Eden Dene, Durham, where there is a heavy clay soil, it would appear that this species has a definite preference for the lighter, well-drained types such as gravel, sand and the calcareous soils.

Clethrionomys glareolus is normally found in woodland and hedgebank habitats, but in contrast to Apodemus, is mainly restricted to areas where the ground cover is dense. Barrett-Hamilton (1910) stated that Clethrionomys constructs a complicated series of shallow galleries partially below the ground. The tunnels concerned are of irregular diameter with numerous openings, blind terminals and enlarged chambers, and may extend for a considerable distance. He suggested that their main function is intercommunication (presumably between patches of ground cover) as the remains of nests or food are often lacking. The nest of Clethrionomys is made of fine grass lined with moss or feathers, and he recorded that it is often built above ground in hedgerows.

The main function of underground tunnels may be to provide maximum protection from predators and the abiotic environment. The Tulare Kangaroo rat (Fitch 1948) constructs entrances which are considerably wider than the body. This permits the animal to turn round and make a rapid escape from danger. Many of their tunnels end in cul-de-sacs, some of which come to within about one inch of the surface. This crust of earth can be broken to make an emergency exit if an individual is pursued in its burrow by a predator. Kootcherook (1960) stated that the chambers and nests of the Russian Steppe animals are constructed at the depth below the ground surface giving the most favourable temperature conditions. He added that steppe rodents are known to reduce air circulation in their burrow systems by blocking entrance holes, and to congregate in winter for thermoregulation. Górecki (1968) stated that most of the diurnal cycle of Clethrionomys glareolus is spent in groups in nests which function as well-insulated thermostats; and found that voles kept in groups of two to four animals lower their metabolic rate by 13%. Olszewski (1963) investigated the air flow in mole burrows, and in all the systems studied air currents were recorded in the main tunnels, but not in the chambers where the young are born.

The effect of burrows on the soil may be extensive. Taylor (1935) stated that animal products such as hair and excreta, and at death the whole body, will be added to the soil along with the remains of nests and food stores, which results in the soil being enriched. In addition the burrows can reduce run-off of surface water after rain and therefore slow down erosion of sloping ground. The soil layer may even be increased in depth by the movement of soil and water down the tunnels. Formozov and Kodachova (1960) stated that burrow systems dug by marmots extend to a depth of 5m on the Russian and Siberian Steppes. Grass is brought into their tunnels and they have underground latrines. Each marmot brings up 0.1 to 0.2 m^3 of subsoil per year which forms mounds rich in carbonates. These mounds tend to trap snow which moistens the soil and makes them suitable for tree growth. In semi-desert areas they bring up salt and the mounds become covered in halophytic vegetation. In areas not affected by human cultivation the density of ground squirrels (marmots and sousliks) is approximately 160 per hectare. Souslik burrows cover up to 10% of the ground in the semi-desert Caspian Plain, and they encourage the growth of bushes and annuals. Popova (1962) recorded that moistening of the soil to a considerable depth beneath small mammal burrow systems occurred during rainy periods, and that rapid drying of the soil along these systems occurred during periods of dry weather. The amount of soil moisture also depended on the character of the burrow system and the permeability of the soil. Stark (1963) found that the location of the nests of the Californian vole (Microtus californicus) depended on soil moisture. They would construct nests underground in burrows if the soil was sufficiently loose and dry, but they seldom burrowed in clay soils, or those that were compacted or very moist.

Fitch (1948) showed for the Kangaroo rat that the number of open holes depended on the soil type and on the population levels of preceding years. Thus the population density in a locality at any given time could not be estimated accurately from the number of holes present, although the number of holes may provide an indication of rodent abundance over several years.

Several methods have been described for establishing whether or not burrows are occupied. Mayer (1957) used paper smoked by a benzene lamp to determine occupancy of burrow systems by ground squirrels. The paper was rolled into a cylinder and inserted in the burrow entrance. Brown (1966) used tracking rolls to establish home range. The rolls were made of a cardboard cylinder lined with stiff aluminium foil which was coated with silicone as

CHAPTER 2 : METHODS

(i) "Non-residential tunnel system". An underground run (see definition below) connected to the surface by a minimum of two holes and which has at least 60 cm of tunnel, or alternatively, if there is only one entrance hole, the length of tunnel must be at least 150 cm.

(ii) "Residential tunnel system". A tunnel system having a minimum of two holes, with at least one chamber which could be used as a nest site, and with a tunnel length in excess of 150 cm. A "chamber" is that part of a tunnel having a diameter at least twice the mean width of the tunnel. A chamber may be used either to store food or as a nesting site.

(iii) "Other tunnels". All other tunnels which are shorter than 60 cm, and those between 60 cm and 150 cm long which have only one entrance hole.

A "run" refers to a "litter run" which is a run constructed in the litter layer; an "underground run" is synonymous with "tunnel" and "underground passage".

Absolute densities, as opposed to indices of density of small rodents, are difficult to determine except by fencing an area and trapping it out. However, Ashby (1967) believed that he was able to obtain approximate estimates of the absolute densities in the various parts of Houghall Wood he studied, by the analysis of the results of a standard trapping technique employed over a period of several years. With reference in the present text to the density levels he estimated, a value in excess of about fifty per hectare is referred to as high, between twelve and fifty moderate, and below twelve per hectare as low.

2.1. INTRODUCTION TO THE STUDY AREA.

(a) Location and description of Houghall Wood.

The study was carried out in the southern end of Houghall Wood which is situated on sloping ground overlooking the River Wear flood plain about one mile south of Durham City. The following types of vegetational cover predominate in various parts of this area, namely oak woodland, sycamore with some beech and birch, and birch woodland. The ground vegetation differs according to the nature of the canopy. The soil is boulder clay containing variable but substantial proportions of fine sand, the presence of which is due to differential resorting of the glacial deposits by water.

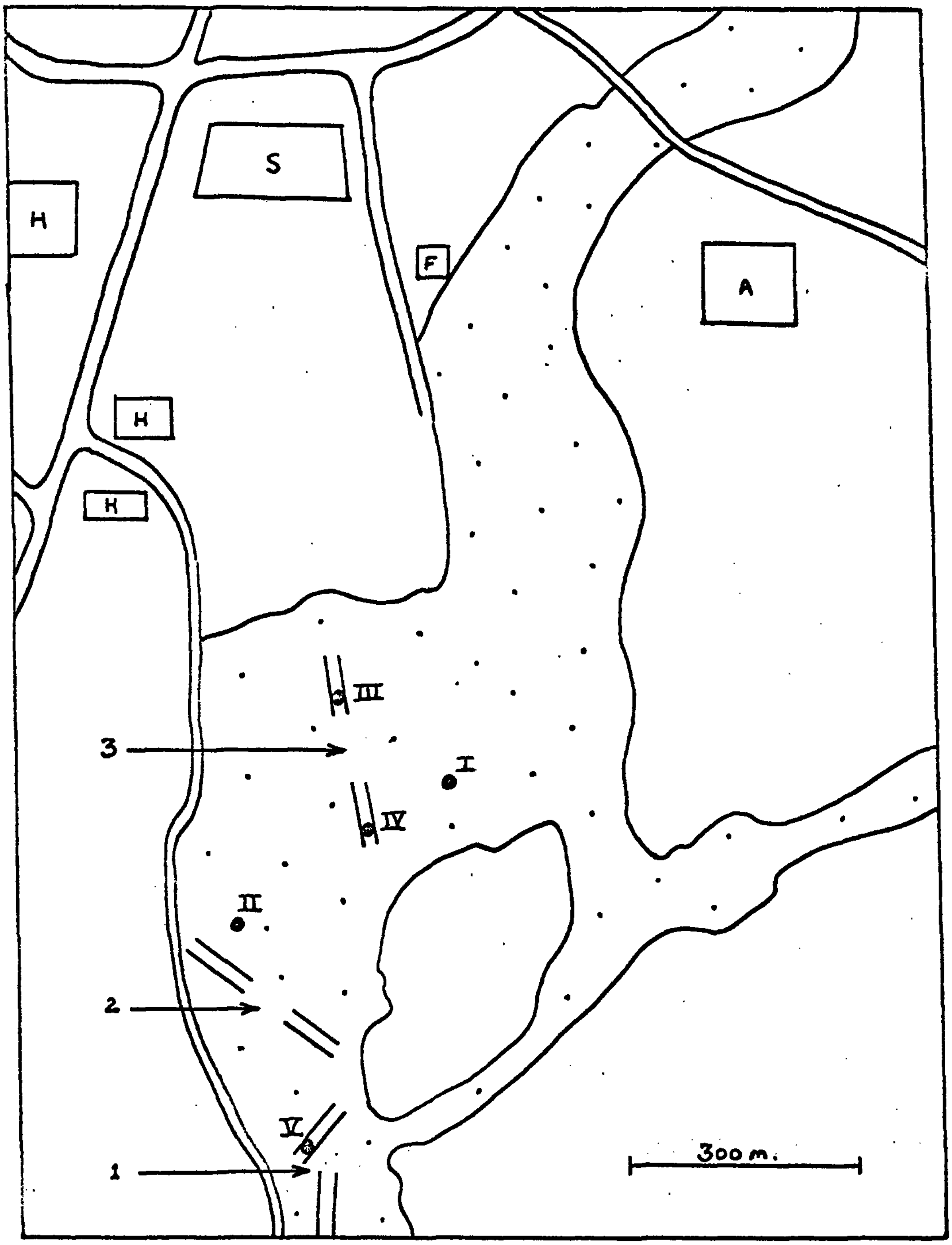
(b) Selection of excavation sites and the abundance of rodents on the sites.

For the purpose of this study, it is more relevant to consider the long-term trapping records of the areas concerned as indices of the population densities of the two species studied, than the trapping results obtained shortly before excavations were undertaken, since at least the deeper tunnels last for many years. The need to use long-term records applies particularly to Apodemus because its numbers are known to fluctuate asynchronously in various parts of Houghall Wood from year to year (Ashby 1967).

Where possible, therefore, the excavation sites were situated within or just outside the three trap transect lines laid down by Ashby (see Fig.1), so that use could be made of his trapping results from 1954 onwards (see Table 9).

Five sites (denoted by Roman numerals) of differing characteristics were excavated. Sites I and II, each $25m^2$, were the major sites used for comparison and were chosen so as to show the maximum disparity in the relative abundance of Apodemus and Clethrionomys. It was possible, as in the case of Site II, to select an area almost exclusively occupied by Apodemus, as the abundance of Clethrionomys is dependent on the density of ground cover. This animal very rarely visits areas such as site II where the cover is slight. Site II was positioned close to the upper half of transect 2 used by Ashby (1967), (see Table 9 and Fig 1) and the densities of rodents in the two areas may be presumed to be the same. But since the distribution of Apodemus is unaffected by the density of cover, and this animal is very much more nearly uniformly distributed in the woodland studied, it was not possible to select an area inhabited only by Clethrionomys. Therefore Site I was located in an area of dense ground cover where Clethrionomys would be abundant, but the Apodemus level would be of the same order as on Site II. No area with sufficiently dense cover was available for excavation near Ashby's transects, so a site which was approximately 100m from his transect 3 was selected (see Fig. 1). Ashby's relative density figures for the two species for areas of dense cover could be presumed to apply to this site, but in order to provide confirmatory evidence, the abundance of rodents in the area of Site I was estimated by live-trapping. This was carried out immediately before excavation using Longworth live traps as in Ashby's standard method described in section 2.2. The trapping results shown in section 3.1(a) confirm that there was in fact a high population of Clethrionomys.

FIG. 1: PLAN OF HOUGHALL WOOD SHOWING POSITIONS OF TRAPPING TRANSACTS 1 TO 3 (ASHBY, 1967) AND EXCAVATION SITES I TO V



Key: 1,2,3 - Positions of trapping transacts used by Ashby (1967).

● - Positions of excavation Sites I-V in present study.

S-University Science Laboratories

H-University Halls of Residence

A-University School of Agriculture

F-University Farm

[. . .] - Houghall Wood

Sites III to V were smaller areas each of $9m^2$ which were selected for excavation within Ashby's transects, that is between his two trapping lines, with a view to amplifying the results obtained on the main excavation sites. Reference to his previous trapping (Table 9) shows that the only part of the area he studied where the mean density of Apodemus was significantly below that elsewhere, was the lower half of his transect 3. This half transect was in a hollow which tends to have a high water table: there was little vegetational cover so the Clethrionomys population was also low. It was therefore chosen as one of these areas and is referred to as Site IV. A further area was located within the upper half of his transect 3, which had a moderate population of both Clethrionomys and Apodemus and is referred to as Site III. Finally, Site V was situated within the lower half of his transect 1, which since 1954 has had a high density of Clethrionomys and might be expected to have a pattern of burrow systems with the same characteristics as Site I. The abundance of rodents in all the sites is summarised with the slope and aspect in Table 1, and the positions of the excavation sites in relation to Ashby's trapping transects are shown in Fig.1.

TABLE 1

THE SLOPE AND ASPECT OF THE SITES AND THE ABUNDANCE OF *CLETHRIONOMYS* AND *APODEMUS*

Site	Slope	Aspect	Rodent Abundance	
			Apodemus	*Clethrionomys*
I	10°	N.E.	Moderate	High
II	12°	E.N.E.	Moderate	Very low to absent
III	25°	E.	Moderate	Moderate
IV	3°	E.	Low	Low
V	25°	E.W.E.	Moderate	High

2.2 ESTIMATION OF THE ABUNDANCE OF APODEMUS AND CLETHRIONOMYS ON SITE 1 BY TRAPPING.

The technique used in this study to obtain an estimate of the rodent abundance on site 1 is the same as that used for fifteen years by Ashby (1967). The reliability of the size of samples obtained by this standard method as indices of the abundance of *Apodemus* and *Clethrionomys* was tested by Ashby using the analysis of variance (described in Ashby 1967: 414-419). He showed that the mean recapture proportions of the two species in sample sizes of many hundreds were almost identical, and that for practical purposes the area sampled could also be assumed to be the same for both species. Further, the analysis of variance indicated that variations in the recapture proportions with season and year did not exceed the level to be anticipated on account of random variability. Therefore, the sample sizes provided indices of population density directly without the Lincoln Index calculation being applied, and the relative proportions of the two species captured approximated to their relative abundance in the population.

The standard trapping method as used by Ashby, and in this study on Site 1, is as follows. Two lines of Longworth live traps (Chitty and Kempson, 1949) were placed nine metres apart, with trap stations at intervals of six metres along each line. Two traps facing the mid-line of the transect were placed at each station. The catchment area is approximately 0.4 hectare (Ashby, 1967). This catchment, in addition to the area within the trap transect, consists of the periphery extending beyond the rows of traps by a distance equal to the mean home range (23m) of the individuals in the population. The traps were pre-baited for two days with grain, set on the morning of the third day, and were visited twice daily for the next two days. A second capture of an individual within each of the periods of 24 hours was ignored.

Details of the vegetation on the sites, recorded prior to excavation, are summarised in Table 2, and the data obtained from soil profiles dug close to each site are given in Tables 3 to 7.

Consideration was given as to whether, instead of choosing areas of the size described, individual square metres should have been taken at random throughout the wood. This would have simplified statistical analysis of the results in some respects, but the extent of some of the tunnels making up the "residential" and "non-residential" tunnel systems was such as to make determination of their length and other physical characteristics impossible from such small areas.

TABLE 2

COMPARISON OF THE VEGETATION AT THE EXCAVATION SITES GIVING COVER ABDUNDANCE VALUES (AUGUST 1969)

Species	Site				
	I	II	III	IV	V
Herbs					
Pteridium aquilinum	5	3		+	2
Rubus fruticosus	3			1	2
Holcus mollis	1	2			3
Deschampsia flexuosa	2		+		+
Endymnion non-scriptus		3			4
Milium effusum		1		3	
Lonicera pericylymenum	2			1	
Dryopteris dilatatum		+		2	
Epilobium angustifolium	+	2			
Vaccinium myrtilus			5		
Oxalis acetosella				5	
Hedera helix					3
Polypodium vulgare			+		
Trees					
Acer pseudoplatanus	3	4		3	
Larix sp.	5			+	4
Fagus sylvaticus		4		5	
Quercus petraea	3		5		
Betula pubescens	3		+	+	
Sambucus nigra					+

Key: + Sparse, very low cover.
1. Common, small cover.
2. Either 5-25% cover or cover low, but high numbers.
3. 25-50%, any number of individuals.
4. 50-75%, any number of individuals.
5. 75-100%, any number of individuals.

TABLE 3
SOIL PROFILE AT SITE I

Horizon	Upper Boundary Depth (cm)	Lower Boundary Depth (cm)	Mean Thickness (cm)	Description
Ao	0	9	9	Friable. Larch needles
A1	9	16	7	Good crumb structure
A2	16	36	20	Sandy loam. Some iron mottling.
B1	36	-	-	Well-drained loam

TABLE 4
SOIL PROFILE AT SITE II

Horizon	Upper Boundary Depth (cm)	Lower Boundary Depth (cm)	Mean Thickness (cm)	Description
Ao	0	8	8	Wet mat of beech and sycamore leaves. Little decomposition.
A1	8	10	2	Friable.
A2	10	35	25	Slight podsolisation
B1	35	-	-	Poorly-drained loam

TABLE 5

SOIL PROFILE AT SITE III

Horizon	Upper Boundary Depth (cm)	Lower Boundary Depth (cm)	Mean Thickness (cm)	Description
Ao	0	3.5	3.5	Loose oak-leaf mould.
A1	3.5	8.5	5	Blackish soil, poor crumb structure.
A2	8.5	34	25.5	Sandy soil, some humic material.
B1	34	-	-	Sandy loam, some iron mottling.

TABLE 6.

SOIL PROFILE AT SITE IV

Horizon	Upper Boundary Depth (cm)	Lower Boundary Depth (cm)	Mean Thickness (cm)	Description
Ao	0	7.5	7.5	Moist, matted sycamore, birch and beech leaves.
A1	7.5	15	7.5	Black mor soil.
A2	15	45	30	Sandy loam, some iron mottling.
B1	45	-	-	Unctuous, heavy loam.

TABLE 7

SOIL PROFILE AT SITE V

Horizon	Upper Boundary Depth (cm)	Lower Boundary Depth (cm)	Mean Thickness (cm)	Description
Ao	0	10	10	Friable. Larch needles.
A1	10	17.5	7.5	Loose, mull-like soil. Good crumb structure.
A2	17.5	27.5	10	Sandy loam, some iron mottling.
A3	27.5	42.5	15	Slight podsolisation.
B1	42.5	-	-	Heavy loam. Signs of leaching.

2.3 ESTABLISHING OCCUPATION OF BURROWS ON SITE I.

The entrance holes on Site I were located, and then an attempt was made to establish occupancy of the burrows by using Longworth traps, tracking rolls and direct observation.

(a) Trapping.

Site 1 was initially examined for obvious entrance holes, The litter layer was not disturbed so that any entrances temporarily blocked or concealed by leaves were not revealed at that stage. Longworth traps were placed adjacent to each hole, set and baited with grain. They were inspected the following morning and the captured animals were marked, recorded and released. The traps were re-set and visited again 24 hours later. Cleminson (personal communication) used this technique and assumed that any individual trapped had been resident in the tunnel adjacent to the trap. However the results obtained in this study and presented in section 3.2(a), suggest that this method may not be very reliable.

(b) Observation of movement after release.

Initially, any individual trapped at an entrance hole was released directly after being examined and its movements observed. The results, which are described in section 3.2(b), suggested that more reliable results would be obtained by returning the captured individual to the trap for five minutes after examination to allow it to become less excited. When the trap door was re-opened the animal could leave the trap when it chose to do so. Observation on animals released in this manner are also given in section 3.2.(b).

(c) Tracking.

Tracking rolls were made of waterproof paper which was coated with silicone, dusted with french chalk and rolled into cylinders. A roll was inserted into each entrance hole so that it could only be marked by animals either entering or leaving the burrow system. Since most tunnels sloped steeply away from the entrance holes, the rolls were often pitched at a steep angle and in some cases were placed vertically. Consequently the prints obtained were a series of short, fine scratches produced by the animals' claws running from one end of the cylinder to the other, and it was not possible to differentiate the tracks of the two species. The last column of Table 28 indicates which of holes 1 to 53 were visited over a period of three days. It can be seen that 31 of the holes were to some degree used over this period.

2.4 EXCAVATION.

(a) Excavation technique.

The boundary of each site was marked by pegs placed one metre apart. Before excavation began the superficial vegetation was cut down to within about one cm of the ground surface. The litter was examined for concealed entrance holes and litter runs, and if any of the latter were found they were followed and recorded before digging commenced.

To prevent damage to litter runs and shallow tunnels, care was taken to avoid treading or kneeling on unstudied ground. For this reason the investigation of a new site was always begun along the lower border and continued up the slope. Two or three square metres were cleared of vegetation at a time. The litter runs were followed and tunnel systems excavated before attention was transferred to a new part of the site. In this way accidental destruction of the burrows was minimised.

The litter runs were followed by lifting the litter with the fingers and turning it to one side. Care had to be taken to avoid producing new "runs" while following their course, as the fingers could easily be pushed through their walls. On removal of the complete litter layer the course of the runs could often be seen as depressions in the surface of the mineral soil, which provided confirmation in doubtful cases.

The excavation of tunnels in the soil was begun at an entrance hole. The direction of the tunnel was ascertained, and the tunnel roof supported by the fingers while a vertical section was made with a trowel. This allowed the soil to be lifted out without debris falling

CHAPTER 3 : RESULTS.

into the tunnel. It was particularly important to prevent this when the passage sloped steeply, as under these circumstances it was liable to get blocked. When the excavation of one section had been completed, the direction of the next section was ascertained and the soil removed as before, the position of any side passages being marked by pegs.

It was found that the deeper tunnels were often crossed by more superficial ones. To avoid destroying the latter, digging was not carried out on those sections of tunnel that exceeded a depth of 15cm until the excavation of the shallower passages had been completed. Exposing the deeper passages required a considerable amount of digging as several horizontal sections had to be taken before a vertical cut could be made. When tree roots were encounted, attempts were made to clear the soil from around them, but often they had to be cut and removed.

(b) Mapping and recording.

The tunnel systems were recorded on a field map at a scale of 1:10. A one square metre quadrat, subdivided into four, was placed over the particular section being mapped as an aid to accurate representation of the tunnels exposed. The width and height of all entrance holes were recorded prior to commencement of digging. The depth of individual tunnels, measured from the ground surface to the tunnel floor, and the width and height of the tunnels were recorded at approximately 15cm intervals. The tunnels that continued beyond the confines of the site were followed to provide data on the size of the "residential" and "non-residential" tunnel systems, but the extra length was not included in the total length per site given in Table 12.

3.1. TRAPPING AS AN INDICATION OF RODENT ABUNDANCE.

(a) Estimation of the abundance of *Apodemus* and *Clethrionomys* in the region of site I.

The traps were arranged in the standard double line as described in section 2.2, and the trapping results are recorded in Table 8.

For a reliable estimate of the population, the percentage of marked animals recaptured on the second day should not in the case of *Clethrionomys* differ significantly from 51% of those marked on the first day, on the basis of the random variability following a poisson distribution. (This value was derived from Ashby, 1967, p418, Table 11, on the basis of the results of trapping several hundred animals over a long series of trapping sessions). Table 8 shows that of fourteen *Clethrionomys* marked on the first day in the present study, eight were recaptured on the second. This recapture proportion does not differ significantly from the value of 51% calculated by Ashby. Two days of trapping would be expected to capture 76% of the population (Ashby, 1967): therefore the eighteen *Clethrionomys* captured over the two days of trapping may be taken as representing this percentage of the population. It was consequently estimated that the density of *Clethrionomys* in Site I was in the order of 60 per hectare. The density of *Apodemus* would appear to have been low. Only four captures, all of different individuals, were made and at this level of capture rate the effect of random variability makes the confidence limits very large in relation to the mean. The trapping indicates very tentatively a density in the order of thirteen per hectare. This accords with the levels of density observed by Ashby (1967) in the late spring and early summer in Houghall Wood.

TABLE 8

TRAPPING RESULTS WITH 40 LONGWORTH TRAPS LAID OUT AS DESCRIBED IN SECTION 2.2. (TRAP NOS. OMITTED IF NO CATCH WAS MADE)

Trap No.	Trap day 1 a.m.	Trap day 1 p.m.	Trap day 2 a.m.	Trap day 2 p.m.
1	Cleth(m)			
2		Apod.(m)		
7			Cleth.(m)*	Cleth.(f)
8		Apod.(m)		Apod.(m)
9		Cleth.(f)		
13	Cleth.(m)			
15		Cleth.(m)		
16		Cleth.(m)		
17				Cleth.(m)*
18		Cleth.(f)		
19				Cleth.(f)*
20	Cleth.(f)			
21	Cleth.(f)		Cleth.(m)	
22				Cleth.(f)*
24	Cleth.(m)			
25		Cleth.(m)		
26				Cleth.(m)
30				Cleth.(m)*
32	Cleth.(m)	Cleth.(f)		
33			Cleth.(m)*	
34				Apod.(m)
35				Cleth.(f)*
37	Cleth.(m)			
38			Cleth.(m)*	Cleth.(m)
39		Cleth.(f)		

Key:- Cleth: *Clethrionomys glareolus*
Apod: *Apodemus sylvaticus*
(m): male
(f): female
* : individual previously marked.

(b) Record of previous trapping.

An indication of the abundance of rodents during the period 1954-64 is given by the mean number of captures per trapping session in each half transect recorded by Ashby (1967) and given in Table 9. These figures were used to estimate the relative population levels of *Apodemus* and *Clethrionomys* which are described for each site in section 2.1(b) and summarised in Table 1.

TABLE 9

MEAN NUMBER OF CAPTURES OF RODENTS PER TRAPPING SESSION OF TWO DAYS PER HALF TRANSECT. OCTOBER 1954 TO MAY 1964 (Table modified from Ashby 1967, Table V)

TRANSECT	1		2		3		Mean
	U	L	U	L	U	L	
Excavation Site		V	(II)*		III	IV	
Clethrionomys							
Oct.1954 - May 1959	3.6	11.9	1.7	5.5	4.2	1.5	4.7
Oct.1959 - May 1964	10.1	15.5	1.0	4.6	3.9	3.8	6.4
Apodemus							
Oct.1954 - May 1959	8.1	7.7	8.7	8.8	7.3	4.2	7.4
Oct.1959 - May 1964	4.9	6.9	8.9	7.7	6.9	4.3	6.6

Key: U: Upper half of transect
L: Lower half of transect
*: Site II nearby.

3.2 ESTABLISHING OCCUPATION OF BURROWS IN SITE I

(a) Trapping at entrance holes.

TABLE 10

TRAPPING RESULTS TO ESTABLISH OCCUPANCY
(TRAPS LAID OUT AS DESCRIBED IN SECTION 2.3(a).
TRAP NO. OMITTED IF NO CATCH WAS MADE)

Trap No. as hole No. on Map 1	Trap. Day 1. Species and mark	Trap. Day 2. Recaptures. Species and mark
5		Apod.(m) L.H.2
6	Cleth.(m) L.H.1	
11	Apod.(m) L.H.2	
13	Apod.(m) L.H.3	Apod.(m) L.H.3
15	Apod.(f) L.H.4	Apod.(m)
29		Cleth.(m) L.H.1
38		Apod.(m)
42		Cleth.(m)
52		Apod.(f)
53	Cleth.(m) L.H.5	Cleth.(m)

Key: L.H.1: Left hind foot 1st digit.
(other abbreviations as used in Table 8).

Table 10 shows that individuals trapped and marked in traps placed adjacent to particular numbered holes (for reference see map I) may be recaptured next day in traps adjacent to quite different ones. One Apodemus was trapped at entrance hole No.11 which had a tunnel of only 8cm, and which was therefore unlikely to have been the tunnel from which it had emerged. In view of these findings it is suggested that this method is unsatisfactory for establishing the occupant of a burrow.

(b) Direct observation.

When the details of the animals trapped at the entrance holes had been recorded, they were released. Both Apodemus and Clethrionomys made their escape extremely rapidly, and in nearly every case disappeared into dense cover outside the study area. Following animals directly after handling therefore appears to be unsatisfactory in establishing residency. One individual Apodemus did however remain within the area searching for food. It entered the largest tunnel system by means of hole 18 (see map I) and emerged one minute later at hole 27: it ate some of the bait scattered around the entrance to the hole and then re-entered it. This behaviour is unusual for Apodemus which is chiefly nocturnal in habit, and may have been elicited by hunger or was possibly a displacement activity due to confinement in the trap.

The release technique was modified as described in section 2.3(b), and the results obtained from using this modified technique are as follows. Three individuals were observed. In each case they emerged cautiously from the trap and moved a short distance from the release point before disappearing down a tunnel entrance, passing several holes on the way. Their movement appeared to be normal, and not to have been unduly affected by trap confinement and handling. One Apodemus male and one Apodemus female which had been returned to the traps in which they had been caught, those at holes nos. 41 and 43 respectively, were seen to move directly to hole 82 and enter it; the distances travelled were 95cm and 145cm. The third individual observed was a Clethrionomys male caught at hole 21; it travelled more than 150cm before entering hole 38.

3.3 GENERAL RESULTS.

The tunnel systems on the five sites are shown in Maps 1-5, and the data concerning the number and length of tunnels and number of exits are summarised in Tables 11 and 12. Table 13 records the mean values of tunnel and entrance hole diameter and transverse-sectional area, and tunnel and chamber depth. In table 11 the data are divided into three categories relating to "residential" and "non-residential" tunnels and "other tunnels", as defined in section 1.3. In order that full details of the lengths of these tunnel types should be recorded in table 11, any data obtained from beyond the site boudaries are included. There was however no need for this additional information to be included in table 12, as it deals with the tunnel systems collectively.

The results in tables 12 are expressed as per site and per hectare. This is to allow direct comparison with the figures of Cleminson (personal communication) who used study areas of a different size, but who expressed his figures as per hectare.

Various features of the tunnel systems and entrance holes are examined statistically in sections 3.4 and 3.5, and the results as a whole are considered in the discussion.

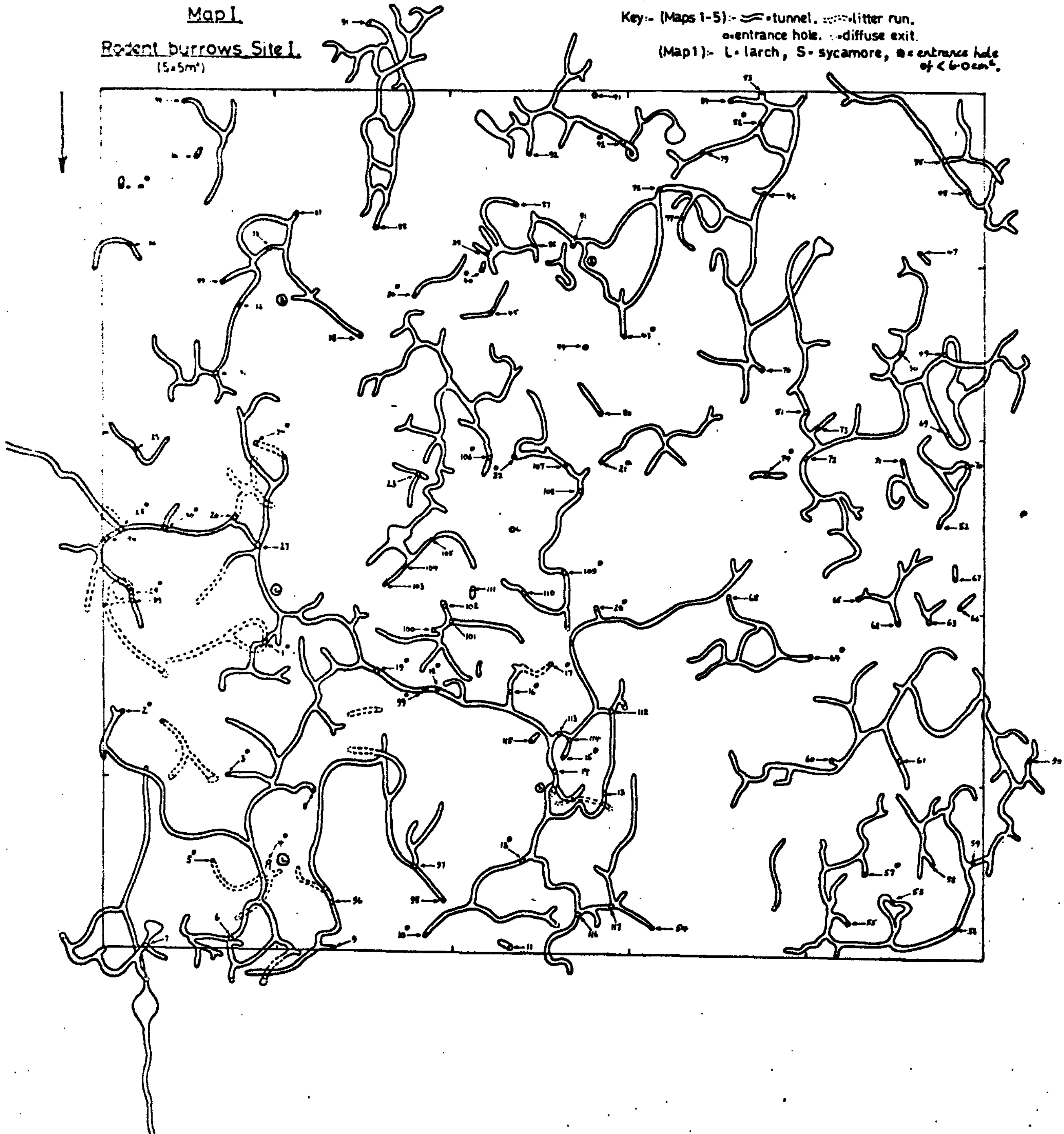
MAPS 1-5 SHOWING SMALL-RODENT BURROWS IN SITES I - V.

Entrance hole numbers are shown on the maps, and arrows show the direction of downward slope.

Map I.

Rodent burrows Site I.
(5x5m²)

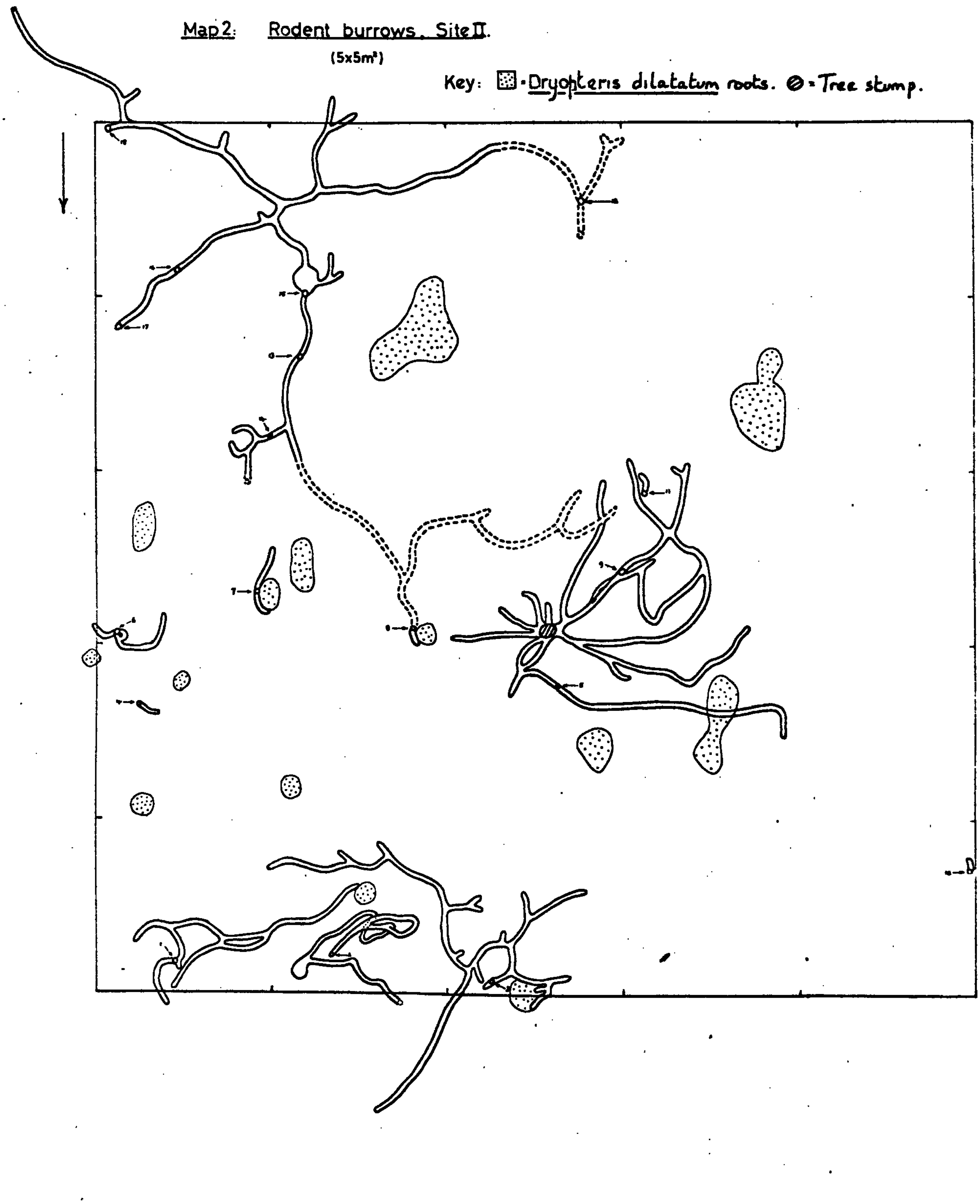
Key:- (Maps 1-5):- ═ = tunnel, ┄ = litter run.
o = entrance hole, ⋮ = diffuse exit.
(Map 1):- L = larch, S = sycamore, ⊛ = entrance hole of < 6·0 cm².



Map 2: Rodent burrows. Site II.

(5x5m²)

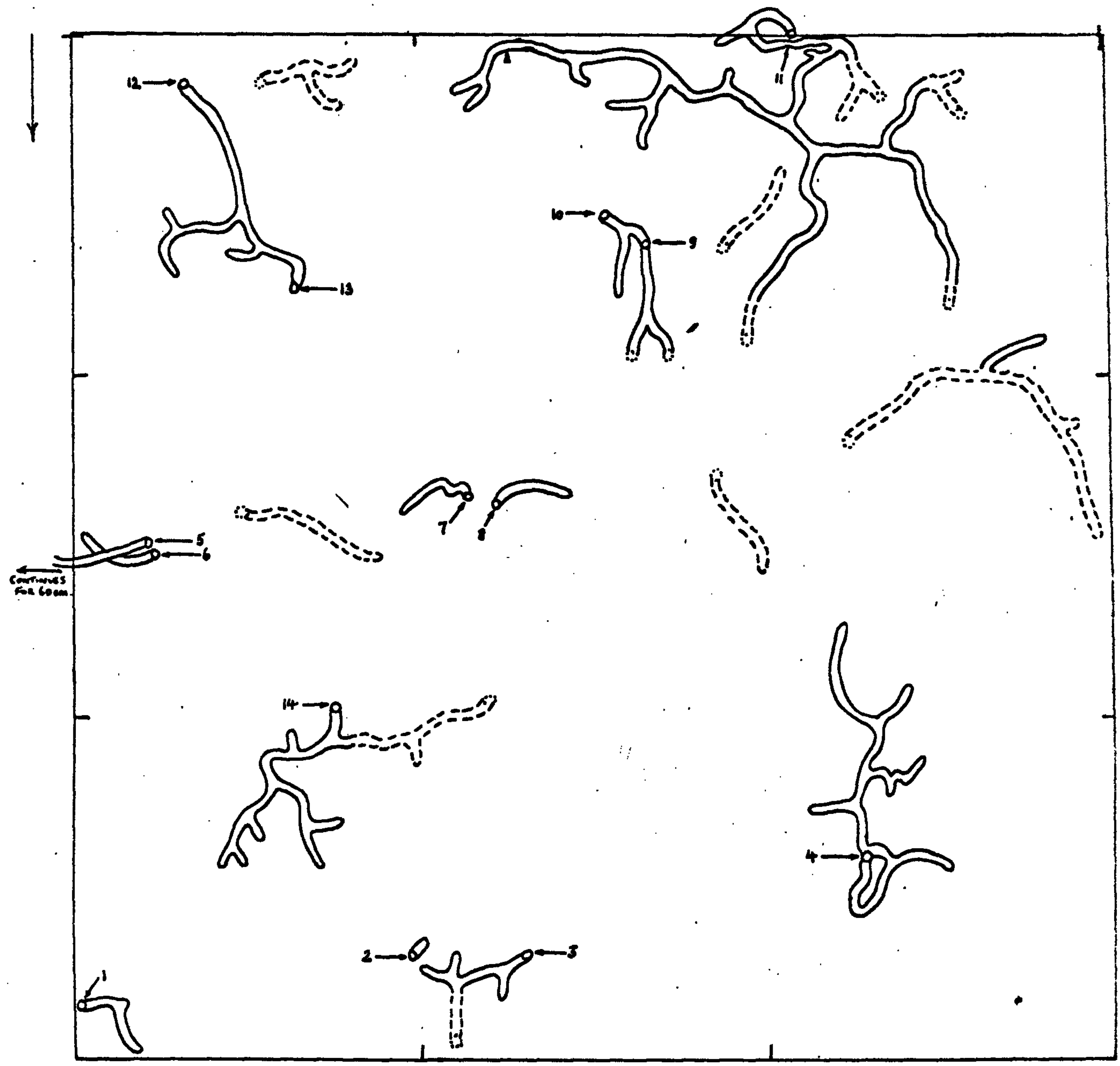
Key: ▨ = *Dryopteris dilatatum* roots. ⊘ = Tree stump.



Map 3:

Rodent burrows. Site III.

(3x3m²)



Map 5:

Rodent burrows,
Site V. (3x3m²).

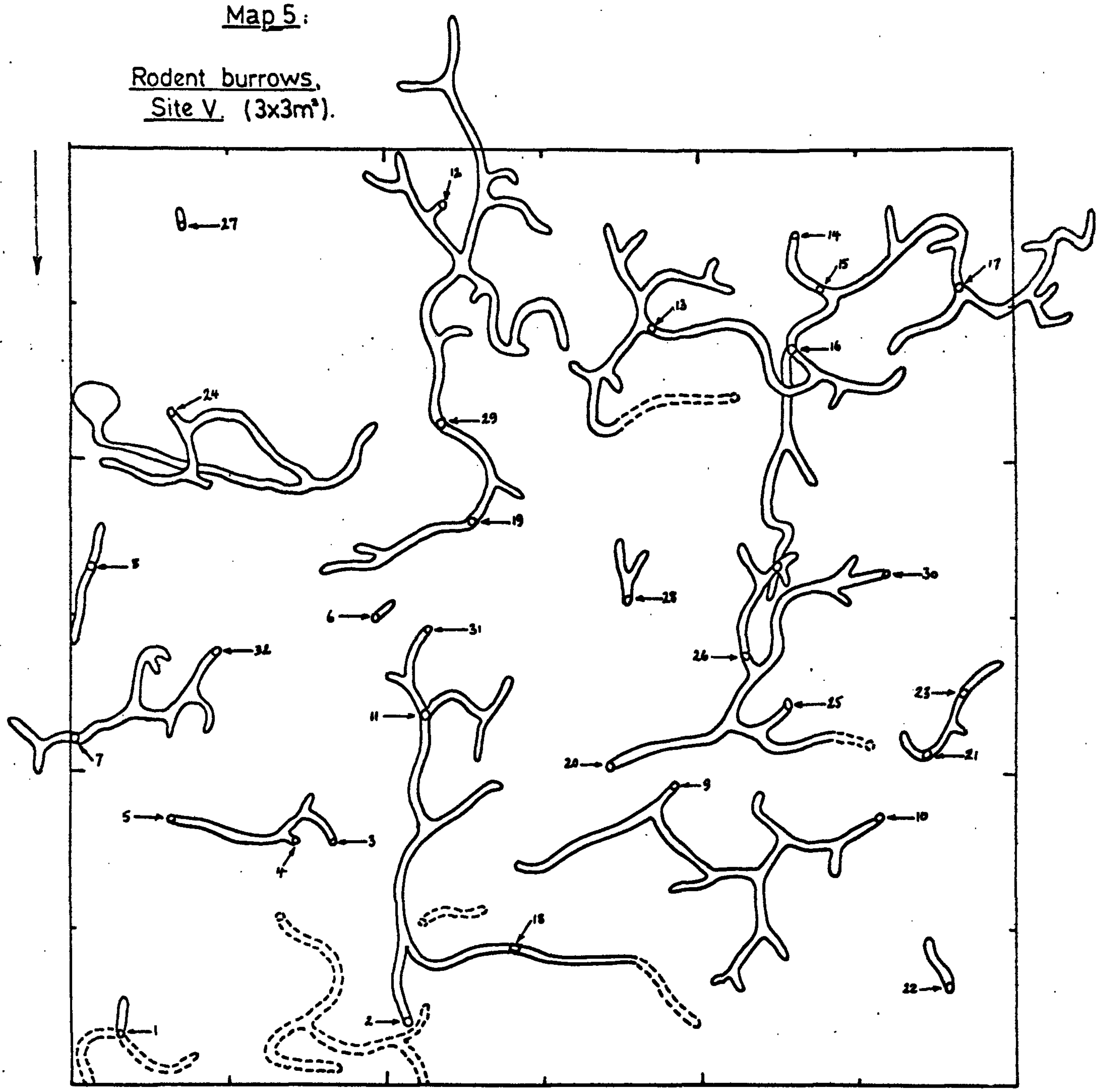


TABLE 11

THE CHARACTERISTICS OF "NON-RESIDENTIAL" AND "RESIDENTIAL" TUNNEL SYSTEMS AND "OTHER TUNNELS" ON INDIVIDUAL SITES.

	Site I ($25m^2$)	Site II ($25m^2$)	Site III ($9m^2$)	Site IV ($9m^2$)	Site V ($9m^2$)
"Non-Residential" Tunnel Systems:					
Number of systems	10	3	4	2	6
Total tunnel length (m)	43.3	16.5	7.6	27.0	19.1
Number of holes	59	4	6	6	23
Number of diffuse exits	7	0	6	7	2
Total number of exits	66	4	12	13	25
Mean tunnel length per exit (m)	0.7	4.1	0.6	2.1	0.8
"Residential" Tunnel Systems:					
Number of systems	6	2	0	0	1
Total tunnel length (m)	41.5	9.4	-	-	2.2
Number of holes	35	8	-	-	1
Number of diffuse exits	3	3	-	-	0
Total number of exits	38	11	-	-	1
Mean tunnel length per exit (m)	1.1	0.9	-	-	2.2
"Other Tunnels":					
Number of tunnels	24	6	8	5	7
Total tunnel length (m)	7.6	1.6	3.1	1.6	1.8
Number of holes	23	6	8	5	8
Number of diffuse exits	1	0	3	1	0
Total number of exits	24	6	11	6	8
Mean tunnel length per exit (m)	0.3	0.3	0.3	0.3	0.2

TABLE 12

THE CHARACTERISTICS OF LITTER RUNS AND ALL TYPES OF SMALL-RODENT TUNNELS CONSIDERED COLLECTIVELY ON INDIVIDUAL SITES.

	SITE I		SITE II		SITE III		SITE IV		SITE V	
	Study Area $25m^2$	Per hectare	Study Area $25m^2$	Per hectare	Study Area $9m^2$	Per hectare	Study Area $9m^2$	Per hectare	Study Area $9m^2$	Per hectare
Underground Tunnels:										
Number of tunnels	40	16,200	11	4,500	12	13,500	7	7,900	14	15,700
Total tunnel length (m)	80.9	32,400	25.0	10,000	10.4	11,700	17.3	19,500	21.7	24,300
Mean tunnel length (m)	2.0	-	2.3	-	0.9	-	2.5	-	1.6	-
Mean tunnel length per m^2 (m)	3.2	-	1.0	-	1.2	-	1.9	-	2.4	-
Number of holes	117	47,400	18	6,300	14	15,700	11	12,400	32	36,000
Number of diffuse exits	11	4,500	3	1,200	9	10,100	8	9,000	2	2,000
Total exits	128	51,800	21	7,400	23	25,900	19	21,400	34	38,200
Mean tunnel length per exit (m)	0.6	-	1.2	-	0.5	-	0.9	-	0.6	-
Number of chambers	8	3,200	2	800	0	0	0	0	1	1,100
Litter Runs:										
Total run length (m)	5.5	2,200	4.1	1,700	3.6	4,100	1.7	1,900	2.8	3,100

TABLE 13

THE MEAN VALUES FOR INDIVIDUAL SITES OF ENTRANCE HOLE AND TUNNEL DIAMTER AND TRANSVERSE-SECTIONAL AREA, AND TUNNEL AND CHAMBER DEPTH.

Parameter	Mean Values (cm)				
	Site I	Site II	Site III	Site IV	Site V
Entrance hole width	3.2	3.0	2.9	3.0	3.1
Entrance hole height	3.0	2.6	2.8	2.8	2.9
Entrance hole transverse-sectional area (cm^2)	7.8	6.4	6.4	6.7	7.1
Tunnel width	4.4	3.6	3.1	3.8	3.6
Tunnel height	3.6	3.2	2.8	3.2	3.3
Tunnel transverse-sectional area (cm^2)	12.4	9.0	6.8	9.8	9.5
Tunnel width (junction)	4.4	4.0	3.3	3.9	3.8
Tunnel width (intermediate sections)	4.2	3.0	2.9	4.1	3.4
Tunnel depth	8.4	13.9	9.2	6.3	9.2
Chamber depth: to floor	18.0	19.5	-	-	15.0
Chamber depth: to roof	10.7	10.3	-	-	5.5

The method used in obtaining the above measurements is given in section 2.4(b).

3.4 DISTRIBUTION OF ENTRANCE HOLES.

Comparison of the distribution of holes with the ideal Poisson distribution.

In the case where a number of holes are randomly distributed over an area divided into equal squares, the number of holes per square would have a Poisson distribution. To test whether in fact the observed distribution was random, or whether there was a definable pattern of aggregation or over-dispersion, the following exercise was conducted.

The observed distribution of holes, i.e. the numbers of square metres with 0, 1, 2 etc. holes, in each study area was compared with the ideal Poisson distribution. (The graph for site 1 only is shown graphically in Fig.8 in the appendix.)

If the frequency distribution of number of holes per unit area followed a Poisson distribution, then the chance of obtaining x holes on a given m^2 would be given by the following formula:

$$\frac{e^{-m} \cdot m^{x}}{x!}$$

where e=base of natural logs.
m=population mean (The best estimate of which is the sample mean)
x=expected no.of holes from 0, 1, 2 .... n.

It was possible in the case of sites I and II to test the goodness of fit of the data concerning the distribution of holes to a Poisson distribution by using the Chi^2 test. Certain of the data had to be grouped to ensure that in any one category the expected number of squares did not fall below five. The observed and expected data for these two sites is given in Tables 14 and 16, and as grouped for the Chi^2 test in Tables 15 and 17. The number of square-metre grid squares was insufficient in Sites III - V for the Chi^2 test to be applied. However the observed and expected number of metre squares with x holes for these sites is given in Tables 25-27 of the appendix.

TABLE 14

THE OBSERVED AND EXPECTED NUMBER OF SQUARE METRES WITH X HOLES ON SITE I

Number of holes (x) in each m^2.	Observed number of m^2 with x holes	Expected number of m^2 with x holes
0	1	0.2
1	2	1.1
2	3	2.5
3	2	3.9
4	1	4.5
5	8	4.2
6	2	3.3
7	3	2.2
8	1	1.3
9	2	0.7
10	0	0.3

TABLE 15

THE OBSERVED AND EXPECTED NUMBER OF SQUARE METRES WITH X HOLES ON SITE I (TABLE CONDENSED FROM TABLE 14 FOR THE CHI^2 TEST.)

Number of holes in each m^2	Observed no. of squares.	Expected no. of squares.
0,1,2 or 3	8	7.7
4 or 5	9	8.7
6,7,8,9,10 or more	8	8.6

For Site I: $Chi^2 = 0.04$, 2d.f. P= <0.98

TABLE 16

THE OBSERVED AND EXPECTED NO. OF SQUARE METRES WITH X HOLES IN SITE II

Number of holes (x) in each m^2.	Observed no. of squares with x holes	Expected no. of squares with x holes
0	10	12.1
1	12	8.7
2	3	3.1
3	0	0.7
4	0	0.3
5	0	0.02

TABLE 17

THE OBSERVED AND EXPECTED NO. OF SQUARE METRES WITH X HOLES ON SITE II (TABLE CONDENSED FROM TABLE 16 FOR THE CHI^2 TEST)

Number of holes in each M^2	Observed no. of squares	Expected no. of squares
0	10	12.1
1 or more	15	12.9

For site II: Chi^2= 0.7, 1 d.f., P= < 0.5

In neither site I nor site II was the difference between the observed and expected figures significant at the level of p=0.05. However this may only be taken as an indication that there is no evidence of the distribution being non-random, given the data available and using one m^2 as the unit size. Studies over a larger area and with a different size of unit area might reveal a deviation from a random distribution that the present study could not detect.

A further test which was applied to the data from all five sites, uses the ratio of variance to mean as an indication of the nature of the distribution. This ratio is unity in the case of a Poisson distribution; aggregation is indicated if the ratio exceeds unity, while if the ratio is less than one, an overdispersed distribution is suggested. A significant deviation is present if the ratio exceeds 1.45 or is less than 0.55 respectively (Glasgow, 1939).

TABLE 18.

THE VARIANCE:MEAN RATIO FOR THE NUMBERS OF HOLES PER METRE SQUARE FOR INDIVIDUAL SITES

Site	Mean no.holes per m^2	Variance	Variance: mean ratio
I	4.68	5.42	1.16
II	0.72	0.44	0.61
III	1.55	0.47	0.30*
IV	1.22	1.95	1.60*
V	3.56	1.14	0.30*

Key: *denotes values departing significantly from unity.

This test gives no evidence suggesting that the distribution of holes on sites I and II was not random (which agrees well with the results of the Chi^2 test): but suggests that on sites III and V the holes were overdispersed, and that on site IV there was a slight aggregation of holes.

3.5 DIMENSIONS OF ENTRANCE HOLES AND TUNNELS.

(a) Width : Height Ratio.

The data for calculating the width:height ratios collected as described in section 2.4(a) are given in detail in Tables 28-32 and 33-37. From this data the ratios of width to height were calculated, and the standard error (S.E.) of the mean (M) derived for the entrance holes and tunnels on each site. If M-2xS.E. is greater than one then they are significantly dorso-ventrally flattened. The figures obtained, which are shown in Table 19, indicate that there was evidence of statistically significant dorso-ventral flattening in every case except for the entrance holes on sites III and IV, and in these cases also the mean width was still greater than the mean height (see Table 13).

TABLE 19

MEAN LESS 2xS.E. OF WIDTH:HEIGHT RATIO OF ENTRANCE HOLES AND TUNNELS.

Mean minus 2xS.E.	SITE				
	I	II	III	IV	V
Entrance holes	1.06	1.06	0.96	1.00	1.04
Tunnels	1.16	1.09	1.05	1.10	1.06

(b) Transverse-sectional area.

To investigate the possibility that Apodemus and Clethrionomys construct entrance holes and tunnels with transverse-sectional areas peculiar to their species, the Kolmogorov-Smirnov test was applied to the data given in Tables 28 to 37 of the appendix. The Kolmogorov-Smirnov test is a reliable technique for finding a confidence band for the distribution F(x) of a continuous variable. In this test the readings for each parameter and site are arranged according to magnitude i.e. $x_1, x_2, \ldots\ldots\ x_r$, and the ordered sample used to obtain the confidence band (a) for F(x) at the 5% level using the following formula :-

$$"a" = \frac{1.36}{\sqrt{n}} \quad \text{where } n = \text{sample size.}$$

(The construction of the confidence band using "a" is shown in Fig.2.)

$$F(xr) = \Phi\left(\frac{xr-m}{s}\right)$$

where x=rthvalue of the ordered sample
m=mean transverse-sectional area of holes or tunnels.
s=standard deviation of the samples from the mean

$$\Phi(=t) = \tfrac{1}{2} + \int_0^t \phi\,(t)dt, \text{ if } t > 0.$$
$$\tfrac{1}{2} - \int_0^{-t} \phi\,(t)dt, \text{ if } t < 0.$$

Φ values are computed from normal area tables, as given in Hoel (1954), and plotted against $\frac{r}{n}$: where r is the numerical position in the ordered sample series. If the constructed line falls within the confidence band "a", then the readings may be assumed to represent one normal distribution, while if it extends beyond these limits the presence of more than one single distribution is indicated.

The Kolmogorov-Smirnov test provides no evidence that the transverse-sectional areas of both the entrance holes and tunnels represented more than one normal distribution, with the exception of the entrance holes in site I (see Fig.2). In this case, the histogram of frequency

FIG. 2: THE KOLMOGOROV-SMIRNOV TEST FOR ENTRANCE HOLE TRANSVERSE-SECTIONAL AREAS ON SITE I

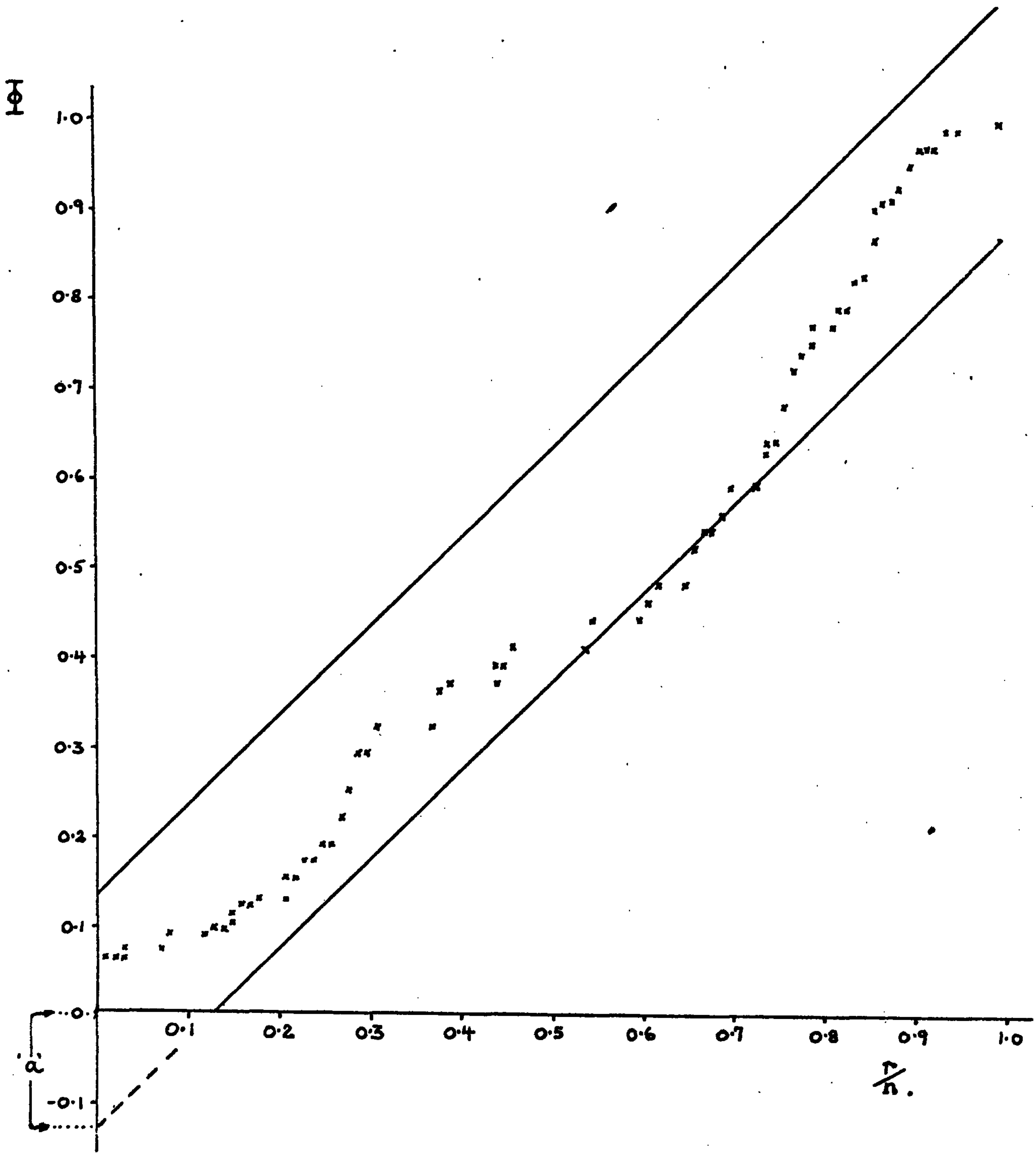


FIG. 3: HISTOGRAM SHOWING FREQUENCY OF OCCURRENCE OF ENTRANCE HOLE TRANSVERSE-SECTIONAL AREAS ON SITE I.

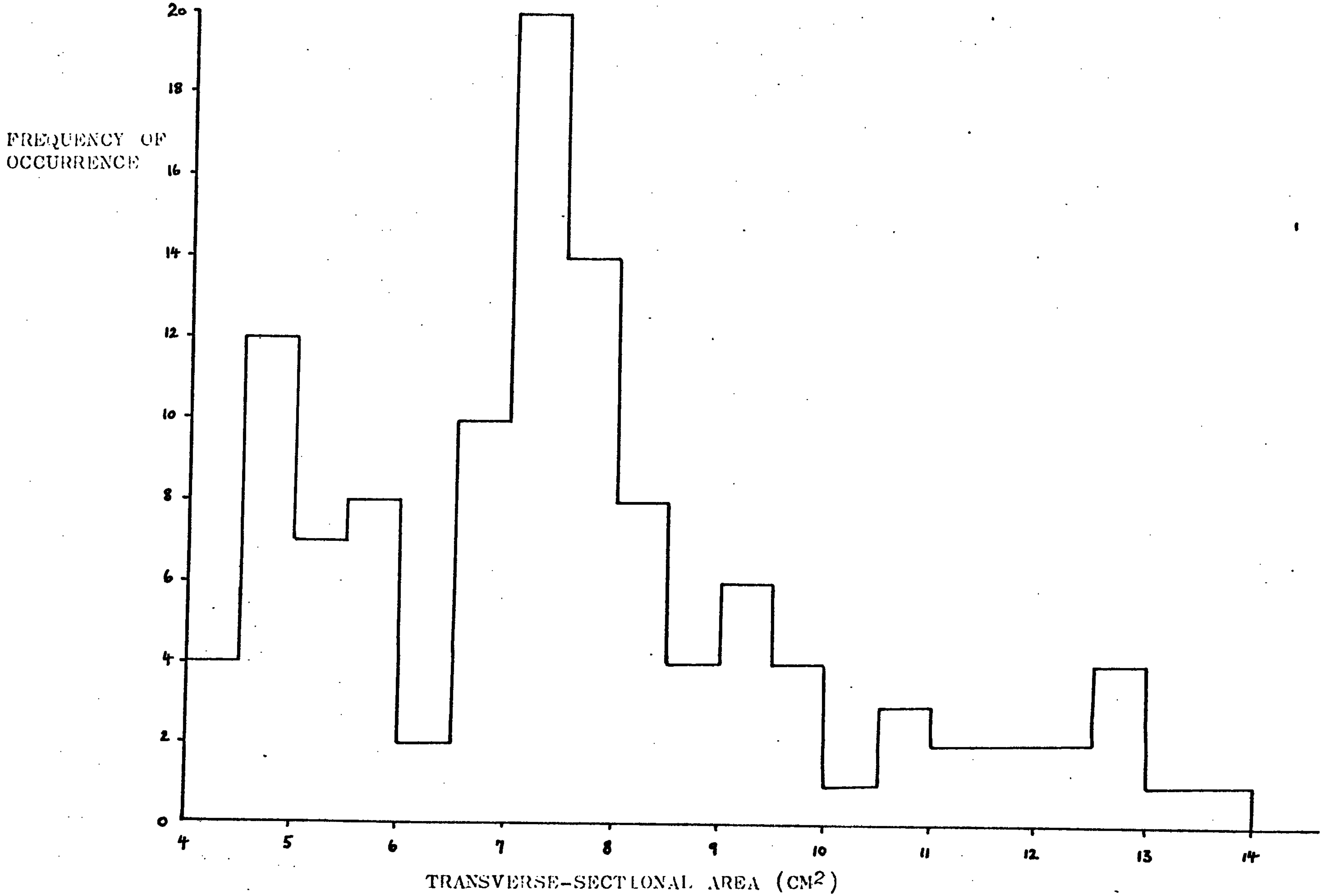


FIG. 3(a): HISTOGRAMS SHOWING FREQUENCY OF OCCURRENCE OF ENTRANCE HOLE TRANSVERSE-SECTIONAL AREAS ON SITES II-V.

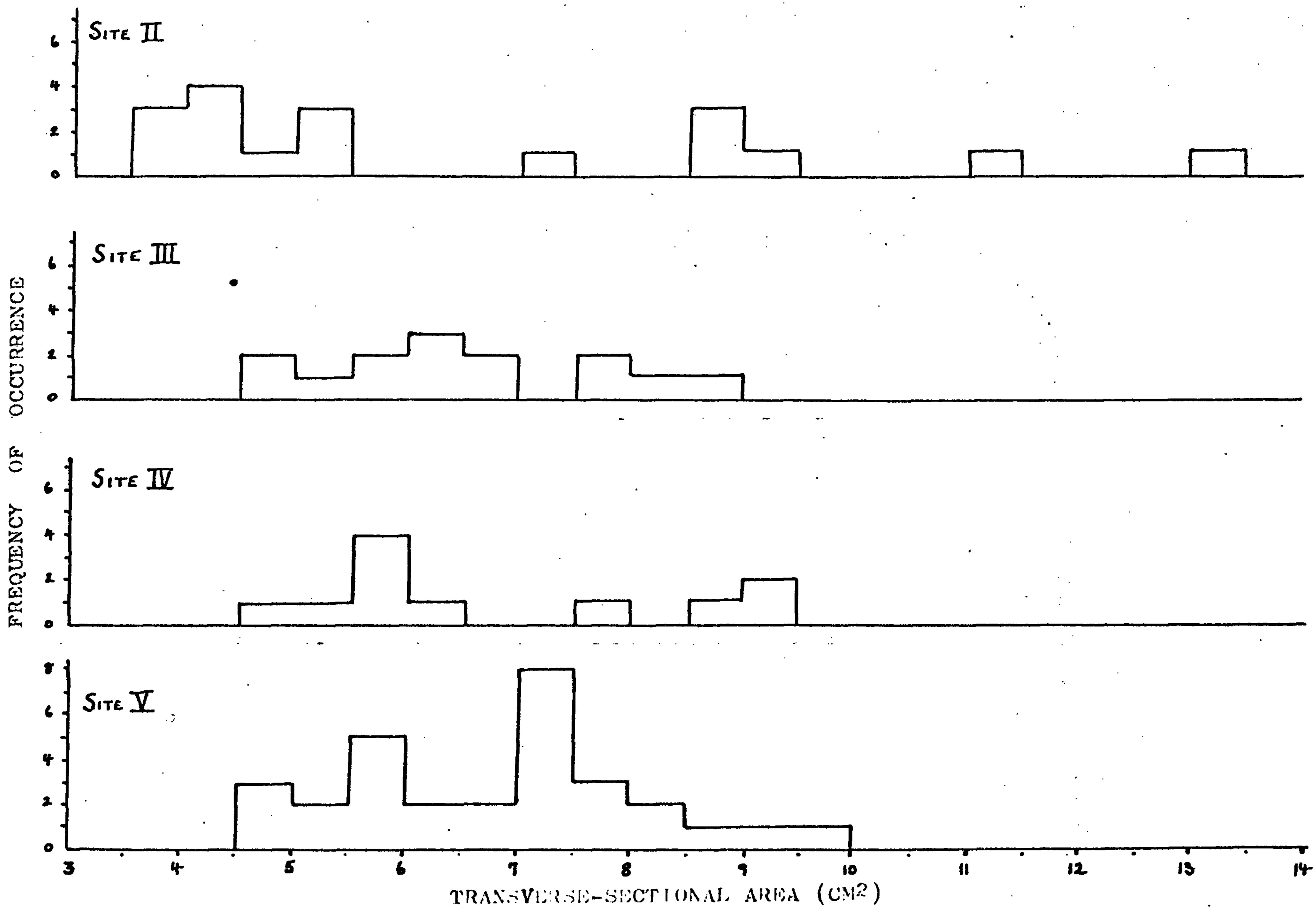
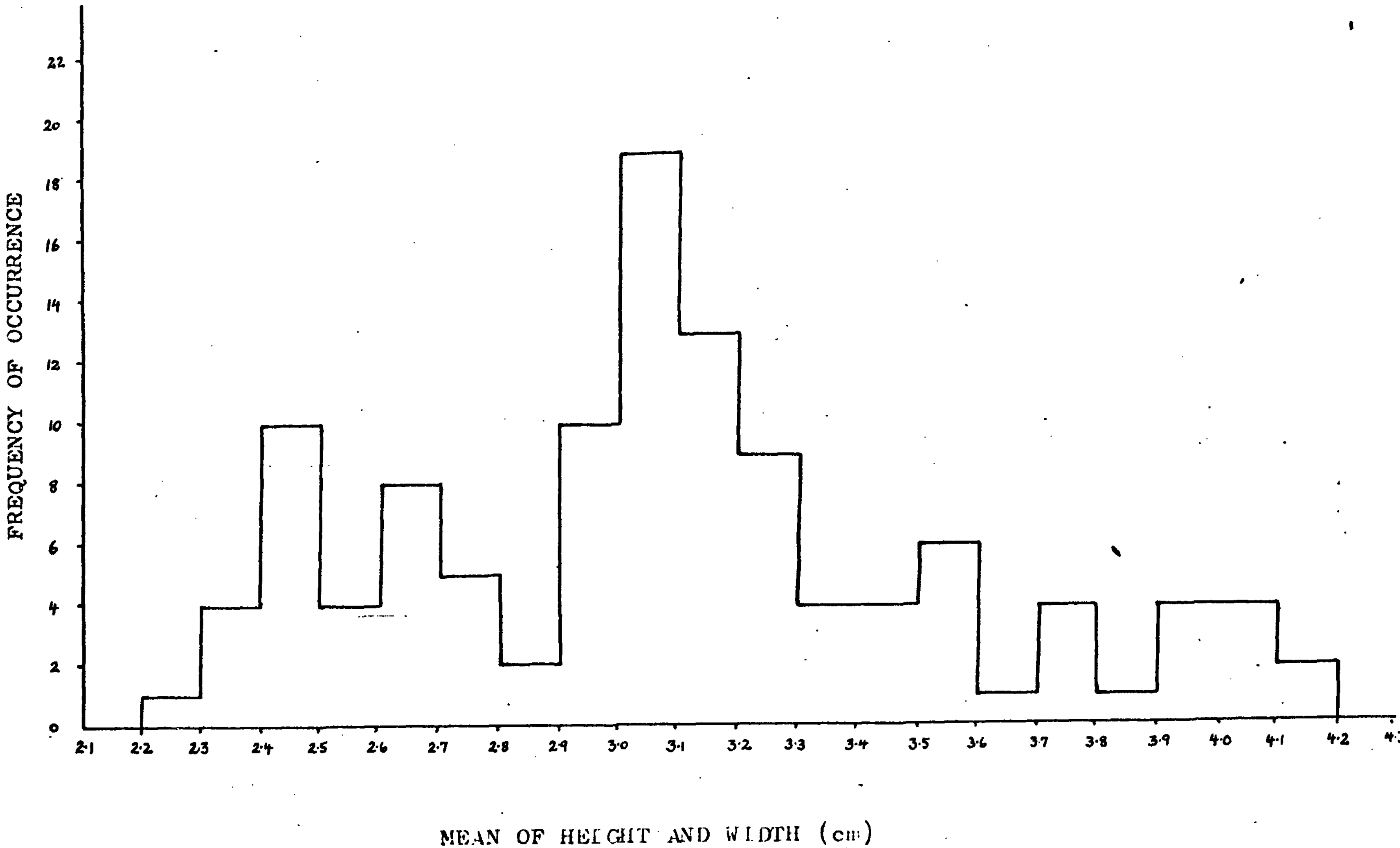


FIG. 4: HISTOGRAM SHOWING FREQUENCY OF OCCURRENCE OF ENTRANCE HOLE DIAMETERS* ON SITE 1.

*Mean of height and width.
(Two entrances with diameters 4.7-4.8 cm not shown)



(c) Tunnel width.

The "t" test was applied to test the possibility that the tunnels are dilated near the junctions, perhaps to enable two individuals to pass one another. The tunnel width measurements were divided into those at "junctions", that is within approximately five cm of a fork in the tunnel, and those in "intermediate sections". The two sets of values from each site are compared in Table 22 below, and the data are presented in Table 38 of the appendix. The results are dealt with in the discussion.

TABLE 22

COMPARISON OF MEAN TUNNEL WIDTH AT "JUNCTIONS" AND "INTERMEDIATE SECTIONS" WITHIN EACH SITE

Site	Parameters compared		"t"	d.f.	P
	Width at "junctions" (cm)	Width at "intermediate sections" (cm)			
II	4.0	3.0	3.3	43	< 0.01
III	3.3	2.9	2.8	12	< 0.02
I	4.4	4.2	not significant		
IV	3.9	4.1			
V	3.8	3.4			

DISCUSSION

(d) Tunnel length in each metre square.

The "t" test was also used to determine if there was a significant difference between sites in the mean length of tunnel per m^2, and the results of the test are shown in Table 23.

TABLE 23

Site	Parameters compared: Mean length (m) per m^2	Site	Mean length (m) per m^2	"t"	d.f.	P
I	3.2	II	1.0	5.69	48	<0.001
		III	1.2	4.11	32	<0.001
		IV	1.9	2.07	32	<0.05
V	2.4	II	1.0	3.03	32	<0.01
		III	1.2	2.86	16	<0.02

The tunnel lengths per m^2 in sites 1 and V are seen to be significantly greater than in the other sites, with the exception of site V compared with site IV.

DISCUSSION

This study deals with the burrow systems of *Apodemus* and *Clethrionomys*. It was possible by comparison of areas with different species abundance to attribute certain features to the burrows of each of the species, but not to establish which rodent species was occupying a particular tunnel system. For this reason the discussion considers the burrows of *Apodemus* and *Clethrionomys* jointly, unless otherwise stated.

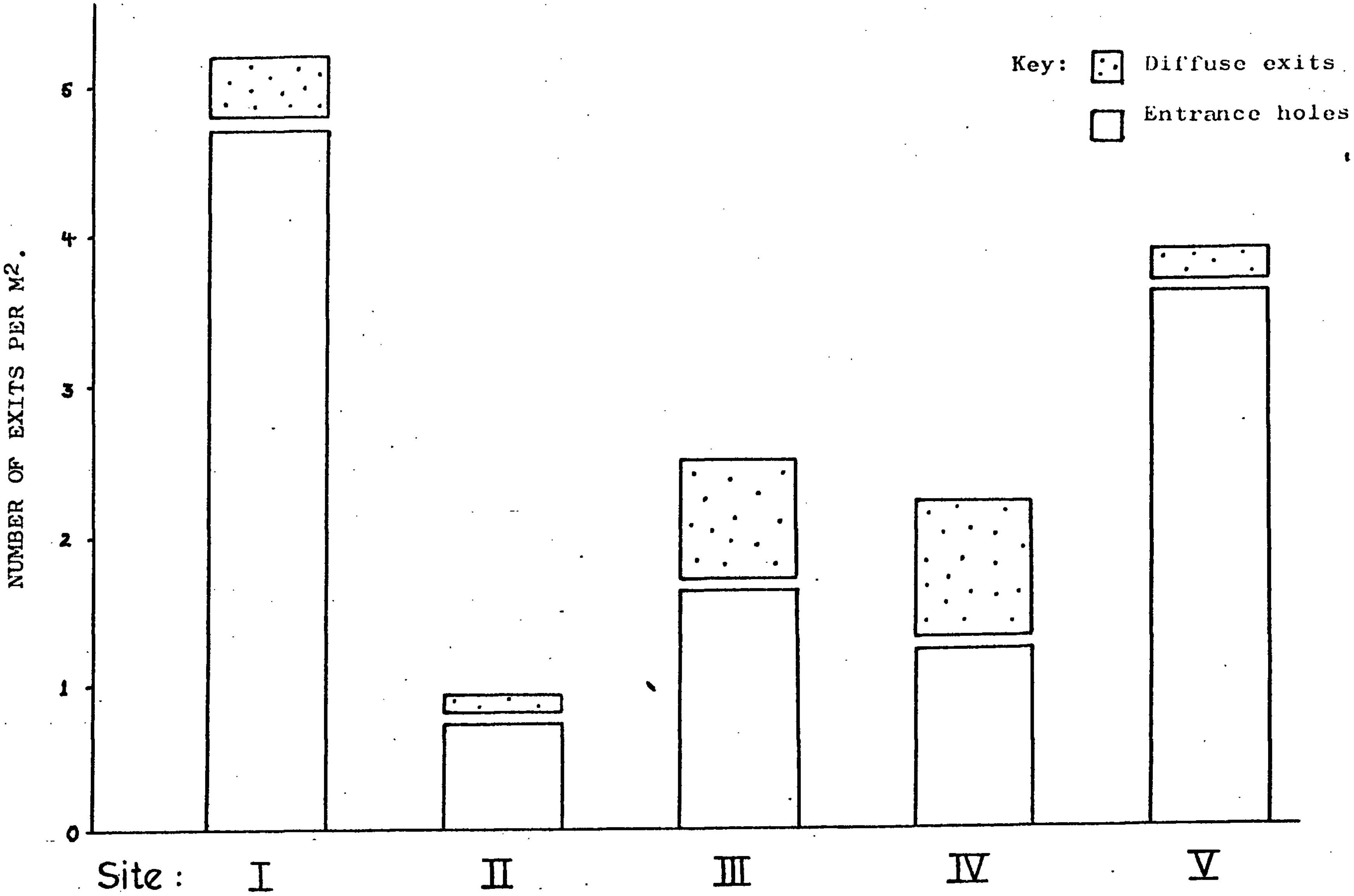
Distribution of entrance holes

The results shown in section 3.4 suggest that the entrance holes were distributed randomly on sites I and II (assuming the expectation of a Poisson distribution), were slightly overdispersed on sites III and V, and were aggregated on site IV. The mean number of holes and diffuse exits per m^2 was very different on the five sites as shown in Fig.5. There does not seem to be any correlation between the density of holes, which was high on site I and low on site II, and their distribution which appears random in both cases. Site IV had a low density of holes which appeared slightly aggregated, while the density was moderate on Site III and high on Site V where an overdispersion of holes is suspected. There is no obvious relation between the type of distribution of entrance holes on the sites and the relative abundance of *Apodemus* and *Clethrionomys*. It is possible that very local factors, such as variations in slope due to uneveness of ground, soil hardness and clumps of vegetation, could have influenced the types of distribution observed on the sites.

Entrance holes and tunnel diameters

The results given in Table 13 show that the entrance holes and tunnels on all the sites were dorso-ventrally flattened. Application of the test described in section 3.5(a) shows that this flattening was significant in all cases except that of the entrance

FIG. 5: HISTOGRAM COMPARING NUMBER OF ENTRANCE HOLES AND DIFFUSE EXITS PER M^2 BETWEEN SITES



holes on sites III and IV.

As the tunnel diameters were not very large, the question arises of how two individuals are able to pass one another in these passages. The possibility that certain sections of the tunnel are expanded to allow passing was investigated in section 3.5(c). The mean tunnel width was greater at "junctions" than at "intermediate sections" in all except site IV (Table 22). Significant results were obtained from Sites II ($p=<0.01$) and III ($p=<0.02$), both of which had a narrower mean tunnel width at "intermediate sections" than the other sites (see Table 22). It appears that widening of the tunnels at "junctions" may be necessary to allow passing, especially when the tunnels are narrow.

Using the techniques described in section 2.3, it was not possible to establish which species lived, or were active, within a particular tunnel. As occupancy could not be established directly, it was necessary to test the data on entrance hole and tunnel traverse-sectional area for bimodality: this was done using the Kolmogorov-Smirnov test as described and applied in section 3.5(b). The test revealed no bimodality in the distribution of the tunnel transverse-sectional areas in any of the sites, and of the entrance hole data, only those from Site I represented other than one normal distribution (Fig 2). Figures 3 and 4 revealed the presence of a bimodal distribution with the possibility of a third peak. Figure 3(a) shows that site II (moderate Apodemus, low Clethrionomys) had a preponderance of small entrance holes, and comparison of its histogram with that for site I (moderate Apodemus, high Clethrionomys) might suggest that the small holes of site I had been made by Apodemus. This hypothesis however lacks support as such small holes are scarce on sites III, IV and V (Fig. 3(a)) which were all used by Apodemus as well as Clethrionomys. Also, the small and large holes on site I (see Map 1) occur along the lengths of the same tunnel systems more or less at random, and are not obviously associated with either long, short or convoluted tunnels. The above points suggest that the bimodal distribution on site I is not to be attributed to construction of different-sized entrance holes by the two species. It was concluded that Apodemus and Clethrionomys burrows could not be distinguished by the entrance hole or tunnel size.

The bimodal distribution of entrance holes may possibly result from differential use of the burrows. Those entrances constantly in use would tend to be enlarged or at least would retain their original size, while those used less frequently would tend to become smaller by the accumulation of debris. With the high number of entrances on site I, it is likely that the proportion not in regular use would have been sufficient to produce a bimodal distribution. The fewer entrances on sites II-V may have resulted in a greater proportion being frequently used, and this could explain why the data from those sites do not exhibit bimodality.

Differences between the burrows of Apodemus and Clethrionomys.

Barrett-Hamilton (1910) suggested that Clethrionomys constructs a complicated network of tunnels which could be used for movement between patches of cover, and that these are generally shallower than Apodemus tunnels. To check whether this difference could be established from the present study, the length and depth of tunnels and their distribution on the five sites are compared.

The best results might be expected from comparison of the data from sites I and II, as the difference in the relative abundance of Apodemus and Clethrionomys was greatest between these two sites; the difference being the greater abundance of Clethrionomys on site I (see Table 1). The soil profiles recorded in Tables 3 and 4 show that the burrowing media were similar on sites I and II, so any difference in the tunnel characteristics between the two sites should be attributable to the population level of Clethrionomys.

The tunnel length per m^2 in site I was more than three times that in site II ($p = < 0.001$), and comparison of Maps I and 2 shows that their distribution was more uniform on site I: the percentage of half-metre squares without tunnels being 0% and 56% respectively. These observations, considered with the knowledge that the mean tunnel depth in site I (8.4 cm) was less than in site II (13.9 cm), are in agreement with the differences between <u>Clethrionomys</u> and <u>Apodemus</u> burrows put forward by Barrett-Hamilton (1910).

Further confirmation is obtained when the results from sites III and V are included in the comparison. The data from site IV are not included in the section, as it was considered that the wetness of the site had to a marked extent influenced the characteristics of the burrows. The effects of waterlogging are discussed later. The soil profiles for sites III and V are presented in Tables 5 and 7.

The order of abundance of rodents on site V was very close to that on site I. A similarly close agreement was found in the tunnel lengths per m^2 shown in Table 12, where the site V value was nearer the site I value than were the other site values, and in the uniform spread of the tunnels (see Map 5) which were distributed throughout all but 3% of the half-metre squares.

The abundance of <u>Apodemus</u> on site III was similar to that on sites I and II, but the density of <u>Clethrionomys</u> was intermediate between that at the two sites. Therefore, continuing the assumption that the differences in the tunnel characteristics between the sites was due to different population levels of <u>Clethrionomys</u>, it would be expected that the site III data would fall between those of sites I and II. It is evident from Maps 1, 2 and 3 that the tunnels on site III were not as uniformly distributed as those on site I, but were not as aggregated as those on site II; the percentages of half-metre squares without tunnels, presented numerically, being 0%, 33% and 56%. In addition, the mean tunnel length per m^2 (see Table 12) and mean tunnel depth values (see Table 13) in site III fall between those for sites I and II.

The above findings suggest that Clethrionomys burrows may be shallower than Apodemus burrows, as was stated by Barrett-Hamilton (1910). It also seems possible that where the Clethrionomys population was high (sites I and V), the tunnels could have provided an adequate network for movement underground from one patch of cover to another. However, these conclusions must be tentative, as inspection of the various maps does not reveal any obvious signs of there being two distinct tunnel types in sites with both species present, and only one type in site II where only Apodemus may be present. It is suggested that the two species may use one anothers burrows successively, and that many burrows may be produced over a number of years by the joint efforts of the two species.

Chambers and tunnel types.

Eleven chambers were excavated of which eight were in site I, two in site II and one in site V. Two of the chambers in site I contained the remains of a nest in the form of shredded grass, but it was not possible to determine whether the remainder had been used for nesting or food storage. Comparison of the chamber and tunnel depth (measured from ground surface to roof) from sites I, II and V combined, showed that the mean chamber depth (9.6 cm) was considerably greater than the mean tunnel depth (6.6 cm). The greater depth of the chambers would provide increased insulation from the abiotic environment.

Details of the various categories of tunnel systems may be found in table 11, and the percentage of the burrows each category represents in the five sites is shown as a histogram (Fig. 6). This figure shows that the percentage of tunnels represented by "non-residential tunnel systems" represented at least 50% of the total. "Residential tunnel systems" were absent from site III, perhaps due to the high density of bilberry roots, and from site IV where the ground is often waterlogged. The other sites had "residential tunnel systems" and were all well drained, which may be an important factor if the chambers are to fulfil their thermo-insulatory function. It may be seen from Maps 1 and 5 that there was a slight tendency in the sites for the tunnels to run up and down the slope rather than across it. This pattern of construction would facilitate drainage during periods of high rainfall.

The effects of waterlogging and soil differences on the characteristics of burrows - a comparison with a previous study.

The results here obtained are compared with those of Cleminson (personal communication), who investigated the burrow systems in two areas of 400 yd^2 in Castle Eden Dene, Durham, which has a heavier and wetter clay than Houghall Wood.

The mean lengths of litter run on the five sites in Houghall Wood are presented in figure 7. From this figure and the soil profiles (Tables 3-7) it can be seen that although site III had the least litter, it had the greatest mean length of litter run per m^2 of all the sites. This may have been to compensate for the very short tunnel length which was thought to be due to the high density of bilberry roots making the digging of tunnels difficult. The data from the other sites suggest that there are more litter runs where there is a lot of consolidated litter than where there is only a little. Cleminson revealed little in the way of litter runs.

FIG. 6: HISTOGRAM COMPARING PERCENTAGE TUNNELS REPRESENTED BY "RESIDENTIAL" AND "NON-RESIDENTIAL" TUNNEL SYSTEMS AND "OTHER TUNNELS" ON SITES I-V.

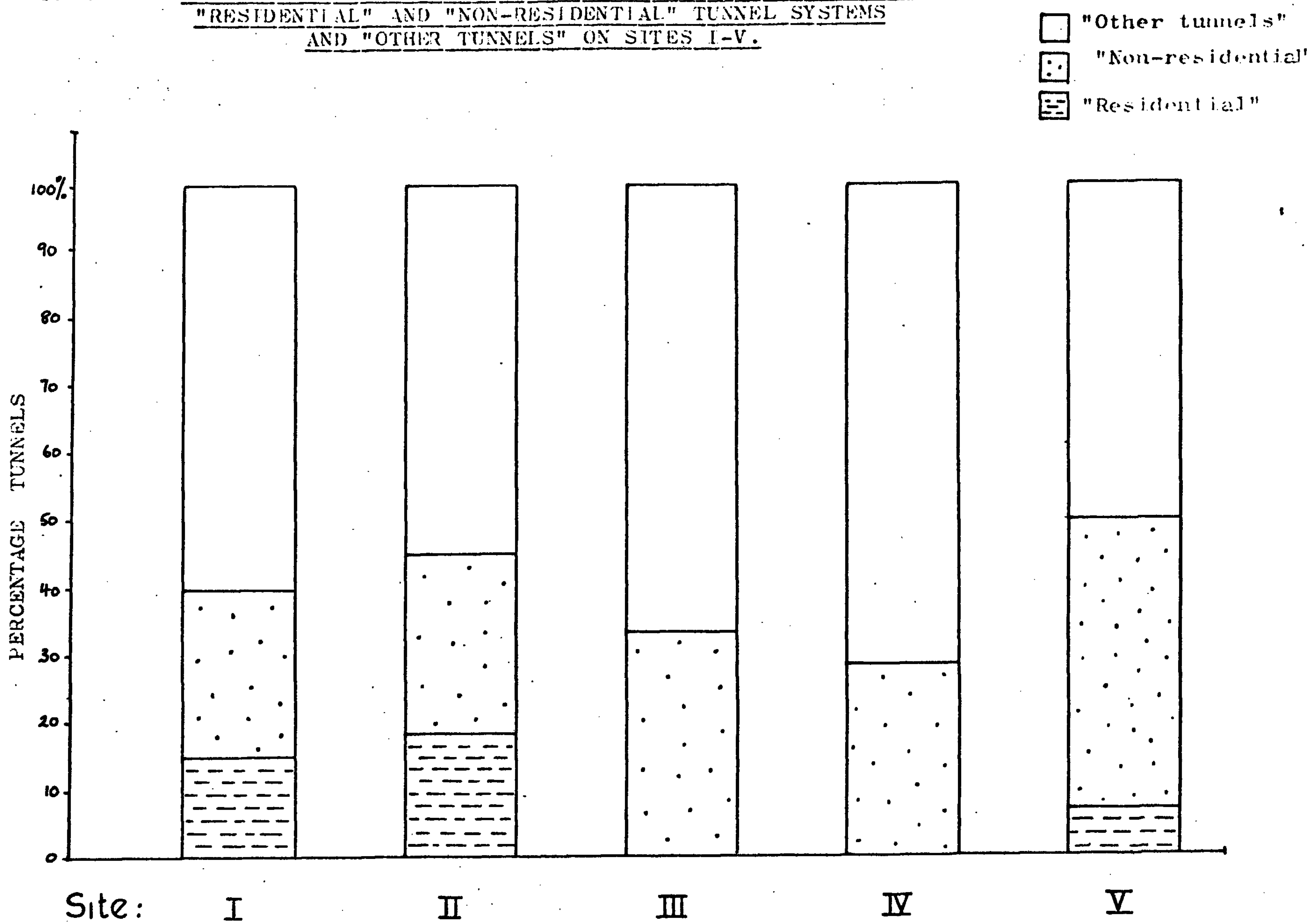
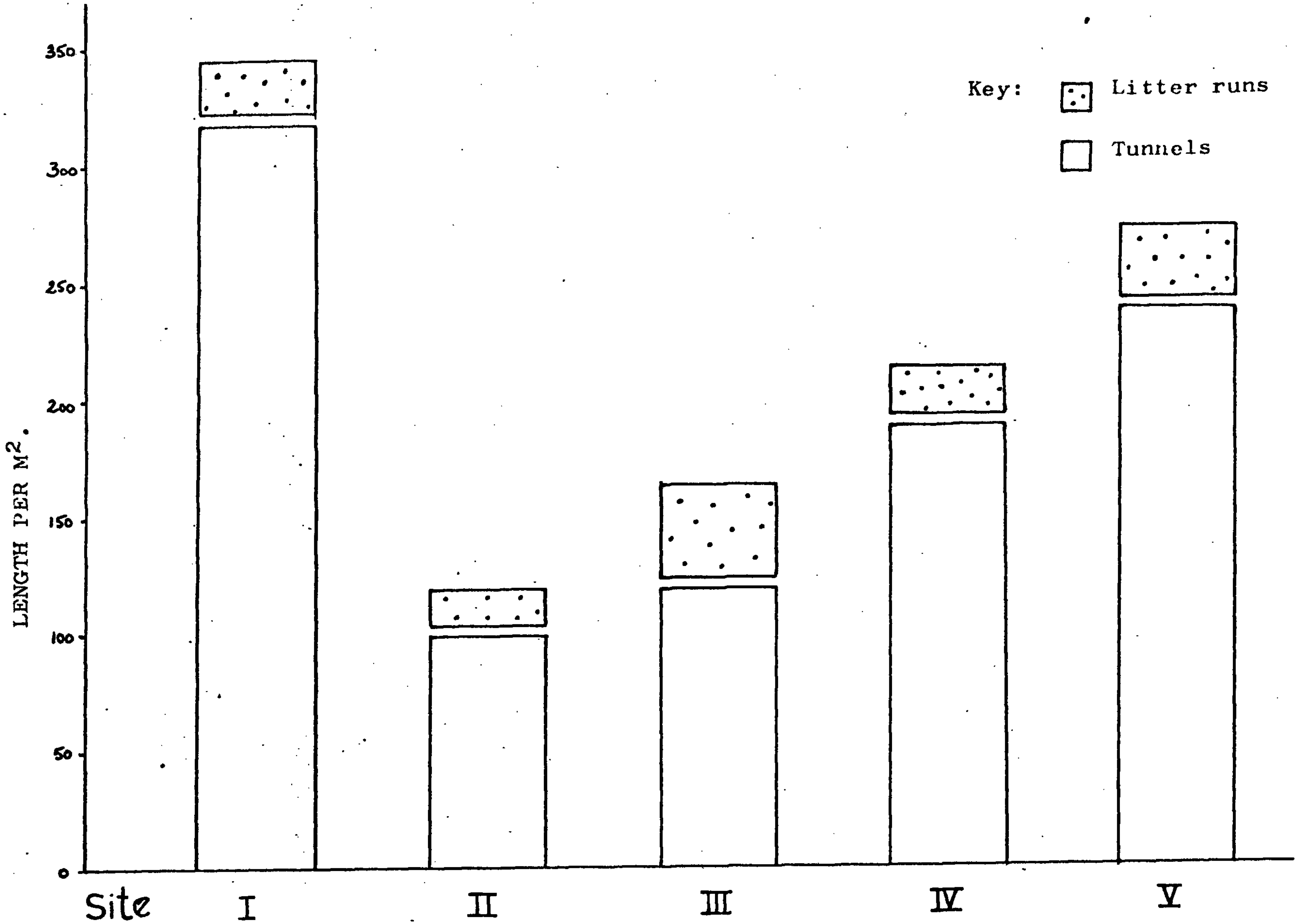


FIG.7: HISTOGRAM COMPARING MEAN LENGTHS OF TUNNELS AND LITTER RUNS PER M² BETWEEN SITES.



SUMMARY

This could be accounted for by the small amount of litter present on one of his areas which was sycamore-ash woodland, but this explanation would not apply on his other area which was larch.

Cleminson recorded a total of 4,000 tunnels per hectare with mean length 95 cm, as compared with the figure of 16,200 tunnels, mean length 200 cm, obtained from site I of this study. Even in his area where Clethrionomys was abundant, there was far more ground which had no tunnel beneath it than was the case in sites I and V in this study. It is suggested that the differences in tunnel abundance and length between the two locations is due to the heavier clay of Castle Eden Dene discouraging digging by both species. In addition, the tunnels recorded by Cleminson are much shallower than was found in the present study in Houghall Wood; this is likely to be due to wetness, water being present within 20 cm of the surface over much of the area following heavy rain. It appears also that wetness explains the shallow nature of the tunnels in site IV (see table 13) as compared with the other sites. This site was situated in a trough draining higher ground which in wet periods has water close to the surface.

SUMMARY

Five sites with differing population levels of *Apodemus* and *Clethrionomys* were excavated in Houghall Wood, Durham. The results were analised in an attempt to distinguish between the burrow systems of the two species.

The results provide no clear evidence of a distinction between burrows made or occupied by *Apodemus* and *Clethrionomys*. The distribution of entrance holes on the sites could not be explained by the relative abundance of *Apodemus* and *Clethrionomys*, and the Kolmogorov-Smirnov test revealed no bimodality in the size distribution (transverse-sectional areas) of entrance holes or tunnels which could be accounted for by a species difference. However, the results suggested that *Clethrionomys* may dig burrows that are shallower than those of *Apodemus*, and that in areas where the *Clethrionomys* population is high the extent of tunnels may be sufficient for considerable movement underground.

The general characteristics of the rodent burrows excavated, with no distinction possible between those dug or used by *Clethrionomys* or *Apodemus*, are listed below:

(1) The entrance holes and tunnels were slightly dorso-ventrally flattened, the average width: height ratio for all the sites being 1.1:1 and 1.2:1 respectively.

(2) The mean chamber depth (9.6 cm) was greater than the mean tunnel depth in the three sites with chambers (6.6 cm), thus giving added protection from the abiotic environment.

ACKNOWLEDGMENTS

ACKNOWLEDGMENTS

I should like to thank Dr. K.R. ASHBY for his supervision of this study and for helpful criticism of the manuscript. Thanks are also extended to Mrs. S. Brooks, Mr. D. George and Prof. J.J. Meester for their valuable assistance.

REFERENCES

(3) Factors other than the abundance of rodents that affected mean length of burrow per unit area and mean tunnel depth, were the presence of standing water near the surface in winter and ease of burrowing.

It is suggested that Apodemus and Clethrionomys may occupy one anothers burrows successively, and that many burrows are dug by the combined efforts of the two species over a period of years. In this case, any differences in the pattern of digging would be obscured.

REFERENCES

ASHBY, K.R. (1967). Studies on the Ecology of Field Mice and Voles (Apodemus sylvaticus, Clethrionomys glareolus and Microtus agretis) in Houghall Wood. Durham. J.zool.Lond.152 : 389-513.

BARRETT-HAMILTON, G.E.A. (1910). A History of British Mammals. Vol II. London : Gurney and Jackson.

BOLAM, G. (1912). Bradford Sci.Journ., Jan.1912 : 213.

BROWN, L.E. (1966). Home range and movement of small mammals. Symp.zool.Soc.Lond. 18 : 111-142.

CHITTY, D. and KEMPSON, D.A. (1949). Prebaiting small mammals and a new design of live trap. Ecology 30 : 536-542.

CRAWLEY, M.C. (1965). Studies on the movements, population dynamics and food of Apodemus sylvaticus (L.) and Clethrionomys glareolus (Schr.). Thesis, Fac.Sci., Univ. Durham.

ELTON, C. et al (1931). The health and parasites of a wild mouse population. Proc.zool.Soc.Lond.1931 : 657-721.

FITCH, H.S. (1948). Habits and economic relationships of the Tulare Kangaroo rat. J.Mammal. 29 : 5-35.

FORMOZOV, A.N. and KODACHOVA, K.S. (1960). Les rongeurs vivant en colonies dans la steppe eurasienne et leur influence sur les sols et la vegetation. Terre Vie 108 : 116-129.

GLASGOW, J.P. (1939). A population study of subterranean soil Collembola. J.Anim. Ecol. 8 : 323-353.

GODFREY, G.K. (1954). Use of radioactive isotopes in small mammal ecology. Nature 174 : 951.

GÓRECKI, A. (1968). Metabolic rate and energy budget in the bank vole. Acta Theriologica Vol.XIII,20 : 341-365.

APPENDIX

GYSEL, L.W. (1961). An ecological study of tree cavities and ground burrows in forest stands. J.Wildl.Mgmt. 25 : 12-20.

HOEL, P.G. (1954). Introduction to Mathematical Statistics. 2nd Edition. New York : Wiley.

JENKINS, D.W. (1954). Advances in medical entomology using radio isotopes. Experimental Parasitology 3 : 474-490.

KOOTCHEROOK (1960). Burrows as means of protection against the unfavourable effect of abiotic environmental factors. Mater. Poznan. Faun. Flor. S.S.S.R., N.S. (Zool.) No. 38.

MAYER, W.V. (1957). A method for determining the activity of burrowing animals. J. Mammal. 38 : 531.

MILLER, L.S. (1957). Tracing vole movements by radioactive excretory products - Ecology 38 : 132-136.

OLSZEWSKI, J.L. and STANISLAW SKOCZEN (1963). The airing of the burrows of the mole Talpa europaea Linnaeus 1758. Acta Theriologica 10 (10/17) : 181-193.

POPOVA (1962). The effect of the digging activity of small-sized mammals on the distribution of soil moisture in areas covered by coniferous and broad-leaved woods. Byull.Mosk.Obstich.lsp. Prir, Otd.Biol. 675 : 29-35.

STARK H.E. (1963) Nesting habits of the Californian vole Microtus californicus, and the microclimatic factors affecting its nests. Ecology 44 : 663-669.

TAYLOR, W.P. (1935). Some animal relations to soil. Ecology 16 : 127-136.

WALKER, E.P. (1964). Mammalia of the World, Vol II. Baltimore : John Hopkins Press.

FIG. 8: FREQUENCY GRAPH SHOWING THE OBSERVED AND IDEAL POISSON DISTRIBUTION OF HOLES ON METRE SQUARES ON SITE 1.

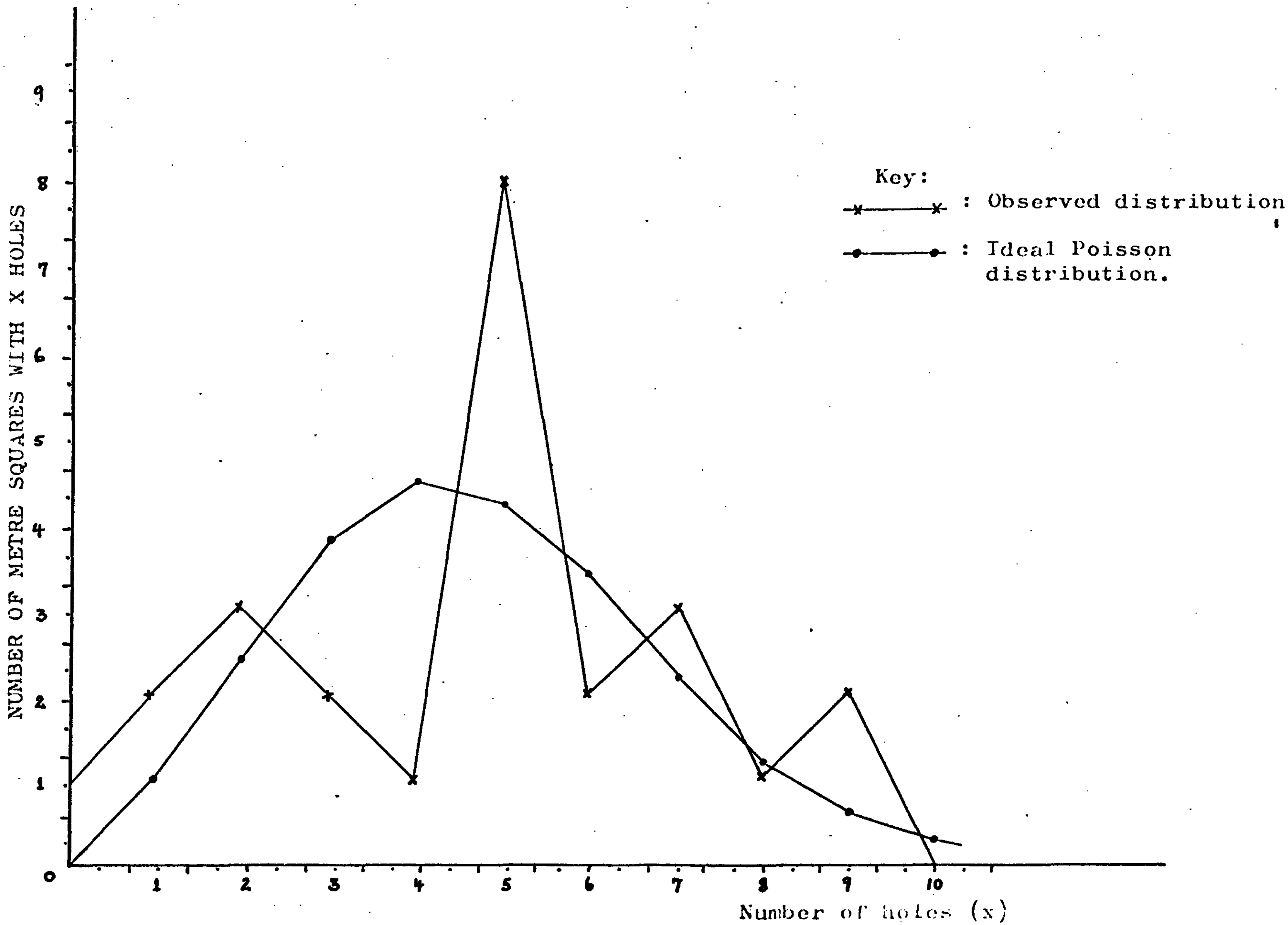


TABLE 24

NUMBER OF HOLES IN EACH SQUARE METRE OF INDIVIDUAL SITES

Number of the m^2	Number of holes (x) per m^2 on site					
	I	II	III	IV	V	
1	5	2	2	0	2	
2	3	1	3	2	4	
3	9	2	2	1	4	
4	5	1	2	0	3	
5	4	1	2	1	5	
6	2	1	1	0	3	
7	2	2	1	4	4	
8	5	1	0	0	5	
9	5	0	1	3	2	
10	6	1	14	11	32	Totals
11	7	1	1.55	1.22	3.56	$\bar{x}$
12	5	0				
13	9	1				
14	8	1				
15	5	1				
16	7	0				
17	1	0				
18	2	1				
19	0	0				
20	1	0				
21	3	0				
22	5	0				
23	7	0				
24	5	0				
25	6	1				
Totals:	117	18				
$\bar{x}$ =	4.68	0.72				

TABLE 25

THE OBSERVED AND EXPECTED NUMBER OF METRE SQUARES WITH X HOLES ON SITE III

No. of holes in each m^2 (x)	Observed no. of metre squares with x holes	Expected no. of metre squares with x holes
0	1	1.9
1	3	3.0
2	4	2.3
3	1	1.2
4	0	0.5
5	0	0.1
6	0	0.04

TABLE 26

THE OBSERVED AND EXPECTED NUMBER OF METRE SQUARES WITH X HOLES ON SITE IV

No. of holes in each m^2 (x)	Observed no. of metre squares with x holes	Expected no. of metre squares with x holes
0	4	2.7
1	2	3.2
2	1	2.0
3	1	0.8
4	1	0.2
5	0	0.1

TABLE 27

THE OBSERVED AND EXPECTED NUMBER OF METRE SQUARES WITH X HOLES ON SITE V

No. of holes in each m^2 (x)	Observed no. of metre squares with x holes	Expected no. of metre squares with x holes
0	0	0.3
1	0	0.9
2	2	1.6
3	2	1.9
4	3	1.7
5	2	1.2
6	0	0.7
7	0	0.4

TABLE 28

TRANSVERSE-SECTIONAL MEASUREMENTS OF ENTRANCES, AND PRESENCE OR ABSENCE OF MARKINGS ON TRACKING ROLLS IN INDIVIDUAL ENTRANCE HOLES SHOWN ON MAP 1 OF SITE I

Hole number as on map 1	Width x cm.	Height y cm.	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z	Tracking roll. (M=marked)
1	2.9	2.3	5.2	1.26	M
2	2.5	2.3	4.5	1.09	M
3	2.5	2.4	4.7	1.04	M
4	2.3	2.4	4.3	0.96	-
5	2.4	2.3	4.3	1.04	-
6	3.4	3.4	9.1	1.00	M
7	2.6	3.0	6.1	0.87	M
8	3.0	3.1	7.3	0.97	M
9	3.4	3.2	8.6	1.06	-
10	2.4	2.5	4.7	0.96	M
11	2.9	3.2	7.3	0.91	-
12	2.8	2.4	5.3	1.17	M
13	3.1	3.0	7.3	1.03	M
14	2.9	3.0	6.8	0.97	M
15	2.2	2.3	4.0	0.96	M
16	3.1	2.4	5.9	1.29	M
17	2.6	2.5	5.1	1.04	M
18	2.6	2.2	4.5	1.18	M
19	2.4	2.3	4.3	1.04	-
20	2.7	2.7	5.7	1.00	M
21	2.8	2.7	5.9	1.04	M
22	2.6	2.7	5.5	0.96	M
23	3.2	2.9	7.3	1.10	-
24	2.4	2.4	4.5	1.00	-
25	3.1	3.2	7.8	0.97	M
26	3.1	3.0	7.3	1.03	M
27	3.3	2.9	7.5	1.14	M
28	2.6	2.4	4.9	1.08	M
29	2.4	2.5	4.7	0.96	M
30	2.3	2.5	4.5	0.92	-
31	3.1	2.6	6.3	1.19	-
32	3.9	3.0	9.2	1.30	-
33	4.1	3.3	10.6	1.24	M
34	3.3	2.9	7.5	1.14	-
35	2.5	2.4	4.7	1.04	-

Continued overleaf ....

TABLE 28 (Cont.)

Hole number as on map 1	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	Width/Height z	Tracking roll. (M=marked)
36	3.4	3.1	8.3	1.10	M
37	2.8	3.6	7.9	0.78	-
38	3.2	3.1	7.8	1.03	-
39	3.4	2.9	7.8	1.17	M
40	2.7	2.6	5.5	1.04	-
41	3.1	2.8	6.8	1.11	-
42	2.7	2.7	5.7	1.00	M
43	2.4	2.4	4.5	1.00	-
44	3.8	4.0	12.0	0.95	-
45	4.0	3.0	9.4	1.33	-
46	4.9	4.5	17.3	1.09	M
47	3.9	2.6	8.0	1.50	M
48	4.0	3.8	12.0	1.05	-
49	3.8	2.7	8.1	1.41	M
50	4.3	5.1	17.2	0.84	-
51	3.4	3.5	9.4	0.97	M
52	4.1	3.7	11.9	1.11	M
53	4.0	4.3	13.5	0.93	-
54	3.3	2.9	7.5	1.14	
55	3.2	3.0	7.5	1.07	
56	3.3	3.1	8.0	1.06	
57	2.9	2.2	5.0	1.32	
58	3.4	3.7	9.9	0.92	
59	3.2	2.8	7.0	1.14	
60	3.3	3.3	8.6	1.00	
61	3.0	2.9	6.8	1.03	
62	3.1	2.9	7.1	1.07	
63	3.0	3.1	7.3	0.97	
64	2.4	2.5	4.7	0.96	
65	3.1	2.9	7.1	1.07	
66	3.4	2.8	7.5	1.21	
67	2.9	3.1	7.1	0.94	
68	3.2	2.9	7.3	1.10	
69	4.1	3.7	11.9	1.11	
70	3.2	2.8	7.0	1.14	
71	3.5	4.0	11.0	0.88	
72	3.4	2.7	7.2	1.26	
73	4.3	3.9	13.2	1.10	
74	2.9	2.3	5.2	1.26	
75	4.1	3.9	12.6	1.06	
76	3.5	3.0	8.3	1.17	
77	3.0	2.9	6.8	1.03	

Continued overleaf .....

TABLE 28 (Cont.)

Hole number as on map 1	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
78	3.7	3.7	10.8	1.00
79	3.0	2.9	6.8	1.03
80	3.7	4.4	12.8	0.84
81	3.4	3.1	8.3	1.10
82	2.7	2.5	5.3	1.08
83	3.9	3.7	11.3	1.05
84	3.0	2.8	6.6	1.07
85	4.0	3.1	9.8	1.29
86	2.8	2.4	5.3	1.17
87	3.2	2.9	7.3	1.10
88	3.5	3.2	8.8	1.09
89	3.3	2.9	7.5	1.14
90	3.4	2.8	7.5	1.21
91	3.2	2.9	7.3	1.10
92	2.8	3.1	6.8	0.90
93	4.1	2.9	9.4	1.41
94	3.3	3.0	7.8	1.10
95	4.1	3.9	12.6	1.05
96	2.9	3.1	7.1	0.94
97	3.4	3.6	9.6	0.94
98	3.4	3.1	8.3	1.10
99	2.7	2.5	5.3	1.08
100	3.2	2.9	7.3	1.10
101	3.5	3.1	8.5	1.13
102	3.4	2.7	7.2	1.26
103	3.3	3.1	8.0	1.06
104	3.2	2.7	6.8	1.19
105	3.0	2.8	6.6	1.07
106	2.4	2.6	4.9	0.92
107	3.1	2.9	7.1	1.07
108	3.0	3.0	7.1	1.00
109	2.9	2.6	5.9	1.12
110	4.4	3.1	10.7	1.42
111	4.1	3.9	12.6	1.05
112	3.5	3.5	9.6	1.00
113	3.7	3.2	9.3	1.16

Continued overleaf ....

TABLE 28 (Cont.)

Hole number as on map 1	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	Width/Height z
114	3.0	2.9	6.8	1.03
115	3.2	3.0	7.6	1.07
116	4.1	3.2	10.3	1.28
117	3.5	2.8	7.7	1.25
Totals N= 117	374.0 $\bar{x}$=3.2	356.7 $\bar{y}$=3.0	909.2 $\overline{T.S.}$=7.8	26.35 $\bar{z}$=1.08

TABLE 29

TRANSVERSE-SECTIONAL MEASUREMENTS OF ENTRANCE HOLES ON SITE II

Hole number as on map 2	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	Width/height z
1	2.6	2.6	5.3	1.00
2	3.4	2.6	8.8	1.31
3	3.0	3.9	9.2	0.77
4	4.5	3.7	13.1	1.22
5	4.5	3.3	11.7	1.36
6	2.6	1.9	3.9	1.37
7	2.7	2.3	4.9	1.17
8	2.9	2.3	5.2	1.26
9	3.4	3.2	8.6	1.06
10	4.0	2.3	7.2	1.74
11	2.3	2.8	5.1	0.82
12	2.3	2.2	4.0	1.05
13	2.3	2.0	3.6	1.15
14	2.3	2.2	4.0	1.05
15	3.5	3.1	8.5	1.13
16	2.4	2.2	4.2	1.09
17	2.3	2.2	4.0	1.05
18	2.5	2.0	3.9	1.25
Totals N = 18	53.5 $\bar{x}$= 3.0	46.8 $\bar{y}$=2.6	115.2 $\overline{T.S.}$=6.4	20.85 $\bar{z}$=1.16

TABLE 30

TRANSVERSE-SECTIONAL MEASUREMENTS OF ENTRANCE HOLES ON SITE III

Hole number as on map 3	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	Width/height z
1	2.4	2.5	4.7	0.96
2	2.5	2.9	5.7	0.96
3	2.6	3.0	6.1	0.87
4	3.2	3.0	7.6	1.07
5	2.9	3.5	8.0	0.83
6	3.9	2.8	8.6	1.39
7	2.6	2.6	5.3	1.00
8	3.2	3.1	7.8	1.03
9	2.4	2.5	4.7	0.96
10	2.7	2.7	5.7	1.00
11	3.1	2.6	6.3	1.19
12	3.1	2.8	6.8	1.11
13	2.9	3.0	6.8	0.97
14	3.0	2.6	6.1	1.15
Totals: N = 14	40.5 $\bar{x}$=2.9	39.6 $\bar{y}$=2.8	90.2 $\overline{T.S.}$=6.4	14.39 $\bar{z}$=1.03

TABLE 31

TRANSVERSE-SECTIONAL MEASUREMENTS OF ENTRANCE HOLES ON SITE IV

Hole number as on map 4	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	Width/height z
1	3.0	2.6	6.1	1.15
2	2.5	2.5	4.9	1.00
3	2.6	2.5	5.1	1.04
4	2.7	2.8	5.9	0.96
5	3.8	3.0	9.0	1.27
6	3.2	3.1	7.8	1.03
7	3.6	3.0	8.5	1.20
8	2.8	2.7	5.9	1.04
9	2.6	2.8	5.7	0.93
10	3.4	3.5	9.4	0.97
11	2.7	2.6	5.5	1.04
Totals: N= 11	32.9 $\bar{x}$=3.0	31.1 $\bar{y}$=2.8	73.8 $\overline{T.S.}$=6.7	11.63 $\bar{z}$=1.06

TABLE 32

CROSS-SECTIONAL MEASUREMENTS OF ENTRANCE HOLES ON SITE V

Hole number as on map 5.	Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
1	2.8	2.5	5.5	1.12
2	3.5	2.6	7.2	1.35
3	2.8	2.8	6.2	1.00
4	3.1	3.0	7.3	1.03
5	3.4	2.9	7.8	1.17
6	3.0	3.0	7.1	1.00
7	2.9	2.5	5.7	1.16
8	2.9	2.4	5.5	1.21
9	3.0	3.1	7.3	0.97
10	3.2	3.3	8.3	0.97
11	2.6	2.5	5.1	1.04
12	3.3	2.9	7.5	1.14
13	3.2	2.9	7.3	1.10
14	3.0	2.5	5.9	1.20
15	3.1	3.3	8.0	0.94
16	4.1	4.0	12.9	1.03
17	3.3	3.7	9.6	0.89
18	3.1	2.6	6.3	1.19
19	3.7	3.0	8.7	1.23
20	3.3	2.8	7.3	1.18
21	2.9	3.2	7.3	0.91
22	3.3	2.9	7.5	1.14
23	2.5	2.4	4.7	1.04
24	2.4	2.4	4.5	1.00
25	2.5	2.4	4.7	1.04
26	3.1	2.9	7.1	1.07
27	4.1	3.9	12.6	1.05
28	3.2	2.7	6.8	1.19
29	2.6	2.6	5.3	1.00
30	2.8	3.0	6.6	0.93
31	4.0	3.0	5.4	1.33
32	2.6	2.7	5.5	0.96
Totals: N = 32	99.3 $\bar{x}$=3.1	92.4 $\bar{y}$=2.9	228.5 $\overline{T.S.}$=7.1	34.58 $\bar{z}$=1.08

TABLE 33

TRANSVERSE-SECTIONAL MEASUREMENTS OF TUNNELS ON SITE 1

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{Height}}$ z
3.6	3.6	10.2	1.00
4.4	3.0	10.4	1.47
4.4	3.8	13.1	1.16
5.0	4.2	16.5	1.19
4.3	2.9	9.8	1.48
4.3	3.6	12.2	1.19
3.9	3.9	12.0	1.00
4.2	3.6	11.9	1.17
3.5	2.9	8.0	1.21
4.3	4.1	13.9	1.05
4.7	4.0	14.8	1.18
3.5	2.7	7.4	1.30
3.6	3.2	9.1	1.13
3.9	3.3	10.1	1.18
3.3	2.2	5.7	1.50
4.0	3.2	10.1	1.25
5.8	5.2	23.7	1.12
5.7	3.4	15.2	1.68
5.3	3.5	14.6	1.51
2.7	3.0	6.4	0.90
4.5	3.5	12.4	1.29
3.4	3.5	9.4	0.97
3.5	3.4	9.4	1.03
4.4	3.9	13.9	1.13
4.1	3.2	10.3	1.28
4.0	3.4	10.7	1.18
4.5	3.6	12.7	1.25
4.6	3.6	13.0	1.28
3.6	3.8	10.8	0.95
4.1	4.0	12.9	1.03
4.4	3.8	13.1	1.16
5.2	4.1	16.8	1.27
4.6	4.2	15.2	1.10
4.6	4.6	16.6	1.00
4.9	3.7	14.3	1.32
3.9	3.7	11.3	1.05
3.4	4.0	10.7	0.85
5.2	3.6	14.7	1.44

Continued overleaf ...

TABLE 33 (Cont.)

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
4.6	3.6	13.0	1.28
4.1	4.6	14.2	0.89
4.5	4.0	14.1	1.13
3.6	3.0	8.5	1.20
3.8	3.0	9.0	1.27
5.5	3.9	16.9	1.41
3.2	3.7	9.3	0.86
3.8	3.1	9.3	1.23
5.0	2.5	9.8	2.00
5.0	4.3	16.9	1.16
5.7	4.3	19.3	1.33
4.7	5.2	19.2	0.90
4.2	3.6	11.9	1.17
5.6	4.9	21.6	1.14
3.8	2.6	7.8	1.46
4.2	2.5	8.3	1.68
4.9	3.0	11.6	1.63
4.5	3.0	10.6	1.50
245.0	201.7	694.6	68.5
$\bar{x}$=4.4	$\bar{y}$=3.6	$\overline{T.S.}$=12.4	$\bar{z}$=1.22

TABLE 34

TRANSVERSE-SECTIONAL MEASUREMENTS OF TUNNELS ON SITE II

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	Width/height z
2.7	3.1	6.6	0.87
3.1	3.1	7.6	1.00
2.7	3.1	6.6	0.87
3.8	3.6	10.8	1.06
4.2	3.4	11.2	1.24
3.3	3.1	8.0	1.06
2.4	2.9	5.5	0.83
2.9	2.7	6.2	1.07
5.0	3.9	15.3	1.28
4.2	3.7	12.2	1.14
3.5	2.9	8.0	1.21
3.7	3.1	9.0	1.19
2.6	2.9	5.9	0.90
2.3	2.5	4.5	0.92
6.3	4.0	19.8	1.58
3.4	3.4	9.1	1.00
2.6	4.0	8.2	0.65
3.2	3.4	8.6	0.94
4.5	5.2	18.4	0.87
3.4	3.1	8.3	1.10
4.5	2.9	10.3	1.55
2.3	2.3	4.2	1.00
5.0	6.6	25.9	0.76
2.8	2.8	6.2	1.00
2.2	1.9	3.3	1.16
2.9	2.9	6.6	1.00
2.6	2.3	4.7	1.13
3.8	2.7	8.1	1.41
4.4	2.7	9.3	1.63
6.3	3.4	16.8	1.85
4.7	4.7	17.4	1.00
5.0	3.6	14.1	1.39
3.6	2.8	7.9	1.29
3.0	2.4	5.7	1.25
5.0	3.2	12.6	1.56
3.5	2.5	6.9	1.40
4.4	3.2	11.1	1.38

Continued overleaf .....

TABLE 34 (Cont.)

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
3.3	3.0	7.8	1.10
4.0	3.1	9.7	1.29
2.7	2.2	4.7	1.23
4.9	4.6	17.7	1.07
2.6	2.6	5.3	1.00
3.5	2.5	6.9	1.40
3.6	3.2	9.1	1.13
3.7	3.1	9.0	1.19
3.4	2.7	7.2	1.26
3.2	2.5	6.3	1.28
170.7 $\bar{x}$=3.6	149.5 $\bar{y}$=3.2	424.9 $\overline{T.S.}$=9.0	54.49 $\bar{z}$=1.16

TABLE 35

TRANSVERSE-SECTIONAL MEASUREMENTS OF TUNNELS ON SITE III

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
3.2	3.2	8.0	1.00
3.3	2.8	7.3	1.18
3.1	3.2	7.8	0.97
3.3	2.7	7.0	1.22
2.7	2.5	5.3	1.08
2.7	2.9	6.2	0.93
2.8	2.5	5.5	1.12
2.6	2.6	5.3	1.00
3.4	3.3	8.8	1.03
3.2	2.9	7.3	1.10
3.6	2.9	8.2	1.24
2.9	2.5	5.7	1.16
2.9	2.7	6.2	1.07
3.1	2.5	6.1	1.24
42.8 $\bar{x}$=3.1	39.2 $\bar{y}$=2.8	94.7 $\overline{T.S.}$=6.8	15.34 $\bar{z}$=1.10

TABLE 36

TRANSVERSE-SECTIONAL MEASUREMENTS OF TUNNELS ON SITE IV

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
2.9	2.4	5.5	1.21
3.4	3.2	8.6	1.06
4.2	3.8	12.5	1.11
3.9	3.3	10.1	1.18
3.6	2.5	7.1	1.44
3.6	3.1	8.8	1.16
4.1	3.9	12.6	1.05
4.0	3.8	11.9	1.05
4.0	3.0	9.4	1.33
4.2	3.5	11.6	1.24
4.9	4.7	18.1	1.04
3.2	3.4	8.6	1.94
3.4	3.4	9.1	1.00
3.4	3.0	8.0	1.13
3.6	3.2	9.1	1.13
5.3	3.2	13.3	1.66
3.0	2.4	5.7	1.25
2.6	2.4	4.9	1.08
3.9	3.5	10.7	1.11
4.4	2.9	10.0	1.52
75.6 $\bar{x}$=3.8	64.6 $\bar{y}$=3.2	195.6 $\overline{T.S.}$=9.8	23.65 $\bar{z}$=1.18

TABLE 37

TRANSVERSE-SECTIONAL MEASUREMENTS OF TUNNELS ON SITE V

Width x cm	Height y cm	Transverse-sectional area T.S. cm^2	$\frac{\text{Width}}{\text{height}}$ z
3.1	2.8	6.8	1.11
3.2	3.1	7.8	1.03
2.8	2.9	6.4	0.97
3.5	2.7	7.4	1.30
2.6	2.5	5.1	1.04
4.2	3.5	11.6	1.20
3.0	3.0	7.1	1.00
4.2	4.5	14.9	0.93
4.1	4.0	12.9	1.25
4.3	3.5	11.8	1.23
3.2	2.8	7.0	1.14
3.4	3.1	8.3	1.10
3.6	3.7	10.5	0.97
3.1	2.6	6.3	1.19
3.2	3.1	7.8	1.03
4.5	4.0	14.1	1.13
4.9	3.9	15.0	1.26
3.1	2.9	7.1	1.07
2.8	2.6	5.7	1.08
3.8	3.9	11.6	0.97
3.7	3.4	9.9	1.09
4.5	3.8	13.4	1.18
78.8 $\bar{x}$ =3.6	72.3 $\bar{y}$=3.3	208.5 $\bar{T.S.}$=9.5	24.27 $\bar{z}$=1.1

TABLE 38

TUNNEL WIDTH MEASUREMENTS AT 'JUNCTIONS' AND 'INTERMEDIATE SECTIONS'

	SITE I		SITE II		SITE III		SITE IV		SITE V	
	Width (cm)		Width (cm)		Width (cm)		Width (cm)		Width (cm)	
	J.	N.J	J.	N.J	J.	N.J.	J.	N.J.	J.	N.J.
	3.3	3.9	3.2	3.6	3.3	2.7	5.2	5.6	2.8	4.2
	4.0	3.6	3.4	3.8	3.1	2.8	2.8	4.5	4.2	3.5
	3.6	4.5	3.7	2.7	2.9	2.6	4.2	4.9	4.9	2.6
	3.4	4.2	5.0	2.9	3.4	2.9	4.0	5.0	3.1	3.1
	3.5	5.6	3.0	2.6	3.6	3.2	4.0	4.2	2.8	3.2
	3.9	3.6	3.5	3.1	3.3	3.2	4.9	2.9	3.8	3.0
	3.4	4.1	4.4	4.5		3.1	3.2	3.4	3.7	4.1
	5.2	5.0	5.0	4.2		2.7	3.4	3.9	4.3	3.2
	4.6	4.3	4.7	3.8			3.4	3.6	4.5	3.4
	4.1	3.9	6.3	2.3			5.3	3.6		3.6
	3.6	5.3	4.4	2.7			3.0	4.1		3.1
	3.8	4.1	3.3	2.7			2.6	4.2		3.2
	5.8	4.5	4.0	3.1			4.4	3.6		4.5
	5.7	3.5	3.3	2.6				3.9		
	4.2	2.7	2.7	2.6						
	4.3	3.5	3.2	2.2						
	5.5	4.1	3.2	2.3						
	3.2	4.6	2.6							
	3.8	4.6	6.3							
	3.8		3.4							
	4.2		4.9							
	4.5		2.9							
	4.4		5.0							
	5.2		3.7							
	5.0		3.5							
	4.5		4.2							
	4.9		5.0							
	5.7		2.9							
	4.7									
	5.0									
Totals	130.8	79.6	110.7	51.7	19.6	23.2	50.4	57.4	34.1	44.7
Means	4.4	4.2	4.0	3.0	3.3	2.9	3.9	4.1	3.8	3.4

Key: J. = "Junction"
NJ = "Intermediate Section"