FEEDING BEHAVIOUR OF THE EUROPEAN HEDGEHOG
(*Erinaceus europaeus* L.)
IN A NEW ZEALAND PASTURE.

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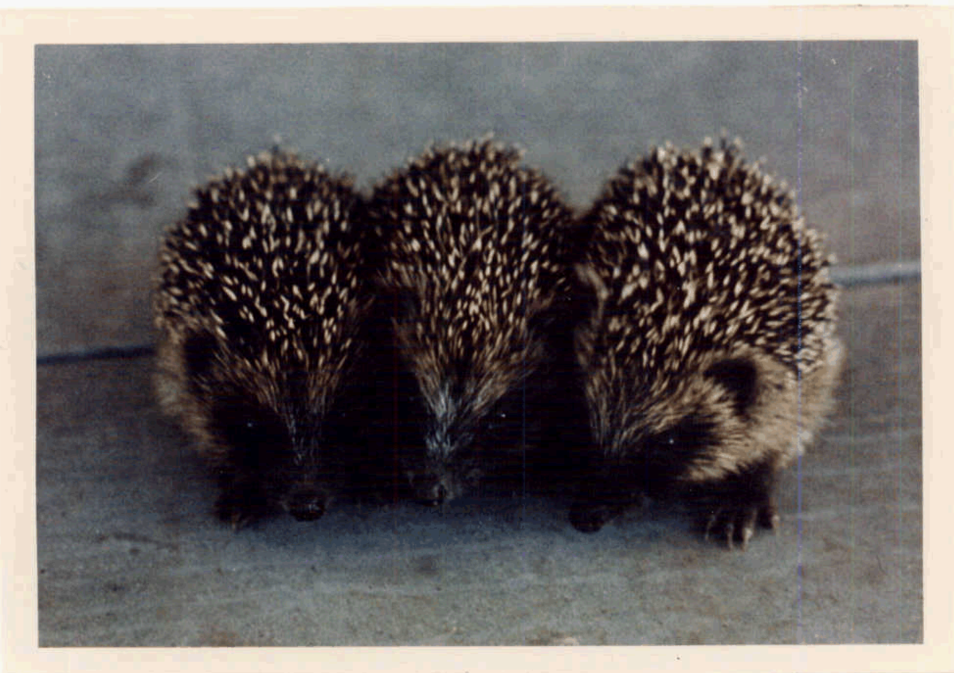
ABSTRACT

The feeding behaviour of the European hedgehog (*Erinaceus europaeus* L.) has been investigated in a pastoral environment. Sampling methods that caused the minimum interference to the natural population were used. The relative importance of the various prey species in the diet were analysed by occurrence, relative volume and direct counting techniques. Problems often associated with the use of direct counting were successfully overcome. It was established that the main animal food items in the hedgehog diet were earwigs, lepidopteran larvae, beetles, harvestmen, dung flies, slugs, and earthworms. Small quantities of a large number of other species were also consumed. Several variations in the diet were found to be related to changes in the availability of food species. Although hedgehogs are capable of consuming large numbers of grass grub beetles (*Costelytra zealandica*) during the flight season it is concluded that they are unlikely to provide any effective measure of biological control of this pasture pest. Hedeghog diet was not influenced significantly by the sex of the animal, or by pasture irrigation. It was demonstrated that the feeding rhythm of captive animals, fed under laboratory conditions, was similar to that observed in the field.

Observation showed that hedgehogs were active for an average of eight hours per night, with a period of maximum activity between 9 p.m. and 11 p.m. Animals tended to follow relatively fixed routes on successive nights.

Excluding nestlings, the population density in an irrigated clover-ryegrass pasture was found to vary from four (winter) to eight (summer) animals per hectare. The average minimum feeding range of these animals was 2.4 hectares, although their feeding ranges overlapped considerably.



<u>Erinaceus europaeus europaeus</u> L.

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CHAPTER I

GENERAL INTRODUCTION

In 1965, the author completed a short laboratory study on the feeding behaviour and food preferences of hedgehogs, as partial fulfilment of the requirements of a B. Sc. (Hons.) degree. The results of this study are contained in an unpublished thesis "Feeding Behaviour of the European Hedgehog (Erinaceus europaeus L.) in New Zealand" (Otway, 1965).

As little subsequent work has been carried out on the feeding habits of the New Zealand hedgehog it was felt that further observations, particularly of animals in their natural habitat, were warranted. The current study is an attempt to elucidate the feeding ecology of the hedgehog, and to establish its significance in a pasture.

The field work was based upon a population, living under natural pastoral conditions, which was exposed to minimum interference. Disturbance of the animals was restricted to such observations as were essential to obtain satisfactory records of their movements and behaviour.

There were five main aims to the study.

(i) To investigate the size, distribution and dispersal behaviour of a population of wild hedgehogs in an irrigated ryegrass-timothy-white clover pasture.

(ii) To qualitatively define the available food supply of the hedgehogs.

(iii) To investigate the feeding behaviour of the population.

(iv) To determine if hedgehogs alter their feeding rhythms when held captive in the laboratory, by comparing their feeding behaviour in the laboratory with that observed in the study area.

(v) To investigate the effect of hedgehog predation on grass grub (Costelytra zealandica) and porina (Wiseana cervinata) populations.

I. TAXONOMY AND DISTRIBUTION

Hedgehogs are small mammals of the Subclass Eutheria, Order Insectivora. Mammals of this order have many primative or pleisiomorphic features. The eight families of insectivores are listed in Table 1.

TABLE 1. FAMILIES OF INSECTIVORES.

FAMILY	COMMON NAME	NATURAL DISTRIBUTION
1. Solenodontidae	Solenodons	Cuba and Haiti
2. Tenrecidae	Bristle hedgehogs	Madagascar
3. Potamogalidae	Otter shrews	West Africa
4. Chrysochloridae	Golden moles	South Africa
5. Erinaceidae	Hedgehogs	Europe, Asia, Africa
6. Macrosceliidae	Elephant shrews	Africa
7. Soricidae	Shrews	Europe, Asia, Africa, America
8. Talpidae	Moles	Europe, Asia, America

Hedgehogs belong to one of the oldest known families of living mammals. Fossil remains of hedgehogs belonging to the same genus as modern hedgehogs have been found in rocks of Upper Eocene and Mid and Lower Miocene age in France, Britain, Germany and Switzerland (Herter, 1938). Two subfamilies are distinguished within the forms of hedgehogs living today. These are the true hedgehogs (Erinaceinae), which are found in Europe, Africa and Asia, and the hair hedgehogs (Echinosoricinae) which are restricted to Asia and will not be considered further.

Thomas (1918) divided the Erinaceinae into five genera:

1. <u>Erinaceus</u> Linnaeus, 1758.
2. <u>Atelerix</u> Pomel, 1840.
3. <u>Hemiechinus</u> Fitzinger, 1866.
4. <u>Paraechinus</u> Trouessart, 1879.
5. <u>Aethechinus</u> Thomas, 1918.

This division has been accepted by Cabrera (1925) and Herter (1938 and 1965).

Thomas (1918) included 13 species within the genus <u>Erinaceus</u>. Cabrera (1925) recognised six of these species, considering the remaining seven to be subspecies, and added four new species. Of Cabrera's 10 species only two, <u>E</u>. <u>europaeus</u> and <u>E</u>. <u>roumanicus</u> are found in Europe.

Further discussion is restricted to these two species. Opinions differ as to whether they should be regarded as separate species, or as subspecies only. Some workers (Rebel, 1933; Schaefer, 1933 and von Wettstein, 1942) considered that both belonged to a single species, while others (including Miller, 1912; Thomas, 1918; Cabrera, 1925; Ognew, 1928; Stein, 1929-30 and Herter, 1938 and 1965) postulated that the two "forms" were different species.

Herter (1938 and 1965) claimed that the two species were distinguished principally by the colour of the hair on the ventral surface, and by the shape of the skull. The under-sides of the species Erinaceus europaeus, the brown-breasted, or western hedgehog, are dark brown or grey, while those of Erinaceus roumanicus, the white-breasted, or eastern hedgehog are white. The skull of E. europaeus is shorter and wider than that of E. roumanicus. Thus the maxillary index (the length of the upper jaw bone, divided by its height) is ≤ 1 in E. europaeus and > 1 in E. roumanicus.

Herter (1938) acknowledged the division of the two species into a number of subspecies as follows:

1. Erinaceus europaeus europaeus Linnaeus, 1758.
2. E. e. hispanicus Barrett-Hamilton, 1900.
3. E. e. italicus Barrett-Hamilton, 1900.
4. E. e. consolei Barrett-Hamilton, 1900.
5. E. e. meridionalis Altobello, 1920.
6. E. e. centralrossicus Ognew, 1928.
7. E. roumanicus roumanicus Barrett-Hamilton, 1900.
8. E. r. transcaucasicus Satunin, 1901.
9. E. r. nesiotes Bate, 1905.
10. E. r. rhodius Festa, 1914.

He stated that the subspecies of E. europaeus differed from each other only in inessential characteristics, and that they had been established in most cases, on the basis of very few specimens. He claimed that the need for a proper statistical analysis in-volving large numbers of the various 'races' before any division into subspecies could be properly justified. He further claimed that it was doubtful how far the subdivision of the species

E. roumanicus was justified, as the reported differences were small and little was certain.

The main factor in the division into subspecies appears to have been geographical isolation.

The present distribution of hedgehogs in Europe, as shown in maps published by von Wettstein (1942) and Herter (1965), can be explained by either of two hypotheses. The first (von Wettstein, 1942) assumes that there is only one European species, while the second (Herter, 1965) regards the surviving forms as two species.

During the Tertiary period hedgehogs were widespread throughout Europe, but fossil evidence has been unable to show whether they were of the European or Roumanian group. Hedgehogs could not have survived in Northern Europe during the most recent advance of the ice, the Würm glaciation. Those that now inhabit this region must have migrated from more southerly refuges following the retreat of the ice.

Von Wettstein (1942) assumed that the recolonising stock had the form of the subspecies now known as Erinaceus europaeus transcaucasicus, and that it survived in areas around the Black Sea.

Herter (1965) postulated that during the 700,000 years of the Würm glaciation hedgehogs survived in two geographically isolated parts of Europe. These were the Iberian peninsula, southern France and Italy; and a region around the Black and Caspian Seas. During that time the two groups diverged and developed independently of each other to form the 'western' europaeus species and the 'eastern' roumanicus species. As the rest of Europe became habitable, the 'western' species spread northwards until it had colonised the whole of Europe, including the British Isles and Scandinavia, which were, at that time, accessible by land bridges. Contemporaneously the 'eastern' species spread northwards and westwards, the two species eventually meeting along a line that more or less corresponded with longitude 14°13'E.

Neither of these hypotheses has yet been proved. If it is conceded that hedgehogs were as likely to survive the Würm glaciation in southwestern Europe, as around the Black Sea, von Wettstein's theory would also have to explain why only one group should emigrate in the post-glacial period.

Herter (1965) states that although the north-south boundary between the two species is comparatively sharply drawn, the 'western' species is sometimes found east of it. He claims that fertile crossings between the two species may be responsible. He also states that hedgehogs bearing the external characteristics of both species, and therefore presumably hybrids, are often found along the biological frontier. He postulated that if a hedgehog of one species invaded the territory of the other and mated with one of the local species, the progeny of the union, if fertile, would be more likely to mate with the local species. This would result in the blood of the invading species being rapidly diluted, and would prevent each species from replacing the other in their respective territories. This case is similar to that of the carrion crow (Corvus cornix) and the hooded crow (Corvus corone) in north west Europe, as cited by Meise (1928) and Mayr (1963).

Herter (1965) has shown experimentally the feasability of first generation crossing. An Erinaceus europaeus female from Saxony was mated in captivity with an E. roumanicus male from Bohemia; the union producing five young. The reverse cross has not been achieved in captivity, but two E. europaeus males and two E. roumanicus females were released on Ruden Island, in the Baltic. No other hedgehogs existed on this island. Two years later six young hybrid hedgehogs were found. Hybrids from both these crosses had the skull characteristics of E. europaeus and the ventral colours of E. roumanicus. It has not yet been shown whether the hybrids are mutually fertile, or whether union between them and members of the two species is fertile.

The concept of 'species' as used by Herter (1938 and 1965) does not concur with that of Mayr (1963). Mayr defines species as 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups'.

Herter was not unaware of this conflict. He was of the opinion (Herter, 1938) that the 'eastern' and 'western' hedgehogs seem to be a borderline case between species and subspecies. He claimed that their morphological differences were great enough to justify division into two species, even allowing for the fact that the two species could interbreed. At the time Herter did not know if interbreeding extended beyond the F1-generation, but he asserted that he would consider the two 'forms' to be separate species, even if unlimited interbreeding was later shown, because failure to do so would result in considerable difficulties with nomenclature. He reiterated these arguments in his later work (Herter, 1965).

The principle of regarding a species as a reproductive community cannot be absolutely maintained, as other, admittedly rare, examples of fertile hybrids have been reported (Gray, 1954 and Mayr, 1963).

The only subspecies of hedgehog to become established in Britain was *Erinaceus europaeus europaeus*. As all hedgehogs introduced into New Zealand came from British stock, future references in this thesis to the term 'hedgehog' refer to *E. e. europaeus* unless otherwise stated.

II. THE HEDGEHOG IN NEW ZEALAND

The European hedgehog is the only insectivore that has become naturalized in New Zealand. The European hedgehog (*E. europaeus*) was first introduced into New Zealand in 1870 (Thomson, 1922) when the Canterbury Acclimatisation Society obtained a pair from England. A year later a further specimen was imported. These three animals died without producing progeny.

In 1885, the Otago Acclimatisation Society attempted to import 100 animals from Britain, but only two males and one female survived the voyage. These survivors were liberated in suburban gardens in Dunedin, but the female soon died. Although no records of further importations exist, hedgehogs were discovered at Sawyers Bay, in 1890 (Thomson, 1922).

In 1892, Peter Cunningham, of Christchurch, imported 12 hedgehogs from Britain, in exchange for a consignment of wekas. These hedgehogs escaped from the pigeon house, in which they had been confined. They thrived, and succeeded in breeding, thus making this the first successful, fully documented introduction of hedgehogs into New Zealand (Thomson, 1922).

There have been many subsequent liberations of local stock into other parts of the country (Wodzicki, 1950). In 1913, W.W. Smith liberated two pairs at New Plymouth. These multiplied rapidly, and, together with hedgehogs liberated about 1910, in the Bay of Plenty, began the colonisation of the North Island.

By 1950, the hedgehog had colonised much of the North and South Islands, and been introduced to Stewart, Chatham and Waiheke Islands. The only areas that remained free of the animal were, in general, the heavy bush and alpine areas (Wodzicki, 1950). Apart from those mentioned, it had not colonised the offshore islands.

A further survey on the distribution of the hedgehog is currently being carried out by Brockie (pers. comm.).

The hedgehog inhabits gardens, orchards, farm paddocks, sand dunes and open tussock country. It has been found in snowgrass at altitudes of up to 6,000 feet in Otago (Wodzicki, 1950).

As natural colonisation by hedgehogs is slow (Wodzicki, 1950) liberations probably account for their wide distribution in New Zealand. Climate appears to have little effect on their distribution, but their incidence is determined by the availability of suitable cover (Wodzicki, 1950).

A comparison of road mortalities in the North Island of New Zealand and Hampshire, England, indicates that hedgehogs are now far more numerous in New Zealand than in Britain (Brockie, 1960).

CHAPTER II

REVIEW OF LITERATURE ON HEDGEHOGS

In this chapter literature on the physiology, anatomy, reproduction, diseases and food of the hedgehog (Erinaceus europaeus) will be briefly reviewed. Particular emphasis is given to the available New Zealand literature.

I. EUROPEAN LITERATURE

The monograph "Die Biologie der Europäischen Igel", (Herter, 1938) contains a very comprehensive study of the systematics, anatomy, physiology, distribution, ecology, behaviour and economic significance of the hedgehog. As it reviews European literature published prior to 1938, it was not considered necessary to obtain this early literature, which, for the most part, dealt with topics not relevant to the present study.

An abridged, popularised version of Herter's monograph appeared in 1963 and was translated into English in 1965, under the title "Hedgehogs - A Comprehensive Study".

"The Hedgehog" (Burton, 1969) summarised the available British literature. Burton discussed general hedgehog ecology, and treated, at some length, a few peculiar aspects of hedgehog behaviour, such as self anointing, suckling of cows and carriage of fruit on the spines.

These two books (Herter, 1965 and Burton, 1969) provide a comprehensive general survey of observations and theories of hedgehog behaviour.

(1) General.

For many centuries the hedgehog has been the subject of folklore and legend. Much nineteenth and early twentieth Century British literature on this animal was compiled by amateur zoologists, who recorded their observations on the behaviour of hedgehogs in popular journals such as "The Zoologist", "Irish Naturalist", "Naturalist" and "Field". They dealt with subjects such as the food of hedgehogs (Atkinson, 1844; Smith, 1853; Spicer, 1858; Alston, 1866; Orr, 1899; and O'Connell, 1900); and methods used to attack bees (Crotch, 1850); wasps (Peacock, 1900); vertebrate prey such as hares (Mathew, 1887); rats (Lilford, 1890; Green, 1892; Mansel-Pleydell, 1895; and Passingham, 1895); and partridges (Grabham, 1898). Other articles described grooming (Bury, 1844); abnormal behaviour, such as licking of boots (Brydges, 1847); suckling of cows (Gurney, 1853); athletic prowess, as shown by a hedgehog scaling a 2.9 m wall (Scott, 1886); or swimming (Peacock, 1901); and hibernation (Grabham, 1896; and Moffat, 1904).

Much of this work, in the light of our present knowledge, is inaccurate, incomplete and inconsequential. However, Barret-Hamilton (1911) provided a useful summary of the literature available at that time. He revised the classification and history of the hedgehog and described its subspecies and local variations.

Ritchie (1931) claimed that hedgehogs were generally more an ally of the farmer than a pest. Vesey-Fitzgerald (1946) confirmed this by stating that 'so far as the gamekeeper is concerned, it does more good than harm'.

The majority of recent literature on hedgehogs deals with laboratory studies, and reports of field studies are comparatively rare. The major British work of relevance to the present study was a thesis and associated papers by Morris (1969). These covered aspects of the ecology of hedgehogs, including the building and use of nests, the incidence of ringworm and its transmission to other hedgehogs, home ranges, and population studies. Home range data were attempted using a radio-tracking technique, but, because of limitations imposed by radio performance, only distances between successive capture points were obtained. As a very limited number of points was recorded for each hedgehog, no accurate assessment of home ranges was feasible. The use of radios did, however, aid in the location of nests, and Morris (1969) provided much useful data on these. His thesis represents a significant advance in field studies on hedgehogs.

(2) Physiology and Biochemistry.

The most studied aspects of the hedgehog are its physiology and biochemistry, and in particular its hibernation mechanisms.

Ranson (1941), Edwards (1957), Morris (1961 a and b) and Dimelow (1963) discussed the care necessary for the handling and breeding of hedgehogs in the laboratory. They found that the hedgehog was easily kept in captivity provided it was fed a balanced diet and, where possible, kept at a constant temperature. These works form the basis for most subsequent laboratory experimental work on hedgehogs.

Because the hedgehog is a readily available, primitive, insectivore which can be easily induced to hibernate, it is an excellent animal for comparing physiological, biochemical and histological changes, between active and hibernating animals. Many of the early papers dealing with these aspects were written in German. During the last three decades, and especially during the last decade, much work in this area has been published by biologists in Scandinavian laboratories.

The earlier papers, such as Proctor (1949) and Suomalainen and Suvanto (1953) discussed temperature changes in hibernating hedgehogs. They found that hedgehogs entered deep hibernation when the temperature of their environment was held between 9° and 2°C, and that the body temperature of the hedgehog followed fluctuations in the environmental temperature. Lyman and Chatfield (1955) studied the physiology of hibernation in several mammals, including the hedgehog. They found that the onset of hibernation was not sudden, but was a result of decreasing activity, which culminated in hibernation when the temperature dropped below a critical level. These papers, which are concise and conclusive, have helped create a new understanding of the mechanisms of hibernation.

(3) <u>Anatomy and Reproduction</u>.

Apart from general texts, little has been written on hedgehog anatomy or on aging techniques. Clark (1932) compared the brains of various Insectivora and concluded that as the olfactory organs of most, including the hedgehog, are large in relation to their other sensory organs, the sense of smell is important to these animals in locating their prey.

Morris (1970) described a method for determining the absolute age of hedgehogs, that used periosteal growth lines in their jaw bones. This technique makes accurate age determination of hedgehogs possible, but unfortunately, as it can only be used with dead animals, it remains difficult to obtain accurate age determinations in the field.

Allanson (1934) investigated the seasonal changes in the reproductive organs of 135 male hedgehogs. She found that sexual maturity was not reached until at least nine months, that the testes of adult males in Britain were fully active from mid April to the end of August then retrogressed to a relatively quiescent condition until the end of December, and that from January until March the testes were preparing actively for the breeding season. Allanson and Deansley (1934) found that changes characteristic of the breeding season could be induced in hedgehogs held captive in the laboratory, by injecting females with the hormone oestrin, and both sexes with urine of pregnancy extract. Deansley (1934) described experiments carried out on 136 female hedgehogs to determine the limits of the breeding season and the nature of the reproductive cycle. She found that female hedgehogs in Britain bred between May and September, had one, or in some cases possibly two, litters per year, that the length of pregnancy was about one month, and that the average litter was five.

These latter three papers are comprehensive reports on hedgehog reproduction.

(4) Diseases.

Considerable work has been done on the diseases carried by hedgehogs. Much British work has been concerned with foot - and - mouth disease and ringworm. Hulse and Edwards (1937) found that hedgehogs carried foot - and - mouth disease, and that the virus could survive in the body of the hedgehog during hibernation. McLaughlan and Henderson (1947) found that foot - and - mouth disease is often fatal in the hedgehog under natural conditions. Skinner (1947) discussed foot - and - mouth disease in wild hedgehogs, and described how it may be introduced experimentally into laboratory animals.

These papers provide interesting information, which could be of real importance should the virus ever gain entry to New Zealand, as hedgehogs could form a reservoir of infection for the disease, and make its eradication more difficult.

The hedgehog has its own specific variety of ringworm, and is a vector for many other human diseases. It can also be infected experimentally with a wide range of economically important diseases, including the common cold and yellow fever.

English et al. (1962) described 13 human cases of clinical ringworm, 12 of which could be traced back to contact with hedgehogs. English (1967) further discussed the incidence of ringworm fungi in wild animals in Britain, and found that five out of 16 hedgehogs were infected. Morris and English (1969) and English and Morris (1970) described the incidence of hedgehog ringworm in Britain, and the isolation of ringworm from winter nests. They found that infected nests correlated with their use by infected hedgehogs. These latter two papers were extensions of Morris's (1969) thesis, which in itself gave a well documented account of the effects of this disease in a wild population of hedgehogs. These papers all add to the understanding of the transmission of ringworm fungi from hedgehog to hedgehog and from hedgehog to human.

(5) Food.

Many articles have been written on the food of hedgehogs, but few have been field studies made in any depth. Kalabukhov (1928), in Southern Russia, recorded that insects comprised 97% of the volume of food eaten by hedgehogs. Liu (1937) analysed the stomachs of 47 hedgehogs in China, and found that 95% of the food items were fly maggots. Shilova-Krassova (1952) examined 262 hedgehog droppings from the southern woodlands of Russia, and found that insects formed the main food items. No plant material was found in the droppings. Dimelow (1963) carried out 167 food preference tests on nine hedgehogs and found that although hedgehogs would eat most of the small invertebrates present in their natural habitat, they consistently exhibited a preference for particular species. From examination of stomach contents of 143 hedgehogs, (37 of which were empty) Yalden (1969) found that the food items occurring most frequently were carabid beetles, earwigs, caterpillars, millipedes, earthworms and weevils. These papers were of considerable value in the present study and provided a good basis for comparison with the food of hedgehogs in New Zealand.

Although there is little evidence, either for or against, the hedgehog has for centuries been blamed for eating the eggs and chicks of ground nesting birds. Buckland (1877) gave several accounts of hedgehogs caught in the act of eating eggs. However, Middleton (1935) found that only 17 of 1,323 partridge nests were disturbed by hedgehogs, while Kruuk (1964) estimated that only about 2.5% of 8,000 gull and tern broods, at Ravenglass in Cumberland, were destroyed by hedgehogs. These latter authors concluded that as a nest robber the hedgehog was a relatively insignificant predator. These papers are contradictory to Axell (1956) who concluded that between 1952 and 1954 the major mammalian predator of tern eggs at Dungeness bird reserve may have been the hedgehog. His evidence was circumstantial as no hedgehog was ever caught in the act. Axell also showed that control of carrion crows and foxes led to more successful breeding within the reserve. Unfortunately Axell does not provide statistics of the relative importance of the various predators, or the number of eggs allegedly eaten by each. The ecological balance in the area studied by Axell had been disturbed by wartime activities, and by post-war attempts to reduce predation. Axell also carried out experiments which showed that although a hedgehog would eat hen eggs when the shells were broken, it could not eat whole eggs. A similar result was reported by Otway (1965). It is unfortunate that Axell used hen eggs, instead of the smaller, thinner-shelled and more sharply pointed tern eggs in his experiments.

In a laboratory study Cott (1951) measured the relative acceptability of the eggs of 25 species of bird, as illustrated by feeding preferences of hedgehogs. He found that hedgehogs had definite preferences which agreed broadly with those of men. This was a well executed experimental study.

II NEW ZEALAND LITERATURE

Until recently, comparatively little work had been done on the hedgehog in New Zealand. Thomson (1922) discussed the introduction and distribution of the hedgehog in New Zealand, and Wodzicki (1950), Davidson (1965), Bull (1968), and Harris (1970) provided general accounts of its ecology and distribution. All of these are brief and descriptive.

Brockie (1958) studied the ecology of the hedgehog in the Wellington district and recorded his results in an unpublished thesis, and several associated papers. Brockie (1957) reported that the food eaten by hedgehogs inhabiting sand dunes on the west coast of the North Island consisted mainly of invertebrates, with slugs providing up to 90% of the food. Brockie (1959) listed the food items eaten by hedgehogs in Wellington province, and concluded that the main items of diet were slugs, millipedes and snails in suburban areas, slugs and lepidopteran larvae in pasture lands and snails, millipedes and frogs in sand dunes. As he found no egg shell in the droppings of wild hedgehogs, Brockie (1959) claimed that hedgehogs were insignificant as predators of ground nesting birds. Brockie (1960) discussed the road mortality of hedgehogs in New Zealand. He found that the mean number of hedgehogs killed per 100 miles of road ranged from zero in winter months to 73 in the spring and summer months. Brockie (1964) examined the dentition of 77 New Zealand hedgehogs, and found that 39 of these showed some dental abnormalities. Brockie's (1958) thesis on the ecology and food habits of hedgehogs is the most comprehensive New Zealand study attempted so far, and his published papers have been widely referred to in overseas literature on hedgehogs.

Herter (1961) compared the anatomy of hedgehogs in Germany with hedgehogs in New Zealand, and concluded that New Zealand hedgehogs did not differ significantly in their bodily characteristics from their west European counterparts. As only six New Zealand hedgehogs were used in the comparisons, Herter's conclusion may be questionable. However, as he provides extensive data on various anatomical measurements of

German hedgehogs, the opportunity exists for New Zealand workers to make more reliable comparisons.

(1) Diseases of New Zealand Hedgehogs.

The most extensively studied aspect of hedgehogs in New Zealand is the diseases they carry. Smith (1964) initiated a new line of investigation when he studied the microbiological aspects of the hedgehog. This study led to the publication of several papers, in conjunction with Marples and others, between 1960 and 1968. Most of these papers, such as Marples and Smith (1960 and 1962), Smith and Marples (1963), English, Smith and Rush-Munro (1964) and English (1964) dealt with the hedgehog as a carrier of ringworm, which is pathogenic to humans. The fungi appeared to be passed from animal to animal by contact, and by the sharing of infected nests. They may be passed directly to man by contact with nesting materials, or with the animals themselves. However, they showed that normal hygiene, such as washing the hands after handling animals, can prevent the spread of ringworm to man.

All of these papers have significantly altered the understanding of this disease and its means of transmission in medical and microbiological terms.

Smith and Marples (1964 and 1965) and Smith (1965) studied the hedgehog as a natural reservoir of penicillin-resistant strains of the bacterium Staphylococcus aureus, and found that 90% of the strains associated with the hedgehog were typable with human staphylophages. These papers could have important implications in the medical aspects of diseases caused by this bacterium.

Webster (1957 a and b) discussed the hedgehog as a potential reservoir of Leptospira pomona, and found that the hedgehog was highly susceptible to L. pomona when inoculated with the culture in captivity, and that it did carry the organism in wild populations.

Smith and Robinson (1964) discussed the incidence of Salmonella typhimurium in New Zealand hedgehogs, and found that 13 of 33 hedgehogs, in the Hamilton suburban area, carried this organism. Smith (1968) reviewed the diseases of hedgehogs and reported that hedgehogs carried many species of viruses, bacteria and fungi, as well as protozoan and metazoan parasites. Heath, Rush-Munro and Rutherford (1971) recorded the hedgehog as a new host for the mite Notoedres muris.

Many of the above disease producing organisms, especially Leptospira pomona and Salmonella typhimurium, have a significant effect on the health of domestic stock. Thus any knowledge on these is of importance to farmers and veterinarians.

(2) Theses.

The remainder of the work on hedgehogs in New Zealand is contained in unpublished theses. The two major works are Brockie (1958) and Smith (1964), which have been reviewed earlier.

Walsh (1963) studied locomotion and rolling mechanisms in the hedgehog, and concluded that the muscles of the back were unusually strong and flexible to enable the hedgehog to roll up, and that the peripheral muscles of the back acted as a drawstring, making it difficult for a predator to unroll the animal.

Otway (1965), the present author, studied the feeding behaviour of hedgehogs in the laboratory, and found that they appeared to have a definite feeding rhythm, and that each animal showed a preference for particular food items.

Woodhouse (1965) found that hibernating hedgehogs, in outdoor pens in Dunedin, did not remain in deep hypothermia for longer than six days at a time. Irving (1967) found that the hibernation period, in the Christchurch area, lasted from mid June to late September, and that food availability was an important external factor influencing the onset of hibernation.

Perry (1967) studied methods of aging hedgehogs by measuring the height of the protoconulid of the first lower molar, and following the sequence of fusion of the epiphyses of the long bones. She found that all methods had disadvantages, and that without known-age specimens it was not possible to accurately determine the ages of animals in all age-classes.

Wood (1970) studied the food preferences of hedgehogs in the laboratory and found that they preferred, in descending order of priority, beetles, snails, spiders, slugs, moths, earwigs, grass grubs and worms.

Parkes (1972) studied some aspects of the ecology of hedgehogs in pastures in Manawatu, and found that the population density was two animals per hectare, and that the average home ranges of males and females were 2.74 and 3.68 hectares, respectively. Brockie is currently completing a Ph. D. study on hedgehog populations in Wellington province.

All of the above theses, except Brockie (1958) and Smith (1964), were short term studies that were consequently very restricted, and therefore of limited importance. However, all add to the fund of knowledge on the New Zealand hedgehog, and introduce possible lines of investigation for future workers.

CHAPTER III

THE STUDY AREA

I. SITE SELECTION

In order to implement the aims of this investigation, it was essential that the study area met the following conditions:

(i) To reduce travelling time to a minimum, it should be readily accessible, but it must be sufficiently distant from built up areas to be classed as open pasture.

(ii) It was to remain in pasture for at least the two year period of the study.

(iii) It must be regularly grazed by stock to keep the pasture short enough for hedgehogs to be visible at night in a spotlight beam.

(iv) It should be subject to normal farming practices, such as haymaking and topdressing.

(v) There should be no difficulties associated with staking the area to form a reference grid, or with stock disturbance while counting hedgehogs at night.

(vi) Insect and invertebrate foods must be available in sufficient numbers to support a sizeable population of hedgehogs.

(vii) Hedges and cover, that could provide nesting sites for hedgehogs, must be available.

(viii) The resident hedgehog population should be sufficient to yield results which could be treated statistically.

As it fulfilled the above conditions, a portion of the Lincoln College experimental dairy farm was selected as a suitable study area. An additional advantage was that the monthly farm bulletin, produced by Lincoln College, gave relevant information on farming activities within the area.

The study area was located at Lincoln College, Canterbury. The map reference of this centre is 853424 on N.Z.M.S.2 Sheet S83/6, Burnham.

The location of the study area is shown in Figure 1. The paddocks used in the study were D9 (1.6 hectares), D10 (2.7 hectares) and D5 (5.2 hectares) of the Lincoln College experimental dairy farm.

Two adjacent four hectare blocks, hereafter referred to as block A and block B, each of which was divided into 100 systematically labelled 20 metre square plots, were set out in these paddocks. Block A was located on paddocks D9 and D10, and block B on D5.

II. SOILS AND VEGETATION

The dominant soil type in both blocks was Wakanui silt loam (Figure 2). Narrow bands of Templeton silt loam occurred along the western edge of each block. The slightly lower-lying eastern third of blok B was Temuka silt loam. The soils of the study area are representative of a large part of Canterbury and North Otago (Ward, et al., 1964 and Kear, et al., 1967).

FIGURE 1. MAP OF LINCOLN COLLEGE DAIRY FARMS.

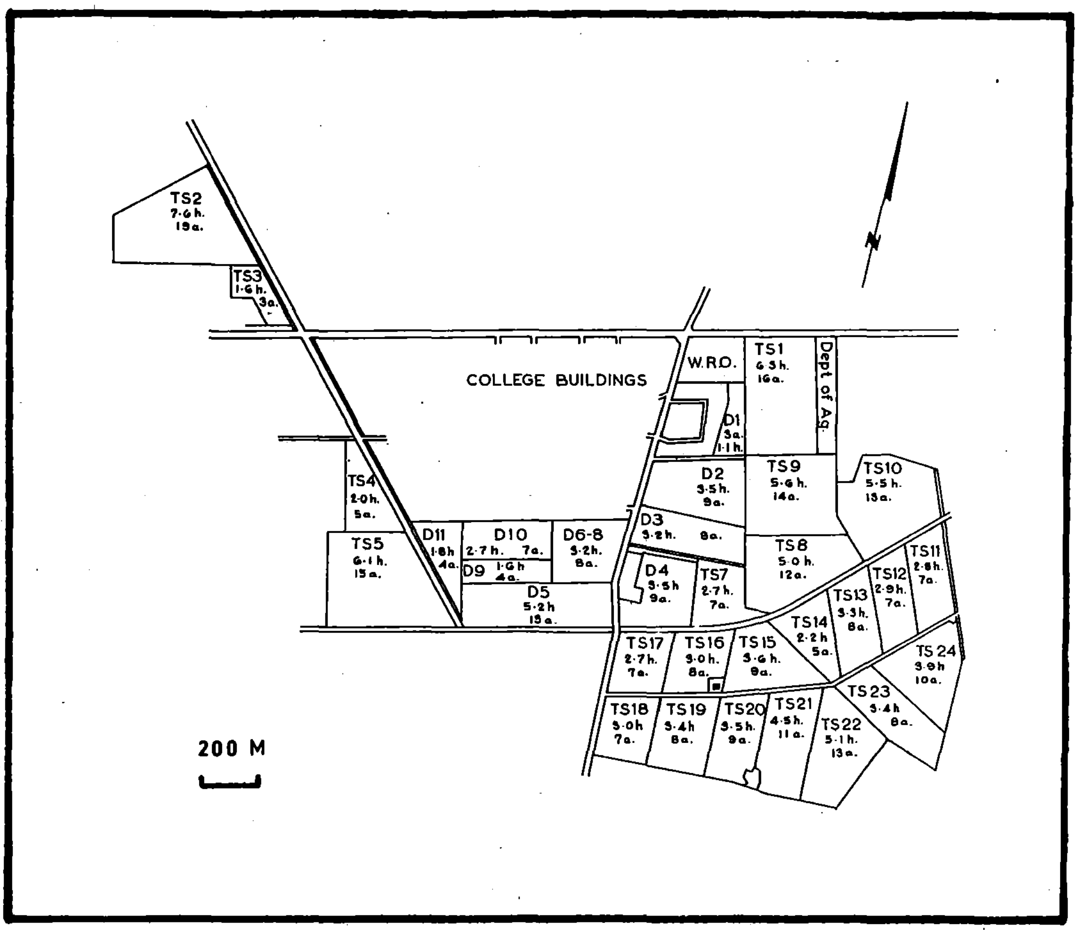
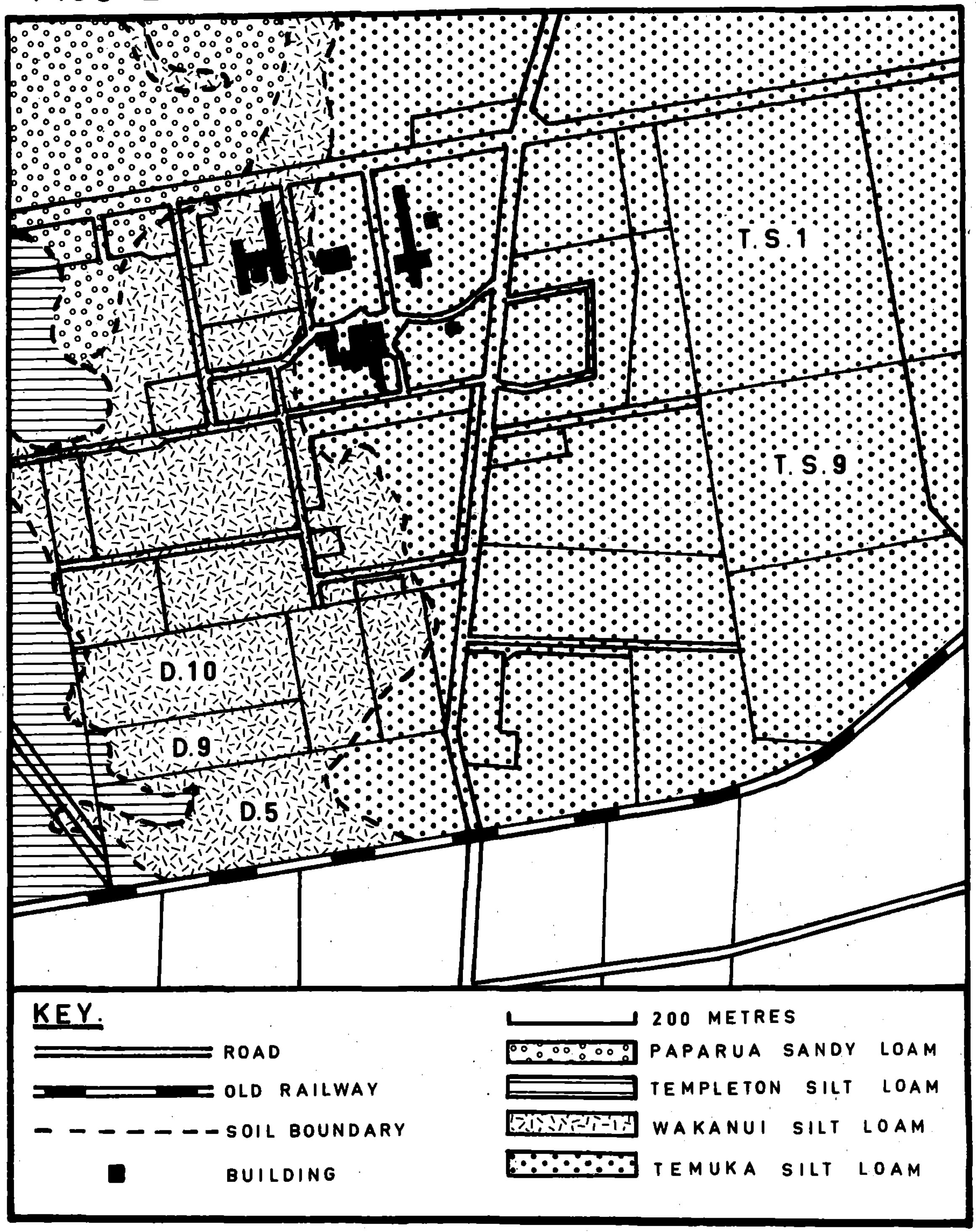


FIGURE 2. SOIL MAP OF THE STUDY AREAS.



The soils vary somewhat in fertility. Land use on these, and related soil types on the younger fan surfaces correlates with the depth and texture of the soils and with the height of the water-table. These factors control the availability of water during the period of summer drought. Soil moisture in the soils of the study area is sufficient to maintain pasture growth during short periods of drought, but spray irrigation may be used to advantage.

Both blocks were sown in Ariki ryegrass (Lolium x hybridum) (13.4 kg/ha) timothy (Phleum pratense) (6.7 kg/ha) and white clover (Trifolium repens) (3.4 kg/ha) pasture. At the commencement of the study on 30/6/69 the ages of the pastures in D9, D10 and D5 were 12, eight and seven years respectively, and consisted of 60% grass and 40% clover.

All these pastures contained the following weed species:

Dock (Rumex obtusifolius)
Barley Grass (Hordeum murinum)
Dandelion (Taraxacum officinale)
Common Daisy (Bellis perennis)
Yorkshire Fog (Holcus lanatus)
Prairie Grass (Bromus unioloides)
Cocksfoot (Dactylis glomerata)
Storks Bill (Erodium moschatum)
Hawkbit (Leontodon taraxacoides)
Wintercress (Barbarea verna)
Scotch Thistle (Cirsium vulgari) and
California Thistle (Cirsium arvense).

Barley grass infestation was largely restricted to the eastern half of D10, while docks were found mainly in the eastern part of D5, which became waterlogged during the winter. Docks were also found along lines of buried irrigation pipes and around their outlets, where water tended to collect.

The clover-ryegrass pasture, together with its various weed species, supported a large variety of insect and invertebrate foods, in numbers sufficient to provide hedgehogs with good foraging for most of the year.

III. LAND USE

The three paddocks of the study area formed part of a four paddock rotation system. They were grazed by the experimental dairy herd throughout most of the year. The number of cows in the herd varied with the season, averaging 43 in the summer season (August to May) and reducing to 24 during the winter period (May to August). After each milking, the herd was usually shifted to a different paddock. The herd usually grazed at least one of the three paddocks each day, keeping the grass reasonably short, and making it possible to locate foraging hedgehogs by spotlight searching.

When irrigation was used, grass growth was sometimes too great for the herd to keep reasonably short. This made it more difficult to locate hedgehogs at night. The same problem occasionally occurred during the winter months as the dairy herd was shifted less frequently and fed a supplementary diet of swede turnips and hay in order to conserve pasture for later winter and spring grazing.

The irrigation system comprised five hydrants, each of which fed six spraying positions, making a total pf 30 spray settings per application. Running each setting for three hours gave a 51 mm rain equivalent. All paddocks were irrigated throughout the drier periods of each year. These were between 23/10/69 and 19/3/70, 2/12/70 and 1/3/71, 30/3/71 and 26/4/71 (D5 only), and 1/10/71 until the completion of the study.

Irrigation of pastures during periods of moisture stress is increasing on farms on the Canterbury plains. Approximately 10% of pastures now receive some form of irrigation. Planning has already commenced on schemes which will eventually irrigate a further 50% of the pastoral and cropping land (G. Frengley pers. comm. and New Zealand Labour Party Manifesto, 1972).

Irrigation has been an important factor in this study, because extension of the grass growing period provided a suitable habitat for insect life for a longer period than would otherwise have occurred. Irrigation also brought additional food species, such as earthworms and lepidopteran larvae, to the surface of the soil, where they were readily available to hedgehogs. Had the soil remained dry, these species would have been inaccessible.

Paddock D5 was closed for hay in November 1969, and cut on December 21st, 1969. All three paddocks were lightly cut for hay on December 15th, 1970. Closure of these paddocks for hay made observations of hedgehogs difficult during the periods involved.

Paddock D10 was ploughed on June 24th, 1971, and was planted in fodder beet on September 15th, 1971. The fallow soil did not support a suitable food supply and very few hedgehogs were observed in this paddock following ploughing.

Apart from hedgehogs, the only non-domestic mammals seen in the study area were hares, opossums and semi-wild cats.

Throughout the study period, five hares (Lepus europaeus) were resident in the study area. During April 1971, two half-grown hares were also observed, but these had disappeared by June. Another quarter-grown leveret was seen in October 1971, but disappeared in November. These hares slept in forms in the paddocks and were frequently disturbed during field work. On each of two occasions an opossum (Trichosurus vulpecula) was seen in the gum trees (Eucalyptus spp.) on the western boundary of D5. These were two different animals as one had a black, and the other a red-brown pelt. Many cats (Felis domesticus) were seen hunting in the area throughout the study period. These were semi-wild cats that were living and breeding in haysheds and outbuildings.

Many species of birds were present at different times of the year, but few of these were resident. During each spring season, two pairs of mallards (Anas platyrhynchos) were present in the study area, and each season at least one pair nested. On 29/10/69, a nest containing four broken, but uneaten eggs, and one whole egg, was found under the hedge on the western boundary of D9. All eggs were rotten, and the nest had been abandoned. On 21/9/70 a nest containing five eggs was located in longish grass near the centre of block B. These eggs were fresh. The duck was apparently disturbed from the nest during the night, but returned later that morning. Two days later, after the herd had eaten the grass surrounding the nest, leaving it very exposed, it was finally abandoned. The eggs were left in the exposed nest for one month, but were not touched by predators. They were then removed for preservation.

Fifteen pairs of skylarks (Alauda arvensis) were resident in the area during the period of the study. The birds were frequently disturbed from their night roosts during the weekly hedgehog counts. During the nesting season (October to December) nests were located by searching the areas from which birds were observed to fly. Five nests were located in the 1969 breeding season, and one in 1971. Two were found in block A, and four in block B. Data from observations made on these nests is listed in Table 2.

TABLE 2. DATA ON SIX LARKS' NESTS FOUND IN THE STUDY AREA

NEST	BLOCK	DATE FOUND	NO. OF EGGS	NO. OF FLEDGLINGS	EGGS HATCHED
1	B	23/10/69	1	-	
2	A	13/11/69	4	-	
3	A	17/11/69	4	-	
4	B	27/11/69	4	3	1/12/69
5	B	3/12/69	2	2	9/12/69
6	B	18/ 1/71	1	1	22/ 1/71

The female from nest one was presumed to have been killed by a cat, as lark's feathers were found nearby. Two eggs disappeared completely from nest two; no broken shell was left. While it is possible that they were taken by a predator, such as a hedgehog, rat, hawk or gull, no evidence of such predation was apparent. The remaining eggs were left in the nest for one month before being removed. During this period they were ignored by predators. Nest three was flooded by irrigation, and was abandoned on 23/11/69. The unhatched egg remained in nest four until removed on 14/12/69 to give the fledgelings more space.

It can be concluded from the above observations that, with the possible (though unlikely) exception of two eggs from nest two, there is no evidence that hedgehogs preyed on the eggs or young of birds. This conclusion is supported by the results of the dropping analyses (Chapter 7). No egg shell was found in any dropping recovered from the study area. Laboratory experiments have shown that hedgehogs that have eaten eggs always passed pieces of shell in the droppings (Otway, 1965).

A flock of geese (Anser anser) was observed several times in block B, during the summer of 1969-70. Up to seven white-faced herons (Ardea novaehollandiae) were occasionally seen in the same area. Large flocks of both adult and juvenile black-backed gulls (Larus dominicanus), and black-billed gulls (Larus bulleri) invaded all three paddocks on different occasions. These invasions were most frequent in late autumn, presumably when their other food supplies were becoming scarcer.

A little owl (Athene noctua) was seen twice in block B, during the winter of 1970, and was heard on four other occasions. A harrier hawk (Circus approximans) was observed in D9 on 10/5/71.

Flocks of passerines including white eyes (Zosterops lateralis), goldfinches (Carduelis carduelis), house sparrows (Passer domesticus) and starlings (Sturnus vulgaris) were observed feeding in the area at different times of the year. Two pairs of white-backed magpies (Gymnorhina tibicen) were seen on many occasions in block B, and occasionally in block A. Song thrushes (Turdus philomelos) and blackbirds (Turdus merula) were frequently observed in both blocks. These probably nested in the hedge between the two blocks.

All species mentioned are probably inhabitants of any typical Canterbury pasture land. Only seven of them were likely to compete with the hedgehog for food. These were the magpie, thrush, blackbird, heron, starling and the two species of gull, all of which catch insects or invertebrates from pastures. The skylark also eats insects, but as it usually catches them on the wing, it cannot be considered a competitor. None of the seven species may be regarded as a serious competitor. The first four were present in such small numbers that they would have had little effect on the food supply. Although the latter three species were present in large flocks, they appeared so infrequently that they too would have had little effect on the total food supply.

IV. NOTE

It was originally intended to compare two non-irrigated blocks C and D, each of four hectares, with the similar, but irrigated blocks, A and B. After consultation with the farm manager these non-irrigated blocks were located in two adjacent paddocks, TS1 and TS9 respectively, of the Lincoln College town supply dairy farm as shown in Figures 1 and 2. Their areas were 6.3 and 5.6 hectares, respectively.

The soil type of these paddocks was Temuka silt loam. TS1 carried a newly sown pasture of tall fescue (*Festuca arundinacea*) and white clover, while TS9 carried a four year pasture of Ariki ryegrass, timothy and white clover.

Pitfall collections obtained from 12 traps in each of blocks C and D yielded the same invertebrate species (with a few very minor exceptions) as those from blocks A and B. Consequently the same types of hedgehog food were present in both areas. Minor variations were that collembola and ladybirds were more numerous in blocks C and D than in A and B, but neither of these species was important in the hedgehogs diet.

Unfortunately this area became unsuitable for study because spasmodic grazing, resulting in excessive grass growth, made it extremely difficult to locate hedgehogs at night in block D. This block was also closed for hay from 18/9/69 to 13/11/69.

As the first drilling of grass in block C did not strike successfully, the paddock was redrilled with Ariki ryegrass on 11/9/69. When this grass germinated it was found to be infested with shepherds purse (Capsella bursa-pastoris) which produced tall seed heads. These threw shadows in the spotlight, again making hedgehog counts very difficult.

After attempting to overcome these counting difficulties for a period of eight months it was decided on 28/2/70 to abandon this area. The low reliability of the data obtained meant that any comparisons with blocks A and B would not be valid. All other non-irrigated pastures within the study area were found to be unsuitable for further comparison with the irrigated pastures in blocks A and B.

CHAPTER IV

POPULATION SIZE, DENSITY AND DISTRIBUTION

I. INTRODUCTION

In order to relate the feeding behaviour of a natural population of hedgehogs to the size and distribution of the population, to their movements within their home ranges, and to their available food supply, it was necessary to know the hedgehog population of the study area throughout the period of the investigation. The different techniques available for this purpose were examined in detail to determine which was most suited to the present study.

The few studies that have already been made on the movements of wild hedgehogs, have been confined in the main to distance travelled, rather than to movements within a home range. The object of this study was, however, to define the extent of hedgehog home ranges in pasture land, and to investigate movements of animals within these home ranges. This data could then be used in conjunction with the diet of the hedgehogs to give an estimate of their control, if any, of pasture pests.

II. LITERATURE REVIEW

(1) Population Estimation.

As Buckner (1966) noted, it is usually very difficult to accurately determine the sizes of small-mammal populations.

Methods used to determine population size for vertebrates have been reviewed by Davis (1963), Eberhardt (1971), Scott-Overton (1971), and in some considerable depth by Southwood (1967).

Dice (1938 and 1941) and Blair (1941) discussed various methods of estimating mammal populations, and concluded that any method must be adapted to suit the particular animal under study, and that in any given study one method will prove to be the most suitable.

Deevey (1947), in a study of the age distribution of mortality in several natural populations of mammals, found that these could easily be condensed into life tables. Hayne (1949 b and c) discussed methods for estimating animal populations, including the strip census method, capture-recapture methods and a removal method. He concluded that each method was suited to different sets of conditions. The above papers provide a general background to small-mammal population studies, and critically review the different methods available for such analyses.

Taylor and Williams (1956) and Howard (1959) described techniques for estimating rabbit populations from the density of faecal pellets on the ground. Batcheler and Logan (1963) used faecal pellet counts to estimate the populations of deer and chamois, both before and after a control campaign, as the means of determining its effectiveness. In the present study an attempt was made to obtain population estimates based on dropping counts, but the values obtained were considered unreliable. The sources of error in these estimates are discussed in detail later.

Jackson (1939) described a technique which gives the absolute number of animals in a population from the percentage of marked animals recaptured. He also extended the technique to measuring birth, death and migration. Adams (1951) discussed the confidence levels for the Lincoln Index as used in animal population studies, and introduced mathematical confinements for this method.

Bailey (1951) described two methods of estimating the size of mobile populations from recapture data. He concluded that the 'triple-catch' method, in which data collection was restricted to only three occasions, was the better.

Leslie and Chitty (1951), Leslie (1952), and Leslie, Chitty and Chitty (1953) discussed estimates of populations from capture-recapture data. They found that when they attempted to estimate two populations of murid rodents, namely the field vole (Microtus agrestis) and the bank vole (Clethrionomys glareolus) by this technique, the former could not be estimated with confidence, as members of the population did not fulfil the requirements of their mathematical model. During the winter months, a difference in behaviour between marked and unmarked animals was noted. This negated the requirements of random sampling.

Kelker (1940) devised a method based on change of composition of a population caused by the selective removal of one distinct group such as one sex, or one age group. As the population must be left undisturbed, to observe the natural behaviour of wild hedgehogs, this method was not acceptable for the present study.

Craig (1953) produced two methods which are based on the frequency of capture of individuals, and differ only in the mathematical treatment of the data. These methods are based on a mathematical model different from the Lincoln Index and demand that while the animals must not leave the habitat, they must be very mobile, thus making their chances of recapture virtually random, almost immediately after release. As the hedgehogs were more likely to be caught within their home ranges, and because they moved out of the study area the conditions of this model were not met.

Jolly (1963) devised a method which is particularly applicable if a large number of individuals have been recaptured several times in a long series of samples. This situation often arises in work on mammals. Jolly's (1963) method is based on a deterministic model while Jolly (1965) is based on a stochastic model. Jolly (1963 and 1965) both cover situations in which there is both loss (death and emigration) and dilution (births and immigration).

Based as it is on an efficient method of grouping the data, and on a fully stochastic model, Jolly's (1965) method would appear to be the most appropriate method for use in studies, such as the current one, involving three or more successive samples, where both dilution and loss are occurring. Thus Jolly's (1965) stochastically based method gives a more realistic, estimate of the variance.

This model assumes that each animal has its own individual survival rate, and deals more with the probability of a population surviving a given interval than with the survival of the individuals. Jolly (1965) uses the final capture only for each animal, and assumes that there is the same probability of capture for marked and unmarked animals. This method assumes that marked animals are not affected by such marking, and that marks are not lost or destroyed. Birth and immigration and death and emigration, as calculated within the model, could not be obtained separately unless either birth or immigration, or death or emigration, was known. None could be determined in this study because of inability to locate nests or sleeping areas, very young hedgehogs and corpses. However, data gathered from pregnant hedgehogs captured outside the study area for stomach contents indicate that the most common litter-size for hedgehogs is four provided all embryos are born alive.

Jolly's (1965) stochastic model had another obvious advantage for use in the present study in that it had been converted to a computer programme by Dr E.G. White, who had used it for population estimates of alpine grasshopper species (White, 1971 a and b). Although this programme was easily adapted to the estimation of hedgehog populations, the smaller numbers involved meant that less information could be obtained from it, and that relatively high standard errors would have to be accepted. The methods Jolly (1965) and White (1971 a and b) were found to be the most suitable for use in the present study, because all their necessary assumptions could be fulfilled and the groupings of capture-recapture data permitted by these methods compensated in part for the small number of individuals in the population. No matter what method was chosen to estimate the population the very small numbers involved would limit reliability.

(2) Home Range.

Many of the problems associated with animal population studies may be solved by a knowledge of the range of movement of individuals. Movements of mammals have been widely studied, and movement data provide basic information on a species which is useful in planning control programmes and management (Sanderson, 1965).

The types of movements most frequently studied are those involving activities, such as feeding, mating, raising young, sleeping and exploring, within a home range area. Dice (1952) defined the home range as "the area covered in the day-to-day travels of the animal". Brown (1956) reviewed many definitions and methods of home range estimation and concluded that the home range was limited by the ability or necessity of the animal to travel for food or protection, by the seasons, by the population density and by the sex and age of the animals. Brown (1962) concluded that an animal does not wander at random but repeatedly travels over the same area. Whether this area is visited each day, or is part of a wider area traversed over several days is a function of the individuals of the species that are present in the area. Other comparable definitions have described home range as "that area about its established home which is traversed by the animal in its normal activities of food gathering, mating and caring for young" (Burt, 1940); and "the area covered in normal daily activities" (Blair, 1953).

The techniques most frequently used in obtaining the extent of home ranges have been reviewed by Sanderson (1965). These involve both direct and indirect observations. The advantages of direct observations are that interference caused by handling is minimised, movements of the individuals are not hampered and direct information is obtained on the activities of the animals. The main disadvantages of this technique are the considerable time required, the limited number of animals that can be observed at any one time, and the influence the observer may have on the individuals being studied. Many techniques for indirect observations have been developed and these include capture-recapture methods, the interpretation of natural signs, and the use of radioactive materials, dyes to render urine and faeces readily visible, photographic devices and radiotelemetry. Repeated live trapping of marked animals is often used in home range studies where large numbers of small animals are involved, although for birds and larger mammals visual observation is often possible.

Justice (1961) described a method of measuring home ranges in mice by using smoked kymograph paper to pick up the tracks of individual toe-clipped house mice (Mus musculus - Rodentia: Muridae). This method avoided the problems associated with trap-shyness or trap-addiction and gave reliable results without in any way altering the normal activities of the animals under study. This simple method was extremely efficient in terms of the information obtained in relation to the amount of effort and expense involved.

The availability of a wide range of radioactive isotopes such as Co^{60}, and Au^{168} that can be detected at distances of up to four metres has made it easier to obtain information on the movements of a single individual especially among insects and in some small mammals having restricted home ranges. Godfrey (1954 a and b) reviewed the use of radioactive isotopes in small-mammal studies. The detection range was too small for radioactive isotopes to be of much value in the present study. Animals could be detected by eye at greater distances.

The most difficult part of any home range study is not the collection of data, but interpretation and the calculation of home range from these data. Statistical approaches to the study of home ranges and movements of mammals have resulted in the development of three generally applicable techniques of defining home range from field data.

Minimum area or convex polygon methods (Dalke and Sime, 1938), define the home range as the area of a convex polygon formed by straight lines joining the points of successive captures. This represents a minimum area as the range of movement of the animal is assumed to be bounded by the known points of capture. Harvey and Barbour (1965) describe a modified minimum area method which was used to determine home range in the vole Microtus ochrogaster (Rodentia:Muridae). This method uses one quarter of the range length as a standard to determine whether outside points in the range were to be connected directly.

Boundary strip methods include an area beyond the minimum area enclosed by the capture points either to compensate for the lack of traps at a boundary, or to allow for the area equidistant between two sets of traps. The inclusive boundary strip method includes the area halfway to the next set of traps (Blair, 1940 and 1943; Haugen, 1942, and Allen, 1943). Hayne (1949a) maintains that the inclusive boundary strip method is too mechanical, as the lines enclosing the home range are drawn according to an arbitrary set of rules, by which the same configuration of capture points produces the same geometrical shape.

Traps which the animal has never visited may be included within the home range. Blair (1942), however, regards these constraints as acceptable in a system which is both simple and objective. Brown (1962) points out that such a mechanical method can not allow for an investigator's informed knowledge of the particular habitat, especially of areas which the animal was known to avoid. In the exclusive boundary strip method allowance is made for observed irregularities, as well as adding some additional area to the minimum area established by trapping (Burt, 1940 and 1943; Evans and Holdenreid, 1943; Baker, 1946; and Stickel, 1954).

To avoid errors introduced by converting linear measurements into areas some workers have preferred range length methods. The maximum distance between points of capture (i.e. the greatest distance that the animal is known to have moved) is used to estimate the home range. These methods may use either the observed range length, or an adjusted range length obtained by the addition of half the distance to the next set of traps. Workers who have made use of these maximum range lengths include Burt, (1940); Holdenreid, (1940); Evans and Holdenreid (1943); Linsdale (1946); and Brown (1956). Where the maximum range length has been used to calculate the home range, it has been assumed to be the diameter of a circle, or the major axis of an elipse (Lay, 1942; Stuewer, 1943; Stickel, 1946 and Fitch, 1947). Brown (1962) points out that personal observation may have shown such an assumption to be incorrect. This method would overestimate the size of narrow and irregular home ranges.

To test the validity of these various methods of calculating home range Stickel (1954) applied them to artificial populations. Using circular ranges she found that the exclusive boundary strip method and the adjusted range length methods gave, more accurately, the true range and length. The minimum area method gave results that averaged 64% too small, while the results from the inclusive boundary strip method averaged 17% too large. Whereas the observed range length method averaged 25% too small, adjusted range length averaged $<3\%$ too large.

Opinions have differed as to the number of captures required to produce a reliable estimate of the home range. Brown (1962) found that the greater the number of captures, the more reliable the boundary for the home range of the animal. Godfrey (1954b) found that it was necessary to have 16 to 19 captures for *Microtus agrestis*, whereas Tanaka (1953) relied on as few as six for *Clethrionomys rufucanus*. Stickel (1954) showed that trap spacing influenced the number of captures necessary to obtain maximum home range values. Haugen (1942) showed that the trap-revealed home range size increased rapidly for the first few captures and then levelled off. Using artificial populations Stickel (1954) demonstrated a similar result. In these artificial populations more than half the maximum values were reached in 12 captures, and all after 33 when traps were visited at random. The same general pattern occurred where traps nearer the centre of the grid were favoured, but the areas levelled off more slowly. All maximum values were again reached after 33 captures. Davis (1953), concluded that there were several statistical deficiencies involved when large areas were covered, or when the number of captures was small.

Hayne (1949a) examined the relative merits of different methods of calculating home range areas from trapping records, and concluded that all made the assumption that an animal would be trapped throughout the biologically important portions of its home range. He suggested than an experimental examination of this assumption was warranted. McNab (1963) examined the size of mammalian home ranges in relation to bioenergetics, and concluded that, as the size was a function of the amount of energy expended by the species. it varied according to the effect on the animal of weather, climate and the available food supply.

Sanderson (1965) reviewed the methods and techniques used in the study of mammal movements and suggested that the sizes and shapes of home ranges had little significance in themselves, and that researchers should concentrate on ecological studies. He stated that herbivores seem to have smaller home ranges than carnivores; that habitat affects the size of home range; and that the average size of home range appears to decrease as the population density increases. He concluded that no one technique for determining location, and no single method of analysing data, gave the best answer for all species and in all situations. He suggested that studies should emphasise a mammal's specific needs under all circumstances throughout the year rather than the distance it moves, the shape of its home range or the area it covered. The information needed would be gained by determining why an animal was at a particular place at a particular time.

Following critical examination of the above papers it was decided that, as there were statistical advantages in dealing with a larger number of captures when the total population was relatively small, and because difficulty was being experienced in finding nests, that the capture-recapture and convex polygon methods would yield the most reliable information on home ranges.

Apart from the home range studies discussed earlier, the only studies that have been made on hedgehog movements are distance movements between successive points of capture. Lüttich (1928-29) found that a marked pair of breeding hedgehogs on the Island of Spiekeroog had a regular summer hunting range of 200 to 300 square metres surrounding their nests. Herter (1938) reported that following the release of several animals in Berlin only three were recaptured, one within a few metres, and the other two within one kilometre of their point of release. He does not give the time between release and recapture. Herter (1938) also reported that, in Silesia, a hedgehog which was caught robbing a fowl house, was subsequently marked and released 2.5 kilometres away, but had returned within two days. Lindemann (1951) claimed that a hedgehog which he had tamed could find its way home from distances of up to one kilometre. Kruuk (1964) found that hedgehogs at Ravenglass, in Cumberland, Britain, wandered over distances of up to four kilometres. Morris (1969) reported that within Bushey Park, in Twickenham, Britain, hedgehogs had been observed to travel up to 600 metres.

Brockie (1958) recorded the results of captures and recaptures of hedgehogs in a range of New Zealand environments. Many of the 42 animals captured in a 6.5 hectare area at Gwavas, near Tikokino, Hawkes Bay, made frequent movements of up to 315 metres, but as this was the maximum possible distance available within the study area, it was possibly an artificial limit. The males tended to cover greater distances than the females. Few of the animals in a 5.7 hectare area of beech forest, bush and domestic gardens in the Point Howard area of Wellington, were recaptured at distances greater than 90 metres from the points of release. The maximum distance travelled was 135 metres. However, these movements may have been restricted by the steep terrain, the dense shrubbery and by the presence of retaining walls. Of five hedgehogs released in an area of 6.5 hectares in the North Paekakariki sand dunes, three were recaptured within 180 metres of their release points, while the remaining two were found to have travelled 540 and 720 metres, respectively. Of seven hedgehogs released in Wilton Bush, on the outskirts of Wellington, six were recaptured within 90 metres of their release points. The seventh, a male, was found to have travelled 900 metres.

Although, all of these reports of hedgehog movements are largely descriptive, they do add to our limited knowledge of the likely distances covered and areas occupied by hedgehogs.

III. METHODS OF STUDY

(1). Dropping Counts.

Dropping counts as used for population estimates of deer (Batcheler and Logan, 1963) and rabbits (Taylor and Williams, 1956) were used to estimate the hedgehog population of the irrigated study area. Droppings were collected weekly over a one year period from a Z-shaped transect in each block. Estimates were based on the formula :

$$P = \frac{N}{7D} \times \frac{A}{a}$$

where P = population estimate

N = number of droppings obtained from the transects per week

A = area of field

D = average number of droppings/hedgehog/day (=3.2)

a = area of transects.

Estimates based on the number of droppings collected from the study area on the mornings following hedgehog counts, gave values which never exceeded 60% and were usually less than half of the number actually seen the previous night. The value D = 3.2 was obtained from 10 animals kept in a field cage over a period of four months and represents the best estimate possible. The mean value for defecation obtained from the food recovery experiments in the laboratory is also similar (Chapter 7).

Possible reasons for these low estimates are:

(i) Hedgehogs do not have a preferred defecating area, and droppings are deposited singly, therefore some may have escaped detection. Since narrow transects (1.2 m) were followed it is unlikely that this was a major source of error.

(ii) Droppings could be destroyed by paddock irrigation, crushing by tractors, irrigation machinery and cows, or covered by cow dung. Of these, losses caused by irrigation and rainfall would be the most serious. The mean monthly rainfall for the Lincoln area (80 year average) ranged from 43 to 68 mm. Field experiments showed that irrigation equivalent to 25 mm of effective rainfall destroyed droppings in less than 90 minutes. Destruction of droppings would cause underestimation of the population.

(iii) Almost invariably animals held in field cages, and those fed in the laboratory were observed to defecate in the vicinity of their nest on first emerging each night. As no nests were found in the study area it is likely that a value less than the average number of droppings/ hedgehog/day should be used in the equation above. Reducing D to 2.2, on the assumption that each hedgehog defecated once/day outside the study area, gave population estimates closer to but still well below those actually observed.

(iv) Each animal in the population may not be present in the study area every day as assumed by the formula.

(v) The number of droppings collected per week was comparatively small. This could lead to large errors in the calculations.

It was concluded that because of these uncertainties dropping analyses were not suitable for estimating the population of this area.

(2) Capture-Recapture.

Capture-recapture methods usually involve trapping and marking animals, releasing them, and then after a given period attempting to recapture them. This is essentially the method used here. However, as the emphasis of this study was the examination of a population of wild hedgehogs in the field, it was essential that the animals suffered the minimum human interference. Trapping would involve hedgehogs being held captive in cages for some time. As this would upset their natural feeding and behavioural rhythms, it was decided that it was an unsuitable technique to use in an investigation of these rhythms. Trapping would also introduce the problems that are associated with trap-shy and trap-prone animals (Brown, 1956). To avoid problems with using traps, hedgehogs were located at night by spotlight, identified (new animals were marked), and immediately released, thus causing the minimum interference with their behavioural patterns. This modification of the capture-recapture method has been little used for small mammals other than hedgehogs.

Several possible alternative methods for tracking hedgehogs were considered, but, for various reasons, all except spotligh searches had to be discarded. As the detection range of radioactive wires (Co^{60}) did not exceed 4 m, (Godfrey, 1954a) these were unsuitable. There was also the possibility that they may have affected the physiology of the hedgehogs, and thus influenced their behaviour. A small, flashing, red light, attached to the hedgehog by an elastic harness was also tried, but again, even in the limited cover provided by pastures, this could not be seen at distances exceeding 6 m. This system was also impractical to use because the most suitable power source, as far as size and weight were concerned, was a small mercury cell, which lasted less than 36 hours.

Although the use of small radio transmitter would have been ideal, and an electronic technician who could manufacture suitable models was available, the method could not be implemented because all attempts to obtain the necessary finance were declined. Lack of available finance also precluded the use of infra-red night scopes. It is particularly unfortunate that tracking by radio was not possible. This would have made it easy to follow the movements of the animals, and would have enabled their nests to be located. Unless the nests, integral parts of the home ranges, were located, it would not be possible to establish birth, death, immigration and emigration.

Strenuous efforts were therefore made to find these nests, and to track hedgehogs to them.

As the investigator's previous experience had shown that red light did not disturb hedgehogs from their normal activities, attempts were made, using a red spotlight, to follow individual animals throughout the night. However, these attempts all failed because the animals were always able to detect the presence of the observer, although care was taken to stand quietly down wind, and as far away as possible. The red light greatly reduced the distance at which hedgehogs could be observed. It was impossible to observe a hedgehog with the red spotlight if the observer remained at a distance sufficient to avoid detection by the animal. When hedgehogs detected the presence of an observer, they resorted to one of two patterns of behaviour; they either froze and refused to move, their patience outlasting that of the observer, or they immediately headed for the nearest cover and usually disappeared. These attempts to follow individual hedgehogs were thus terminated.

When the grass length exceeded 15 cm the tracks of hedgehogs could often be observed winding through the grass. Under these conditions it was possible to record the movements of the animal, and often to follow it for some distance. Similarly, on nights of heavy dew it was possible to follow the tracks of hedgehogs, where the dew had been brushed off the grass. These observations showed that the animals tended to follow relatively fixed routes each night. Unfortunately, however, all tracks were lost when they entered the long cover adjacent to the study area. Only two nest sites were located during the study. One of these was under a large bluegum stump in the plantation on the western boundary of block B. Frequent searching both by day and by night, including attempts with a rabbiting dog failed to locate any further nests in this area. Wet sand was spread around many of the stumps in the plantation, and although illdefined tracks through it suggested that some animals were using the cavities under the stumps, no tracks could be positively identified as those of hedgehogs. It is unlikely that these tracks were caused by hedgehogs, since tests carried out with adult hedgehogs showed that they left identifiable impressions in wet sand. Spores of cats in the sand, and the close proximity to the western boundary of the plantation of the Lincoln College dump, suggest that the unidentified tracks were probably caused by rats.

During the period of the study the mummified corpses of 24 hedgehogs were found in four hay barns located between 0.04 and 0.7 km from the western boundary of block A. These corpses had been dislodged when hay was removed for winter feeding of stock. The second nest was located in one of these barns by a Lincoln College employee. It contained a female and two living young. The employee noticed that the animal had been marked. These observations suggest that a considerable number of hedgehogs preferred to nest in these barns, rather than in natural cover. This possibility had been overlooked at the start of the investigation.

The hay was periodically probed in attempts to locate animals. This was unsuccessful, and the only reliable method of determining the numbers of animals nesting in these barns would have been to remove all bales. This was neither practical nor permitted. The barns were examined daily while hay was being fed to stock and although 24 unidentifiable corpses were recovered, over the three winters, no live animals were observed. Live animals could presumably have burrowed deeper into the remaining bales before being uncovered.

Brockie (pers. comm.) has found that if hedgehogs are located at night, held captive until daylight, and then released, they make straight for their nests. This information was not received until the study had been completed. Use of this method could, however, have disturbed the behavioural rhythms of the animals, which was contrary to one of the aims of the study. Inability to find nests has meant that analyses of the data yields minimum feeding ranges, rather than home ranges. It has also meant that births (and deaths, as many hedgehogs die in their nests) could not be recorded with any certainty.

Grass growth varied throughout the year and was most vigorous in spring and early summer. Unfortunately these times coincided with the breeding periods of the hedgehogs. This meant that the young hedgehogs were smallest when the grass was longest. They were therefore difficult to locate, and few were found in the present study. This problem could be overcome in future studies if it was possible to arrange for very heavy stocking, or regular mowing at such periods. In this study regular mowing would have altered the natural pasture situation and would have interferred with the profitable operation of the experimental dairy farm, and possibly interferred also with the hedgehog population. Without reliable data on birth and death, immigration and emigration could not be calculated.

(3) Method of Counting Hedgehogs.

Blocks A and B (as described in Chapter 3) were systematically searched every Monday night from 30/6/69 to 29/11/71 using a spotlight powered by a six-volt, wet-cell, spotlight battery.

Each block was divided into 100 systematically labelled 20 m square plots. Two plots on either side of the track were searched as the observer moved forward. The overlapping that occurred while returning along the reciprocal track guarded against hedgehogs avoiding detection by crossing from an unsearched to a searched plot. The grass conditions of the blocks were noted on each count night as an indication of the efficiency of the count. The time at which each animal was located was recorded, as was its position in relation to the nearest peg.

Preliminary field observations made between October 1968 and March 1969, inclusive, indicated that the period of maximum hedgehog activity occurred between 9 p.m. and 11 p.m. Wood (1970) observed maximum activity between 9 p.m. and midnight. Subsequent grid searches were therefore timed to coincide with this activity maximum. Each search usually required one and a half to two hours for completion. Towards the end of the study period a series of all-night counts were carried out, to check if searching had caused any variation in the time of maximum activity previously observed.

Eleven all-night counts were carried out on 12th, 13th, 14th, 19th, 20th and 21st October, 1970, 23rd and 30th of March 1971, and 6th, 12th and 27th of April, 1971. As both blocks had to be counted in each one hour period from 7 p.m. to 7 a.m. during these searches (instead of the normal 1.5-2 hours) they were carried out at times when grass growth conditions were most suitable. Block A was counted in the first half of each hour, and block B in the second.

Fifty seven hedgehogs were observed in the study area during the all-night counts. Eighteen of these animals were also captured 10 or more times during the determination of home ranges. These animals were considered to be resident in the study area and accounted for 90% of the observations recorded in Table 3.

TABLE 3. DATA FROM ELEVEN ALL-NIGHT COUNTS OF HEDGEHOGS IN THE STUDY AREA.

	DATE OCTOBER 1970						MARCH 1971		APRIL 1971			
	12	13	14	19	20	21	23	30	6	12	27	Total
TIME	NUMBER OF HEDGEHOGS OBSERVED IN ONE HOUR PERIODS											
7- 8p.m.	0	0	0	0	0	0	0	0	0	0	0	0
8- 9p.m.	3	4	2	3	4	1	1	3	6	5	3	35
9-10p.m.	4	4	5	6	2	6	0	5	10	9	8	59
10-11p.m.	7	8	6	8	7	8	4	7	6	7	6	74
11-12p.m.	4	4	5	4	6	5	6	10	7	5	5	61
12- 1a.m.	3	3	2	3	4	3	4	7	6	5	4	44
1- 2a.m.	4	2	3	3	3	2	4	6	5	4	4	40
2- 3a.m.	2	3	1	3	1	4	3	6	5	3	4	35
3- 4a.m.	3	3	1	2	1	2	3	6	4	3	3	31
4- 5a.m.	1	2	1	1	1	2	1	5	4	4	3	25
5- 6a.m.	0	0	0	0	0	0	1	1	3	3	2	10
6- 7a.m.	0	0	0	0	0	0	0	0	0	0	0	0

The data presented in this table shows that the largest numbers of hedgehogs were active in the study area between 8 p.m. and 3 a.m., with the maximum activity occurring between 10 p.m. and 11 p.m. This table appears to suggest that the population contained natural early and late feeders. Examination of the times when each animal was observed showed that there were considerable differences in behaviour between individuals. After making allowance for animals known to have disappeared from, or become resident in the area between the two count periods, it was calculated that each of the 18 resident animals was present in the study area, on average, on only 50% of the nights when searches were carried out. Three of these animals were observed in the area on every count night, while at the other extreme one resident was observed as infrequently as one night in six. The time per night actually spent in the study area by the residents on the nights they were present ranged from one to 11 hours with a mean of 6.5 hours. All 18 residents tended to be most active between 9 p.m. and 3 a.m., and seven of them were never observed in the study area before 9 p.m. or after 5 a.m. Thus the animals that appear earliest in the study area each night tend also to be the last to leave. It would appear, therefore, that the presence in the population of animals that spend larger and shorter periods each evening in the study area, rather than the presence of natural early and late feeders is responsible for the distribution pattern shown in Table 3.

The laboratory feeding experiments discussed in Chapter 5 suggested a possible correlation between time spent feeding and body weight. Unfortunately the only weight data available for the 18 resident animals were their weights at the time of first capture. As the animals had been captured over a period of 15 months prior to starting the all-night counts, and as hedgehog weights vary seasonally, it was considered unrealistic to attempt to correlate length of time spent feeding with these available weights.

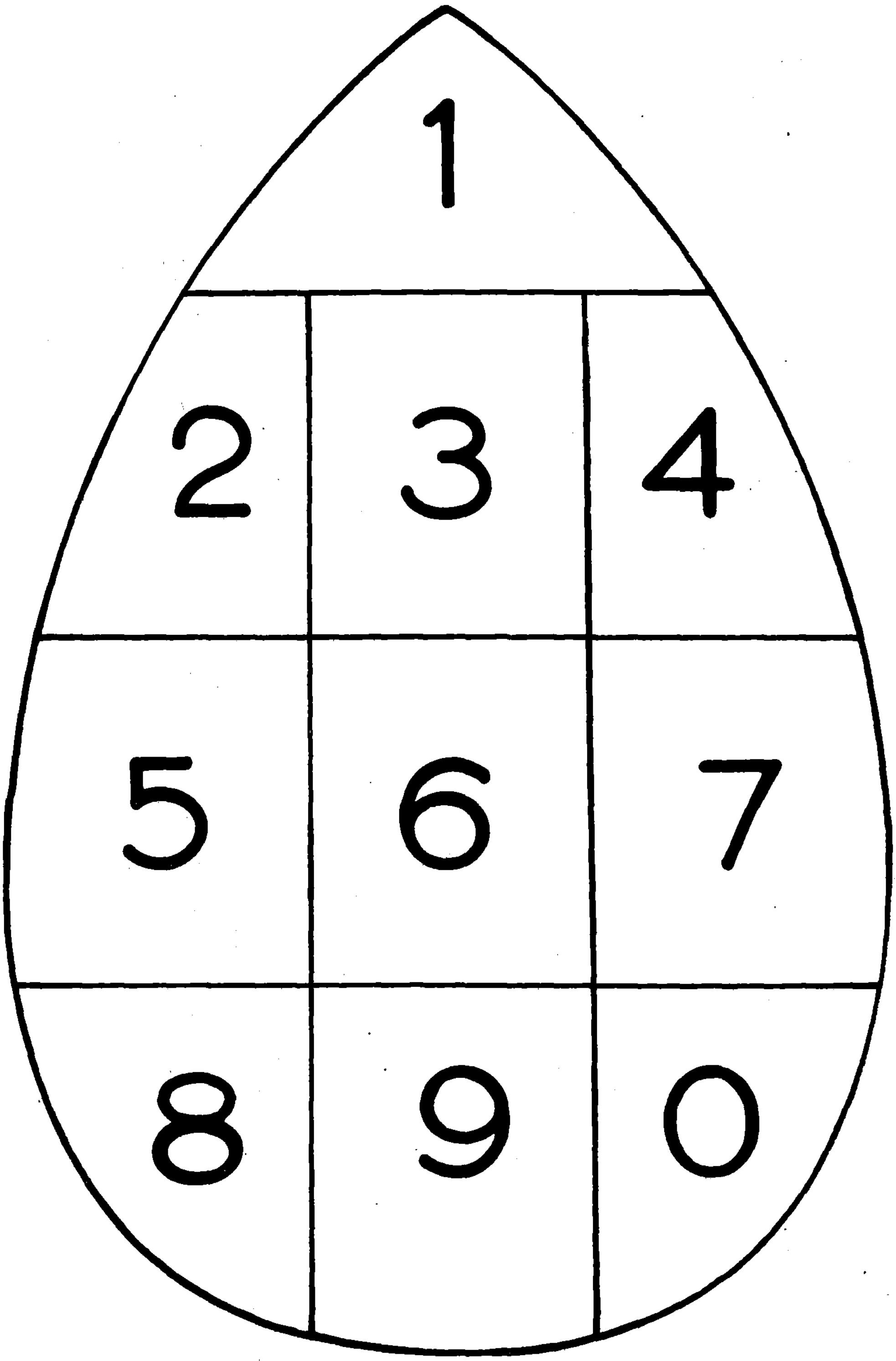
As it is unlikely that many hedgehogs would be hibernating in October and March, the absences of resident animals from the study area that were discussed above suggest that the home ranges of many of the animals included areas outside the selected study area. The absence of nests within the study area supports this conclusion. The observed variations in the frequency with which individual animals returned to the study area are in agreement with the conclusion of Brown (1962). It is concluded that the 'home ranges' as determined in this study are in effect minimum feeding ranges traversed as part of a larger home range.

(4) Hedgehog Marking System.

All hedgehogs located were weighed, sexed, marked by spine clipping and silver paint and then released. Each hedgehog was given an individual mark, using a system of spots and crosses in 10 different areas of the body (Figure 3). The marking code used was as follows:

Numbers from one to nine were indentified by a single spot on the appropriate part of the body. For numbers greater than nine, two spots were used, that for the tens digit being larger than that for the units. Where both digits were the same, a single cross replaced the spots. By this combination up to 100 hedgehogs could be marked.

FIGURE 3. AREAS OF THE BODY USED FOR THE NUMERICAL MARKING OF HEDGEHOGS.



Spine clipping and spraying with silver paint were found to be the most suitable methods of marking, as other methods, including ear-tagging, coloured leg bands etc. were difficult to apply without rendering the animal unconscious, and thus causing disturbance. Brockie (1958) found that white enamel paint markings were indentifiable for up to 16 months, while clipped spines were visible for more than 12 months. Aluminium paint was used in this study, as it was a better reflector of the spotlight.

Spines were clipped with a pair of scissors, and, although new spines grew to replace those clipped, replacement was slow, taking more than 12 months. However, to ensure that no marks were rendered unidentifiable, all recaptured animals were re-marked about every three months. This was essential with young hedgehogs as their spines grew much faster than those of adults, and could be partly replaced in about six months.

IV. RESULTS AND DISCUSSION

A total of 24 time intervals was used, with the odd numbers representing mark periods, and the even numbers representing recapture periods. As the numbers in the weekly counts of hedgehogs were too small, the weekly counts were aggregated into four-weekly totals. During the winter months, when very few hedgehogs were observed, eight-weekly totals were used. When all-night counts were carried out, and larger numbers of hedgehogs obtained, two-week or two-night counts were employed. These differences in time intervals did not affect the calculations as each was designated as either a mark period or a recapture period.

One hundred hedgehogs were caught in the study area over the two and a half year period. Of these 25 animals were captured once only, 35 were captured two to four times, 20 were captured five to nine times and 20 were captured 10 times or more.

The calculated home range areas were dependent on the number of captures as shown by the regression equation:

$A = 0.064\ C + 1.06$, where A = area of home range (hectares)

and C = number of captures.

The correlation coefficient was significant at the 0.1% level. It follows from this high degree of correlation that insufficient captures were made to reach the plateau proposed by Haugen (1942) and Stickel (1954). Thus the full home range was not obtained for any hedgehog. As the fewer the number of captures, the smaller the fraction of the home range that would be obtained, it was considered that areas based on fewer than 10 captures would be meaningless, and that areas calculated from the results of 10 to 46 captures should be considered only as minimum feeding ranges. No further treatment of this data was warranted.

Only 82 animals could be used for the population estimates, as the remaining 18 were caught only in recapture periods. All hedgehogs captured in mark periods were recorded, but because the same data was used for calculating home ranges, any hedgehogs initially caught during recapture periods were marked, but ignored in the population size calculations, unless later caught in a mark period.

Analysis of the data was carried out to give estimates of the population as a whole, and as all possible combinations of two areas (blocks A and B), two stages (adult and juvenile) and two sexes. The results from the complete analysis, together with the adult, juvenile, female and male populations, are shown in Table 4, with a pictorial summary in Figure 4. Population estimates were calculated for mark periods only, except for time one, for which insufficient data was available. All population estimates excluded nestlings.

The 11 weeks between 30/6/69 and 14/9/69 were not considered, as too few hedgehogs were captured. Similarly, the nine weeks between 4/11/69 and 4/1/70, the six weeks between 3/11/70 and 13/12/70, and the five weeks between 17/8/71 and 19/9/71, were not used. During most of these periods, grass growth made counting impossible. No population estimates have been calculated for time 21, because no new animals were captured. This means that the total population estimate equals the estimate of the number marked in that time.

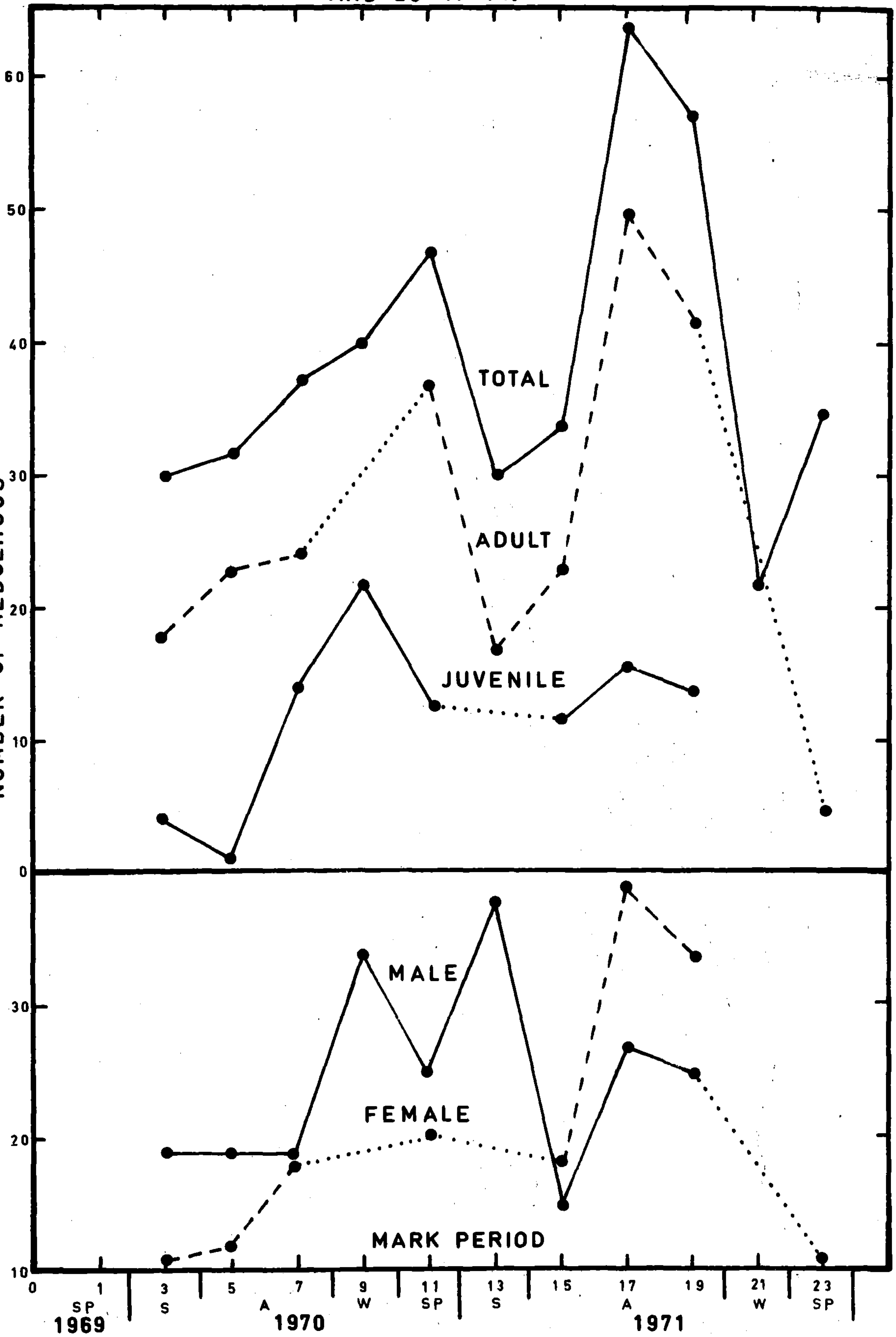
Although 100 hedgehogs were actually caught in the study area, many of these appeared to be transients, which were caught once or twice only. This was especially true of adult males during the breeding seasons. These animals appeared to expand their ranges during such periods. Similar results were obtained by Haugen (1944) when he related highest highway mortality to increased activity and extension of home ranges during the breeding season. Similarly, many juveniles were caught once or twice only. These may have been young which emigrated from the area, or alternatively they may have been merely transients. Transients, especially as immature animals, represent a definite part of normal population (Brown, 1962).

TABLE 4.

ESTIMATES OF THE SIZE OF A POPULATION OF WILD HEDGEHOGS IN THE STUDY AREA BETWEEN 30/6/69 AND 29/11/71.

TIME	INCLUSIVE DATES	PROPORTION RECAPTURED	PROBABILITY OF CAPTURE	NUMBER MARKED	TOTAL POPULATION	ADULT POPULATION	JUVENILE POPULATION	FEMALE POPULATION	MALE POPULATION
1	15/ 9/69- 6/10/69	-	-	-	-	-	-	-	-
2	13/10/69- 3/11/69	-	-	9	-	-	-	-	-
3	5/ 1/70-26/ 1/70	0.36	0.47	11	30± 9	18± 4	4± 4	11± 8	19± 7
4	2/ 2/70-23/ 2/70	-	-	16	-	-	-	-	-
5	2/ 3/70-23/ 3/70	0.44	0.57	14	32± 7	23± 4	1± 2	12± 4	19± 5
6	30/ 3/70-20/ 4/70	-	-	23	-	-	-	-	-
7	27/ 4/70-18/ 5/70	0.50	0.48	19	37± 8	24± 5	14± 7	18± 5	19± 6
8	25/ 5/70-15/ 6/70	-	-	29	-	-	-	-	-
9	22/ 6/70-10/ 8/70	0.80	0.12	32	40±17	-	22±21	-	34±34
10	17/ 8/70- 5/10/70	-	-	20	-	-	-	-	-
11	12/10/70-19/10/70	0.56	0.34	27	47±12	37±15	13± 4	20± 8	25± 9
12	20/10/70- 2/11/70	-	-	23	-	-	-	-	-
13	14/12/70- 4/ 1/71	0.86	0.23	26	30± 8	17± 5	-	-	38±38
14	11/ 1/71- 1/ 2/71	-	-	22	-	-	-	-	-
15	8/ 2/71- 1/ 3/71	0.58	0.55	20	34± 7	23± 7	12± 6	18± 4	15± 5
16	8/ 3/71-23/ 3/71	-	-	23	-	-	-	-	-
17	29/ 3/71-30/ 3/71	0.38	0.37	24	64±16	50±16	16± 5	39±15	27± 8
18	5/ 4/71- 6/ 4/71	-	-	34	-	-	-	-	-
19	12/ 4/71-19/ 4/71	0.67	0.47	38	57±12	42±11	14± 4	34±12	25± 7
20	26/ 4/71-27/ 4/71	-	-	25	-	-	-	-	-
21	3/ 5/71-24/ 5/71	-	-	22	22±	-	-	-	-
22	31/ 5/71-21/ 6/71	-	-	21	-	-	-	-	-
23	28/ 6/71-16/ 8/71	0.83	0.17	29	35±30	5± 2	-	-	11± 9
24	20/ 9/71-29/11/71	-	-	-	-	-	-	-	-

FIGURE 4. ESTIMATES OF THE SIZE OF A POPULATION OF WILD HEDGEHOGS IN THE STUDY AREA BETWEEN 30-6-69 AND 29-11-71.



The total population shows a definite increasing trend towards a peak in March and April 1971. It increases steadily, from about 30 animals in January 1970, to about 47 animals in October 1970. This steady increase is to be expected as more of the animals of the population are captured in each successive time period. This leads to more reliable results.

During the summer period, December 1970 to March 1971, when the population could be expected to be near a maximum, the data show it passing through a minimum. This is probably an incorrect result, however, as the low number of captures which resulted in this low value, were probably a function of hedgehogs escaping observation in grass, which was sufficiently high (through the use of irrigation) to make counting difficult. Although the population would be expected to be highest in late summer to early autumn, the maximum values of about 64 in March, and about 57 in April 1971, may be in part a function of the ideal counting conditions prevailing at these times.

As well as natural mortality, the ploughing of half of block A may have contributed to the sudden drop in population size between April and June 1971. This would force many animals to search elsewhere for food. No hedgehogs were seen in the ploughed area during these months and no new animals were captured. For this reason the lowest level of population, of about 22, was probably unrealistic, and the minimum population was probably nearer the figure estimated for the June to August period.

The percentages of standard errors of the mean for the total population ranged from 21 to 86, while those for the stages and sexes ranged from 17 to 100. These standard errors, which were all very high, were a function of the small numbers of animals involved. However, definite population trends, (an initial gradual increase due to a greater percentage of the population being marked, followed by a maximum in the late summer-early autumn, and a minimum in the winter), were apparent, despite these large standard errors.

Both the adult and juvenile populations followed the trends of the total population, with the following exceptions. At time five the juvenile population shows a decrease, while at time nine it shows a large increase. However, the standard errors are so high in these instances that the estimates must be suspect. These high standard errors were due to the very small numbers of juvenile animals captured during these time periods. Although the female population followed the trends of the total population, the male population showed some exceptions. It appeared to remain static at about 19 animals between January and June 1970. With two exceptions it then followed the trends of the total population. During the June to August 1970 period, and the December 1970 to January 1971 period, the male population showed sudden increases. As both gave large standard errors they were therefore suspect. However, the second of these increases may have been partly due to transient males in the breeding season.

The values for the populations of the individual blocks (A and B) were of limited value. As many of the hedgehogs were captured in both areas, the population estimates of each block were very high and had high standard errors. They often actually exceeded the estimates of the total population. The birth-immigration, death-emigration, and survival rates, as calculated, could not be used in this study because insufficient data was available to make them realistic. Since the term 'home range' as applied to data obtained in this study should be taken as referring to a minimum feeding range, rather than the complete home range, projecting statistical parameters on such data would introduce large errors, for little gain. If the corner pegs of the plots are considered equivalent to trap sites boundary strip or extended range length methods could be used. However, there is little to be gained in increasing the areas by these means since in most (and possibly all) cases it is unlikely that the expanded areas would include the nest sites. Many of the nests may have been located in hay barns, the nearest of which was 40 m west of the study area. The paddock containing these barns was non-irrigated and was used as an emergency holding area for cattle in winter. Its pasture had degenerated over a long period and now contained mainly weed species. Searches were regularly attempted in this area but only one hedgehog (number 5) was ever found moving through this area. Whenever, boundaries were crossed by hedgehogs efforts were made to follow them, but because of dense cover such efforts were often unsuccessful. Boundaries did not form barriers to hedgehog movements, as the animals readily passed through hedges, dry ditches and long grass. The gorse and macrocarpa hedges did, however, prove to be barriers to the observer and generally meant the loss of the hedgehog under observation. The probability elipse method of Jennrich and Turner (1969), as used by Parkes (1972), could not be applied, as its assumption that the animal preferred movement in one direction was, in most cases, not fulfilled, as shown when the data is treated by the convex polygon method. The topography of Parkes (1972) study area, a narrow strip between the Manawatu River and a series of pine plantations, probably influenced the movements of the resident hedgehogs.

As home ranges in the present study are incomplete, and as sizes and shapes of home ranges have little significance in themselves (Sanderson, 1965) they have simply been represented as convex polygons constructed by joining the external points of capture. These, as has been stated, should be regarded as representing minimum feeding ranges. Because it is difficult to compare visually a series of irregular polygons, circles having the same areas have also been constructed about the centres of gravity of the polygons. While these circles allow the areas of the various feeding ranges to be compared more readily, it is not intended to imply that their centres represent centres of activity.

The stage, sex, dates of first and last captures, numbers of captures, and home range areas for the 20 animals captured 10 or more times are listed in Table 5. The polygonal home range of each animal, together with the points of capture and the equivalent circular home ranges are shown in Figures 5 to 24. The track followed by the observer in searching each block is also shown in Figure 5.

The 20 hedgehogs have been subdivided into four groups; adult males (seven), adult females (seven), juvenile males (three) and juvenile females (three). The circular home ranges of these groups are compared in Figures 25 to 28 respectively. Examination of these figures and home range data listed in Table 5 shows that the areas of the home ranges vary considerably within each group. Statistical analyses, for comparing

TABLE 5. HOME RANGE DATA FOR 20 HEDGEHOGS IN THE STUDY AREA BETWEEN 30/6/69 AND 29/11/71.

HEDGEHOG NUMBER	STAGE	SEX	DATE OF FIRST CAPTURE	DATE OF LAST CAPTURE	NO.OF CAPTURES	AREA OF HOME RANGE IN HECTARES
1	A	F	7/7/69	20/ 7/70	36	4.0
19	A	F	19/1/70	24/ 7/71	19	2.9
23	A	F	26/1/70	3/ 5/71	10	2.6
29	A	F	16/2/70	7/ 6/71	30	1.8
30	A	F	16/2/70	14/ 6/71	21	2.4
42	A	F	13/4/70	12/ 7/71	46	4.6
50	A	F	4/5/70	17/ 5/71	15	1.3
4	A	M	15/9/69	31/ 5/71	41	3.6
6	A	M	22/9/69	17/ 5/71	16	3.6
7	A	M	22/9/69	13/ 4/70	12	2.4
17	A	M	12/1/70	12/ 7/71	32	3.5
22	A	M	26/1/70	13/10/70	10	1.5
37	A	M	23/3/70	17/ 5/71	15	1.6
78	A	M	29/3/71	28/ 6/71	13	0.8
26	J	F	16/2/70	18/10/71	33	2.7
63	J	F	1/3/71	8/11/71	11	2.1
70	J	F	15/3/71	12/ 4/71	14	1.3
33	J	M	9/3/70	18/10/71	15	1.9
39	J	M	13/4/70	19/ 4/71	16	2.8
54	J	M	6/7/70	4/ 1/71	23	1.1

A = ADULT. J = JUVENILE. F = FEMALE. M = MALE.

FIGURE 5. "HOME RANGE" OF HEDGEHOG 1. (ADULT FEMALE).

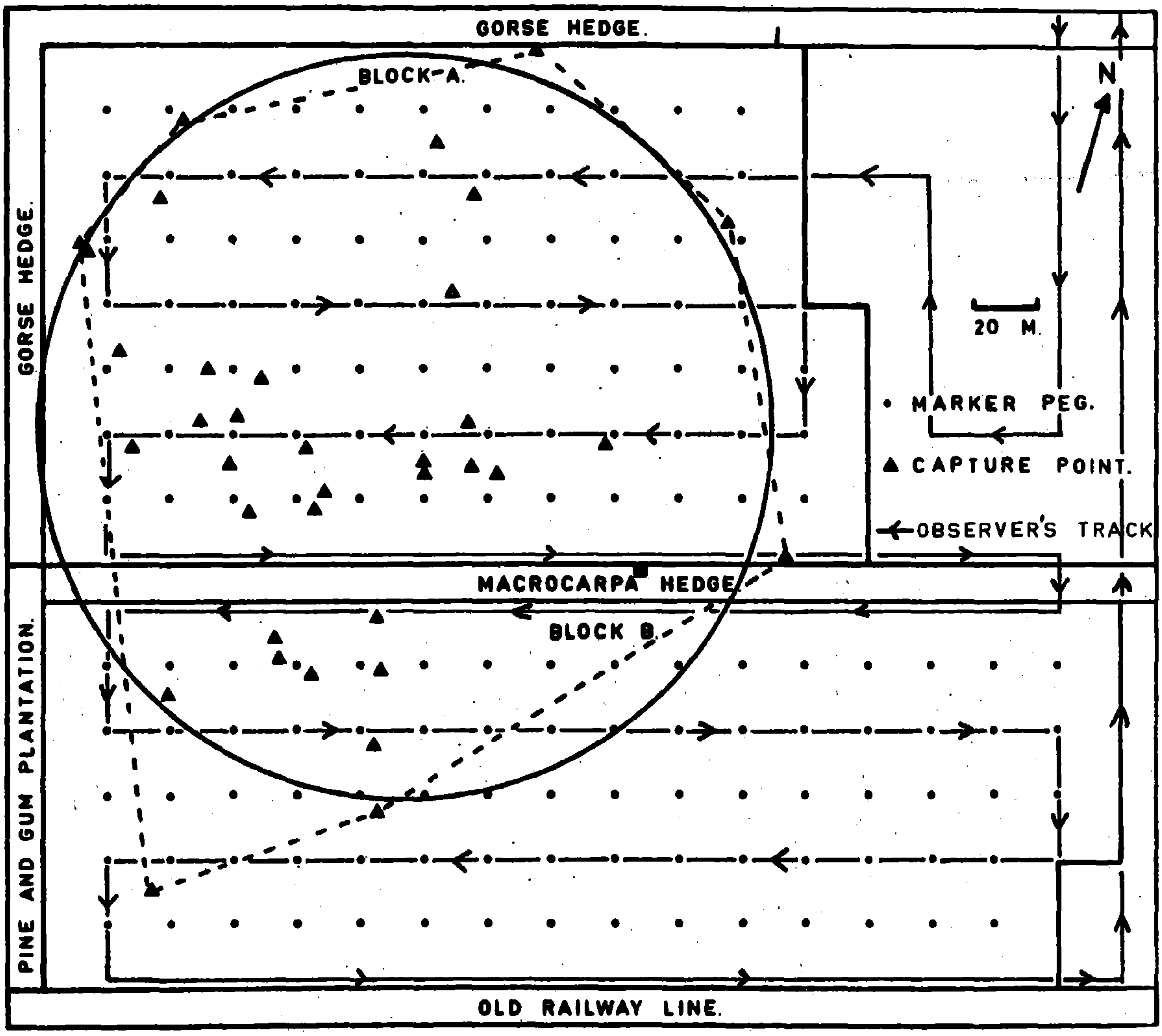


FIGURE 6. "HOME RANGE" OF HEDGEHOG 4. (ADULT MALE).

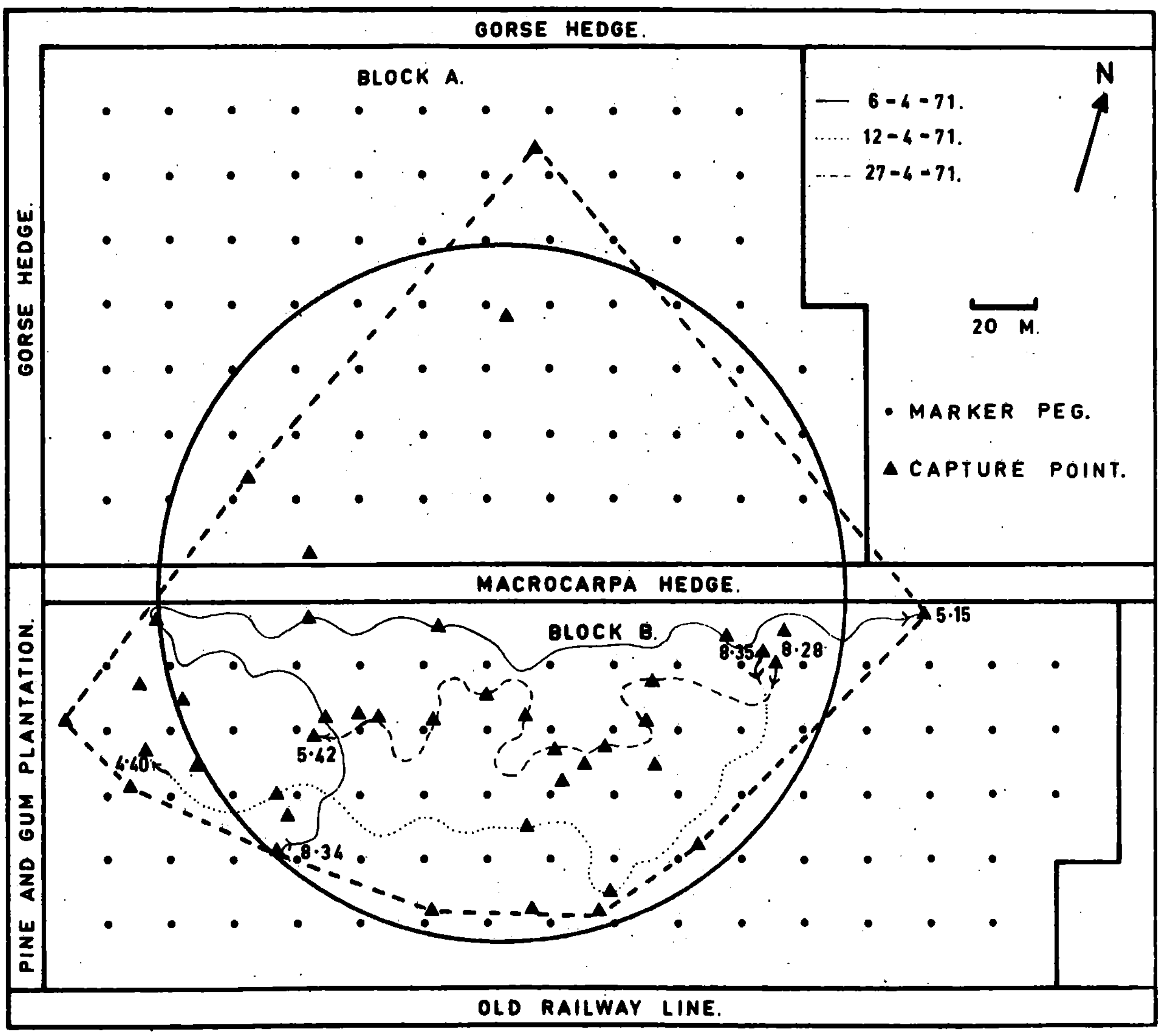


FIGURE 7. "HOME RANGE" OF HEDGEHOG 6. (ADULT MALE).

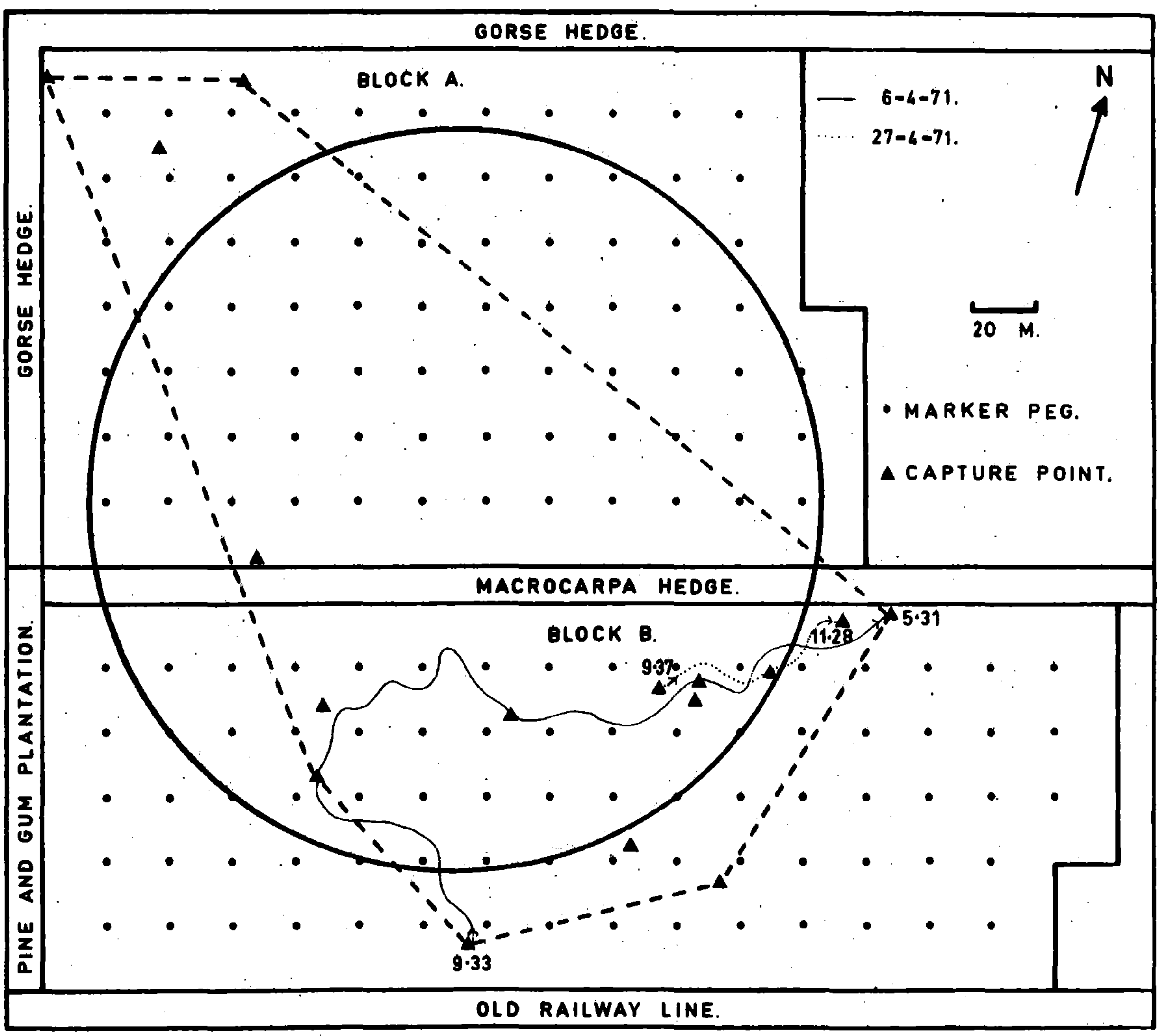


FIGURE 8. "HOME RANGE" OF HEDGEHOG 7. (ADULT MALE).

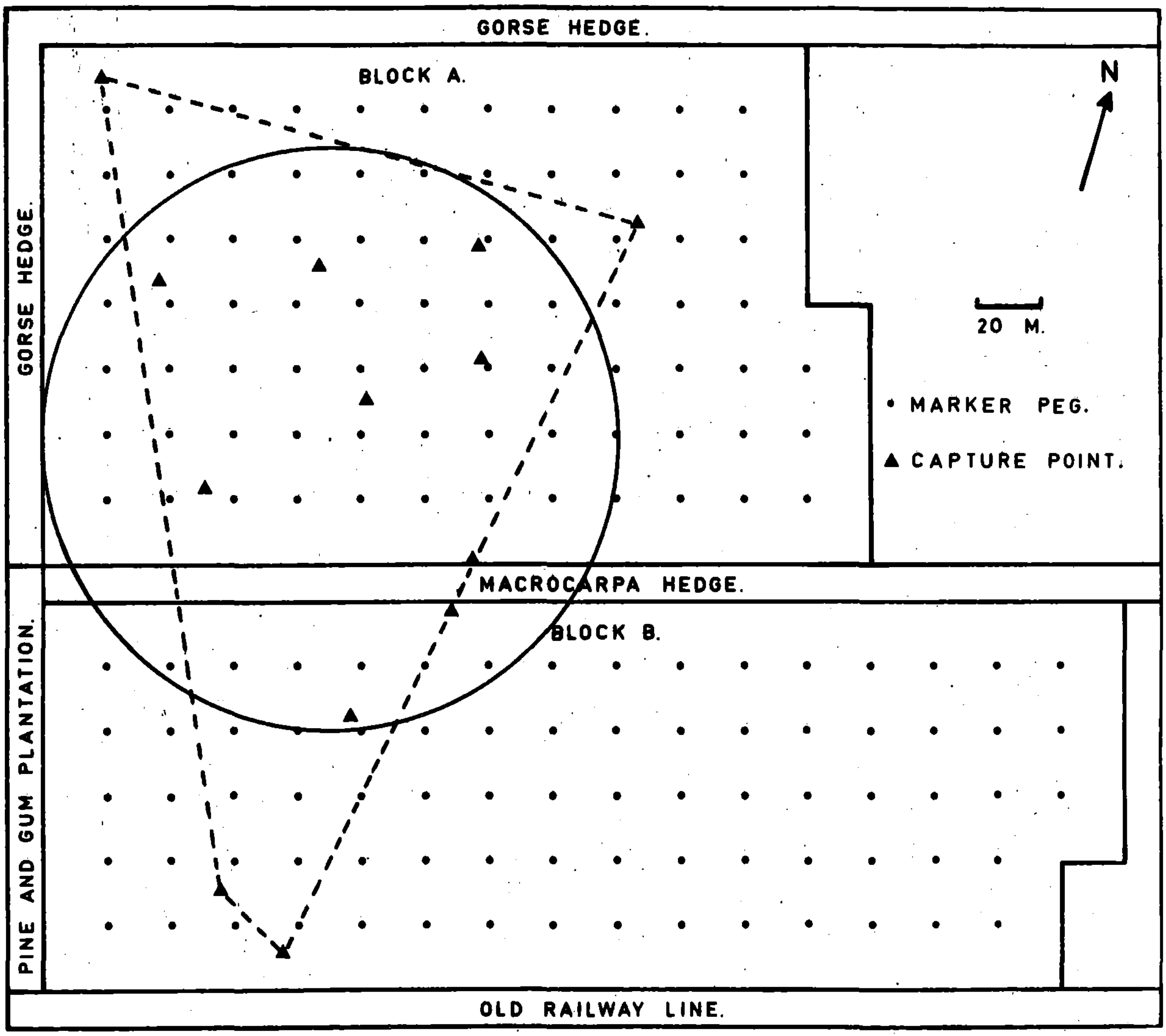


FIGURE 9. "HOME RANGE" OF HEDGEHOG 17. (ADULT MALE).

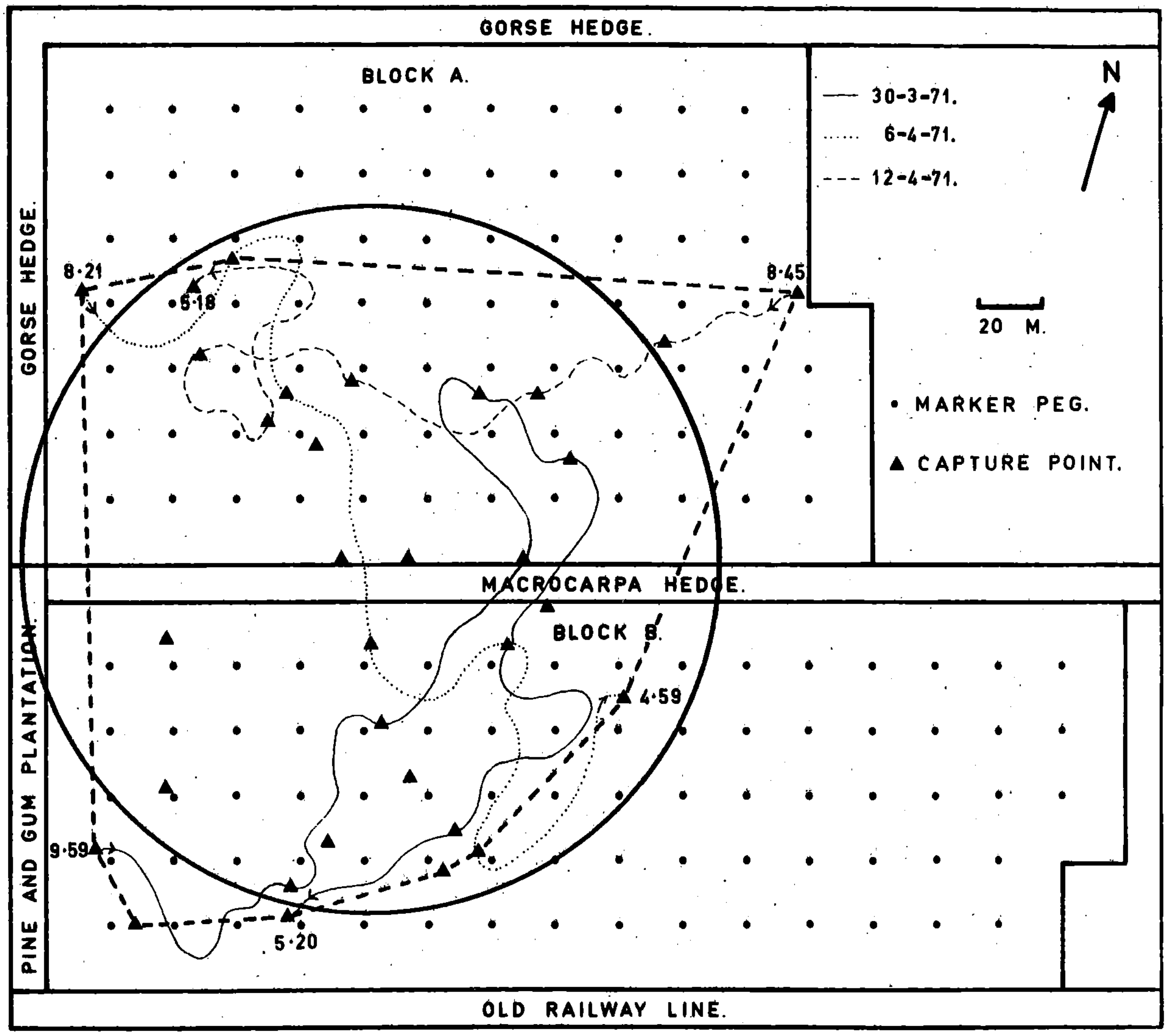


FIGURE 10. "HOME RANGE" OF HEDGEHOG 19. (ADULT FEMALE).

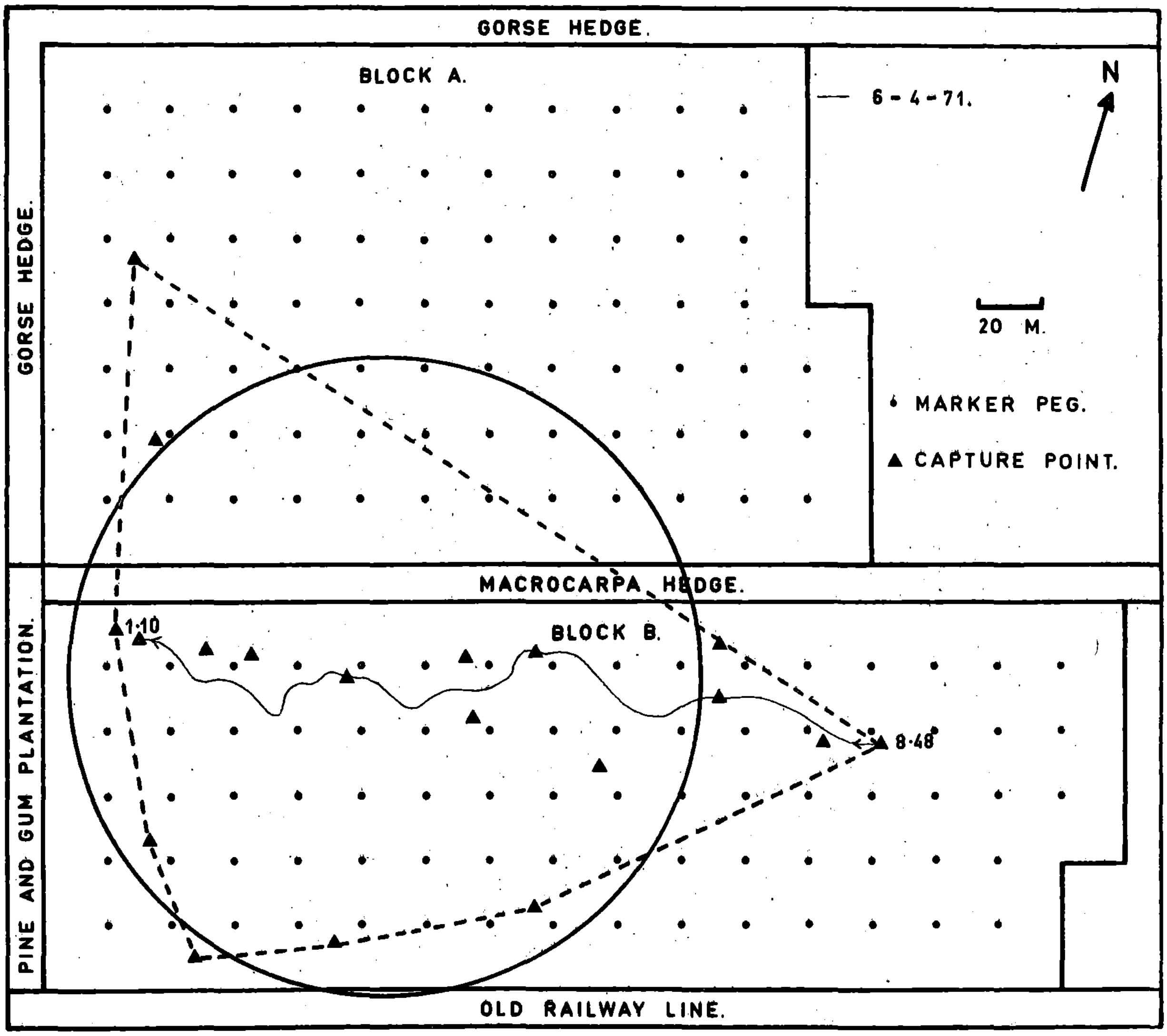


FIGURE 11. "HOME RANGE" OF HEDGEHOG 22. (ADULT MALE).

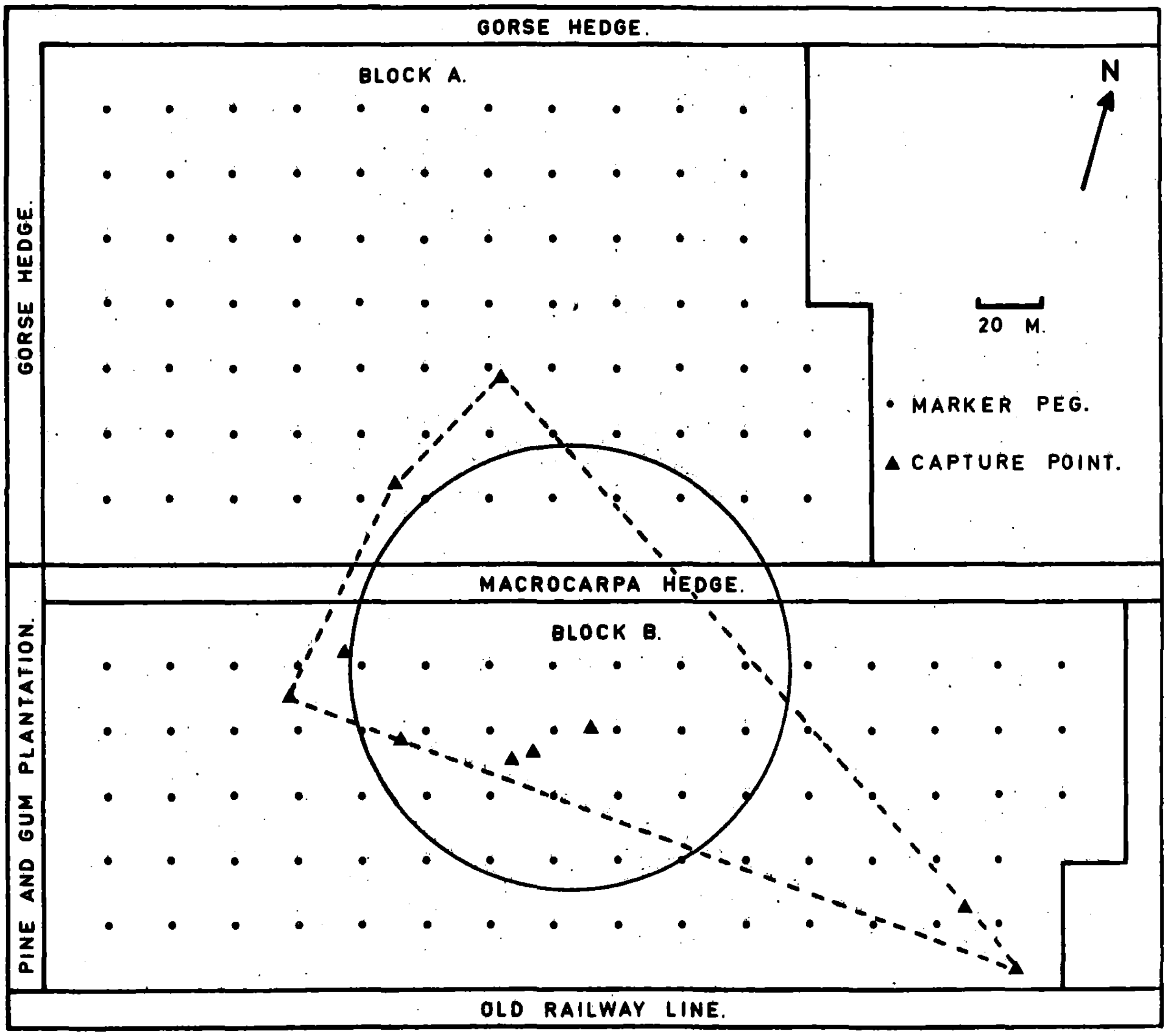


FIGURE 12. "HOME RANGE" OF HEDGEHOG 23. (ADULT FEMALE).

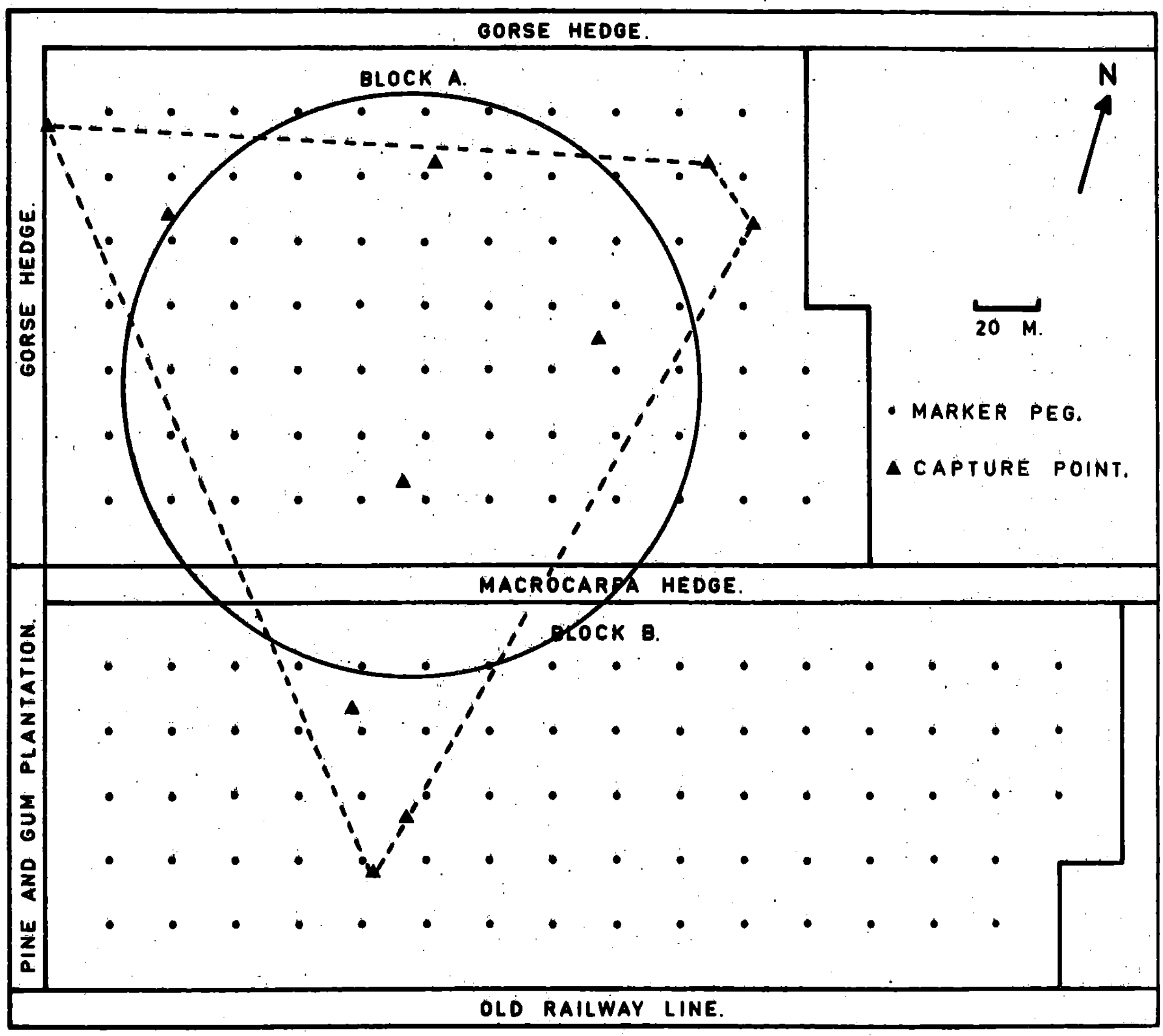


FIGURE 13. "HOME" RANGE" OF HEDGEHOG 26. (JUVENILE FEMALE).

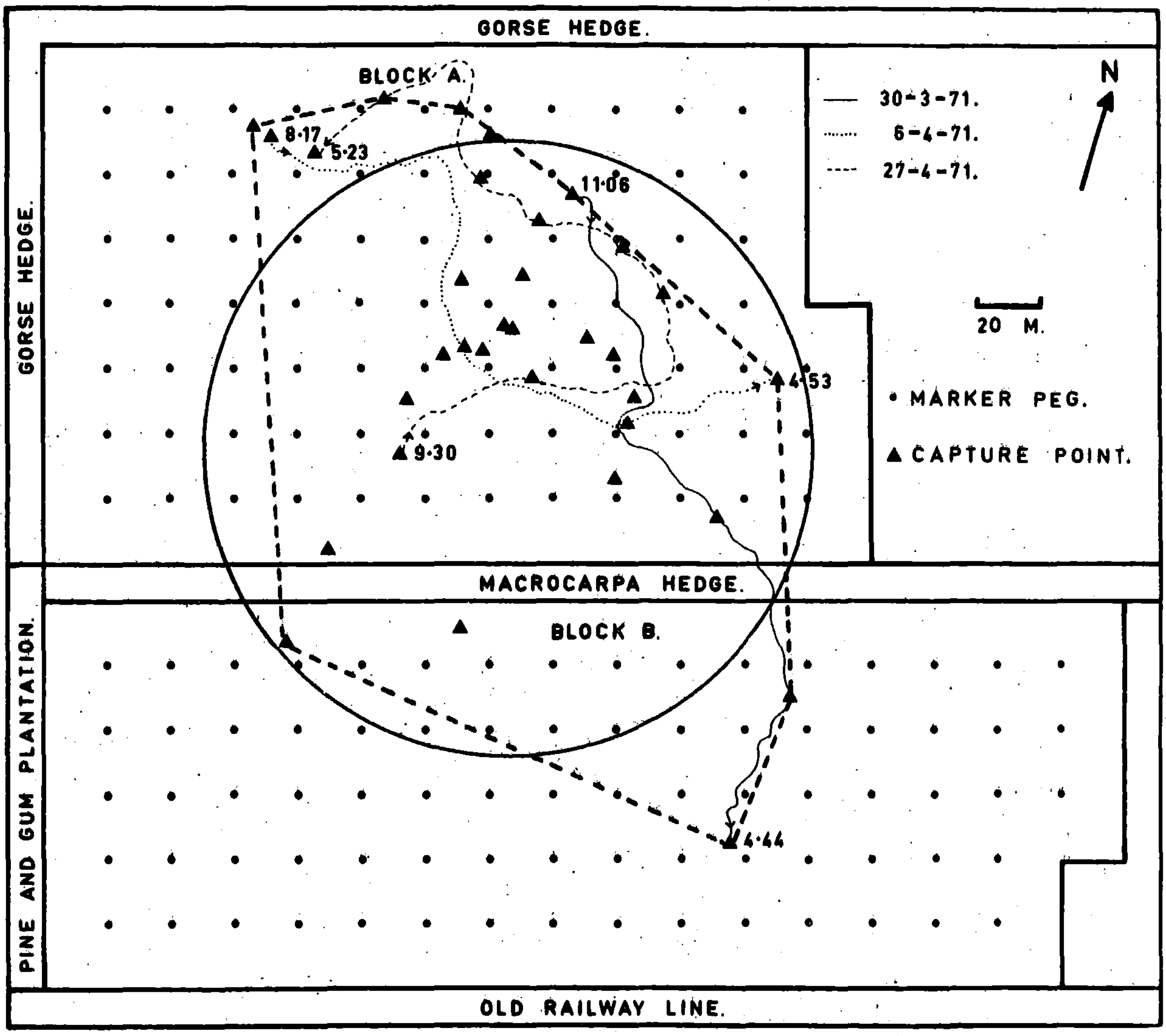


FIGURE 14. "HOME RANGE" OF HEDGEHOG 29. (ADULT FEMALE).

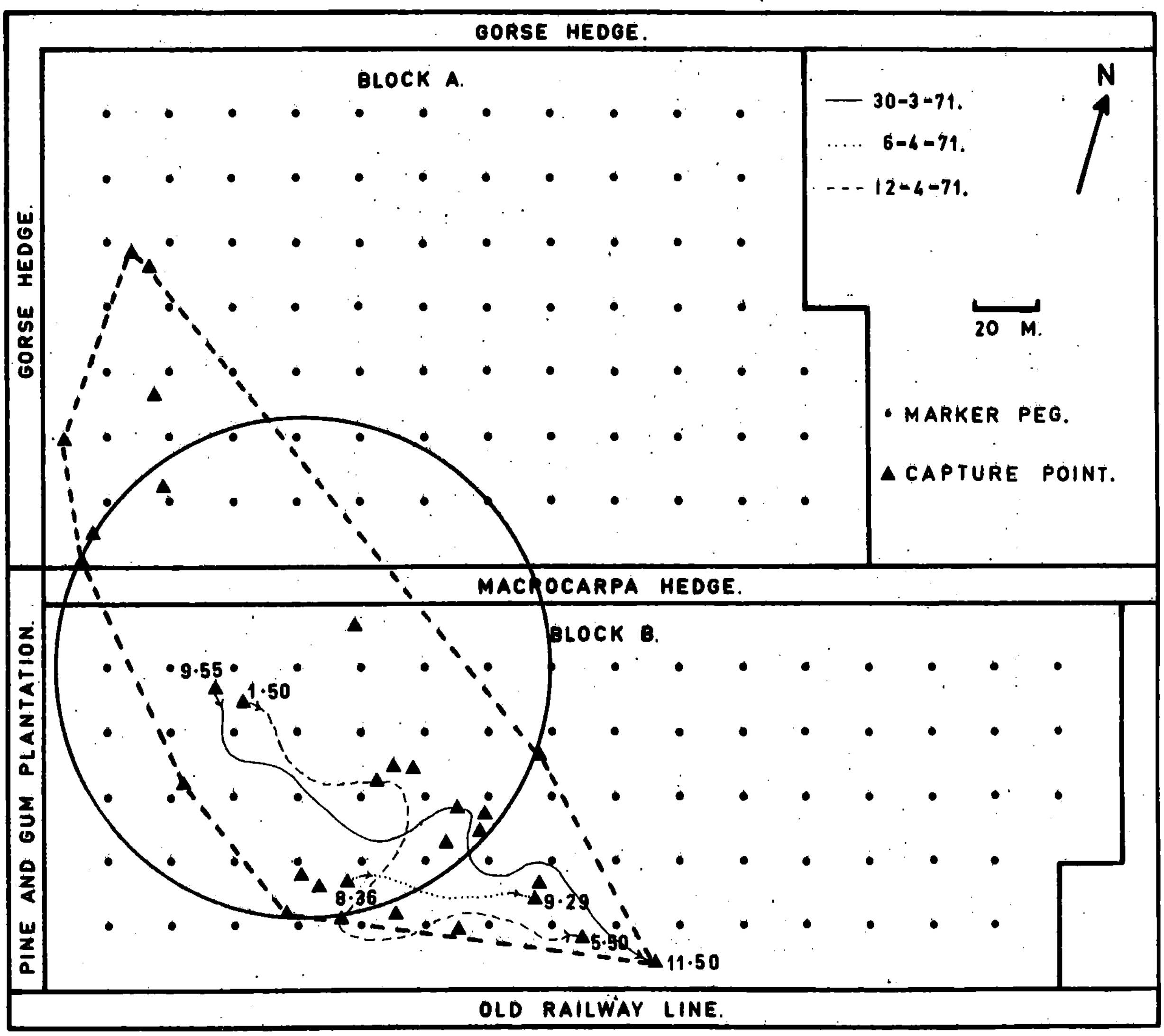


FIGURE 15. "HOME RANGE" OF HEDGEHOG 30. (ADULT FEMALE).

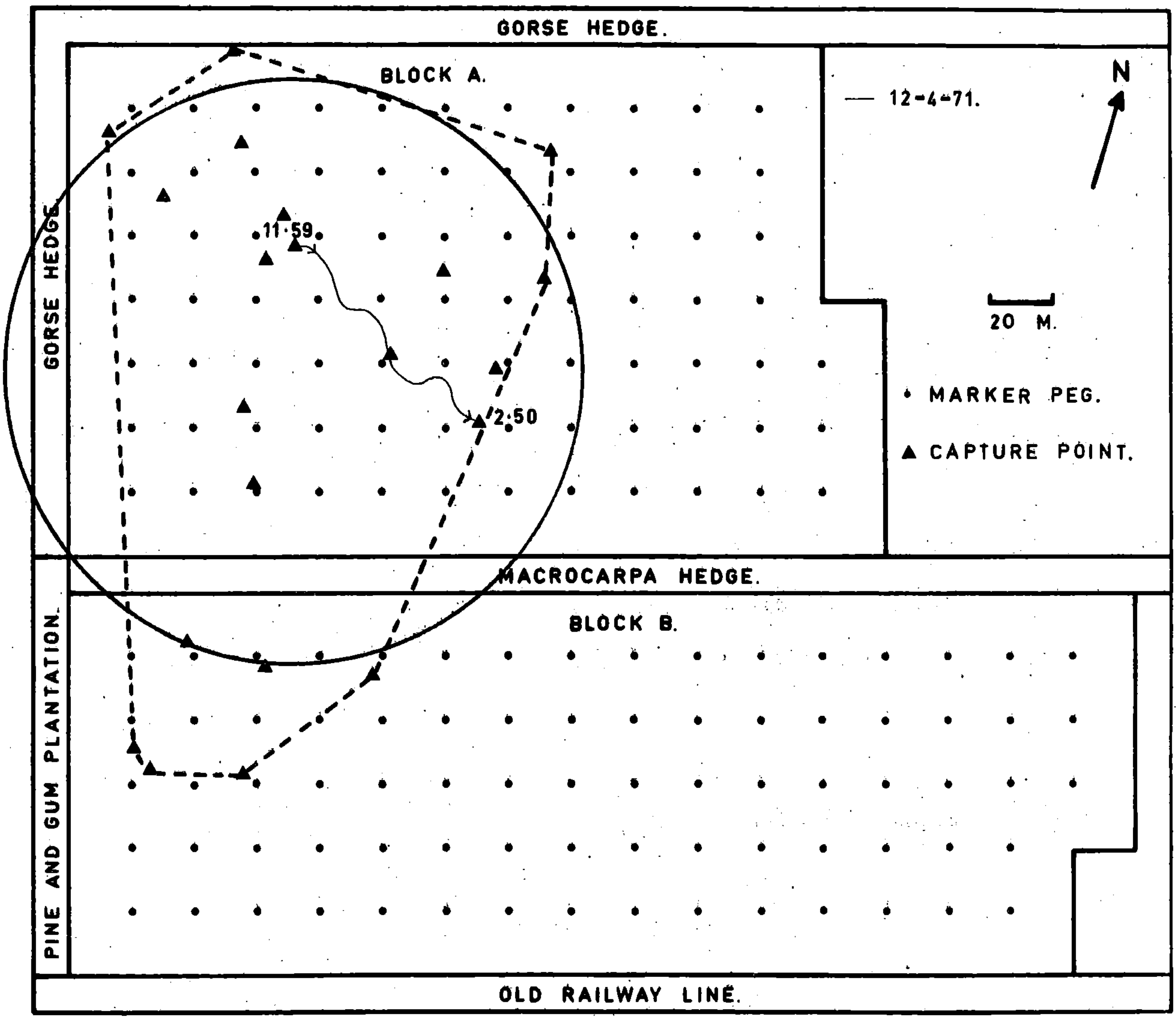


FIGURE 16. "HOME RANGE" OF HEDGEHOG 33. (JUVENILE MALE).

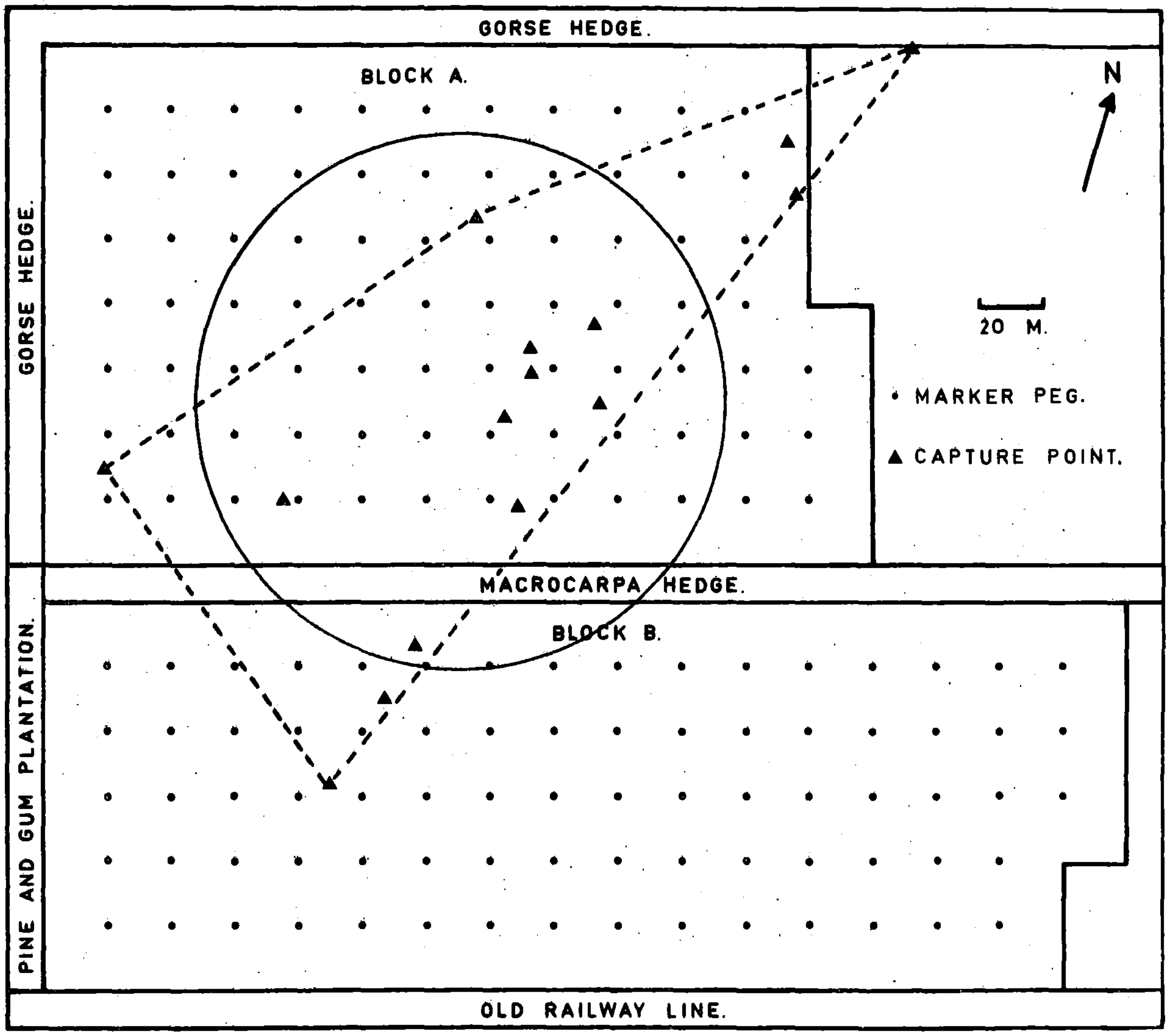


FIGURE 17. "HOME RANGE" OF HEDGEHOG 37. (ADULT MALE).

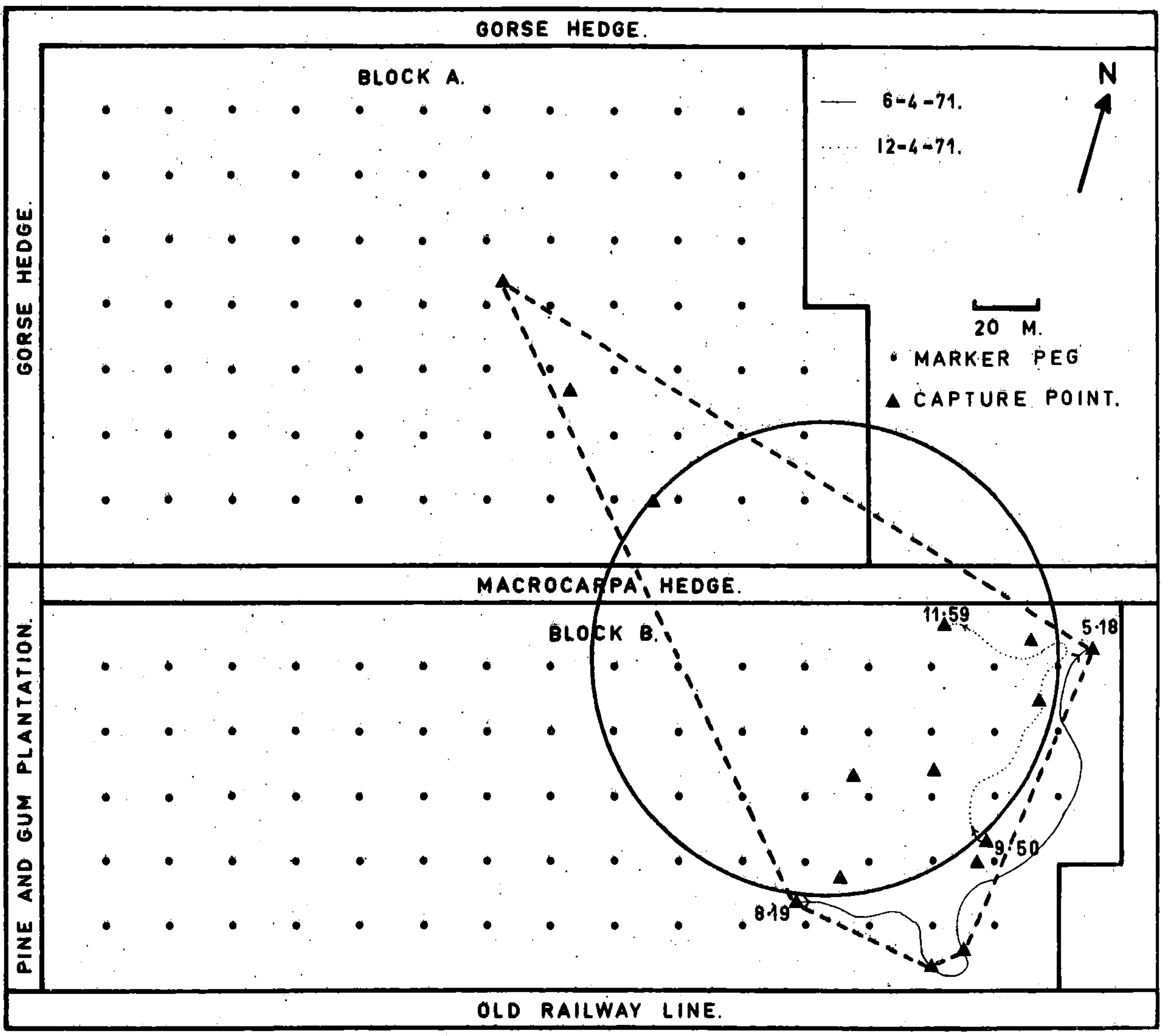


FIGURE 18. "HOME RANGE" OF HEDGEHOG 39. (JUVENILE MALE).

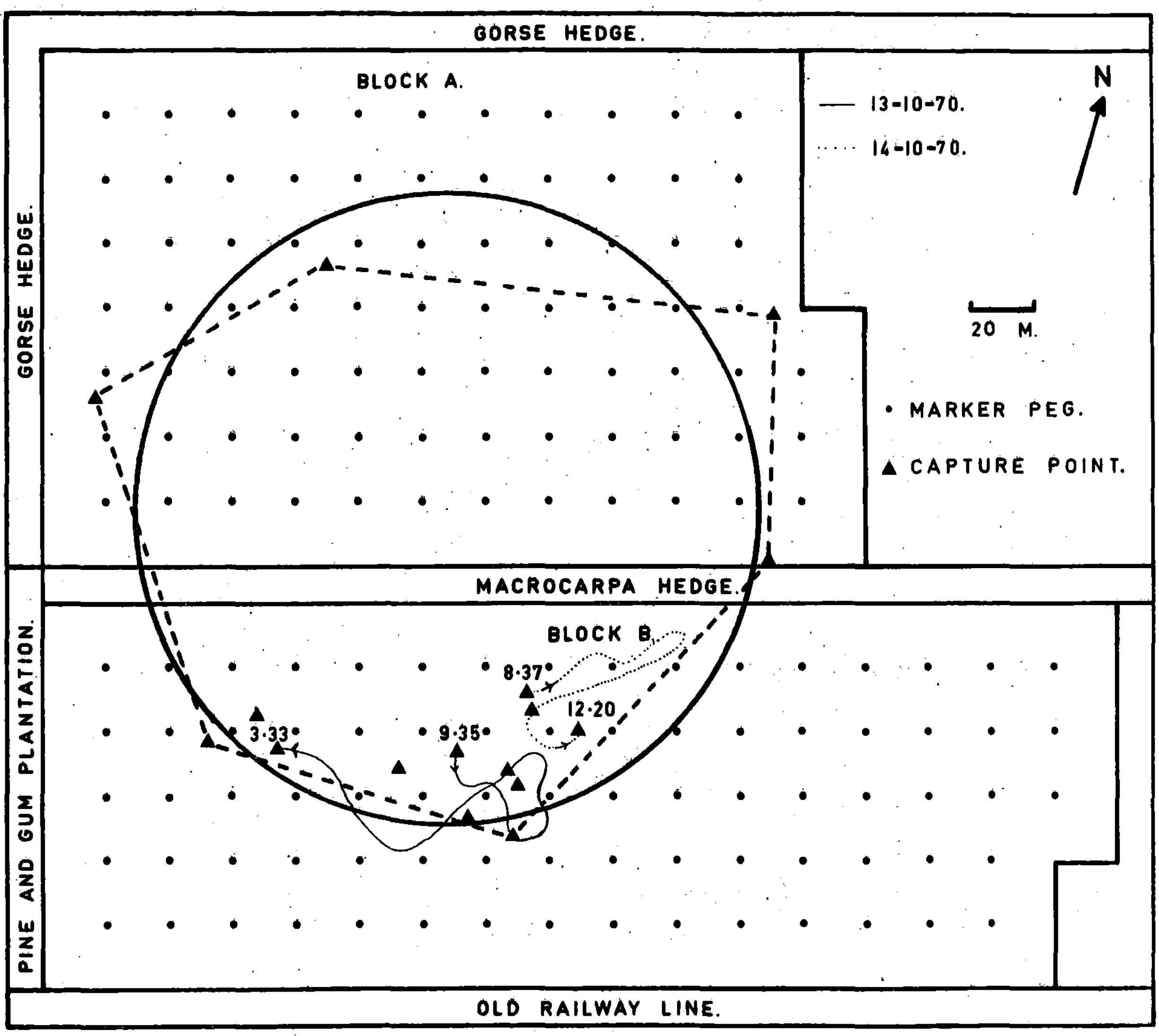


FIGURE 19. "HOME RANGE" OF HEDGEHOG 42. (ADULT FEMALE).

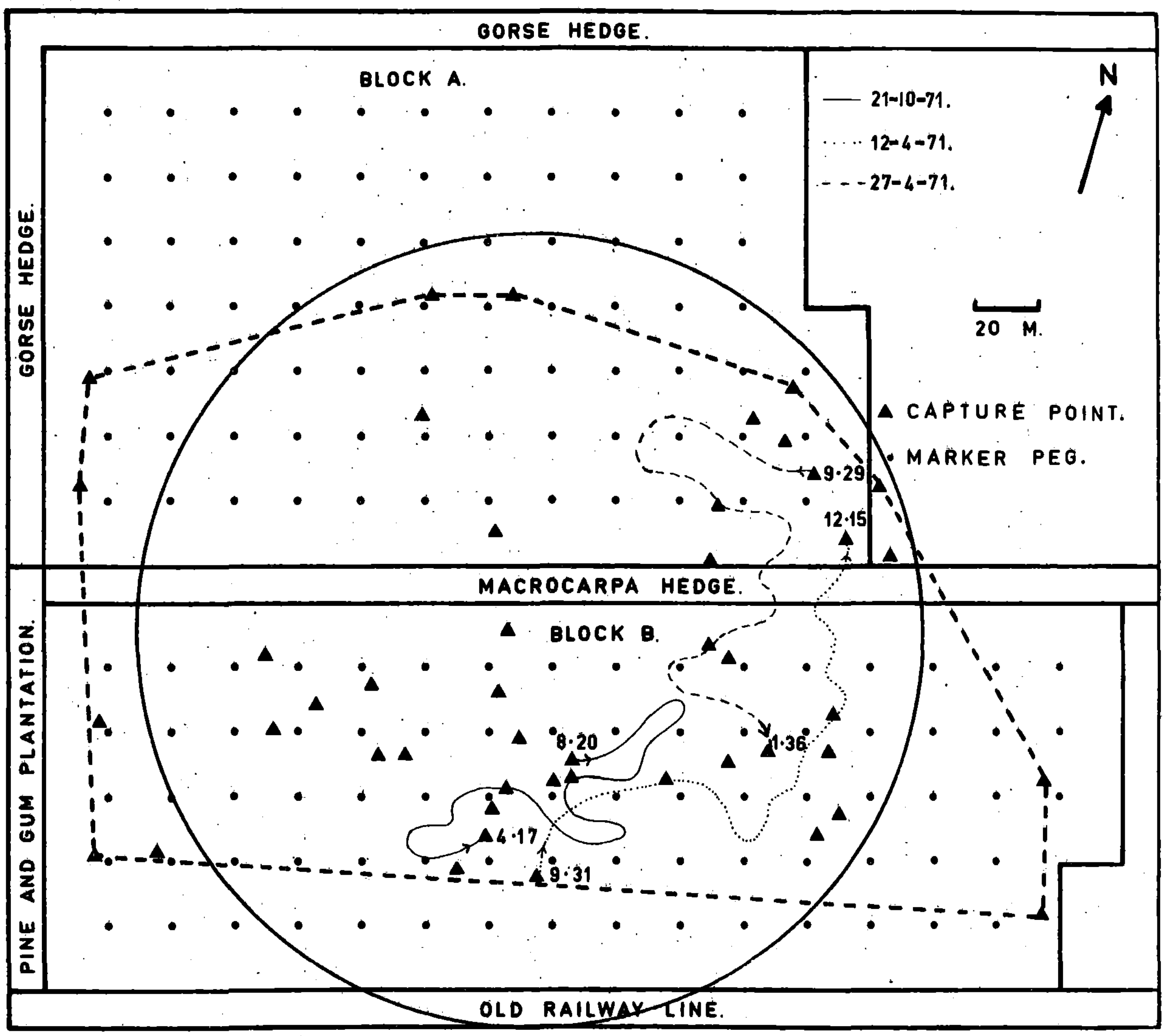


FIGURE 20. "HOME RANGE" OF HEDGEHOG 50. (ADULT FEMALE).

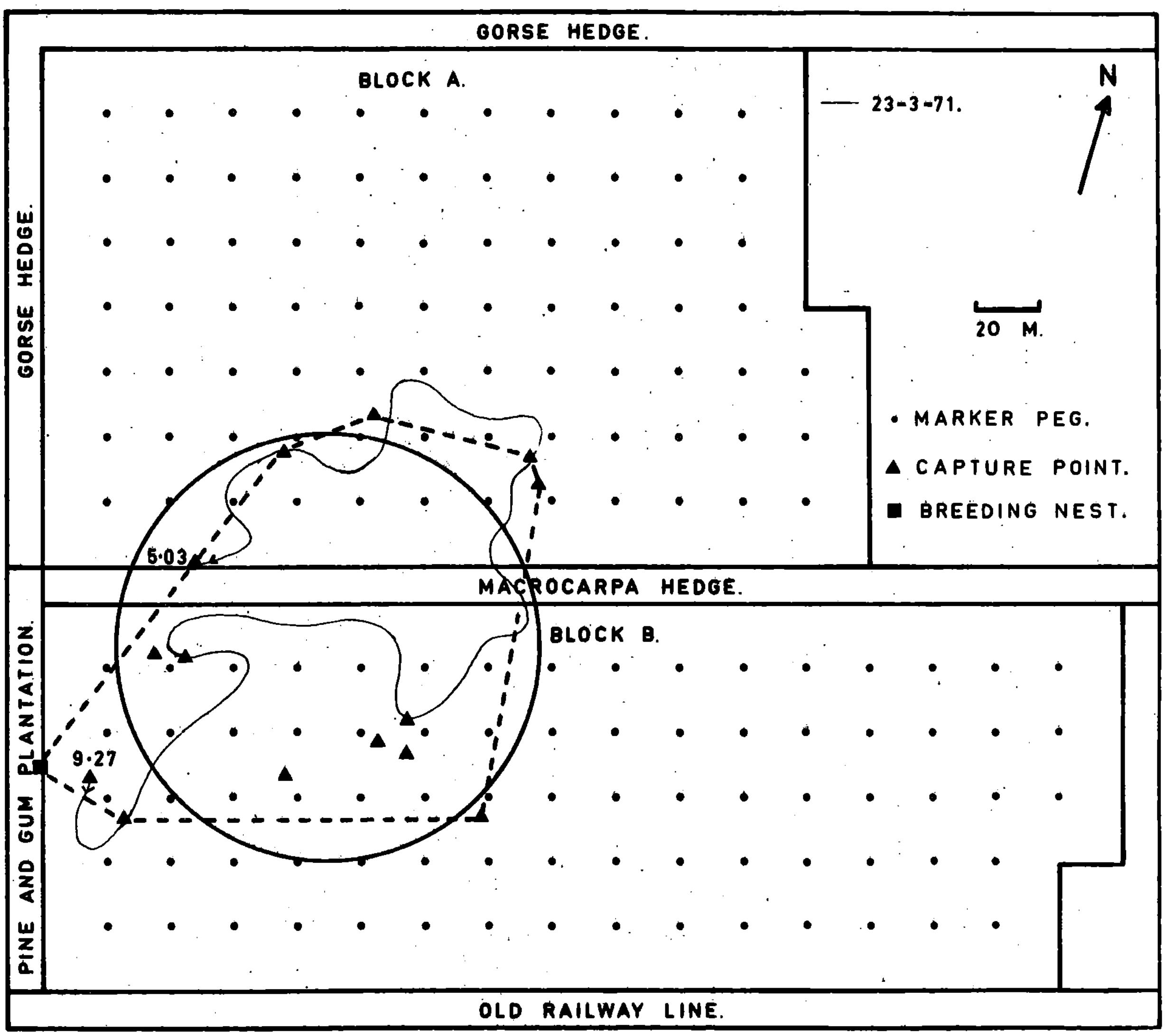


FIGURE 21. "HOME RANGE" OF HEDGEHOG 54. (JUVENILE MALE).

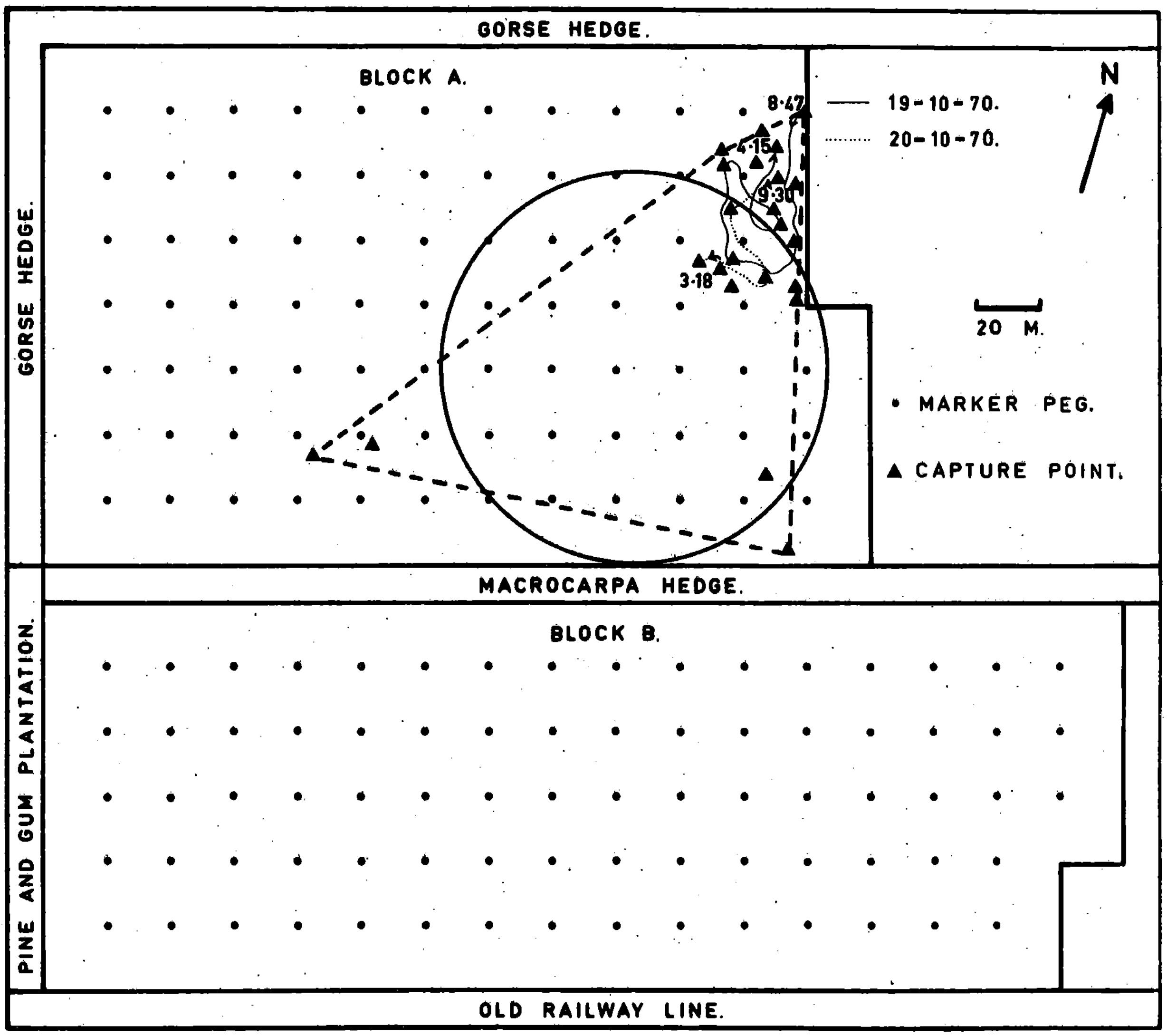


FIGURE 22. "HOME RANGE" OF HEDGEHOG 63. (JUVENILE FEMALE).

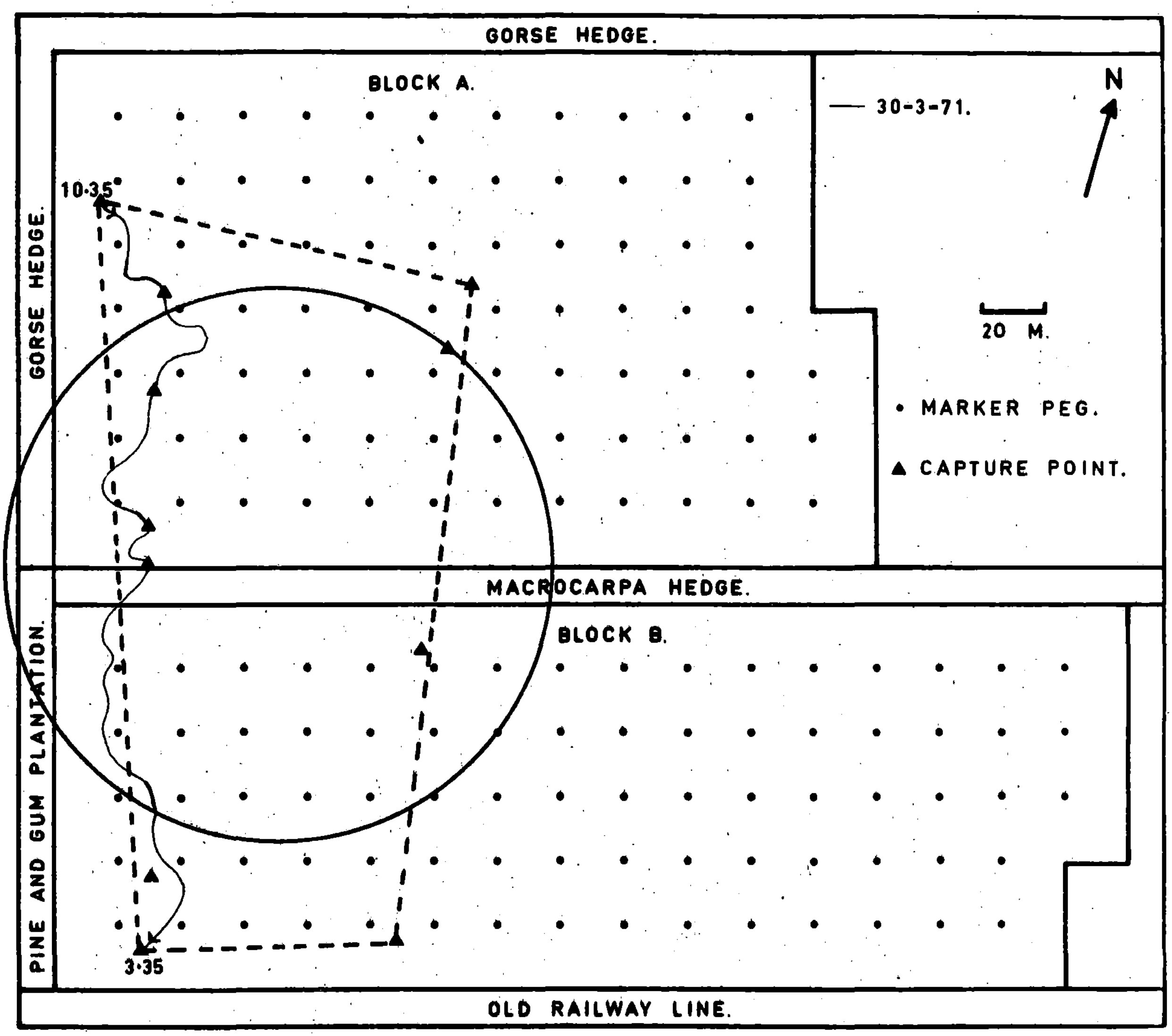


FIGURE 23. "HOME RANGE" OF HEDGEHOG 70. (JUVENILE FEMALE).

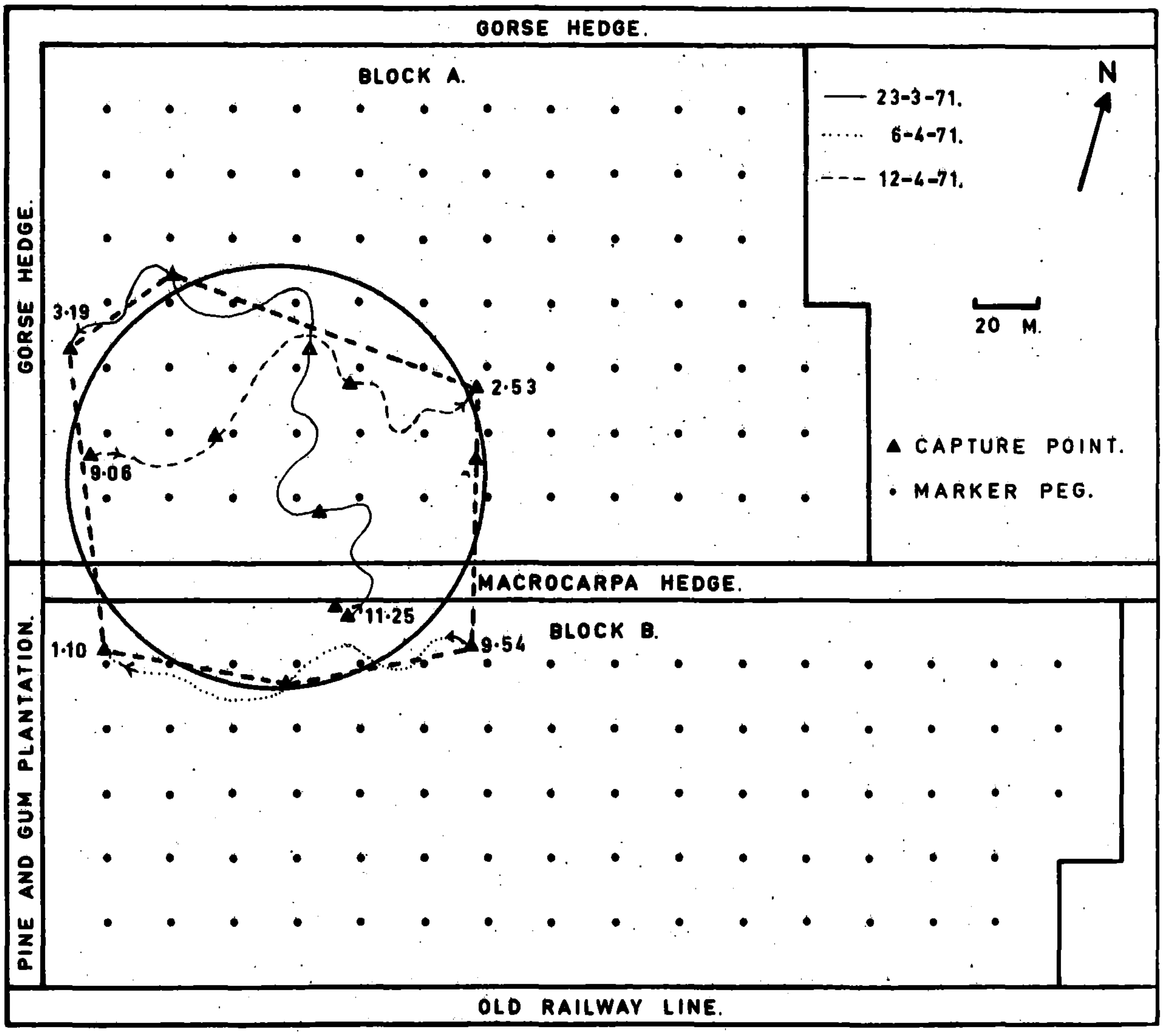


FIGURE 24. "HOME RANGE" OF HEDGEHOG 78. (ADULT MALE).

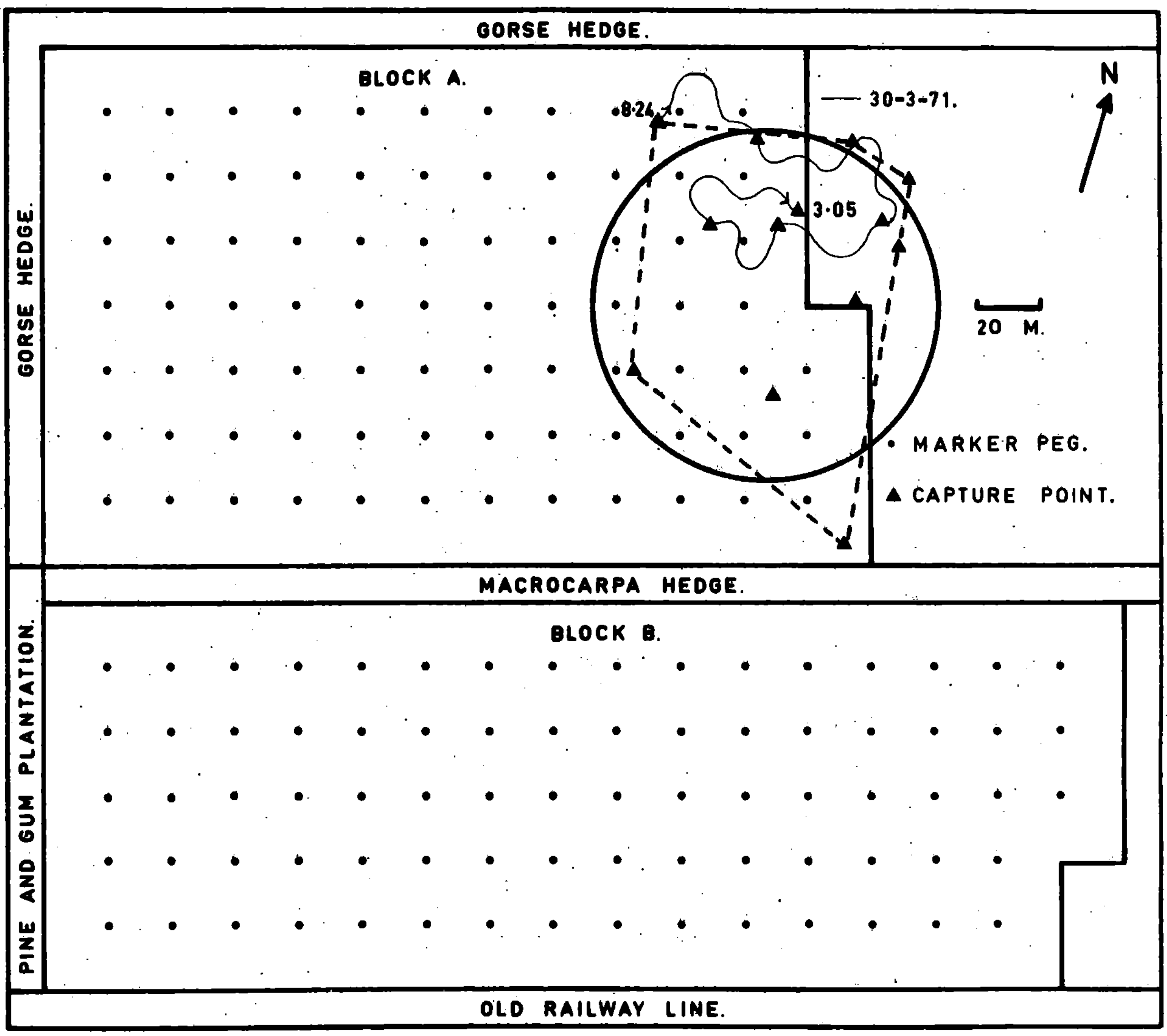


FIGURE 25. "HOME RANGES" OF 7 ADULT MALE HEDGEHOGS.

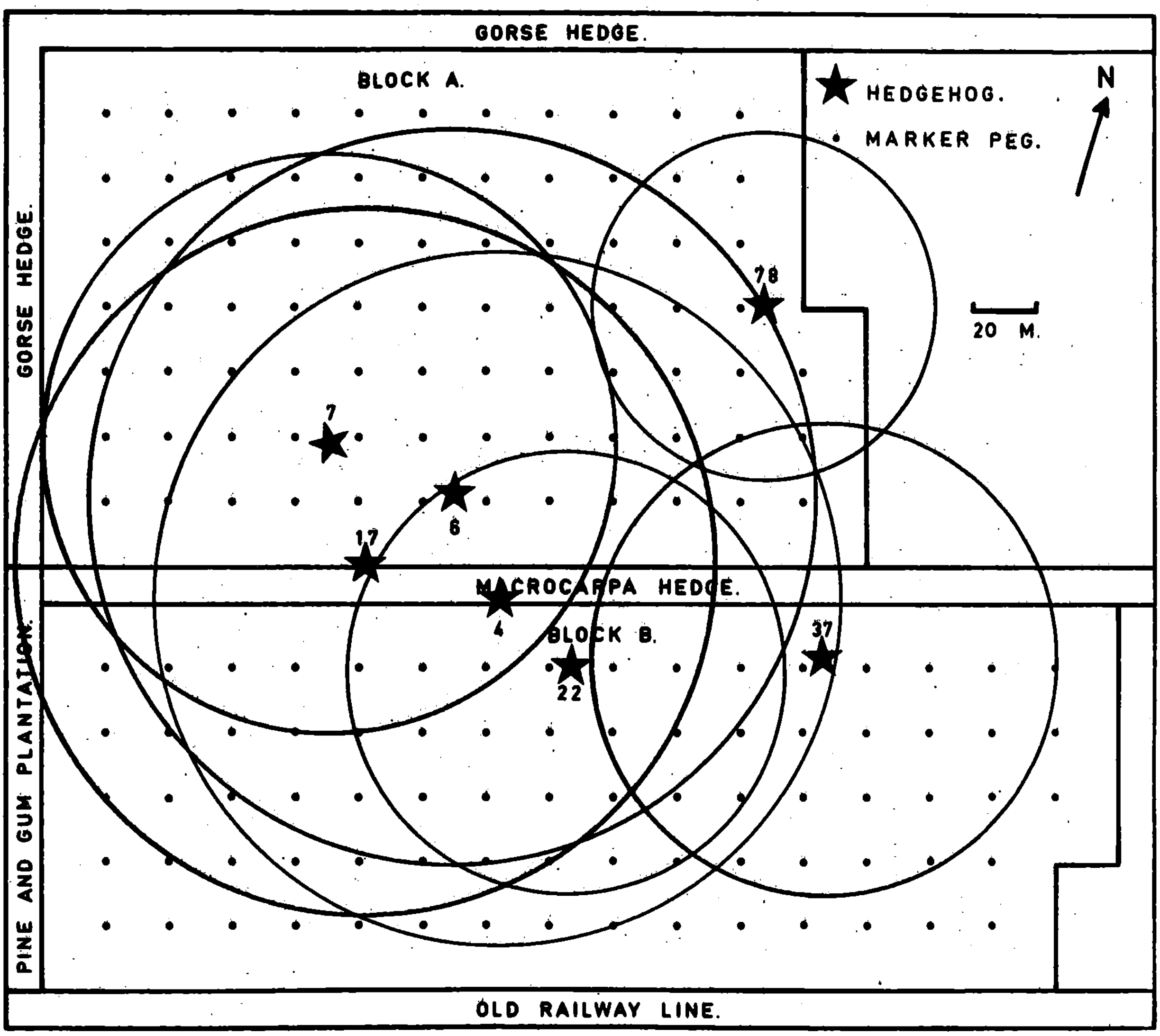


FIGURE 26. "HOME RANGES" OF 7 ADULT FEMALE HEDGEHOGS.

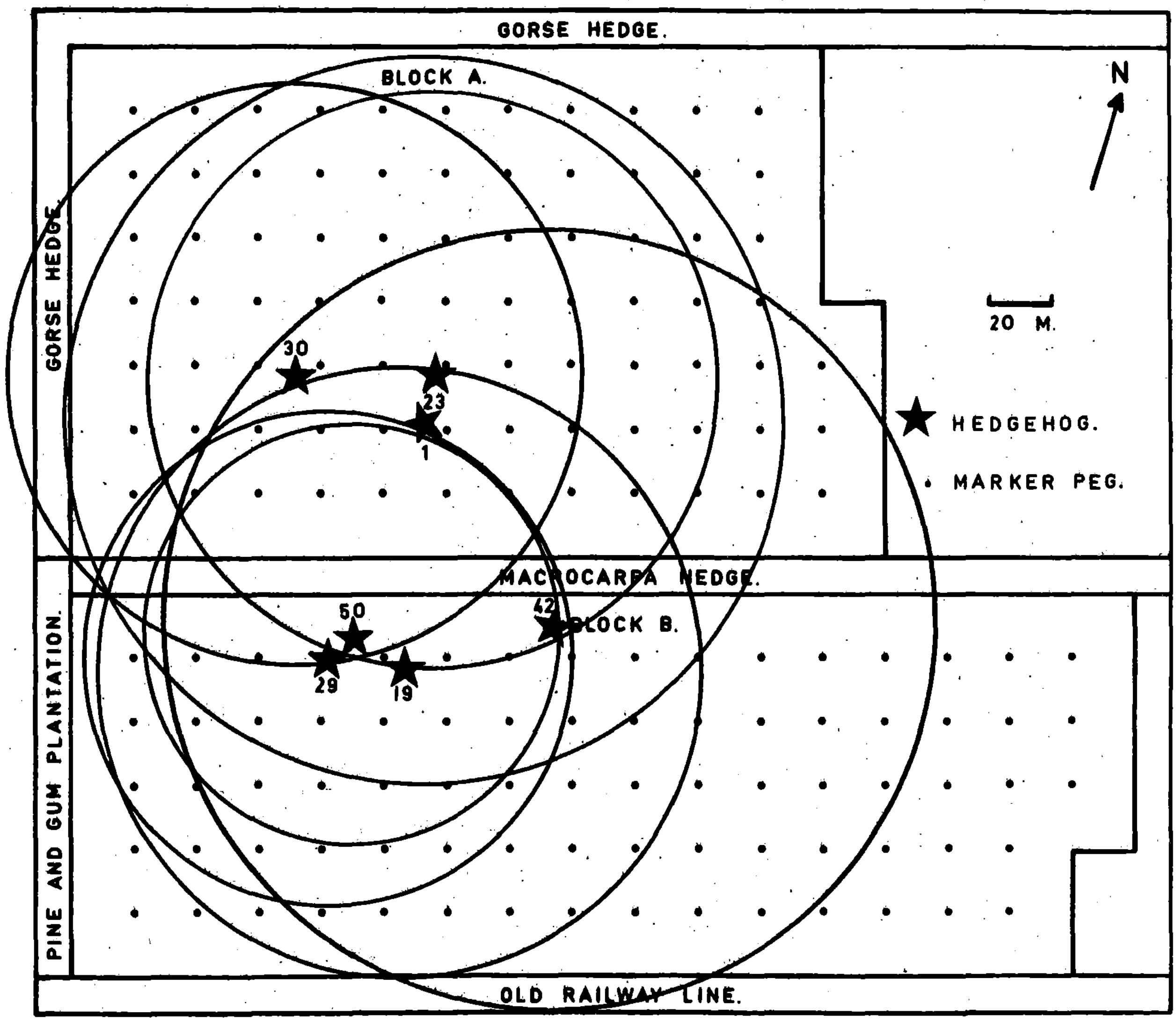


FIGURE 27. "HOME RANGES" OF 3 JUVENILE MALE HEDGEHOGS.

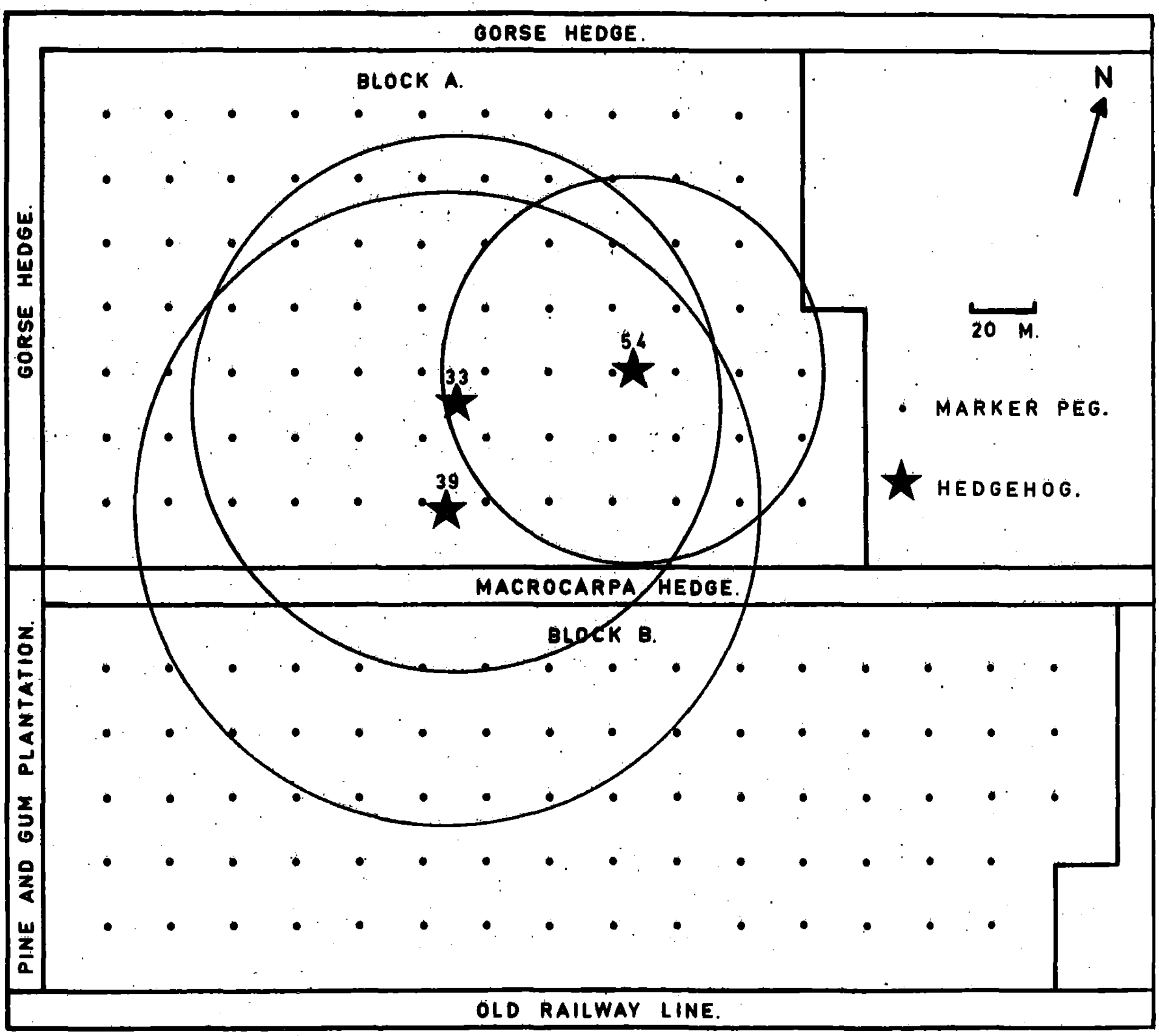
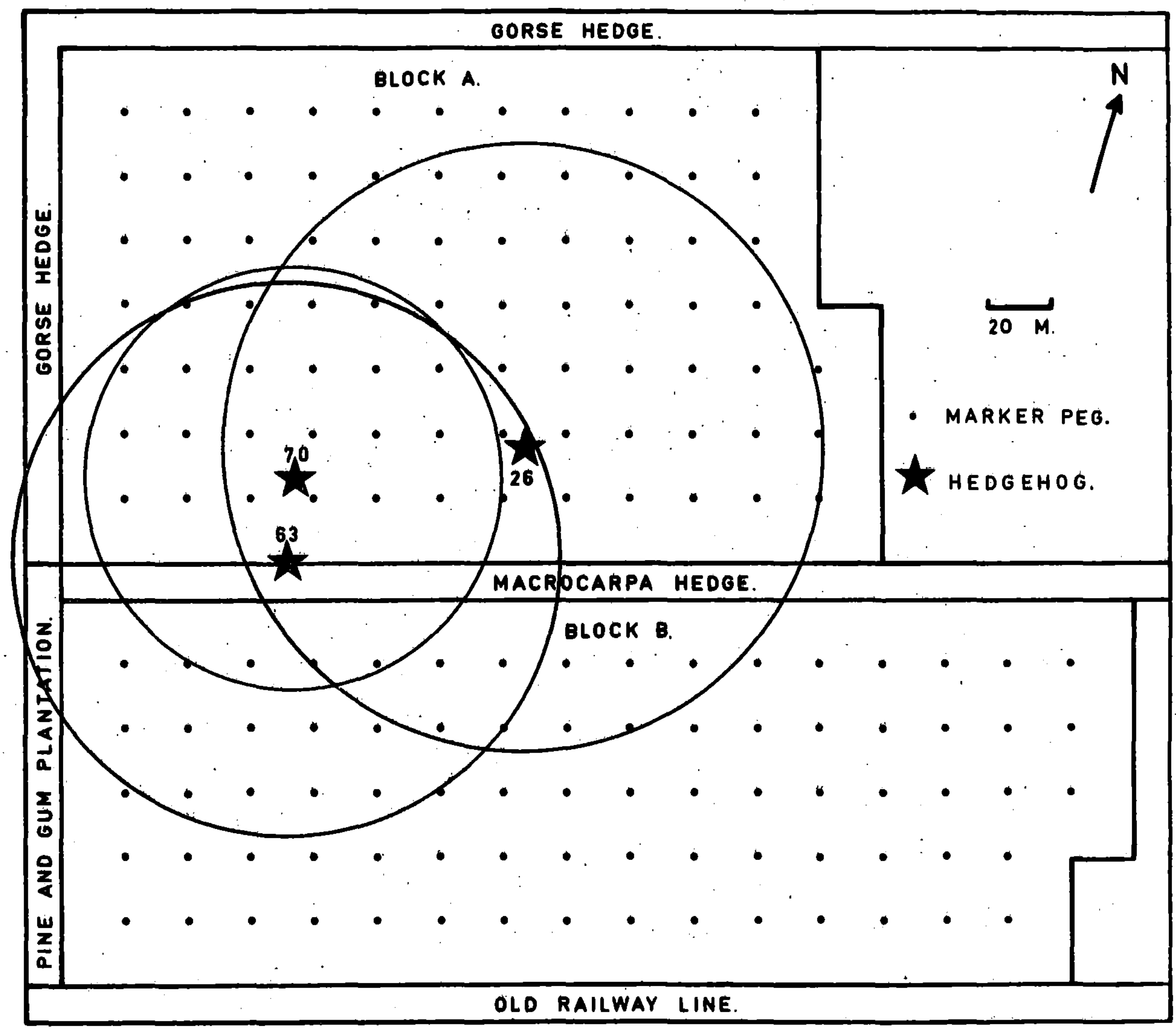


FIGURE 28. "HOME RANGES" OF 3 JUVENILE FEMALE HEDGEHOGS.



the variations from the means of each group, using the standard "t" test of Snedecor and Cochran (1967), showed that the differences were not significant at the 5% level. Data for the statistical analyses are given in Appendix II. These non-significant differences are to be expected, as the home range areas of these hedgehogs vary from 0.8 hectares to 4.6 hectares, with an average of 2.4 $\pm$ 1.1 hectares.

The sizes of the home ranges plotted, are however, dependent to some extent on the number of captures, as in general, the greater the number of captures, the larger the home range, as shown by the correlation calculation given earlier. This agrees with the observations of Haugen (1942) and Stickel (1954). The home ranges also show a large degree of overlap (Figures 25 to 28). This allows full exploitation of feeding areas by the whole population. This overlap was frequently observed in the field, when, on many occasions, several animals were found feeding within a few metres of each other, and was particularly obvious when up to 12 animals were observed, feeding in the vicinity of irrigation pipes, which had recently been turned off. Although the average home range area was 2.4 hectares, as many as 21 hedgehogs were captured in a single night, in the eight hectare study area.

Although the home ranges showed this high degree of overlap, fighting between hedgehogs was never observed. On meeting hedgehogs usually sniffed at each other, then continued on their separate ways. The only significant encounters were those between male and female during the breeding seasons, when typical courting behaviour took place. The lack of fighting, when two hedgehogs encountered each other during their feeding forays, suggests that hedgehogs do not have a definite, defended territorial area, but simply a home range.

The size of these home ranges is almost certainly influenced by the habitat and the available food supply. High hedgehog populations found in suburban areas are probably a function of restriction of movement and of the larger food supply, created by the diversity of plants and animals available in gardens.

In the study area there were no restrictions on movement, and the food supply was probably greater than that of many similar areas, because irrigation increased the availability of foods such as earthworms, slugs and soil-dwelling larvae. Thus the home ranges in the irrigated study area were probably smaller than those in non-irrigated but otherwise comparable pastures.

Because hedgehogs apparently disappeared from the study area during the winter months, it was not possible to determine if there were seasonal variations in their ranges. The home ranges as calculated, therefore, were essentially summer feeding ranges. Few hedgehogs were observed in the study area during the winter months, but most reappeared in the spring.

As many non-resident males passed through the study area during the breeding seasons, it seems logical to conclude that adult males expand their ranges during these periods. However, no direct evidence of such range expansion was found during this study, and some hedgehogs, especially males, were probably nomadic, as found by Parkes (1972).

Of the hedgehogs found in the study area, 68 were captured over periods of less than six months. This figure includes the 25 animals captured once only, and those animals which were first captured less than six months before the end of the study period. Of the remainder, 12 hedgehogs were captured over a six to 12 month period, 14 over a 12 to 18 month period, and the remaining six were captured over an 18 to 24 month period. As four of this latter six, were mature adults when first captured, it suggests that they, at least, survived to over three years of age. The other two, were over six months old when first captured, and as they were still active at the end of the study period, they too were at least three years old at the end of the study. It follows therefore, that some hedgehogs may become resident in a particular area, and remain there for long periods, possibly throughout their life spans.

In relation to its size, a hedgehog has a relatively large home range. During the course of the nightly search for food, a hedgehog appears to cover a large part of this home range. On many occasions, when a hedgehog could be tracked through long or dew-covered grass it was found to cover routes similar to those covered by the same animal on previous nights. This suggests that each animal regularly followed a relatively fixed route. It is not known whether hedgehogs actually mark these routes with scent or by other means, or whether they follow visual land marks. Lindemann (1951) suspects that both olfactory and visual cues are used. Examples of some of these tracks and the times of captures, where applicable, appear in Figures 5 to 24.

This use of fixed routes agrees with observations reported by Lindemann (1951) who found that two tame hedgehogs regularly followed the same paths about 50% of the time. During the present study it was found that it was possible to predict the area within which a particular hedgehog could be found at a given time. These predictions were found to be correct on many occasions, especially with hedgehogs 1, 4, 26, 29, 30 and 54. Thus, it seems likely that many hedgehogs do regularly follow relatively fixed routes.

The actual hedgehog tracks followed meandering courses. The animals were observed to sniff constantly and regularly pause to grub in the vegetation for food, which was eaten immediately and noisily. Prey species were eaten too quickly to permit identification by an observer standing far enough away to avoid detection. The olfactory is probably the most important sense used by hedgehogs in location of food, or other hedgehogs. This observation is substantiated by the work of Clark (1932) who reports that the olfactory lobe of the hedgehog brain is relatively larger than the other sensory lobes. Field observations also indicated that although the eyesight of hedgehogs was poor, their hearing was acute. When searching for food within its home range, a hedgehog moved slowly along its meandering path, but when in transit from one point to another, or when escaping to cover, each animal adopted a fast purposeful gait along a straight path.

V. SUMMARY AND CONCLUSIONS

The size of a population of wild hedgehogs, in the eight hectare irrigated pasture near Lincoln College, ranged from 35 in the winter months when the population was at its lowest, to 64 in the late summer-early autumn months. The population appears to fluctuate annually between these two levels. These estimates give population densities of from four to eight animals per hectare. It is considered that these values would be higher than could be expected for non-irrigated pasture lands, because of the increased food availability caused by irrigation.

Both adult and juvenile, and male and female numbers followed the trends of the total population. A tendency for many juveniles to emigrate, together with the difficulties encountered in finding them, may be responsible for the resident population containing more adults than juveniles. There were fewer females than males recorded in the population from the commencement of the study until February 1971, after which time there appeared to be fewer males than females. The sex ratio of the 100 animals captured was 42 females to 58 males. As many of these males were transients, as discussed earlier, the sex ratio was actually closer to 1 : 1. The sex ratio of the 20 resident hedgehogs was exactly 1 : 1. The period of highest mortality was winter, after which many dead animals were found. The main causes of death were probably respiratory diseases, such as pneumonia to which hedgehogs are most susceptible during winter. This population appeared to follow the laws of natural regulation by fluctuating between an upper and a lower limit. However, several more years of observation would be needed to confirm this.

As the hedgehog nests were never found, and the animals could not be tracked outside the study area, it was difficult to obtain reliable home range areas. Those calculated are minimal, and are essentially summer feeding ranges. Their sizes varied from 0.8 hectares to 4.6 hectares. The mean sizes for adult males, adult females, juvenile males and juvenile females were 2.4, 2.8, 1.9 and 2.0 hectares, respectively. These home ranges overlapped considerably. Each hedgehog appeared to cover a large part of its home range on each feeding night, and appeared to follow a meanering track along a relatively fixed route. The home range sizes were probably smaller than those in comparable, but non-irrigated, pasture lands. This conclusion is similar to that reached by Allen (1939) who found that in a rabbit population the most favourably located animals had the smallest home ranges.

As a result of the strong correlation between number of captures and minimum feeding range areas, conclusions reached indicate that a larger study area and more observations would be necessary to obtain more adequate data on hedgehog home ranges.

CHAPTER V

FEEDING BEHAVIOUR EXPERIMENTS

I. INTRODUCTION

Observations by Herter (1938) and Burton (1969) have shown that, in their natural habitat, hedgehogs show a definite feeding rhythm. A preliminary study (Otway, 1965) suggested that captive hedgehogs, fed under laboratory conditions, also exhibited this feeding rhythm. A series of experiments was devised to test this hypothesis. Its aims were:

(i) To establish when hedgehogs began and finished their daily feeding, and to determine whether these times were dependent on the light intensity in the laboratory, or the time of sunset.

(ii) To investigate if laboratory fed hedgehogs exhibited a definite feeding rhythm or if they fed randomly throughout the night.

These experiments were carried out between 1/7/69 and 30/11/69, inclusive. The periods used to test the second part of the hypothesis were 16/7/69 to 31/7/69 and 1/9/69 to 30/11/69 inclusive; a total of 107 nights.

II. METHODS OF STUDY

Four adult hedgehogs, two males (A and D) and two females (B and C) were conditioned to captivity for 15 days before commencing the study. These animals were kept in a temperature controlled room maintained at 18 $\pm$ 2^{o}C to prevent hibernation and lessen the risk of respiratory disease. The only lighting in the room was daylight from an east-facing window. A selenium photocell was used to measure the light intensity in the room under varying weather conditions. A calibration curve, microamps to lux (Figure 29) was obtained by photometer.

Each hedgehog was housed in a separate 120 x 30 x 30 cm cage (Figure 30), that had a nest box at one end and a pressure pad connected to a four-pen event recorder at the other. The nest box was filled with shredded paper and its 15 cm square entrance was covered with a light-proof curtain. The top of each cage was open, but an 8 cm baffle board prevented escape. A removable, paper-covered metal tray beneath each cage simplified daily cleaning. The cages were scrubbed and disinfected and the nesting materials changed each week.

A long narrow food tray, placed at the extreme end of the cage forced a feeding animal to activate the pressure pad. When placed in position the food tray was too narrow for an adult hedgehog to be able to have all four feet in it at one time. The spring-loaded pressure pad was depressed when 100 g was applied to the forward (food tray) end. Observations made during the conditioning period confirmed that the hedgehogs were actually feeding when the pressure pads were depressed. The event recorder was programmed to operate between 6 p.m. and 7 a.m. daily. Diversions on paper tape (Figure 31) recorded when, and for how long each animal fed.

The animals were fed a daily diet of 300 g of a 1 : 1 : 3

FIGURE 29. CONVERSION CURVE FOR THE LIGHT INTENSITY INSIDE THE LABORATORY.

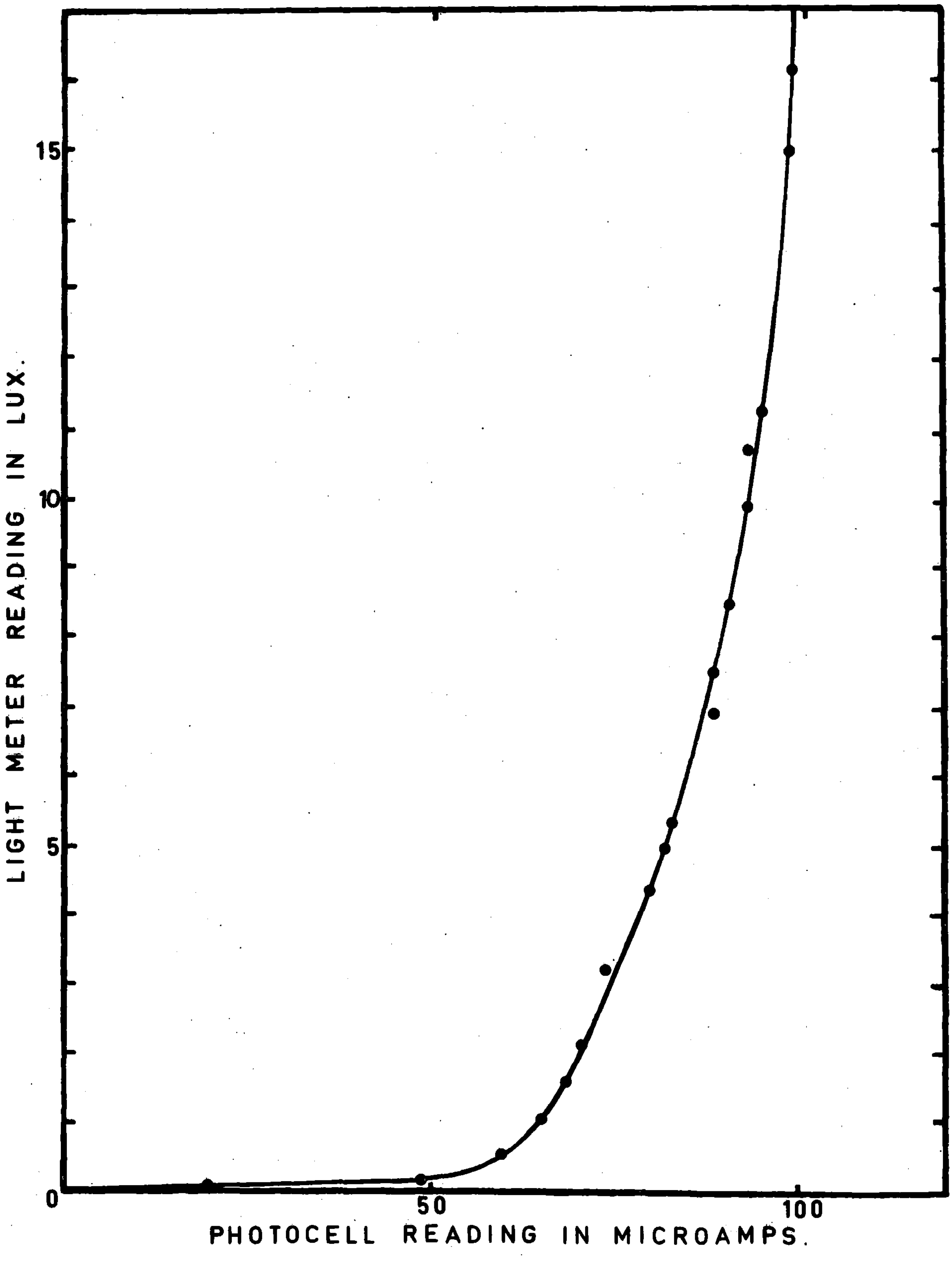


FIGURE 30. DIAGRAMMATIC LATERAL VIEW OF A TEST CAGE.

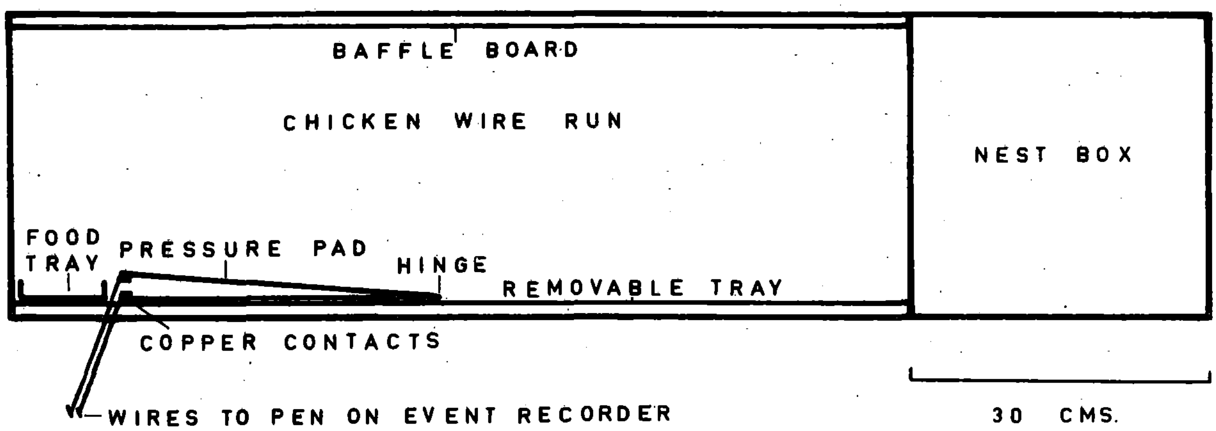
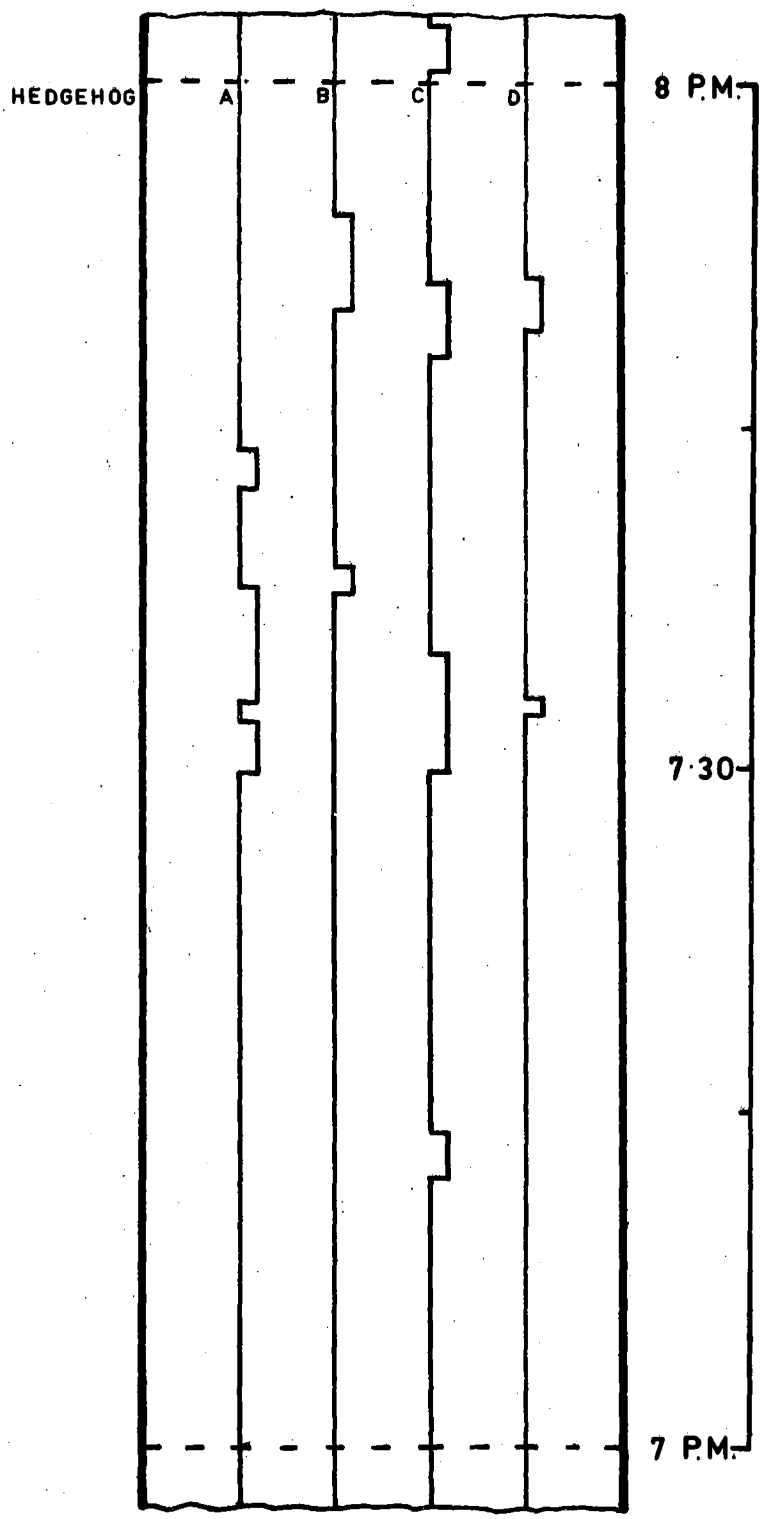


FIGURE 31. ACTIVITY RECORDING ON THE TAPE FOR 30-9-69 BETWEEN 7 P.M. AND 8 P.M. (ACTUAL SIZE).



volume mixture of cooked mince, bread and milk. Small quantities of mineral salts, cod-liver oil and chopped liver were added at monthly intervals. Food consumption was recorded daily. The animals were weighed weekly.

Advice was obtained from a statistician in planning this trial. This enabled a valid modified 't' distribution test to be used to test for significance when only four animals were involved. Four hedgehogs was the maximum number that could be accommodated in the available constant temperature environment.

III. RESULTS AND DISCUSSION

Weekly hedgehog weights and average daily food intake, at weekly intervals, are listed in Table 6. Each animal consumed between 100 and 300 g of food per day. Weight increases of 28%, 43%, 18% and 81% between capture and release occurred with hedgehogs A to D respectively. Weight fluctuations during the trial were related to food intake.

The tape from the event recorder showed the actual times of commencement and termination of every feed, for each of the four hedgehogs, over the 107 nights study period.

From these times the following information was calculated:

(i) The times of the first and last feed each night.

(ii) The number of feeds per night and the average number of feeds per night.

(iii) The total time spent feeding per night.

(iv) The duration of each feed and the duration of the average feed.

TABLE 6.

WEEKLY WEIGHTS AND AVERAGE DAILY FOOD INTAKE, IN GRAMS, OF FOUR HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

DATE 1969	HEDGEHOG A WEIGHT	HEDGEHOG A FOOD* INTAKE	HEDGEHOG B WEIGHT	HEDGEHOG B FOOD* INTAKE	HEDGEHOG C WEIGHT	HEDGEHOG C FOOD* INTAKE	HEDGEHOG D WEIGHT	HEDGEHOG D FOOD* INTAKE
At Capture	1189		942		767		685	
23/7	1212	271	1039	239	782	209	731	168
30/7	1262	292	1143	256	802	202	840	203
1/9	1525	274	1355	269	918	227	1041	206
8/9	1620	272	1334	273	963	229	1146	242
15/9	1637	279	1305	253	962	228	1167	241
22/9	1686	279	1330	259	1018	229	1206	242
29/9	1700	272	1308	258	1009	227	1261	237
6/10	1746	274	1411	261	1006	200	1281	236
13/10	1725	273	1312	225	1001	198	1335	240
20/10	1802	273	1370	253	968	167	1275	235
27/10	1598	193	1232	184	901	131	1175	158
3/11	1640	242	1306	231	919	189	1257	203
10/11	1642	267	1310	255	920	229	1206	242
17/11	1687	280	1349	260	968	220	1278	239
24/11	1640	274	1313	246	893	187	1225	248
1/12	1602	275	1347	259	905	224	1240	247
AVERAGE	1583	268	1277	249	924	206	1138	224

* FOR THE PREVIOUS WEEK.

(v) The average number of feeds in each one hour period throughout the night.

(vi) The average time spent feeding in each one hour period throughout the night.

The results were analysed in two parts corresponding with the two aims of the experiment.

The first aim of this series of experiments was to find out when hedgehogs began and finished feeding, and whether or not these times were dependent on light intensity.

To avoid disturbing the animals once the trial began light intensity readings, both outdoors and in the laboratory, were taken from sunset until dark (zero lux), and each morning from one hour before sunrise to sunrise, during the initial 15 day acclimatisation period.

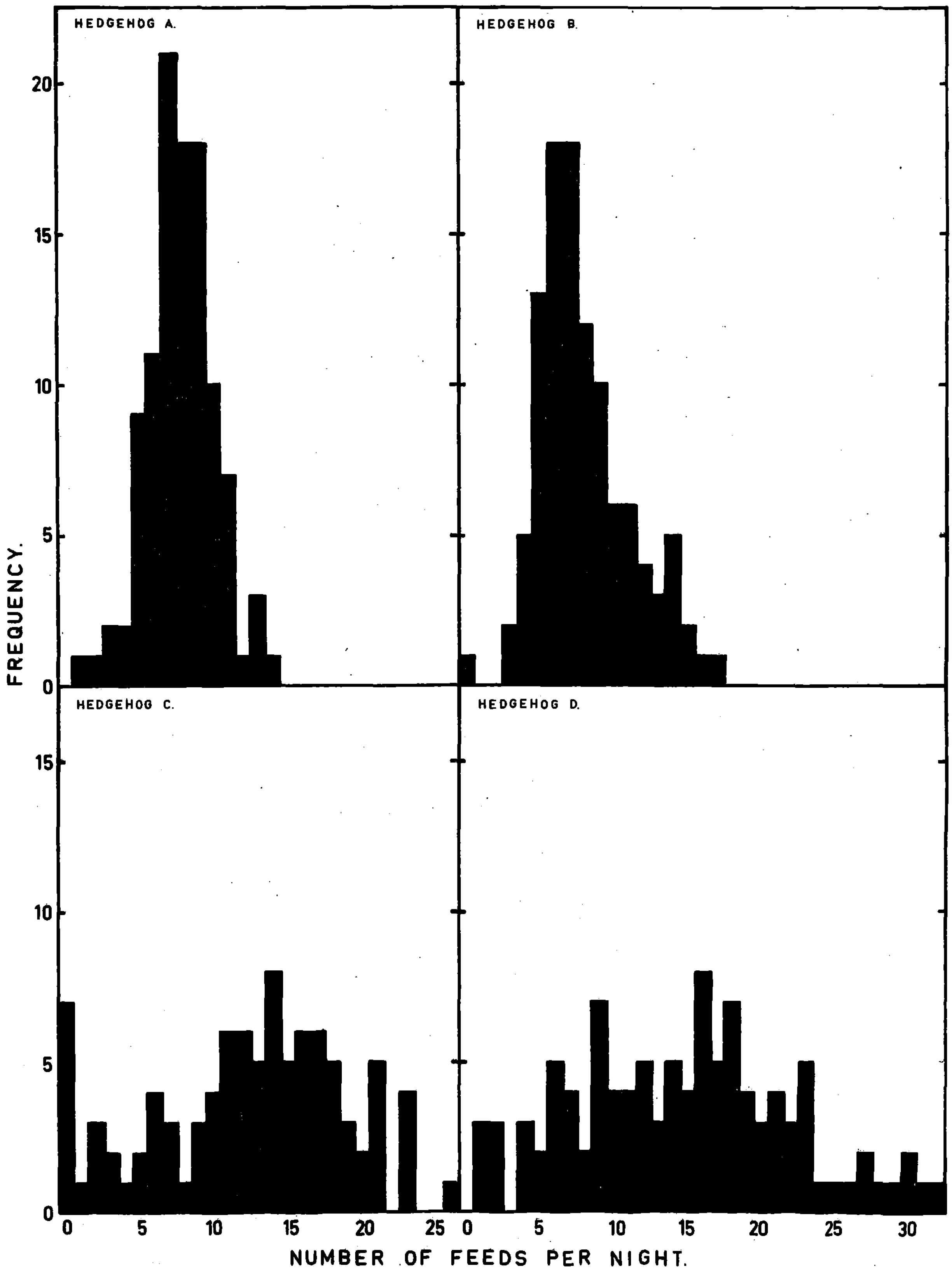
Outdoor light intensity readings exceeded full scale deflection of the micrometer until about half an hour after sunset, while no readings were obtained until about half an hour before sunrise. These readings indicated that the hedgehogs did not feed if the light intensity in the laboratory exceeded zero lux. This result was confirmed by repeatedly switching on a dimmed light during the night while the animals were feeding. This light could be activated from outside the room, to prevent other disturbance of the animals. The times when this light was on were carefully noted and the tape subsequently examined to see if feeding had been interrupted. Animals caught feeding when this light was activated always stopped and retired from the pressure pad.

At first it was suspected that the initiation of feeding in hedgehogs would be related to sunset. However, times of the first feed for each animal for the first 30 days of the study, when sunset varied from 5.02 p.m. to 5.25 p.m., showed no such relationship, as initiation of feeding ranged from 30 minutes to 232 minutes after sunset with an average of 116 minutes. There appeared to be no relationship between the amount of cloud cover and the time after sunset that feeding commenced. The animals would begin feeding at widely scattered times on the same night. There were no consistent early or late feeders, and any animal was liable to feed early or late irrespective of whether the outside conditions were bright or dull. The average of almost two hours after sunset for the initiation of feeding meant that there was little advantage in treating data in terms of time from sunset, hence the simpler time of day was used. Commencement of feeding did not appear to be related to food intake during the previous night.

The second aim of this series of experiments was to determine if laboratory fed hedgehogs exhibited a definite feeding rhythm or if they fed randomly throughout the night.

Frequency distribution histograms of the number of feeds per night (Figure 32) show that the feeding behaviour of hedgehogs A and B differs from that of C and D. The former pair averaged eight feeds per night, and the latter pair 12 and 15 respectively. There was no significant difference between the means of hedgehogs A and B, or C and D, when tested by a modified 't' test. Differences between the means of hedgehogs A and D (the two males), and hedgehogs B and C (the two females) were significant at the 0.1% level. The difference in behaviour was not sexual, and as the hedgehogs fed in a random order it was unlikely that any animal

FIGURE 32. FEEDING FREQUENCY PER NIGHT FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR A PERIOD OF 107 DAYS.



influenced the behaviour of any other.

A possible cause of these differences is the variation in body weight of the four hedgehogs. Hedgehogs A and B were heavier than C and D, and had higher daily food intakes (Table 6). This may have led to the development of differing feeding habits. There is a tendency for the lower the average weight of the animal the greater the average number of feeds per night, and the shorter the average duration of each feed. This explanation is consistent with Rubner's surface area law (Blaxter, 1962), which states that the smaller an animal the greater its surface area in relation to its volume, and consequently, the greater its heat loss. In order to maintain a stable basic metabolic rate, smaller animals need to feed more frequently and for shorter periods, than do larger animals.

An alternative and more probable explanation is that had a greater number of hedgehogs been used, a whole range of behaviour patterns, both within and beyond those of the four animals used, may have resulted.

Frequency distribution histograms of the total time spent feeding per night (Figure 33) were constructed from the data listed in Appendix IV. Differences between the means of hedgehogs C and D were significant at the 1% level. Differences between the means of the other pairs of hedgehogs were not significant at the 5% level. This means that the total time spent feeding per night differs significantly only between hedgehogs C and D.

Frequency distribution histograms for the duration of the first feed each night (Figure 34) show that the duration

FIGURE 33. TOTAL TIME SPENT FEEDING PER NIGHT BY FOUR HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

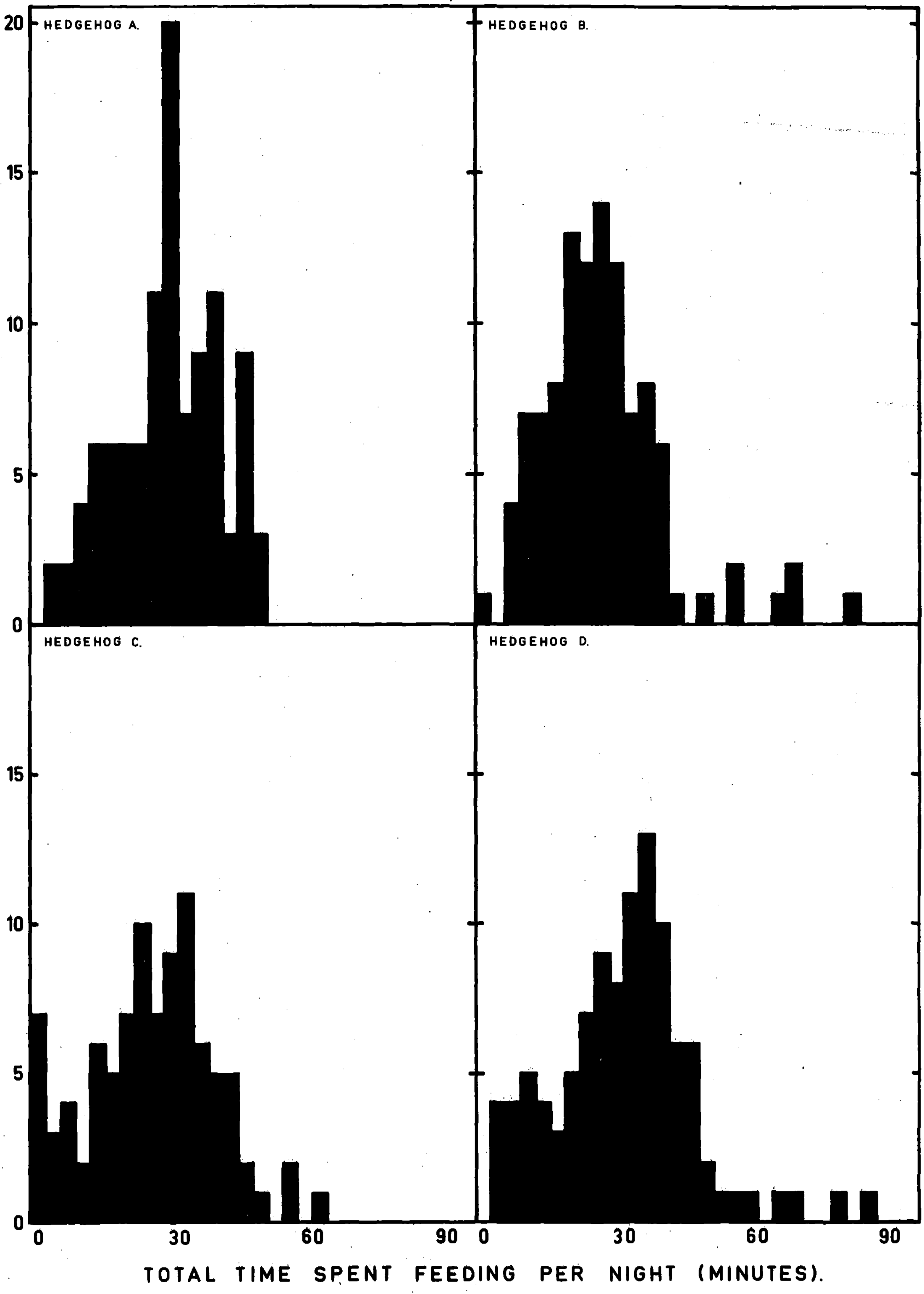
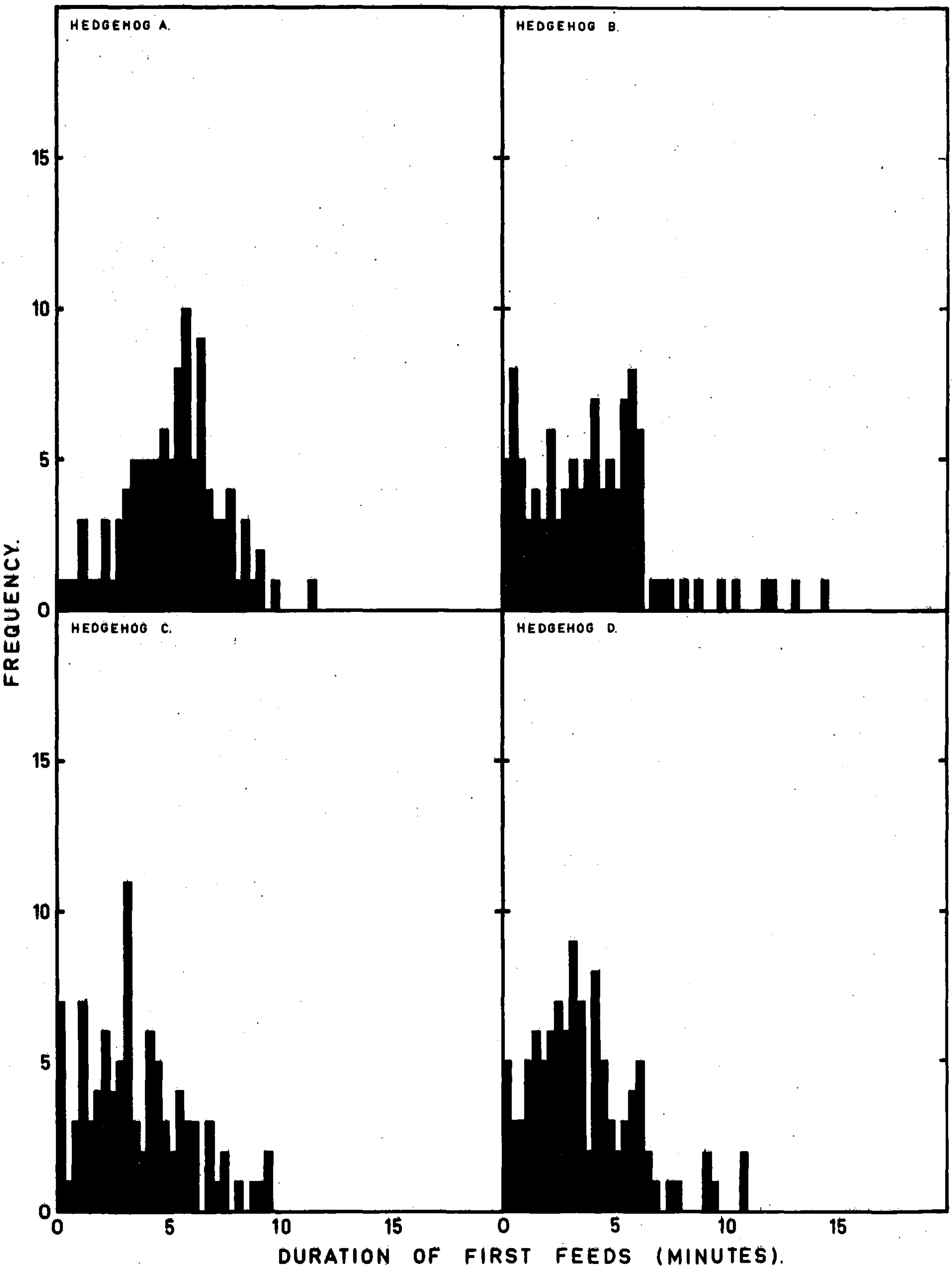


FIGURE 34. FREQUENCY OF THE DURATION OF THE FIRST FEED EACH NIGHT OF 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.



of these feeds ranged from one to 15 minutes. Those of hedgehogs A and B tended to be longer than those of C and D. Differences, significant at the 0.1% level, occurred between the means of hedgehogs A and B, A and C, and A and D. Differences between the means were not significant for other pairings. Hedgehog A thus had a different behaviour pattern from the others as regards its first feed each night.

Frequency distributions for the duration of each feeding period, excluding the first, are shown in Figure 35. The average feeding durations are 3.3, 3.0, 1.8 and 1.9 minutes for hedgehogs A to D respectively. Differences between the means of the two male hedgehogs, and between those of the two female hedgehogs were significant at the 0.1% level. Differences between the means of A and B, and C and D were not significant. The heavier pair, A and B, fed for significantly longer periods than did the lighter pair. Comparison of Figure 34 with Figure 35 shows that the first feed each night tended to be longer than subsequent feeds.

The average number of feeds, and the average time spent feeding in one hour periods throughout the night are shown in Figures 36 and 37 respectively. Hedgehogs A and B fed less frequently than did C and D. For all four animals the greatest number of feeds, and the maximum time spent feeding occurred between 8 p.m. and 9 p.m.

The four hedgehogs fed most frequently in the early part of the night; feeding activity then declined, but a second smaller peak of activity occurred about 3 a.m.

Plots of the average number of feeds in one hour periods throughout the night against the duration of the average feed

FIGURE 35. FREQUENCY OF INDIVIDUAL FEEDS OF 4 HEDGE-HOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

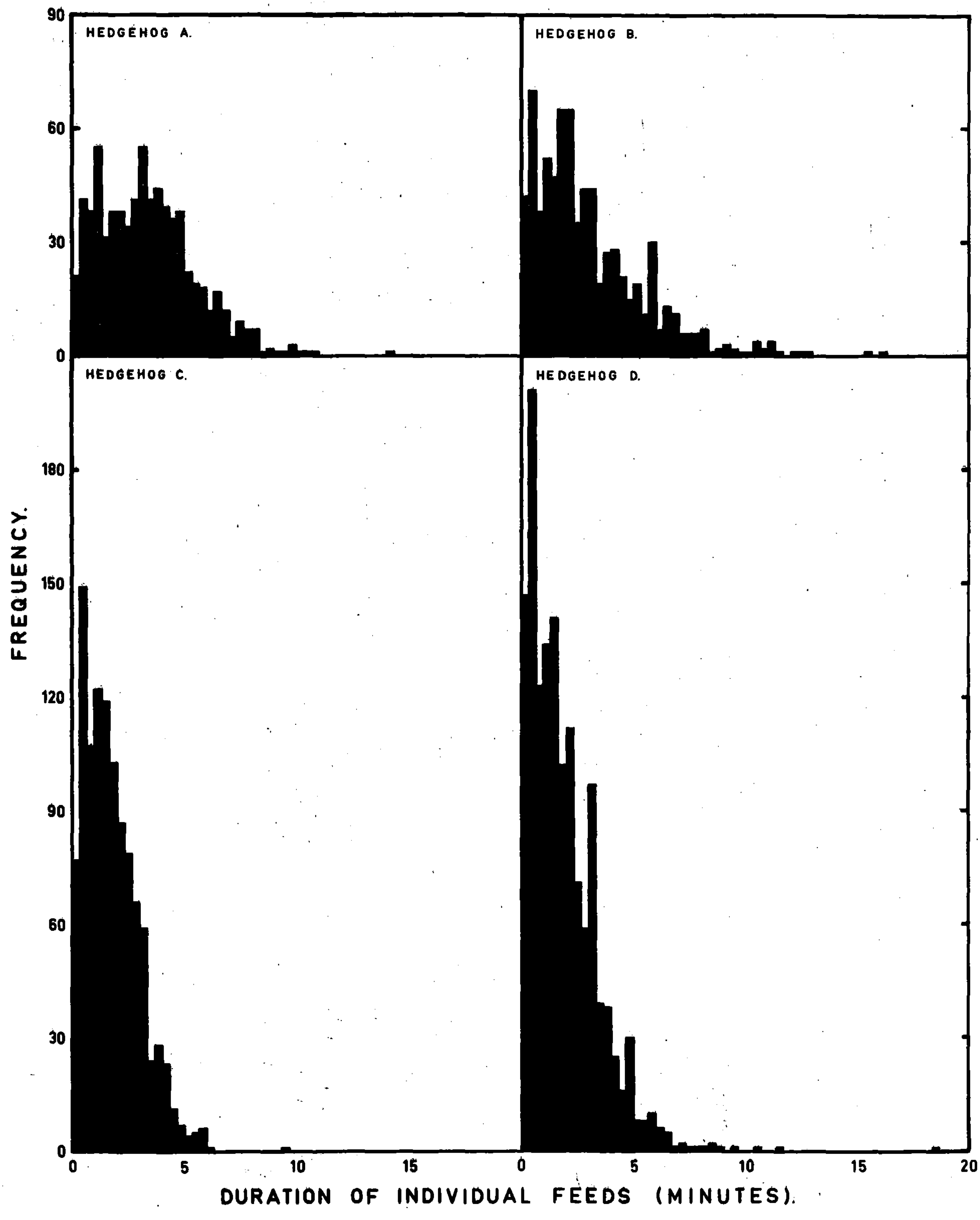


FIGURE 36. AVERAGE NUMBER OF FEEDS IN ONE HOUR PERIODS THROUGHOUT THE NIGHT FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

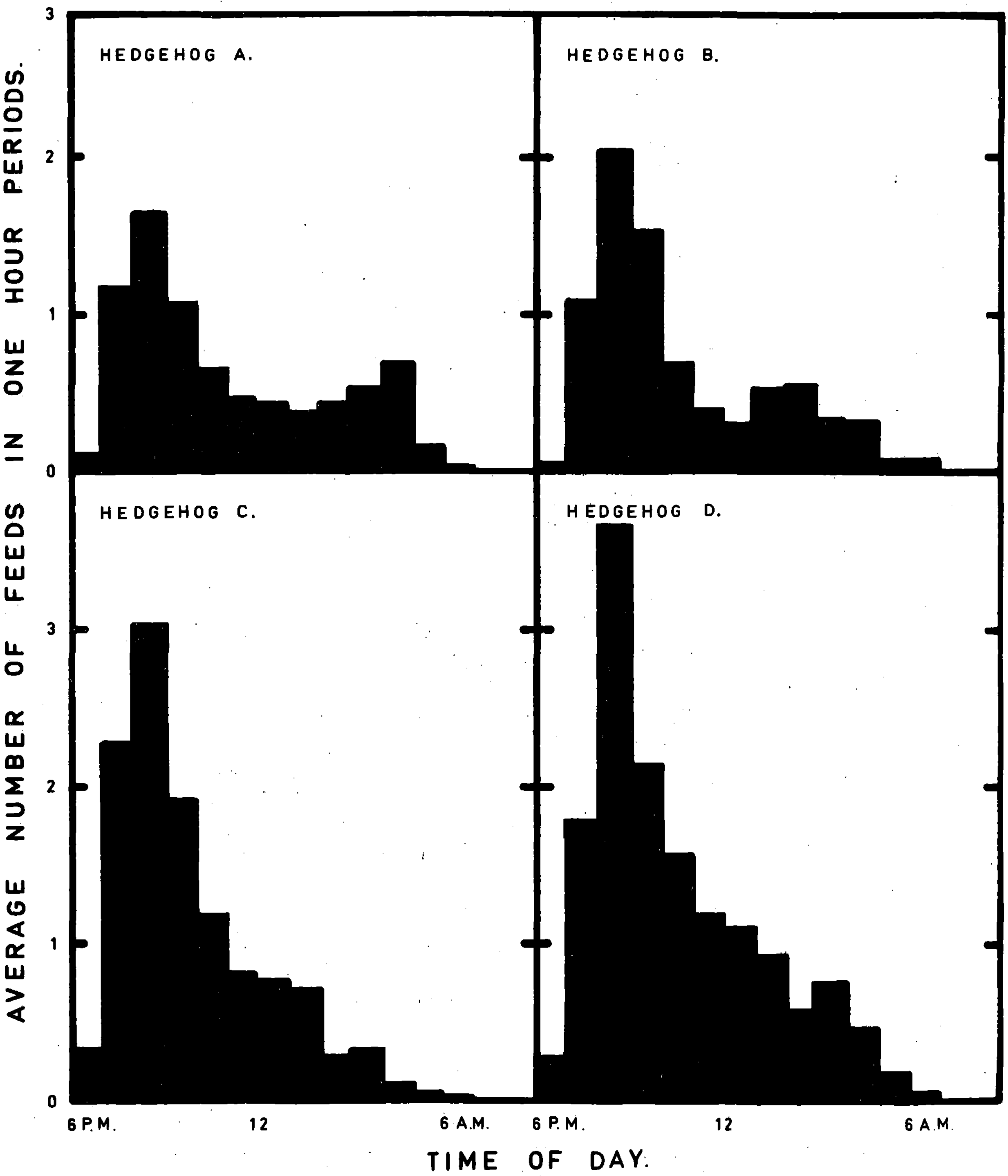
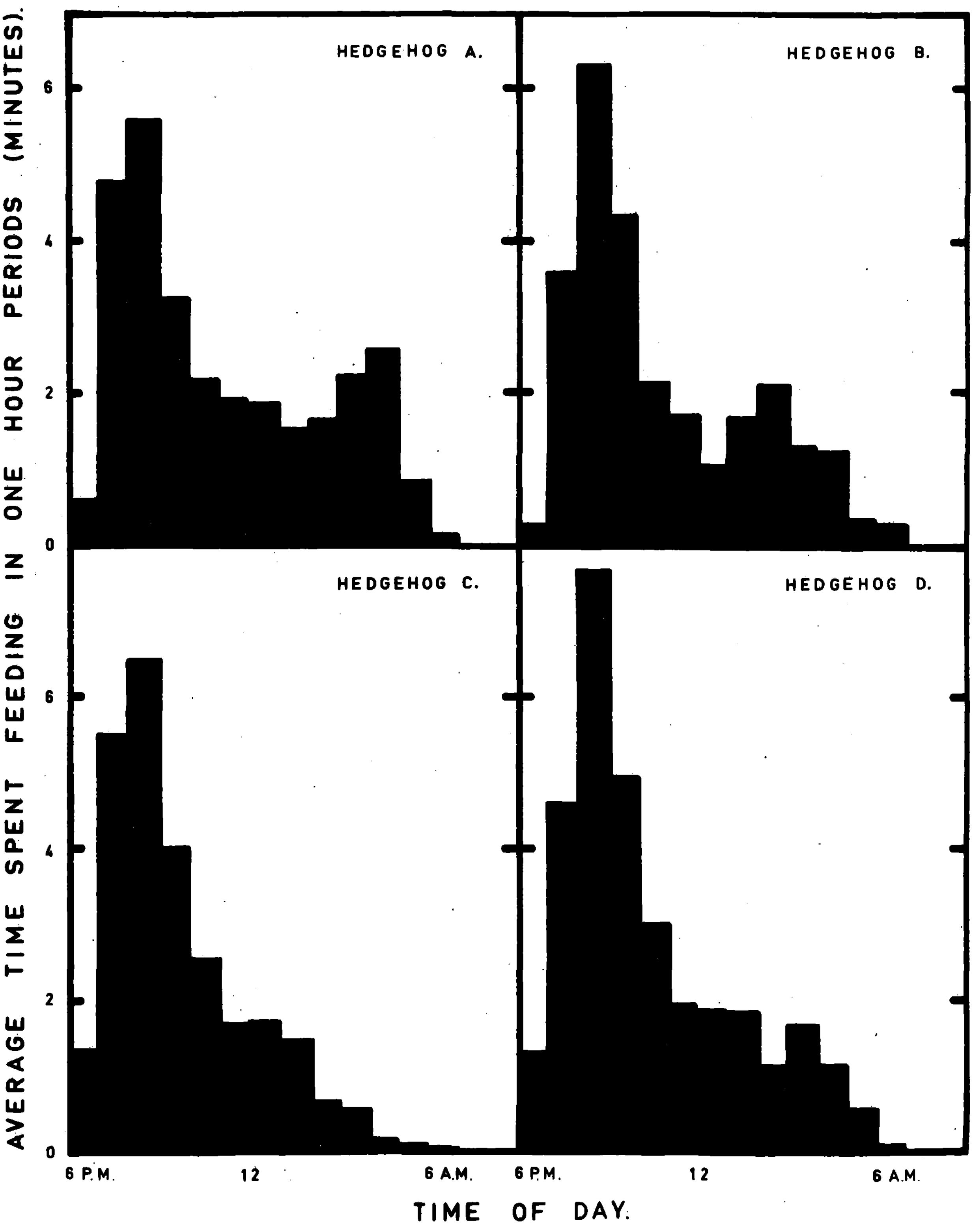


FIGURE 37. AVERAGE TIME SPENT FEEDING IN ONE HOUR PERIODS THROUGHOUT THE NIGHT BY 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.



in those periods are shown in Figure 38. Correlation coefficients were calculated for these lines, and all were significant at the 0.1% level. An analysis of covariance was carried out. Comparison of the residual mean squares by Bartlett's test showed no sign of real differences between the gradients. Homogeneity was thus assumed and the gradients compared with the F-test. They were significantly different at the 1% level. The regression equations predicting the average duration of feeding per hour (Y), from the number of feeds in each one hour period (X), are:

Hedgehog A: $Y = 3.4X + 0.2$

Hedgehog B: $Y = 3.0X + 0.2$

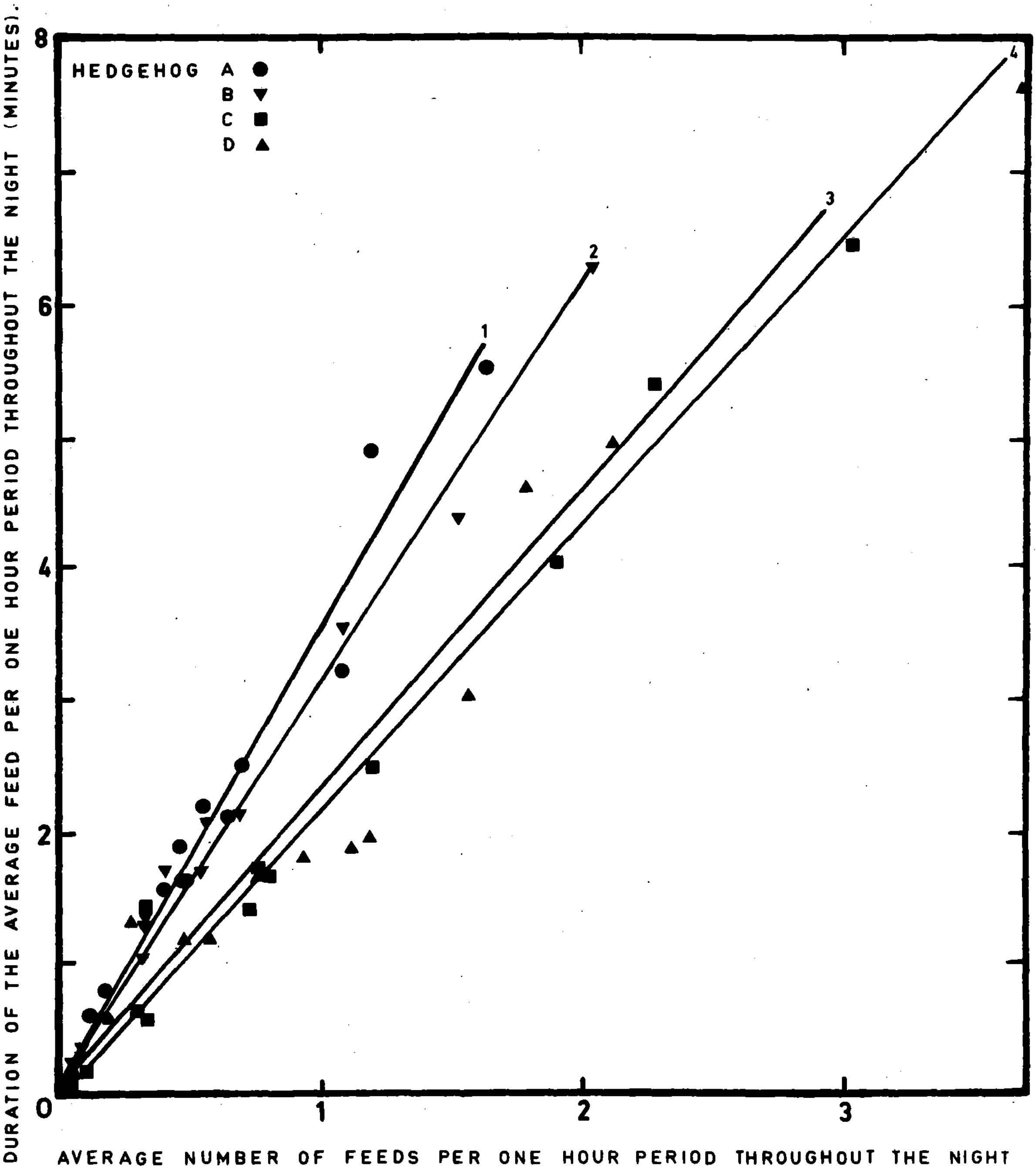
Hedgehog C: $Y = 2.2X + 0.2$

Hedgehog D: $Y = 2.1X + 0.1$

These equations indicate that the duration of feeding is dependent on the frequency of feeding.

Data for Figures 32 to 38 are given in Appendices III to IX and statistical data (after Snedecor and Cochran (1967)) are shown in Appendices X to XIII, respectively. The number of nights used in preparing Figures 32 to 37 for hedgehogs A, B, C and D were 105, 107, 100 and 104, respectively. Recorder pen malfunctions caused incomplete tracings on two nights for hedgehog A and three nights for hedgehog D. Hedgehog C did not feed on seven nights. These latter were recorded as zeros for the number and durations of feeds.

FIGURE 38. CORRELATION BETWEEN THE AVERAGE NUMBER OF FEEDS AND AVERAGE DURATION OF FEEDING, IN ONE HOUR PERIODS THROUGHOUT THE NIGHT, FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.



IV. SUMMARY AND CONCLUSIONS

Feeding occurred in the laboratory only when the light intensity was very low. This agreed with observed field behaviour. On each count night data on wind direction and strength, rainfall, dew, moonlight, amount of cloud and maximum, minimum and minimum grass temperatures were noted, or obtained from data available from the Lincoln College meteorological station. Even on nights with strongest moonlight an effective light intensity of zero lux was obtained at grass level. With the exception that the lowest minimum grass temperatures coincided with the disappearance of hedgehogs from the study area (presumably into hibernation) there was no apparent correlation between any of these factors and hedgehog activity.

Although variations occurred between individuals, the feeding behaviour of all four hedgehogs followed the same general pattern. They fed mainly for short periods, with the first feed each evening tending to be longer than later feeds. Between 6 p.m. and 7 p.m. feeding was infrequent, with the duration of feeds greater than average; between 7 p.m. and 10 p.m. feeding activity was at a maximum; while between 10 p.m. and 7 a.m. feeding activity generally declined. There was, however, a tendency for a slight increase in activity around 3 a.m.

Comparison of data from all-night counts (Table 3) with that in Figures 36 and 37 shows that the maximum feeding activity in the field occurred about two hours later than in the laboratory. The earlier feeding of the laboratory animals was probably caused by the earlier reduction of the light intensity in the laboratory, which had its only window shaded by a baffle.

Burton (1969) observed that wild British hedgehogs had a main feeding period from dusk to soon after midnight, and a second period of less intense feeding for an hour or so before dawn. Similar behaviour was reported for German hedgehogs by Herter (1938). The present laboratory studies were in agreement with these observations. A smaller peak of activity in the early morning was not apparent in the present field studies.

When food was constantly available it appears hedgehogs obtained most of their daily requirements early in the night, and then ate a smaller quantity in the early morning, presumably after some of the evening intake had been digested.

Differences in behaviour between the two heavier hedgehogs A and B, and the lighter pair C and D, may possible have been due to differing body weights. However, it is more likely these differences were due to the two groups being simply points in a series. The use of only four hedgehogs greatly limits variability between sexes and ages.

While the conclusions reached from the experiments in this chapter are of very limited value, because of the small sample and the short time involved, the knowledge and experience gained was extremely necessary for easier handling of the feeding experiments in Chapter 7.

CHAPTER VI

QUALITATIVE ESTIMATION OF HEDGEHOG FOODS IN THE STUDY AREA

I. INTRODUCTION

Many workers (including Herter, 1938; Brockie, 1958; and Burton, 1969) have found that invertebrates, especially insects, form a large part of the diet of hedgehogs. As an important area of this study concerned feeding behaviour of hedgehogs in the field, a programme was initiated to identify the species of invertebrates present in the study area, and thus determine the potential food available to hedgehogs in the study area. This data, together with that in Chapter 7, was essential to determine the size range of the food items commonly eaten by hedgehogs.

II. METHODS OF STUDY

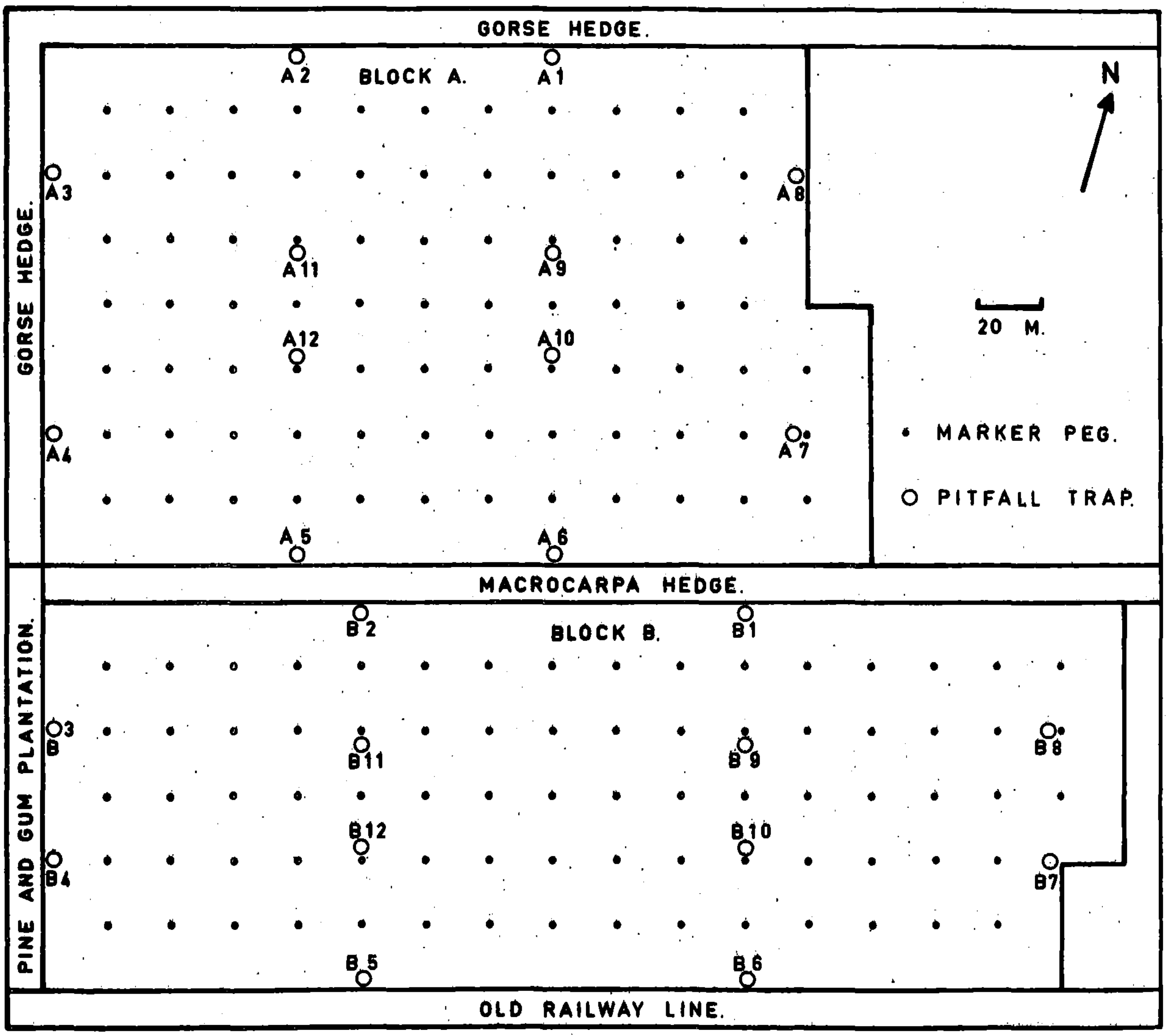
Collections were made using pitfall traps, and supplementary sweep netting.

(1) <u>Traps</u>.

From data gained from dropping analyses it was determined that pitfall trapping was an ideal method of collecting the major invertebrate food items in hedgehog diet. As these collections were for qualitative estimates only, 24 traps were sufficient to adequately cover the study area.

Twelve pitfall traps, arranged as shown in Figure 39,

FIGURE 39. MAP OF THE STUDY AREA SHOWING THE POSITIONS OF THE PITFALL TRAPS.



were placed in each of blocks A and B. Half the traps were positioned along the edges to reveal if nearby ditches and hedges were causing edge effects.

Each pitfall trap consisted of a pint Agee jar containing about 150 ml of 4% formalin. A 10 cm square cover of 5 mm hardboard, held about 2 cm above the lip of the jar by two 8 cm galvanised nails, reduced evaporation, bird predation and contamination by soil, grass and cow dung. Traps were identified by systematic labelling.

(2) Collections.

The traps were cleared each Monday evening and Tuesday morning. This gave an overnight catch on the night of each hedgehog count, and the catch for the remainder of the week.

Net sweeps carried out one hour after sunset every Tuesday evening supplemented the collections from the pitfall traps. Ten sweeps were made in each of four different areas of both blocks, to catch flying insects, some of which may have avoided the pitfall traps. A reference insect collection was prepared by mounting adult specimens of the various species. The antennae, mouthparts, legs and wings of some of these species were removed for reference, and, together with soft-bodied species and larvae, were preserved in 70% alcohol and glycerine. This reference collection was an essential aid in the accuracy and speed of identification of species eaten by the hedgehogs in the analyses of their diet.

To determine if porina and grass grub were present in the study area, five sets, each of 20 random 20 cm spade-square samples, were taken from each block during the study period. Three sets were taken in the summer in October, December and

February, and two in the winter, in April and June. In addition, 12 10 cm core samples, each taken to a depth of 10 cm, were removed from each block in August, 1969. The animals in both the spade-square and core samples were separated from the matrix by flotation.

The traps were first set at 7 p.m. on Monday, 1/9/69, and the initial overnight catch was cleared at 7 a.m. the following morning. The traps were then reset for the first weekly catch. Net sweeps commenced on the night of Tuesday, 2/9/69. As the traps were not cleared in the last two weeks of December, the collection made in the first week of January 1970 contained animals collected over a three-week period. Over the one year period, 51 sets of weekly collections were obtained.

III. RESULTS AND DISCUSSION

The collections yielded 101 identifiable species, together with many species of very small dipterans, a pseudo-scorpion, and larvae of various species. As they were never found in the droppings or stomach contents of hedgehogs, no attempt was made to identify these small flies, and other miscellaneous species. The identifiable species included 76 insects, 16 arachnids and nine other invertebrates.

The 76 species of insects belonged to nine orders and 42 families. The 16 arachnids included two species of harvest-men and 14 species of spiders. The remaining nine species included one annelid, one isopod, one amphipod, one chilopod, two diplopods, two species of collembola and one mollusc.

All identified species are listed and classified in Appendix XIV. The insect classification follows that in C.S.I.R.O. (1970), "The Insects of Australia". The collections from both the pitfall traps and sweep netting declined from the beginning of June, and few species were caught between then and the end of August.

The occurrences throughout the year of the 20 most frequently captured species are shown in Figure 40. The animals collected on Monday evening had been caught during the previous week. Each weekly collection was tabled as finishing on Monday evening, while the Monday night collections were regarded as belonging to the following week. The 20 species were present in the study area for more than 10 weeks of the study period. The weekly catch is shown by the solid black line, the nightly catch by the stippled line, and the sweep netting catch by the cross-hatched line. A dotted line means that the species was assumed to be present at the time but was not actually caught. The months of occurrence of all species are included in Appendix XIV. Although grass grub and porina larvae were not found in the soil samples, some were present in the area as both species were caught in the pitfall traps and by sweep netting. Dung flies, aphids and Argentine stem weevils were mainly caught by sweep netting. Table 7 shows the pitfall traps in which the most common species were caught. Some of these species show the presence of edge effects. Earth worms and slugs were often found under the pitfall traps in all parts of each block, and although they are not listed in Table 7, they were present in the area throughout the study period.

FIGURE 40. AVAILABILITY OF 20 INVERTEBRATE SPECIES FOUND IN THE STUDY AREA BETWEEN SEPTEMBER 1ST., 1969, AND AUGUST 31ST., 1970.

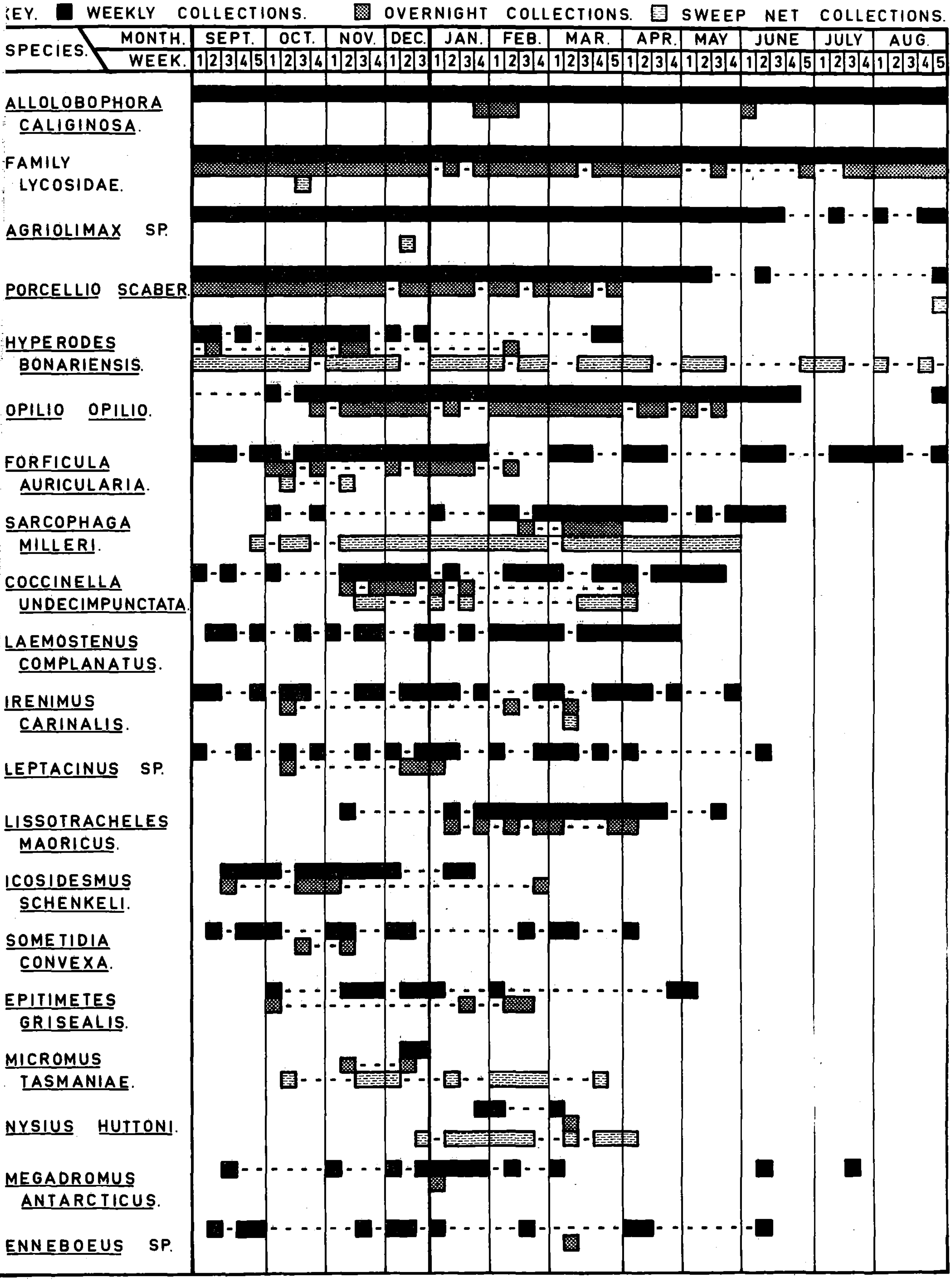


TABLE 7.

THE PITFALL TRAPS IN WHICH THE MOST COMMON FOOD SPECIES WERE CAUGHT.

SPECIES TRAP	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12
LYCOSIDAE	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
PORCELLIO SCABER	X		X	X	X	X	X	X	X	X			X	X	X	X	X		X					X
HYPERODES BONARIENSIS	X	X	X	X	X	X	X		X		X	X	X	X			X	X	X		X	X	X	
OPILIO OPILIO	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
FORFICULA AURICULARIA			X	X	X	X	X						X	X	X		X				X			X
SARCOPHAGA MILLERI	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
COCCINELLA UNDECIMPUNCTATA	X	X	X	X		X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X
LAEMOSTENUS COMPLANATUS					X	X				X			X	X	X	X								
IRENIMUS CARINALIS					X	X					X		X	X	X			X						X
LEPTACINUS SP.	X	X	X	X	X				X	X		X			X			X		X	X		X	X
LISSOTRACHELES MAORICUS	X	X	X	X	X	X		X	X	X	X	X			X	X	X	X				X	X	X
ICOSIDESMUS SCHENKELI				X		X							X	X										
SOMETIDIA CONVEXA							X						X	X	X	X			X					X
EPITIMETES GRISEALIS		X	X			X							X	X	X									
NYSIUS HUTTONI					X	X						X	X											
MEGADROMUS ANTARCTICUS			X	X		X							X		X		X							
ENNEBOEUS SP.	X	X			X			X		X			X		X				X			X		

Most of the 200 spade-square samples contained only earthworms. The numbers present ranged from 22 to 49, with an average of 32, per spade-square sample (i.e. 800/ m^2). Most belonged to the species Allolobophora caliginosa; other species, and earthworm cocoons, being present in very small numbers only. A few of the spade-square samples contained small numbers of larvae of tipulids, muscids and noctuids. All animals were found in the top 8 cm of the soil and most in the top 5 cm. The core samples also, contained mainly earthworms. The numbers present per sample ranged from 0 to 26, with an average of six. The only other species recovered from the cores were one ichneumid, (Salius sp.), one wireworm larva (Aeolus sp.), one tipulid larva, one muscid larva, one millipede (Schedotrigonia sp.), one staphylinid (Leptacinus sp.) and several earthworm cocoons.

Of the 20 most frequently occurring species, the earthworm (Allolobophora caliginosa) and spiders of the Family Lycosidae, were present throughout the year. Six other species, the slug (Agriolimax sp.), slater (Porcellio scaber), Argentine stem weevil (Hyperodes bonariensis), harvestman (Opilio opilio), earwig (Forficula auricularia) and dung fly (Sarcophaga milleri) were present for the major part of the survey period. These six species were captured in more than 70% of the weekly collections. It was assumed that a lessening in activity during the colder months explained their absence from some collections during this period. Some of these species hide in the grass, leaf litter and soil during the winter, but may emerge spasmodically on warmer nights. Slugs were more active on nights when dew was heavy, or when light rain was falling. On these nights larger numbers were seen in the spotlight beam. They were less active on cold, frosty nights. This would explain their erratic occurrence between mid June and mid August.

Eleven-spotted ladybirds (Coccinella undecimpunctata), ground beetles (Laemostenus complanatus) and weevils (Irenimus (Catoptes) carinalis) were caught in approximately half of the weeks surveyed.

The remaining nine, of the 20 most commonly occurring species, were caught in between one third and one quarter of the study period. All occurred over different periods during the summer, but three of them, the large ground beetle (Megadromus antarcticus), the tenebrionid (Enneboeus sp.) and the staphylinid (Leptacinus sp.) were also caught in the second week of June, and Megadromus was caught in the third week of July. This suggests that the latter three species, at least, become active during the winter, if a period of warmer weather occurs.

Two species of Collembola (Hypogastrura rossi and Entomobrya nivalis) were found in varying numbers throughout the study period. They were occasionally found in hedgehog stomachs and droppings but, because of their very small size, it is assumed that they were ingested accidentally.

For all the foregoing species, it does not necessarily follow that they were inactive or absent from the study area in those weeks when no captures were recorded.

Edge effects were caused by the macrocarpa hedge between blocks A and B, and by the gorse hedge and pine and blue gum plantation on the western boundaries of blocks A and B, respectively. The remaining boundaries of both blocks were far enough away from ditches and hedges to avoid any edge effects. The click beetle (Lacon variabilis) was caught only near the gorse hedge, the gum ladybird (Rhizobius ventralis) only near the plantation, and the amphipod (Orchestria tenuis) only near the macrocarpa hedge. However, as these species were caught in only small numbers, they may have been present in other areas as well.

The carabids Megadromus, Laemostenus and Solinochilus and the millipede Icosidesmus schenkeli were caught in drier areas near the hedges and the plantation, although the former two were each caught on one occasion well away from these boundaries. Slaters and earwigs were caught throughout the two blocks but both species were caught in much greater numbers near the hedges. It seems, therefore, that although these species prefer a drier, more sheltered habitat, they may be found in the open pasture.

IV. SUMMARY AND CONCLUSIONS

As all the species mentioned in this chapter, with the exception of Laemostenus complanatus, appeared to be at least partly active at night, all would be available as food for hedgehogs. Even those which were inactive would still be available, as hedgehogs search for their food and turn over cow dung, and other debris. Several hedgehogs were observed scrabbing in muddy patches, and one had excavated a 5 cm diameter hole to a depth of 6 cm, in an attempt to catch a tipulid larvae. This was still in the bottom of the hole when the animal was disturbed. Digging was relatively easy throughout most of the year as irrigation kept the soil friable in the summer. Irrigation was also responsible for earthworms being readily available throughout the year. To prevent dessication earthworms tend to live deeper in the soil during the summer, but in irrigated pasture they are forced into the top layers to prevent drowning.

Although grass grub and porina larvae were absent from the soil samples, two porina larvae were actually found in the area. One of these was found in pitfall trap A5, on the southern boundary of block A, near the macrocarpa hedge, while the second was found dead in the grass near trap B5, on the southern boundary of block B. This indicates that larvae may have been present in the drier parts of the study area. Adults of both porina and grass grub were caught in the sweep nets during the flying season of each species. Porina moths were quite numerous but may have flown in from neighbouring paddocks. Both species, but especially the porina moths were attracted to the spotlight, and both species were occasionally caught in the pitfall traps. The adults of both species were, therefore, available to hedgehogs as food, and both were eaten in large numbers, as shown by stomach content and dropping analyses in Chapter 7.

CHAPTER VII

DIET OF A NATURAL HEDGEHOG POPULATION

I. INTRODUCTION

One of the objects of this study was to determine the number of different food items, and the quantities of each, eaten by a natural population of hedgehogs in pasture lands. Although dropping analyses are satisfactory indicators of the relative importance of a single food item between different seasons, or localities, they should be used cautiously for the quantitative assessment of the different food items in the diet, unless the reliability of the method has been confirmed by food recovery experiments using captive animals, as was done in the present study.

However, as hedgehog droppings were readily available in the irrigated study area they presented an opportunity to examine the diet of that population without causing it any interference. Because of the excessive grass growth, and the possibly lower hedgehog population, only two droppings were found in the non-irrigated area. As this number was, of course, quite inadequate to allow any comparison of diet between the animals from the two areas, some alternative method had to be found. Analyses of the stomach contents of animals captured from comparable, but non-irrigated pastures located a short distance from the irrigated study area was chosen as the most satisfactory of those available, and 45 animals were subsequently obtained. As stomach contents of 15 animals captured from non-irrigated pastures near Kaikoura were available, the opportunity was taken to analyse these to test whether a similarity in diet was shown between animals from two widely separated dry land localities.

By considering these analyses it was hoped to obtain information on the effect of hedgehogs on the populations of pasture pests.

II. LITERATURE REVIEW

Much of the literature in this field discusses the diet of invertebrates and vertebrates other than mammals. Papers which contained techniques relevant to the present study are reviewed below.

Most workers have treated their data by one or more of the following methods:

(i) Occurrence (or presence or absence)
(ii) Relative volume (or point count)
(iii) Direct count (or number)
(iv) Weight
(v) Dominance
(vi) Fullness.

Hymes (1950) reviewed these six methods in relation to the assessment of the diet of fish. He concluded that the relative volume method was the most suitable, since it was rapid, easy to apply, did not involve counting large numbers of small and fragmented organisms, and made no spurious claims of unwarranted precision.

Godfraux (1969 and 1970) used stomach content analyses to determine the diet of predatory fish in the Hauraki Gulf. He concluded that the 'occurrence' and 'volume' methods were the most useful. The pictorial methods of data presentation used in these two papers permit ready assimilation of the results.

Although McAtee (1912) wrote a very early paper he does provide an excellent review of the relative strengths and weaknesses of different methods of stomach content analyses in birds, and concludes that a combination of numerical and volumetric methods is preferable. Such a combination has been used in this study.

Hamilton (1930 and 1941) studied the diets of many North American small mammals, by analyses of their stomach contents. He found that in spite of severe fragmentation, painstaking work enabled most of the food items eaten to be identified. Insects formed a major part of the diet of most of the species that he investigated, with values over 50% being recorded for shrews.

Miller (1954 and 1958) found that insects formed a large part of the diet of the wood mouse (Apodemus sylvaticus) and bank vole (Clethrionomys glareolus) in Wytham Wood, Berkshire, England and that with the exception of arachnids in the diet of the wood mouse, these were the only animal food items represented.

Drummond (1960) from dropping analyses found that the dominant species taken throughout the year by the brown rat (Rattus norvegicus) in Bridgemarsh Island was Spartina townsendii. This was supplemented by varying amounts of dicotyledonous plants, crustacea and insects. By analysing the droppings of the desert fox (Dusicyon sechurae) of northwestern Peru, Huey (1969) found that they ate mainly the seed pods of perennial shrubs. In coastal areas he found that they supplemented this largely herbivorous diet with carrion, crustacea and some insects. The papers of Drummond (1960) and Huey (1969) also provided concise pictorial methods of data presentation.

In a study involving 444 common shrew (Sorex araneus) stomachs, Rudge (1968) compared three techniques of analysis. He found that the effects of fragmentation and of the varying rates of digestion of different prey species, together with rapid passage through the gut made it difficult to obtain quantitative data. He concluded that the results obtained by the occurrence technique were the most reliable. By analysing the contents of 276 stomachs, Best (1969) found that the diet of the black rat (Rattus rattus) in two forested areas of the South Island of New Zealand, consisted of arthropods, berries and seeds. For reasons similar to those given by Rudge (1968), he too had difficulty in obtaining quantitative results.

As the studies of Hamilton (1930 and 1941), Miller (1954 and 1958), Rudge (1968) and Best (1969) all involved insect-eating mammals, they encountered problems similar to those encountered in the present study. However, the development of the freeze-drying technique, together with the percentage recovery experiments using a captive animal, enabled the present author to overcome most of these difficulties, and obtain reliable quantitative results.

III. METHODS OF STUDY

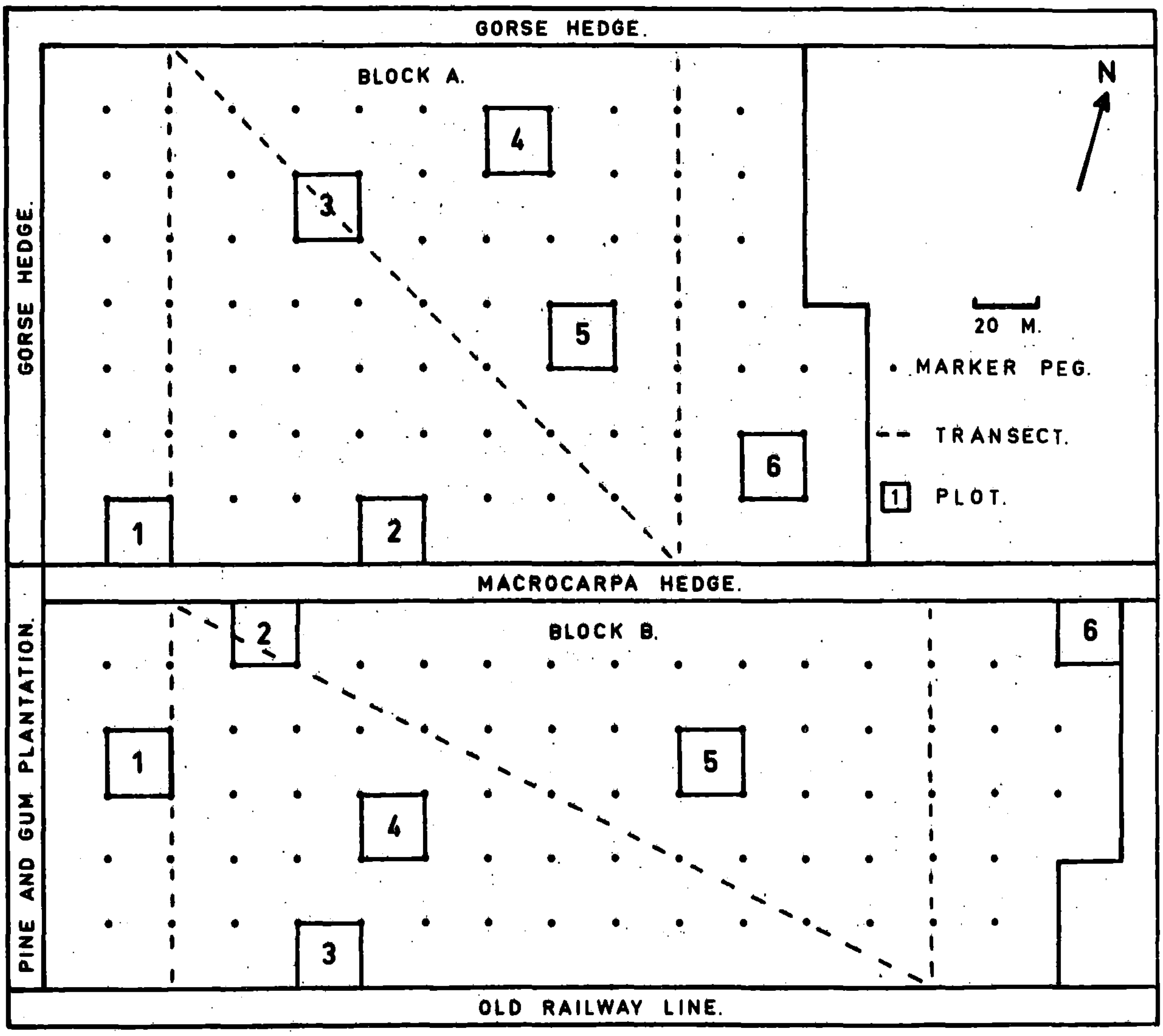
(1) Sample Collection.

(a) Droppings. A total of 230 droppings was collected from the irrigated study area. A 0.53 km Z-shaped transect was plotted in each block (Figure 41). Each week, from 2/9/69 to 31/8/71, inclusive, droppings were collected from an area of up to 60 cm on each side of these transects. In addition six, randomly selected, 20 m square plots (Figure 41) from each block, were grid searched once a week, from 2/9/69 to 30/11/69, inclusive. To enable a comparison to be made between the number of droppings obtained and hedgehog activity, droppings were collected every Tuesday morning, following the Monday night hedgehog counts. All droppings collected from the transects and plots were less than one week old. From their relative hardness, moisture content and colour, it was possible to estimate their approximate age. Random droppings from elsewhere in the study area were also collected when observed.

After three months an evaluation was made of the relative merits of the collections from the transects and plots. As it was found that two thirds of the droppings had been collected from the transects, which could be searched in half the time of the plots it was decided to discontinue searching the plots.

With the exception of eight double droppings, all were single. In the field, forceps were used to place each dropping in a vial, which was then sealed, labelled with the date, number, collection point and estimated age of the dropping. Each vial was placed in a deep freeze as soon as possible, and

FIGURE 41. MAP OF THE STUDY AREA SHOWING THE DROPPING TRANSECTS AND PLOTS.



subsequently freeze-dried and its contents analysed.

(b) Animals. Because of the disturbance to the population under study, hedgehogs could not be collected from the study area. Between September 1970 and February 1971, inclusive 45 hedgehogs (S1 to S45 inclusive, Table 8) for use in stomach content analyses were collected from non-irrigated but otherwise comparable pastures to those of the irrigated study area. These animals from surrounding areas were representative of a dry land population. Of the 45 animals 28 were male and five juvenile. They were collected from suitable paddocks located as close as possible (0.4 to 1.4 km) to the irrigated study area. A major road, and two deep ditches, in which drowned hedgehogs were occasionally observed lay between the two areas. No hedgehogs marked in the study area were subsequently found in this ditch, or in any of the paddocks used for collection. The paddocks of the abandoned non-irrigated study area (TS1 and TS9) were included in this collection area.

The paddocks used for captures (Figure 1) supported the following pastures:

TS1	S170 tall fescue	16.8 kg/ha
(New pasture)	White clover	3.4 kg/ha
	(Overdrilled with Ariki ryegrass)	22.4 kg/ha
TS 8-10	Ariki ryegrass	13.4 kg/ha
(2,4 & 2 year pastures)	Timothy	4.5 kg/ha
	White clover	3.4 kg/ha

TABLE 8.

COLLECTION DATA FOR 60 HEDGEHOGS KILLED FOR STOMACH CONTENT ANALYSES.

NUMBER	DATE	STAGE	SEX	WEIGHT (gm)	NUMBER	DATE	STAGE	SEX	WEIGHT (gm)
S 1	5/ 9/70	Adult	Male	774	S31	3/ 2/71	Juvenile	Female	280
S 2	5/ 9/70	Adult	Male	632	S32	7/ 2/71	Adult	Male	681
S 3	19/ 9/70	Adult	Male	510	S33	7/ 2/71	Adult	Male	664
S 4	19/ 9/70	Adult	Male	842	S34	7/ 2/71	Adult	Male	771
S 5	26/ 9/70	Adult	Male	812	S35	7/ 2/71	Adult	Female	618
S 6	11/10/70	Juvenile	Male	378	S36	7/ 2/71	Juvenile	Female	337
S 7	11/10/70	Adult	Female	588	S37	15/ 2/71	Adult	Female	803
S 8	15/10/70	Juvenile	Male	446	S38	15/ 2/71	Adult	Male	757
S 9	18/10/70	Juvenile	Male	400	S39	15/ 2/71	Adult	Female	665
S10	18/10/70	Adult	Male	603	S40	15/ 2/71	Adult	Female	837
S11	24/10/70	Adult	Male	585	S41	15/ 2/71	Adult	Female	962
S12	30/10/70	Adult	Male	820	S42	15/ 2/71	Adult	Female	681
S13	31/10/70	Adult	Male	610	S43	22/ 2/71	Adult	Female	709
S14	14/11/70	Adult	Female	742	S44	22/ 2/71	Adult	Male	683
S15	14/11/70	Adult	Female	547	S45	28/ 2/71	Adult	Female	697
S16	8/ 1/71	Adult	Male	786	S46	21/11/70	Adult	Female	673
S17	8/ 1/71	Adult	Male	699	S47	21/11/70	Adult	Female	514
S18	14/ 1/71	Adult	Male	634	S48	21/11/70	Adult	Male	628
S19	20/ 1/71	Adult	Female	571	S49	21/11/70	Adult	Male	596
S20	20/ 1/71	Adult	Male	782	S50	28/11/70	Adult	Male	683
S21	20/ 1/71	Adult	Female	648	S51	28/11/70	Adult	Female	530
S22	20/ 1/71	Adult	Male	675	S52	28/11/70	Adult	Female	623
S23	30/ 1/71	Adult	Male	504	S53	28/11/70	Juvenile	Female	405
S24	30/ 1/71	Adult	Male	579	S54	28/11/70	Adult	Female	756
S25	30/ 1/71	Adult	Female	503	S55	28/11/70	Adult	Male	699
S26	30/ 1/71	Adult	Male	835	S56	5/12/70	Adult	Male	631
S27	30/ 1/71	Adult	Male	823	S57	5/12/70	Adult	Female	569
S28	3/ 2/71	Adult	Female	830	S58	5/12/70	Adult	Male	762
S29	3/ 2/71	Adult	Male	855	S59	5/12/70	Adult	Female	569
S30	3/ 2/71	Adult	Male	545	S60	5/12/70	Adult	Female	583

D1	S170 tall fescue	13.4 kg/ha
(9 year pasture)	White clover	3.4 kg/ha
D2 & 3	Ariki ryegrass	13.4 kg/ha
(New pasture)	Timothy	6.7 kg/ha
	White clover	3.4 kg/ha

The ryegrass pastures showed first year ryegrass dominance, second year clover dominance, and thereafter a 60% grass : 40% clover composition. The fescue pastures showed first year clover dominance with a subsequent 50% grass: 50% clover composition.

All collection paddocks were part of a rotational grazing system with 56 cows per hectare grazing at intervals of 21 days in summer and 60 days in winter.

The soils of the collection paddocks were Temuka silt loam. Apart from being non-irrigated these grass-clover pastures were comparable with those of the irrigated study area. Comparison of dropping analyses from the study area with stomach content analyses from these pastures allows a comparison of hedgehog diet between irrigated and non-irrigated pastures.

Collections obtained over the eight month period from the pitfall traps that had been placed in blocks C and D yielded the same invertebrate species as those from blocks A and B. Although collembola and ladybirds were more numerous in blocks C and D, neither was an important constituent in hedgehog diet. Thus essentially the same hedgehog food supply was present in both the irrigated and non-irrigated areas.

To avoid taking animals with empty stomachs, or with the contents largely digested, hedgehogs for stomach content analyses were collected between 10 and 11 p.m. Animals were located by spotlight and killed with chloroform as soon as possible, and always within 30 minutes of capture.

Following the abandonment of blocks C and D, it was initially intended to collect four animals per week throughout a one year period commencing in June 1970, as this would yield information on any seasonal variation in the diet. However, it proved impossible to collect sufficient hedgehogs during the winter months for any comparison involving this season to be valid. Therefore, hedgehogs were collected as available between September 1970 and February 1971.

Exact aging of hedgehogs in the field is difficult, but with experience it was relatively easy to distinguish between adults and juveniles by means of size, weight, pigmentation and the relative hardness and colour of spines. Animals were tentatively classified as adults in the field if their weight exceeded 500 g. This classification was later confirmed by laboratory examination of the gonads.

Mr Don McKinnon, of Kaikoura, contacted the author and reported that he had observed hedgehogs eating large numbers of grass grub beetles in his paddocks. He agreed to catch, kill and forward a number of animals. These samples, collected from pastures badly affected by grass grub, during the flight season of this pest, allowed a comparison to be made with the Lincoln samples where examination had failed to detect its presence. These hedgehogs (S46 - S60, inclusive) were collected from non-irrigated ryegrass - timothy - clover pasture lands on Waimakariri shallow soils, between 21/11/70 and 5/12/70, inclusive. Six of the animals were male, and 14 were adult.

(2) Identification of Food Items.

The weight, sex, stage of development, and date of capture of the hedgehogs used for stomach content analyses are listed in Table 8. Stomachs were removed by cutting the oesophagus where it passes through the diaphgram and cutting immediately below the pyloric sphincter muscle of the stomach. The stomach and its contents were weighed. The contents were then removed by dissecting the stomach lengthwise, scraping out the contents with a blunt scalpel, and placing them in a labelled pomade. The empty stomach was then weighed and the weight of its contents calculated by difference.

The usual technique for analysing the contents of stomachs and droppings is to place each sample in alcohol, and then separate the components with mounted needles. It was found that this technique had several major disadvantages. Moistening the samples caused them to become slimy and give off a repulsive odour. This made them very unpleasant to handle. A certain amount of fragmentation of the components inevitably occurred during separation of the small and fragile animal parts from the rather sticky and slimy matrix. The large amount of mucus from the stomach lining made the stomach samples even more difficult and unpleasant to handle than the droppings.

Attempts were made to improve this analytical technique, both to reduce the amount of fragmentation, and if possible to make the samples more pleasant to handle. Use was made of an ultrasonic generator to free animal parts from the matrix, and of a series of six sieves ranging in mesh size from 2 to 0.1 mm to aid their sorting. The sieves did permit much of the stomach mucus to be washed from samples by running water, but their use and that of the ultrasonic generator increased fragmentation without making the analyses significantly more pleasant. These methods were discarded.

It was found that if both stomach and dropping samples were freeze-dried before being placed in a mixture of alcohol and glycerine, the insect parts could be readily separated, with little fragmentation, and the material was odour free and reasonably pleasant to handle. The stomach mucus was reduced to a fine powder which was readily removed from the samples with a bulb pipette. This freeze-drying technique then, both rendered the droppings relatively pleasant to handle, and by loosening the matrix, significantly reduced fragmentation of insect parts. It is claimed that this freeze-drying technique is a major improvement of the method used to analyse the contents of stomachs and droppings.

Labelled samples were stored in a deep freeze. Prior to analysis they were dehydrated in a Cuddon freeze-dryer for 24 hours. The freeze-dried samples were then placed in a white dish, moistened with 70% alcohol and 2% glycerine and the insect and invertebrate parts they contained teased apart under a binocular microscope (magnification 144 times) using mounted needles and fine number three forceps. As complete samples could be analysed it was not necessary to sub-sample.

The intestines of six hedgehogs were analysed as well as the stomachs. The same prey species appeared in both. The quantities found in the stomachs were approximately twice those in the intestines. Fragmentation of food items in the stomachs was less than in the intestines. Thus it was decided to use only stomach contents.

The immense task of identifying the various parts of the many insects and invertebrates was greatly eased by use of the reference collection from the study area. Initially all different parts were placed in separate pomades in 70% alcohol and 2% glycerine, and later compared with the insects and invertebrates in the reference collection. The legs, mouthparts, wings etc. of the most common species were dissected off and used for comparison. Gradually, with experience, an increasing number of parts and species were identified until most were eventually identified. When necessary the help of experienced entomologists was obtained.

To find which parts were most commonly found in identifiable condition in droppings, and to find the relationship between material ingested and that recovered from the droppings, a series of laboratory food recovery experiments was initiated. All recognisable animal parts evacuated in the droppings were counted. From this data diagnostic parts were selected for each prey species. These were defined as those parts which were evacuated in the largest numbers in a relatively undamaged form in the droppings from the food recovery experiments. The numbers of diagnostic parts were divided by the number of parts per animal to give the number of animals represented in the droppings. Each diagnostic structure was counted only if more than half of it was present. These diagnostic parts for the prey species used are listed in Table 9. The foreleg tibiae

TABLE 9.

THE DIAGNOSTIC PARTS OF THE 12 PREY SPECIES USED IN HEDGEHOG FOOD RECOVERY EXPERIMENTS IN THE LABORATORY.

SPECIES	DIAGNOSTIC PART	NUMBER PER ANIMAL
Agriolimax sp.	Radula	1
Porcellio scaber	Telson	1
Wiseana cervinata	Antennae	2
Musca domestica	Forewings	2
Costelytra zealandica	Foreleg Tibiae	2
Allolobophora caliginosa	Setae	8 (per segment)
Megadromus antarcticus	Antennae	2
Laemostenus complanatus	Antennae	2
Forficula auricularia	Forceps	2
Pleioplecton sp.	Anal Cerci	2
Lycosidae	Leg Tibiae	8
Opilio opilio	Leg Tibiae	8

of the grass grub beetles were quite distinct from the tibiae of the other pairs of legs.

(3) Correction for Losses Between Ingestion and Recovery from Droppings.

Because of differential losses between ingestion and recovery from the droppings, the relative proportions of the various prey species, as determined by dropping analyses, may not provide a quantitative measure of the prey species actually consumed. Laboratory food recovery experiments were used to determine the ratio between food input and dropping output for the more important prey species of hedgehogs. Multiplying the data from dropping analyses by the correction factors obtained from these ratios would give a quantitative measure of the food actually consumed. A similar attempt to find correction factors was carried out by Rudge (1968) who fed known combinations of prey species to shrews. Whereas Rudge killed the shrews at intervals and examined the stomach and gut contents, the present author allowed the food to be evacuated as droppings, which were subsequently analysed. These experiments were carried out between 1/10/71 and 30/11/71.

The quantities of the various prey species available meant that only one animal, a healthy, mature male aged between one and two years, could be used for these experiments. When captured on 1/10/71 its weight was 973 grams.

Two cages were necessary for this set of experiments. A glass aquarium tank, 60 x 30 x 30 cm, was used for the actual feeding of the prey species. It was closed by a wooden lid containing two 20 cm square hatches. One hatch was permanently covered with 2 mm wire mesh, which prevented the escape of any food species, but provided ventilation. The second hatch, which allowed access, was covered by a 21 cm square sheet of perspex. The glass floor of this cage was covered with 3 cm of grass turf to provide as natural an environment as possible, and to enable the prey species to hide in available cover. The turf was replaced for each feeding experiment. The second cage used was as described in Chapter 5. Both cages were kept in a controlled-environment room, maintained at a temperature of 21 $\pm$ 2°C, and a relative humidity of 65 $\pm$ 2%. Fluorescent tubes, controlled by a time switch to operate between 6 a.m. and 9 p.m. daily, provided the only lighting.

To accustom the hedgehog to captivity, it was fed a diet of 300 grams of a 1:1:3 volume ratio of cooked mince, bread and milk for nine days. To clear the animal's alimentary canal of food, it was starved on the tenth day and on the eleventh night fed the first of the prey species.

Every second evening, after being starved for one day, the hedgehog was placed in the feeding cage, together with the selected prey species. The following morning the hedgehog was transferred to the second cage. Thereafter the animal was starved and fed on alternate nights. The starvation period was provided to allow all the food consumed during each feeding experiment to pass completely through the alimentary canal. As a further precaution, different prey species were fed to the animal at each successive feed. This ensured that any food from the previous feed would be easily recognised. The starvation period also ensured that the hedgehog was hungry and would consume all the food provided.

Droppings evacuated in both cages, over the two day period of each trial, were collected and analysed. At the conclusion of each food recovery experiment the feeding cage was searched to confirm that all the food presented to the hedgehog had been consumed.

Each of the following major prey species was presented to the hedgehog as 200 live animals: slugs (*Agriolimax* sp.), slaters (*Porcellio scaber*), porina moths (*Wiseana cervinata*), houseflies (*Musca domestica*), grass grub beetles (*Costelytra zealandica*) and earthworms (*Allolobophora caliginosa*).

Houseflies were substituted for dung flies (Sarcophaga milleri), as these latter were not obtainable in sufficient numbers.

Other minor prey species, such as large ground beetles (Megadromus antarcticus), smaller ground beetles (Laemostenus complanatus), earwigs (Forficula auricularia), wetas (Pleioplecton sp.), spiders of the Family Lycosidae and harvestmen (Opilio opilio) , were fed to the hedgehog in smaller numbers, in mixed groups totalling 200 live animals per feed.

The prey species used in the food recovery experiments were obtained as follows: slugs were trapped under sacks laid in the study area; earthworms were dug from the irrigated parts of the study area; porina moths were caught in a mercury vapour light trap and male grass grubs in attractant traps in a garden at Lincoln; houseflies were bred in the Department of Entomology at Lincoln College; and the other species were collected by hand under hedges bounding the study area.

To increase the reliability of the results, each of the major prey species was fed to the hedgehog on three occasions. Two lots of 40 of each major species were also fed to the hedgehog, in combinations with some of the minor species. Each minor species was fed to the hedgehog four times, in two different combinations. From these replicates the average percentage of recovery from the droppings was calculated for each species. As the hedgehog obtained sufficient moisture from its food, water was not provided.

At the completion of these experiments, the animal was fed for four nights on the cooked mince mixture to enable it to regain its former weight. It was then released near its point of capture on 6/12/71.

IV. RESULTS AND DISCUSSION

(1) Food Recovery Experiments.

Descriptions of the droppings produced from the six major prey species in the feeding experiments, and the average number of droppings obtained from each of these species, are given in Table 10.

TABLE 10.

DESCRIPTIONS AND AVERAGE NUMBERS OF DROPPINGS CONTAINING THE SIX MAJOR PREY SPECIES FED TO A HEDGEHOG IN THE LABORATORY.

PREY SPECIES	DROPPING COLOUR	CONSISTENCY	AVERAGE NUMBER OF DROPPINGS
Agriolimax sp.	Greenish-black	Slimy	2.0
Porcellio scaber	Greyish-black	Gritty	1.3
Wiseana cervinata	Brownish-black	Scaly	5.0
Musca domestica	Black	Flaky	2.3
Costelytra zealandica	Brown	Crumbly	5.3
Allolobophora caliginosa	Pinkish-black	Greasy	2.3

The number of prey species presented to the hedgehog and the percentage recovery of the diagnostic parts from the droppings, are given in Table 11. These recovery percentages have been used to calculate correction factors. Multiplying the numbers of the various species recovered from droppings by these correction factors yield the actual numbers that were recovered from droppings by these correction factors yields the actual numbers that were consumed.

TABLE 11.

RELATIONSHIP BETWEEN THE NUMBERS OF VARIOUS PREY SPECIES FED TO A HEDGEHOG IN THE LABORATORY AND THE RECOVERY OF DIAGNOSTIC PARTS FROM ITS DROPPINGS.

	TOTAL NUMBER FED	NUMBER OF DIAGNOSTIC PARTS RECOVERED	PERCENTAGE RECOVERY OF DIAGNOSTIC PARTS	CORRECTION FACTOR
Wiseana cervinata	680	125	18	5.56
Opilio opilio	160	72	45	2.22
Porcellio scaber	680	331	49	2.04
Lycosidae	160	80	50	2.00
Pleioplecton sp.	160	100	63	1.59
Costelytra zealandica	680	477	70	1.43
Musca domestica	680	513	75	1.33
Laemostenus complanatus	120	99	83	1.21
Forficula auricularia	160	140	88	1.14
Megadromus antarcticus	80	72	90	1.11
Agriolimax sp.	680	666	98	1.02

Earthworms could not be counted as individuals since only the setae were recovered from the droppings. Recoveries for the remaining species ranged from 18% for porina moths to 98% for slugs. Slug radulae were easily recognisable in the droppings and usually remained intact, or nearly so. Their extremely high rate of recovery is probably a function of their small size, horny nature and flexibility. The hard, but thin, internal shells were usually crushed into small pieces. The high recoveries of antennae of the ground beetles, forceps of earwigs, cerci of wetas and foreleg tibiae of grass grub beetles were probably related to their relative hardness and small surface areas. The wings of houseflies appear to be relatively indigestible compared with the bodies, and were passed into the droppings in easily recognisable condition.

The telsons of slaters are small and very brittle, and many were crushed into small pieces. The long leg tibiae of spiders and harvestmen were easily broken, and few countable (half or more) units survived. This explains the low recovery rate for these parts.

All parts of porina moths are soft. Their antennae are long and many-segmented, thus the chance of recovering pieces containing 20 or more segments was low. Although the recovery rate of parts for this species was very low, its presence was easily recognised from scales and small fragments of wings, and antennae.

Plates 1 to 6 illustrate the remains of 5 insect species which have passed through the alimentary canal of a hedgehog into the droppings. Where plates are divided by a horizontal line, items shown above this line have been dissected from reference specimens of the insect, while those below the line have been recovered from droppings. Thus, it can be seen that, with practice, these latter parts are readily identifiable, and many are present as comparatively large fragments.

PLATES 1 - 6.

Insect parts as recovered from hedgehog droppings.

(Where plates are divided by a horizontal line, items shown above this line have been dissected from reference specimens).

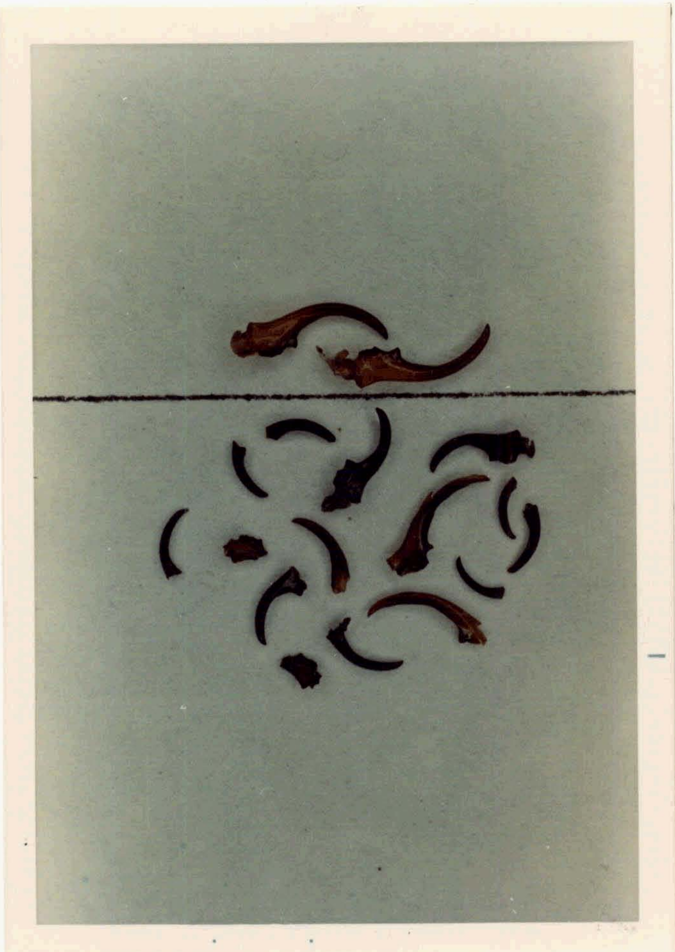


PLATE 1.
Earwig (Forficula auricularia) forceps (Male)
(x4).

PLATE 2.
Earwig (Forficula auricularia) forceps (Female)
(x3).

PLATE 3.

Lepidopteran larvae.

(x5).

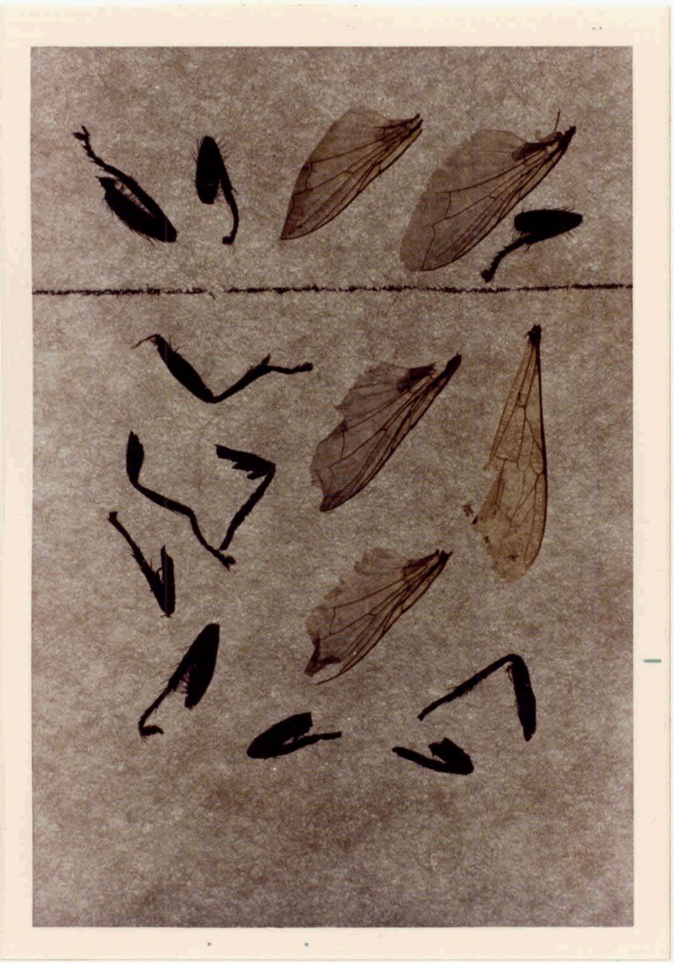


PLATE 4.

Dung fly (Sarcophaga milleri) legs and wings. (Adult).

(Honey bee (Apis mellifera) wing, right centre).

(x6).

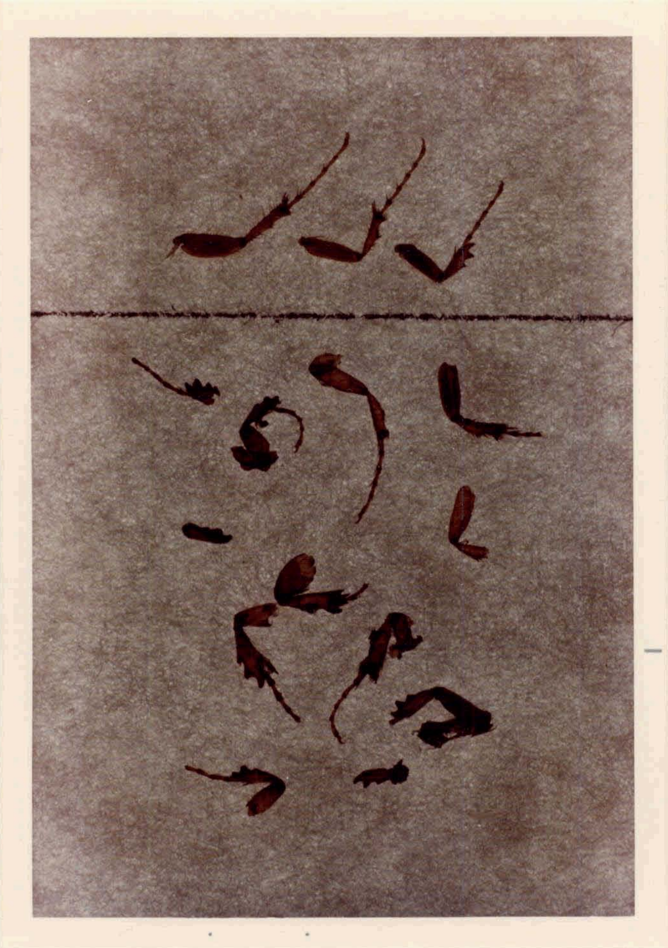


PLATE 5.

Grass grub (Costelytra zealandica) legs. (Adult). (x4).

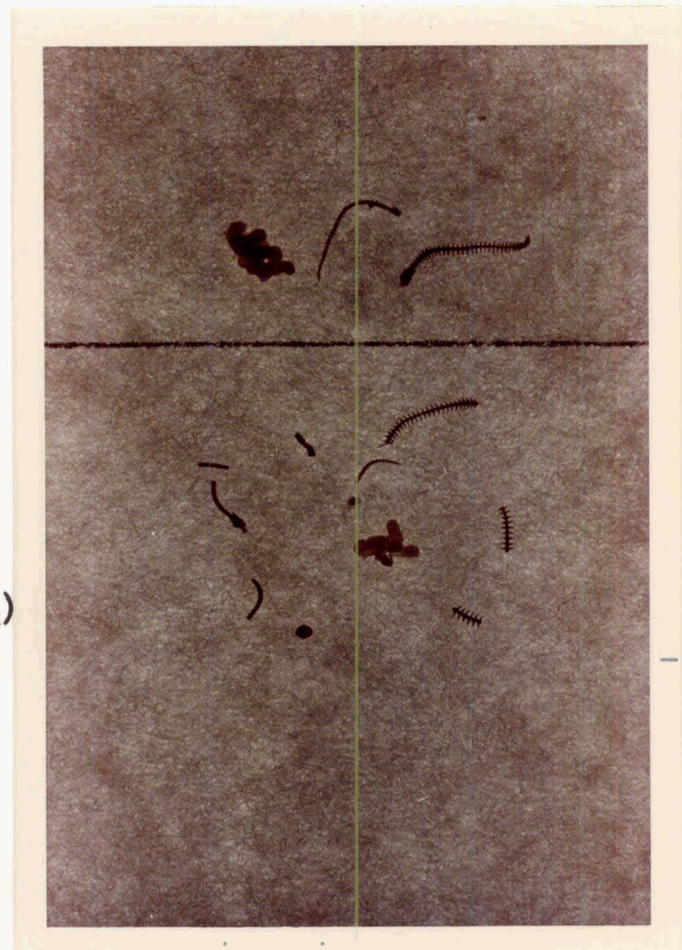


PLATE 6.

Porina moth (Wiseana cervinata) antennae and eggs. (x4).

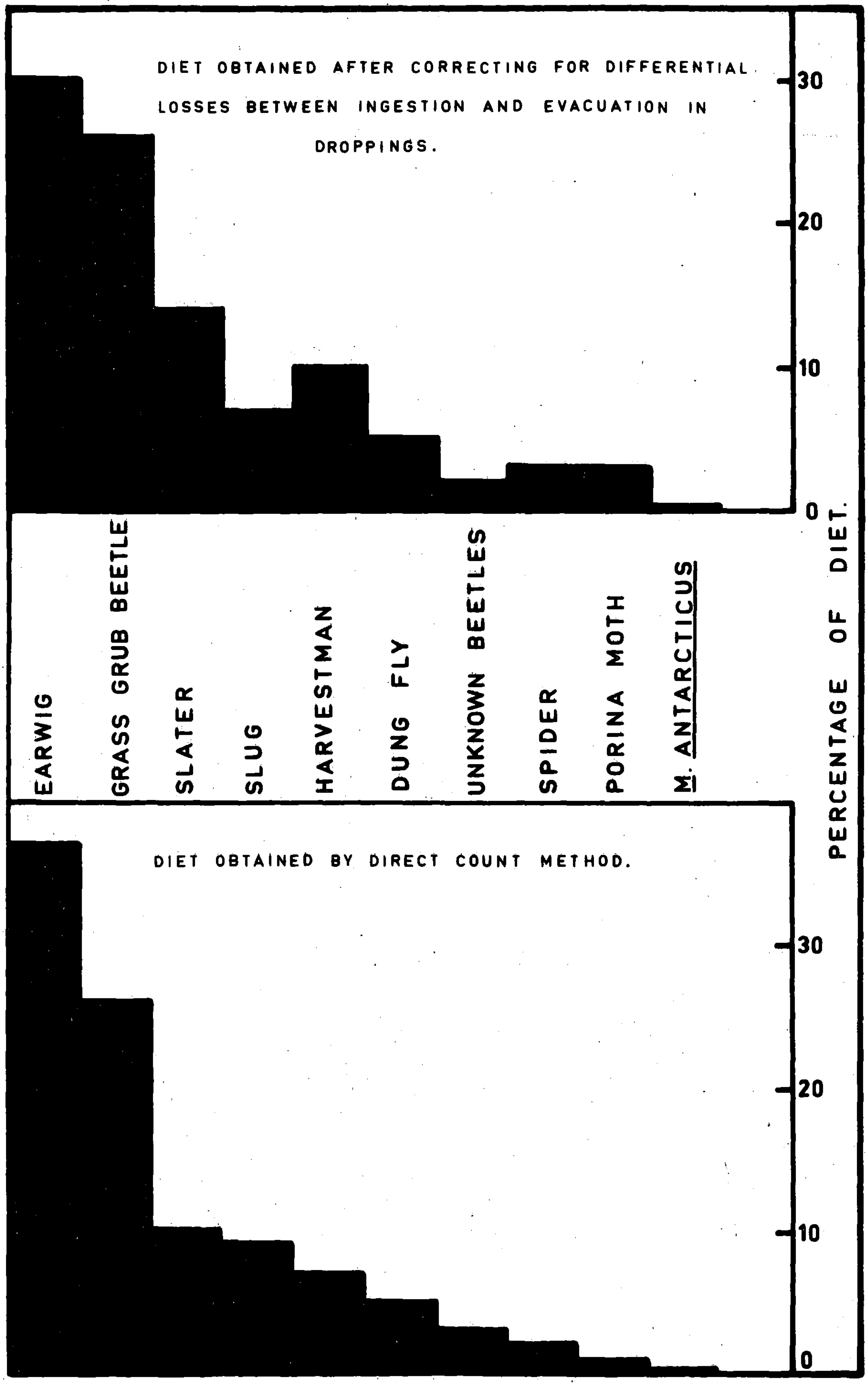
The sex of earwigs may be easily determined by the shape and curvature of the forceps as illustrated in Plates 1 and 2. The wings of flies and other insects can be distinguished by their venation, as shown in Plate 4, and by comparison with a reference collection.

The tibiae of adult grass grub legs are easily identifiable, especially the foreleg tibia, as shown at top right of Plate 5. Male porina moth antennae, as shown at top right of Plate 6, are larger and wider than the female antennae, shown at top centre.

Because of these differential losses between ingestion and evacuation as droppings, uncorrected direct count data would underestimate, and for species like the porina moths seriously underestimate, the numbers of the different prey species that were in fact eaten. Figure 42 shows the effect of applying the correction factors given in Table 11 to the data from the analyses of the 230 droppings collected from the study area (Appendix XVI). Applying these correction factors has decreased the relative importance in the diet of the more resistant species, earwigs, slugs and unknown Coleoptera, and increased the relative importance of slaters, harvestmen, spiders and porina moths, which are of lesser resistance.

The effect that differential losses would have on the reliability of the percentage of diet values obtained from uncorrected direct count data would depend on the nature of the more important diet components. If these species all possessed fairly similar recovery percentages, failure to correct the direct count data would not introduce serious error. However, if porina, or some other species with a much lower recovery than

FIGURE 42. EFFECTS OF APPLYING CORRECTION FACTORS TO DATA FROM ANALYSES OF 230 DROPPINGS COLLECTED FROM PASTURE LANDS.



the remaining species was present as a major diet item, failure to apply correction factors could give a false impression of the diet.

As correction factors were obtained only for the droppings, the numbers for the direct counts of animal food items in the stomachs could not be corrected. The food items from stomachs were less digested, and the values obtained should have been nearer those of the actual quantities eaten than is the case with those obtained from the droppings.

(2) Treatment of Data.

Data from the stomach content and dropping analyses were treated by three different methods.

(a) The occurrence method. The number of samples in which each item occurred was listed as a percentage of the total number of samples. The number of occurrences of all food items was then summed and reduced to a base of 100, enabling the individual food items to be expressed as a percentage composition of diet. This method was rapid and relatively simple to apply, requiring only a careful examination. Individuals did not have to be counted, or subjective assessments made. Use of this method allowed comparisons with the work of Brockie (1958) and Wood (1970).

(b) The relative volume method. In this method allowance was made for both the size and abundance of individual food items. A five point scale, indicating the volume of the identifiable material only of the stomach or dropping occupied by each item was used. This scale was as follows:

1 = <20% of the volume of the sample

2 = 21-40% of the volume of the sample

3 = 41-60% of the volume of the sample

4 = 61-80% of the volume of the sample

5 = 81-100% of the volume of the sample.

Rankings were made on the basis of a subjective assessment by eye. The sum of the points gained by each individual food item expressed as a percentage of the total number of points gained by all items represented its percentage composition of the diet. The advantages of this method were again that it was rapid and relatively easy to apply. The major criticism of the method is that the investigator may be influenced by prejudice in the allocation of points. Where, as in the present work, a large number of samples (290) were analysed over a period of months this possibility is reduced. Use of this method again allowed comparison with data presented by Brockie (1958) and Wood (1970). Rudge (1968) found relative volume estimates misleading.

(c) The direct count method. The number of each animal food item found in every sample were counted. The percentage composition of diet was then obtained by expressing these totals as percentages of the sum of all items found in all samples. The method was both tedious and exacting, as it involved the careful and painstaking separation, identification and counting of the items present in the partly digested food remains.

This method of diet analysis has not been as widely used as the preceding methods, as the inevitable fragmentation of food items caused by ingestion, digestion, and the necessary separation makes their identification and counting difficult.

Rudge (1968) found that fragmentation was too great for direct counts to be obtained from the stomach contents of shrews. The development and use of a freeze-drying technique which reduced fragmentation during separation made it possible to use direct counts in this study.

Most investigators of the diets of mammals are primarily interested in the mammals themselves, rather than in the species that form their diets. Unless care is taken, subjective inaccuracies can occur in the identification of the fragmented remains. The preparation of a reference collection of the species present in the study area, and the concept of diagnostic parts, which could be used for the identification and counting of the various food items, that was developed during the food recovery experiments, reduced these problems in the present study. Application of the correction factors, also obtained from the food recovery experiments, has enabled the numbers of the various prey species actually consumed to be obtained from the dropping analyses.

As only setae survived in the stomach contents and droppings the importance of earthworms in the hedgehog diet could not be determined by this method. With the exception of seeds, it was impossible to obtain absolute numbers for the various plant food items in the samples. Thus use of the direct count method was restricted to the animal foods.

Weight methods, where the weight of the individual food items, or of the total food of each animal are obtained were not used in this study. Because of differential losses following ingestion, caused by varying proportions of soft parts, a percentage of diet based on the weights of separated food items, would not necessarily be proportional to the weights of the various prey species consumed. Should weight data be required for any future comparative study, they could be obtained by multiplying the corrected direct counts by the mean weights of the species concerned, as has been done by Ricker (1937) and Neill (1938). However, it is volume, not weight, which limits the feeding capacity of an animal.

The dominance method was not used for two reasons. In 54% of the samples there was no dominant food item, and of all the prey species eaten, only two, earwigs and grass grub beetles tended to be dominant when present. This method would have shown earwigs as forming nearly half of the diet, and grass grub beetles, although present for less than two months of each year, clearly in second place. Many species, eaten regularly, but in smaller quantities would not appear.

Some workers have attempted to demonstrate seasonal variation in food intake by arbitrary estimation of the fullness of the stomach. As it was intended to compare the result of the stomach content and dropping analyses, this method which could not be applied to the latter was not used.

The results obtained from the 230 droppings collected from the irrigated study area are listed in Appendix XV (occurrence and relative volume) and Appendix XVI (direct count). The results of the stomach content analyses of the 60 hedgehogs captured at both Lincoln and Kaikoura appear in Appendix XVII (occurrence and relative volume) and Appendix XVIII (direct count). A summary of all occurrence and relative volume data is presented in Table 12. In Table 13 data obtained from the dropping analyses are subdivided according to season, while in

TABLE 12.

SUMMARY OF ANALYSES OF 230 HEDGEHOG DROPPINGS FROM IRRIGATED PASTURES, AND THE CONTENTS OF 59 HEDGEHOG STOMACHS FROM NON-IRRIGATED PASTURES. (AS PERCENTAGE COMPOSITION OF DIET).

FOOD ITEM	DROPPINGS		STOMACH CONTENTS			
	LINCOLN (230)		LINCOLN (44)		KAIKOURA (15)	
	OCCURRENCE	RELATIVE VOLUME	OCCURRENCE	RELATIVE VOLUME	OCCURRENCE	RELATIVE VOLUME
GRASS	17	14	12	12	12	10
CLOVER	10	8	2	1	3	2
SEEDS	5	4	6	5	4	3
MISCELLANEOUS PLANTS	3	2	4	3	8	6
DIRT AND GRIT	9	8	6	5	10	8
EARWIGS	10	15	9	12	8	6
LEPIDOPTERAN LARVAE	8	10	9	13	9	8
HARVESTMEN	6	5	7	6	5	5
SARCOPHAGA MILLERI	6	5	2	3	1	1
SLUGS	5	7	5	4	3	3
UNKNOWN COLEOPTERA	4	3	7	6	8	6
EARTHWORMS	4	5	2	1	6	5
SPIDERS	3	2	6	5	7	5
SLATERS	3	3	1	1	1	1
GRASS GRUB BEETLES	3	6	3	3	10	28
HONEY BEES	1	1	4	3	1	1
MEGADROMUS ANTARCTICUS	1	<1	3	3	-	-
ORIBATID MITES	1	<1	2	2	-	-
PORINA MOTHS	<1	<1	2	2	-	-
SALIUS Sp.	<1	<1	-	-	-	-
ODONTRIA STRIATA	<1	<1	3	2	1	1
THRIPS	<1	<1	1	1	-	-
UNKNOWN LARVAE	<1	<1	-	-	-	-
BLOWFLIES	<1	<1	-	-	-	-
WETAS	-	-	1	1	2	1
METAGLYMMA MONILIFER	-	-	2	2	-	-
CENTIPEDES	-	-	<1	<1	1	1
LAEMOSTENUS COMPLANATUS	-	-	<1	<1	1	1

(STOMACH CONTENT DATA FOR SAMPLE S8 HAVE BEEN DELETED. SEE TEXT).

TABLE 13.

ANALYSES OF 230 HEDGEHOG DROPPINGS FROM IRRIGATED PASTURE LANDS ACCORDING TO SEASON. (AS PERCENTAGE COMPOSITION OF DIET).

FOOD ITEM	OCCURRENCE								RELATIVE VOLUME							
	SPRING 1969	SUMMER 1969-70	AUTUMN 1970	WINTER 1970	SPRING 1970	SUMMER 1970-71	AUTUMN 1971	WINTER 1971	SPRING 1969	SUMMER 1969-70	AUTUMN 1970	WINTER 1970	SPRING 1970	SUMMER 1970-71	AUTUMN 1971	WINTER 1971
GRASS	15	14	17	23	19	17	19	20	12	9	14	18	13	17	23	16
CLOVER	5	8	12	16	10	4	10	20	4	5	10	13	7	3	8	16
SEEDS	6	5	4	3	6	4	4	-	5	5	4	3	4	3	5	-
MISCELLANEOUS PLANTS	8	3	1	2	-	-	-	-	6	2	1	2	-	-	-	-
DIRT AND GRIT	10	8	9	11	6	9	8	5	8	5	8	9	4	7	6	5
EARWIGS	11	13	11	6	10	13	8	-	19	20	17	9	7	17	14	-
LEPIDOPTERAN LARVAE	8	9	7	9	3	9	14	11	8	13	8	11	2	13	17	11
HARVESTMEN	<1	8	9	2	1	13	12	-	<1	5	9	2	1	10	9	-
<u>SARCOPHAGA</u> <u>MILLERI</u>	1	5	10	3	1	4	12	-	<1	3	9	2	1	3	9	-
SLUGS	8	-	4	8	7	4	1	37	8	-	6	13	11	5	<1	37
UNKNOWN COLEOPTERA	7	2	2	5	14	6	1	-	5	1	1	2	10	5	1	-
EARTHWORMS	2	2	5	8	3	-	1	16	3	2	6	9	2	-	<1	16
SPIDERS	4	-	3	2	3	2	4	-	3	-	3	2	2	2	3	-
SLATERS	4	8	3	1	6	4	-	-	4	5	3	2	7	3	-	-
GRASS GRUB BEETLES	5	9	-	-	11	6	-	-	11	18	-	-	32	8	-	-
HONEY BEES	2	2	<1	-	-	2	-	-	2	1	<1	-	-	2	-	-
<u>MEGADROMUS</u> <u>ANTARCTICUS</u>	1	3	<1	<1	-	-	-	-	1	2	<1	1	-	-	-	-
ORIBATID MITES	1	-	<1	<1	-	2	1	-	1	-	<1	1	-	2	<1	-
PORINA MOTHS	2	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-
<u>SALIUS</u> Sp.	-	2	<1	-	-	-	2	-	-	1	<1	-	-	-	1	-
<u>ODONTRIA</u> <u>STRIATA</u>	<1	-	<1	<1	-	-	1	-	<1	-	<1	1	-	-	<1	-
THRIPS	<1	-	-	1	-	-	1	-	<1	-	-	1	-	-	<1	-
UNKNOWN LARVAE	<1	-	1	-	-	-	-	-	<1	-	1	-	-	-	-	-
BLOWFLIES	<1	2	-	-	-	-	1	-	<1	1	-	-	-	-	<1	-
NUMBER OF SAMPLES	50	11	74	37	15	8	32	3	50	11	74	37	15	8	32	3

Table 14, data from the stomach content analyses of the hedgehogs captured at Lincoln are subdivided by season, sex and age. The seasons as referred to in Tables 13 and 14 are:

Spring:	September - November
Summer:	December - February
Autumn:	March - May
Winter:	June - August

Items are listed in the same order in all tables to facilitate comparison.

With the exception of hedgehog hair, and a few animal species, each found in only one sample, all materials observed in the samples are included in Appendices XV - XVIII and Tables 12-14. Hedgehog hair was present in 50% of the droppings and 30% of the stomachs. This has been excluded from consideration as it was assumed that it had been ingested accidentally during grooming. The stomach of S8, however, contained only hedgehog hair and blowfly eggs. When captured this animal was feeding on a dead flyblown male hedgehog. This sample has been excluded from the tables. The animal species excluded were aphids, (three species) Argentine stem weevil (*Hyperodes bonariensis*), clover case bearer, (*Coleophora alcyonipennella*), collembola (*Entomobrya nivalis* and *Hypogastrura rossi*), damsel fly (*Xanthocnemis zealandica*) and staphylinids (*Leptacinus* sp. and *Atheta* sp.). With the exception of the damsel fly, these species, because of their small size, were probably ingested accidentally while the hedgehog was catching other prey. Oribatid mites and thrips, although of comparable small size and also probably eaten accidentally, have been included as

TABLE 14.

ANALYSES OF THE STOMACH CONTENTS OF 44 HEDGEHOGS FROM NON-IRRIGATED PASTURE LANDS ACCORDING TO SEASON, SEX AND AGE. (AS PERCENTAGE COMPOSITION OF DIET).

FOOD ITEM	OCCURRENCE						RELATIVE VOLUME					
	SEASON		SEX		AGE		SEASON		SEX		AGE	
	SPRING 1970	SUMMER 1970-71	MALE	FEMALE	ADULT	JUVENILE	SPRING 1970	SUMMER 1970-71	MALE	FEMALE	ADULT	JUVENILE
GRASS	10	13	12	13	12	9	10	14	13	12	13	7
CLOVER	3	1	3	-	2	4	3	1	2	-	1	4
SEEDS	3	7	5	8	6	4	2	6	4	6	5	4
MISCELLANEOUS PLANTS	3	5	4	6	4	4	2	4	3	4	3	4
DIRT AND GRIT	8	4	5	7	5	9	7	4	4	7	5	7
EARWIGS	9	9	10	7	9	9	13	12	15	7	13	7
LEPIDOPTERAN LARVAE	6	10	8	10	9	9	11	15	12	16	12	25
HARVESTMEN	-	10	6	9	7	4	-	9	5	8	6	4
SARCOPHAGA MILLERI	-	3	<1	6	2	-	-	4	<1	7	3	-
SLUGS	6	4	5	5	5	-	8	3	4	6	5	-
UNKNOWN COLEOPTERA	6	7	7	6	7	4	6	6	7	6	6	4
EARTHWORMS	3	1	2	2	2	-	3	1	2	1	2	-
SPIDERS	5	6	7	6	6	9	5	5	5	4	5	7
SLATERS	1	1	1	2	1	-	1	1	1	1	1	-
GRASS GRUB BEETLES	4	2	3	2	3	4	5	2	3	2	3	4
HONEY BEES	3	5	4	5	3	9	2	4	3	4	3	7
MEGADROMUS ANTARCTICUS	3	4	4	3	3	4	2	3	3	3	3	4
ORIBATID MITES	2	2	2	2	2	4	2	2	2	1	2	4
PORINA MOTHS	3	1	2	1	2	4	4	1	3	1	2	4
ODONTRIA STRIATA	5	1	3	2	3	4	5	1	3	1	2	4
THRIPS	3	<1	2	-	1	-	2	<1	2	-	1	-
WETAS	1	1	1	1	1	-	1	1	1	1	1	-
METAGLYMMA MONILIFER	4	-	2	-	1	4	6	-	3	-	2	4
CENTIPEDES	1	-	<1	-	<1	-	1	-	<1	-	<1	-
LAEMOSTENUS COMPLANATUS	1	-	-	1	<1	-	1	-	-	1	<1	-
NUMBER OF SAMPLES	14	30	27	17	40	4	14	30	27	17	40	4

they were found in larger numbers. Dirt and grit were found in 50% of the samples. It is likely that these were also ingested accidentally during feeding, but some may have been consumed deliberately to help grind the food in the stomach.

Plant materials, and dirt and grit account for a substantial part (26-44%) of the undigested residue from the food of hedgehogs (Table 12). It would, therefore, have been unrealistic to have included a summary of the direct count data, which can not assess these materials, in Table 12. To facilitate comparisons of the relative importance of the more important animal foods in the hedgehog diet, as determined by the three methods of data treatment used in the study, only these items are considered in Table 15. The percentage of diet values shown in this table have been calculated on the basis of the total animal foods only.

The hedgehogs obtained from Kaikoura were all captured during the flight season of grass grub. To ascertain if there was any major change in the diet of the hedgehogs in the irrigated study area at this time, droppings collected between 10/11/69 and 11/12/69, and between 2/11/70 and 14/12/70, both inclusive, were considered separately and the results included in Table 15. The dates chosen represented the first and last occurrence of grass grub beetles in the droppings each year.

(3) Comparative Discussion.

The relative importance of the various food items in the hedgehog diet, as determined by the three methods of data treatment used, show some variation. While this is often insignificant, or may result from the limits of experimentation, some major discrepancies are apparent. Such discrepancies

TABLE 15.

RELATIVE IMPORTANCE OF THE MORE IMPORTANT ANIMAL FOOD ITEMS IN HEDGEHOG DIET AS DETERMINED BY DIFFERENT METHODS OF ASSESSMENT. (AS PERCENTAGE COMPOSITION OF DIET).

FOOD ITEM	LINCOLN									KAIKOURA		
	230 DROPPINGS			33 DROPPINGS †			44 STOMACHS			15 STOMACHS		
	OCCURRENCE	REL. VOL.	CORRECTED DIRECT COUNT	OCCURRENCE	REL. VOL.	CORRECTED DIRECT COUNT	OCCURRENCE	REL. VOL.	UNCORRECTED DIRECT COUNT	OCCURRENCE	REL. VOL.	UNCORRECTED DIRECT COUNT
EARWIGS	18	24	25	18	16	11	13	18	28	12	8	1
LEPIDOPTERAN LARVAE	15	15	13*	8	5	3*	13	18	22	15	11	3
HARVESTMEN	11	8	9	6	3	2	10	9	5	8	7	1
SARCOPHAGA MILLERI	10	7	4	2	2	<1	4	4	9	1	1	<1
SLUGS	9	11	6	6	5	2	7	6	3	5	5	<1
UNKNOWN COLEOPTERA	7	5	2	15	9	2	10	9	9	12	8	1
EARTHWORMS	7	7	n.d.	-	-	-	3	2	n.d.	9	7	n.d.
SPIDERS	5	4	2	2	1	<1	9	7	3	11	7	1
SLATERS	5	5	12	7	5	6	2	1	1	1	1	<1
GRASS GRUB BEETLES	4	10	22	25	47	69	4	4	3	16	39	93
HONEY BEES	1	1	<1	2	1	<1	6	5	3	1	1	1
MEGADROMUS ANTARCTICUS	1	<1	<1	2	1	<1	5	4	3	-	-	-
ORIBATID MITES	1	<1	1*	2	1	1*	3	2	2	-	-	-
PORINA MOTHS	1	<1	3	3	2	4	3	3	4	-	-	-
ODONTRIA STRIATA	1	<1	<1	-	-	-	4	3	2	1	1	<1

†: COLLECTED 10/11/69 - 11/12/69 AND 2/11/70 - 14/12/70, BOTH INCLUSIVE.

*: UNCORRECTED

n.d.: NOT DETERMINED

are the result of biases inherent in each of the methods.

In the occurrence method there are only two categories available, an item is ranked as either present or absent. No weight is given to size or abundance. Each occurrence is thus given equal importance. This method overestimates the importance of frequently occurring items that are present in minor amounts. In the present study this has resulted in lower values being obtained by this method for the percentage of hedgehog diet attributed to grass grub beetles, in the 230 droppings collected over a two year period at Lincoln, (Tables 12, 13 and 15) than were obtained by either of the other two methods. When present, grass grub beetles usually formed the major part of the sample (Appendix XVI). As their availability was restricted to the two month flight season, the total number of recorded occurrences was low. If only those droppings collected during periods when they were available, or the Kaikoura stomach contents, are considered (Tables 12 and 15) the relative importance of this species is still underestimated, as the very presence of small numbers of many other species greatly increases the total number of occurrences.

Conversely, grass which exceeded 20% of the content in < 7% of droppings, and yet occurred most frequently (95% of the samples), and clover which never exceeded 20% of content, but was the third most frequently occurring item (Appendix XV), tend to be given more importance by this method (Table 12) than by relative volume.

Although the relative volume method makes allowance for quantity as well as presence it too can be influenced by the frequent occurrence of many minor diet components.

Although this method provides a more realistic estimate of the relative importance of the various food items than does the occurrence method, it still overestimates the importance of minor food items, since items regularly occupying less than 5% of the volume were ranked at half the value of items occupying 21-40% of the same volume. This effect is clearly demonstrated in the stomach content analyses of the Kaikoura hedgehogs, where grass grub beetles are shown to form a much smaller percentage of diet, when the data are treated by relative volume rather than by the direct count method.

Increasing the number of ranked categories beyond five would have reduced the tendency to overestimate minor components, but would have increased the possibility of prejudice in the allocation of rank.

The main disadvantages of the direct count method are that a major diet component (earthworm) could not be determined and that by failing to allow for variations in size it tends to overestimate the importance of the smaller species. Thus the larger species would tend to show lower percentage of diet values when data were treated by this method, than when compared by relative volume. Slugs, which are one of the larger species encountered in this study show lower percentage of diet values by this method than by the others (Table 15).

(4) Plant Materials.

Plant materials formed 21% of the diet of hedgehogs from all three environments (Table 12) when they are compared by the relative volume method. The proportions of plant materials as determined by the occurrence method are in better agreement with those obtained by relative volume for the stomach content samples, than for the droppings. This closer agreement has occurred because larger quantities of grass were found in the stomach contents and because clover was present in a smaller percentage of these samples.

Grasses, dominantly ryegrass, formed the bulk of this plant material, while white clover, seeds and miscellaneous plant remains were present in smaller quantities. The proportions of the different plant materials recovered generally corresponded to those present in the pastures. The seeds found included those of grasses, clover, dock and other weeds. One dropping (number 56) contained over 600 raspberry seeds. These would have been ingested at the Lincoln College dump, which is located behind the plantation and 0.2 km from the western boundary of block B.

Plant materials were a major food item of the hedgehog in the irrigated Lincoln pastures throughout the year (Table 13). The quantity consumed tended to be lowest in summer and highest during the winter months.

As most of the plant materials were passed into the droppings in a relatively undigested form, it is likely that little nutrition was actually gained from them. Some material, however, appeared to be predigested. These predigested materials were more abundant during the late autumn and winter months. It is suspected that they were obtained from cow dung. This conclusion correlates with the observed activities in the field, as during the colder months, when animal foods tended to be scarce, hedgehogs were seen to grub under and turn over cow pats.

Because plant material passed through the alimentary canal in bulk, in a relatively undigested state, all vegetable matter will give very biassed results, when compared with animal material, which was comparatively well digested except for hard parts. Thus plant material will be greatly overestimated in all calculations.

(5) Animal Foods.

All methods of data treatment show earwigs as the most important animal food in the diet of the hedgehog from irrigated Lincoln pastures (Table 15). The occurrence and direct count methods show lepidopteran larvae clearly in second place, but the direct count method ranks grass grub beetles second. The lepidopteran larvae were mainly noctuids, and hepialids, with a few representatives of other families. The analyses of the 33 droppings collected during the grass grub flight seasons, show that at these times, this species is the dominant food item in the diet. Its seasonal appearance is also apparent from Table 13. Large numbers were consumed during these periods and most droppings were more than half full of the beetles (Appendix XV). It is possible that when these beetles are flying, hedgehogs gorge themselves on this abundant, preferred, and easily captured prey. It was not possible to determine the sex of the beetle remains as $<$ 50% of the male genitalia survived during the food recovery experiments. However, both sexes were observed on the ground at night and both were available to the hedgehogs.

The more important of the remaining food items (listed in decreasing percentage of diet as determined by relative volume) were slugs, harvestmen, earthworms, Sarcophaga milleri, slaters, unknown Coleoptera, and spiders (Table 15). None of the remaining species exceeded 1% of the diet. These minor species were honey bees, Megadromus antarcticus, porina moths, Odontria striata, Oribatid mites, Salius sp., thrips, unknown larvae and blowflies. The honey bees were probably moribund workers, as these bees seldom fly at night, and no hives were located in, or near to, the study area. The unidentified beetles were mostly from the Family Carabidae, with small numbers of Scarabaeidae, Tenebrionidae and Curculionidae. The unidentified larvae included wireworm larvae and dipterous larvae such as tipulids, muscids and tachinids.

With the exception of grass grub beetles, the dominant food item during their flight season (Table 15), most of the major animal food items were consumed throughout the year (Table 13). The generally lower values for animal foods during the winter of 1970 (winter 1971 contains insufficient samples for reliable conclusions) are a consequence of the higher intake of plant materials at that time (Table 13). Earwigs are of lesser importance during the winter, and harvestmen during the winter and spring. Species which increase in importance during particular seasons are dung flies (autumn), earthworms (winter), slugs (winter and spring) and unknown Coleoptera (spring). The increased consumption of earthworms and slugs during the colder months is probably a consequence of the lower availability of insect species at this time. When allowance is made for their low recovery rate in droppings (Table 11), porina moths became a relatively important food item during the spring (Table 13). Porina eggs are rendered inviable by the digestive juices of hedgehogs. The white eggs show up very clearly in the droppings. This shows that gravid females are eaten by the hedgehogs. Lepidopteran larvae remain a major diet constituent throughout the year.

Earwigs and lepidopteran larvae were also the animal species making the greatest contribution to the diet of hedgehogs in the non-irrigated pastures at Lincoln (Tables 12,14 and 15). Beetles (unknown Coleoptera and Megadromus antarcticus), and spiders were more important in the diet, and dung flies, earthworms, slaters and slugs less important, as compared with hedgehogs from the irrigated pastures. The higher ranking of earthworms and slugs in the diet of hedgehogs from the irrigated pastures is probably a function of their greater availability in those areas caused by the use of irrigation. This use of irrigation might also explain the failure to locate grass grubs in the soil samples from the irrigated area. The higher ranking of dung flies in samples from the irrigated area, is a function of the more intensive grazing that occurred in that area. This inevitably resulted in the availability of greater quantities of cow dung.

Species found only in stomach content samples from the non-irrigated area were centipedes, Laemostenus complanatus, Metaglymma monilifer and wetas, whereas blowflies, Salius sp. and unknown larvae were obtained only from the droppings from the irrigated area. Of these, only the beetle species Metaglymma monilifer exceeded 1% of the diet (Table 12).

The diets of the male and female hedgehogs from the non-irrigated Lincoln pastures were essentially similar (Table 14). Earwigs were, however, more important in the male diet, and dung flies and harvestmen in the female. The number of juveniles captured (4) was insufficient to allow any valid comparison between their diet and that of adults (Table 14).

Species which formed a more important part of the diet of these animals during the spring were earthworms, Metaglymma monilifer, Odontria striata, porina and slugs, while dung flies and harvestmen were more important during the summer. These were the only seasons for which samples were available. The variations observed for dung flies, earthworms, harvestmen, porina and slugs were similar to those in the irrigated pastures. Metaglymma monilifer and Odontria striata, were both important animal foods in the diet of hedgehogs from the non-irrigated pastures during the spring (Table 14). The former was never observed in droppings from the irrigated pastures, while the latter never exceeded 1% of the diet.

Grass grub beetles are the dominant animal food item in the diet of the hedgehogs from Kaikoura (Tables 12 and 15). This is a consequence of those samples being obtained during their flight season. The maximum number of these beetles observed in any stomach was 284. Seven of the 15 stomachs examined contained an excess of 100 beetles. Other species important in the diet of these animals (listed in order of decreasing percentage of diet) were lepidopteran larvae, earwigs, unknown Coleoptera, earthworms, harvestmen and spiders. The number of samples obtained was too small to allow subdivision on the basis of age or sex.

Although small prey species, such as Argentine stem weevils, Oribatid mites, aphids, thrips and collembola, were extremely numerous in both irrigated and non-irrigated areas, these were not deliberately eaten by hedgehogs. The size of food items eaten by hedgehogs in Lincoln pastures ranged from a minimum of the larger species of the Genus Salius (0.8 cm) and small slaters (1 cm) to a maximum of <u>Megadromus antarcticus</u> (3 cm) and large earthworms (12 cm). However, Brockie (1957) showed that frogs were a preferred prey species in the sand dunes of the West Coast of the Wellington Province, and Otway (1965) found that pheasant and bantam eggs (5 cm x 3.5 cm) were favoured. It seems therefore that the lower size limit in the range of foods eaten by hedgehogs is determined by the nutrient value of the prey species, while the upper limit is set by the gape of the hedgehog's jaw.

(6) <u>Correlation With Other Work</u>.

Brockie (1958) and Wood (1970) have investigated the diet of hedgehogs in pasture lands within New Zealand. The former analysed droppings collected from areas in the Wellington province, and the latter, the stomach contents of animals captured near Christchurch. Both assessed their data by occurrence and by relative volume methods, but the resulting values were not scaled to yield percentage composition of diet. This scaling was carried out (Table 16) to facilitate comparisons with the results obtained in the present study (Table 12).

Little information is provided by either Brockie (1958) or Wood (1970) on the nature of the pastures from which they obtained their samples. Both obtained a total of 10 samples collected, in each case, from six separate locations. It appears likely that most of the animals captured by Wood were observed on the verges of country roads.

The quantity of plant material in the hedgehog diet, as separated by Wood (1970), is comparable to that obtained in the present study, while that found by Brockie (1958) was

TABLE 16.

DIET OF HEDGEHOGS IN PASTURES AS FOUND BY BROCKIE (1958) AND WOOD (1970).
(AS PERCENTAGE COMPOSITION OF DIET).

FOOD ITEM	BROCKIE		WOOD	
	OCCURRENCE	RELATIVE VOLUME	OCCURRENCE	RELATIVE VOLUME
GRASS	7	5	20	20
CLOVER	-	-	4	2
SEEDS	4	2	4	2
MISCELLANEOUS PLANTS	4	4	4	2
EARWIGS	7	4	8	6
LEPIDOPTERAN LARVAE	20	32	12	17
FLIES	4	2	6	6
SLUGS	11	8	8	11
UNKNOWN COLEOPTERA	13	7	2	2
EARTHWORMS	-	-	10	17
SPIDERS	7	5	4	2
SLATERS	-	-	4	4
ORIBATID MITES	2	1	-	-
MOTHS	2	6	-	-
UNKNOWN LARVAE	6	8	-	-
WETAS	-	-	2	2
CENTIPEDES	-	-	2	1
COLLEMBOLA	-	-	4	2
WEEVILS	-	-	2	1
MILLIPEDES	2	2	-	-
*SNAILS	4	6	-	-
*APHIDS	-	-	2	1
*ANTS	4	2	-	-
NUMBER OF SAMPLES	10		10	

* NOT OBSERVED IN PRESENT STUDY.

approximately half. The major animal foods found in the present study correlate reasonably well with those reported by both Brockie (1958) and Wood (1970). Some differences, and changes in ranking occur, and these are probably due to variations in the availabilities of the species involved, and to some extent, to the small number of samples analysed by both Brockie and Wood. Neither of these workers records harvestmen, and Brockie did not record earthworms. Lepidopteran larvae were ranked as the most important animal food by both Brockie and Wood, and both ranked earwigs lower than in the present study. Ants, snails and millipedes, which together provided 10% of the diet in the droppings analysed by Brockie (1958) were not observed in any samples from the present study or in those from Wood (1970). No snails or ants were found in any of the collections from the pitfall traps in either the irrigated, or non-irrigated study areas at Lincoln. Two species of millipedes were present in the study area, but as these differed from those reported by Brockie (1958) they may have been less palatable to hedgehogs. Alternatively, more abundant, more palatable, or easier captured prey may have been available at Lincoln. Wood (1970) did not find any evidence of millipedes in the diet of hedgehogs. From food choice experiments he concluded that they were not a preferred item. The only animal food reported by Wood (1970) that was not found in the present study was aphids.

V. SUMMARY AND CONCLUSIONS

(1) General Aspects.

The colours and consistencies of droppings were found to vary with the prey species consumed. It is therefore possible from macroscopic examination to roughly determine the main prey species present in droppings. Porina eggs and grass grub beetles are easily identifiable in this way.

The freeze-drying technique developed in this study is a major improvement in the methodology of dropping and stomach content analyses. Its major advantages are that there is a considerable reduction in the breakage of delicate parts while separating them from the matrix, and that the samples are rendered reasonably pleasant to handle. As far as the author can determine freeze-drying of such samples has not previously been used.

Although only a limited number of replicates was used in the food recovery experiments, the results obtained do give a reasonable estimate of the recovery percentages of different insect and invertebrate parts separated from the droppings of hedgehogs. These estimates were used to obtain correction factors that enabled the food consumed by hedgehogs in the field to be assessed more reliably from analyses of their droppings.

Plant materials, especially grass, were important, but overestimated, items in the diet of hedgehogs, and the quantities consumed were greatest in winter. It seems that little nutrition was actually gained from these materials, as most passed relatively undigested into the droppings. Although some grass may have been ingested accidentally, the occurrences were too consistent and frequent to be entirely accidental. Grass may have a medicinal function for hedgehogs, as does that eaten by cats and dogs, or it may be eaten as a stomach-filler.

The animal foods consumed by the hedgehogs in the irrigated and non-irrigated pastures at Lincoln were essentially similar. Earwigs and lepidopteran larvae were the most important items in both areas. Other important animal foods were beetles (especially grass grub), dung flies, earthworms, harvestmen, slaters, slugs and spiders. Remaining animal foods formed a relatively small part of the diet. During their flight season grass grub beetles were the dominant animal food item. Porina moths were also a relatively important item at such times. With the exception of changes caused by the appearance of these seasonal species, only minor variations occurred in the diet of the hedgehogs during the year. Similarly difference in sex caused little variation in their diet. This essential similarity between the analyses from the irrigated and non-irrigated pastures indicates that the irrigation played little part in determining the diet of the animals, other than possible differences in searching time and relative abundance of some species at specific times of the year. The dominance of grass grub beetles in the diet of the Kaikoura hedgehogs, was a function of all these samples being collected during the grass grub flight season.

The results obtained in the present work agree reasonably well with those of Brockie (1958) and Wood (1970).

(2) Economic Aspects.

Two of the major pasture pests in New Zealand are grass grub and porina. As hedgehogs are capable of destroying considerable numbers of these pasture pests, they may exert slight pressure on their populations.

During the grass grub flight season hedgehogs tend to eat this species almost exclusively. One of the hedgehogs captured at Kaikoura (S57) contained 284 grass grub beetles in its stomach and 140 in its intestine. This animal was captured at 10.30 p.m., and would presumably have eaten more than 424 grass grubs during the night had it escaped capture. The percentage recovery of grass grub beetles from droppings is 70% (Table 11); the recovery from stomach and intestine contents may be greater. Other Kaikoura hedgehogs, caught during the grass grub flight season, also contained large numbers of these beetles in their stomachs (Appendix XVIII). It was assumed from these values that a hedgehog has the potential ability to consume more than 424 grass grubs in a single night.

East (1972), in the only quantitative study on grass grub predation to date in the Canterbury area, found that starlings helped to control grass grub populations in irrigated local areas, such as at Winchmore, but found that hedgehogs were not important. He estimated the grass grub population of a non-irrigated four year, clover-ryegrass pasture on Templeton silt loam within 2 km of the present irrigated study area at 100 - 400 adults/m^2. This represents an adult grass grub populations of 1-4 x 10^6/ha. He also reported that the populations in irrigated pastures could reach twice this level. East (1972) also calculated a potential daily consumption of

850 adult grass grubs per hedgehog per day. If it is assumed that the value of 8 hedgehogs/ha found in irrigated pastures in the present study is representative of their potential density in pasture lands during late spring and summer months, and that each hedgehog could eat as many as 850 adult grass grubs per day over an estimated two months flight season, they would have the potential to destroy 5-40% of the adult population. The actual destruction caused by hedgehogs will, however, be considerably less than these potential values, due to the presence of alternative foods and fluctuations in beetle populations during these periods.

In an irrigated ryegrass, browntop, white clover pasture at Winchmore, Mid Canterbury, East (1972) found that, over a two year period, the average number of eggs laid per female grass grub beetle was 25.5 and the constant mortality rate of the species in this pasture 92.2%. The corresponding figures for Lincoln non-irrigated pastures were 22.7 and 91.2%, with a total generation mortality rate of 75.7%.

Regulation of a pest species occurs when variable mortalities, added to the more constant blocks of mortality, cause generation mortality to fluctuate around the constant mortality rate. From the point of view of a farmer control means reduction of a pest population below the level where it causes significant damage. This does not necessarily imply regulation. If the total generation mortality of a species exceeds the constant mortality rate the population will decrease, while a total generation mortality rate which is less than the constant mortality rate will enable the population to increase.

It is difficult here to compare directly the work of East (1972) with that of the present study, as East found no hedgehogs in his irrigated Winchmore pastures, and few grass grubs were found in the present irrigated study area. However, it is possible to hypothesize on a situation where both were present. In the case of East's (1972) irrigated Winchmore area he found that a combination of mortality factors such as irrigation, high stocking rates, and intelligent management, together with density dependent starling predation of third instar larvae, gave effective biological control (East and Pottinger, 1972). If contemporaneous hedgehog predation on adult beetles is added, a more effective biological control could be achieved, and could regulate the population and determine whether upward or downward trends occurred in such a population. In this case hedgehogs would help achieve control.

East (1972) suggests that since hedgehogs are active while grass grub beetles are present in large numbers at an approximately equal sex ratio on the pasture surface, these nocturnal insectivores could have a significant effect on grass grub population by destroying females before they can lay eggs. Those females which escape predation lay about 70% of their eggs in the first cluster, then fly to "feed" trees, and after feeding, make dispersal flights to neighbouring areas to start new populations in new pastures with the remaining 30% of their eggs. If hedgehogs destroy these females before their remaining eggs are laid, they would hinder the establishment of new populations. It takes a grass grub population three or four years to build up to a level where it can damage pasture (R.P. Pottinger, pers. comm.) and six to seven years to reach a maximum epidemic level.

The hedgehog alone can not be claimed to exert any measure of control on pest species. However, it can be claimed that it is a beneficial predator.

Many of the lepidopteran larvae eaten by hedgehogs were almost certainly porina. Species identification of these larvae was difficult, as most head capsules were missing. However, the size and general body features were similar to those of porina larvae. Adult porina, and in particular gravid females, were also eaten, and the recorded percentages of these in the diet of hedgehogs (Tables 12-15) are probably underestimated because of the very low recovery percentage for porina moth parts (Table 11). Again hedgehogs can not be claimed to exert any measure of control on this pest species. Hedgehogs do not appear to deliberately eat Argentine stem weevils, a pest species which forms a major item of the diet of Starlings (East, 1972). However, they do eat many species of beetles, and other invertebrates, some of which are pastures pest species, such as wireworm. This ability to destroy large numbers of pasture pests makes the hedgehog a beneficial animal in pastures.

Balanced against these beneficial effects should be the following disadvantages. The hedgehog carries many diseases, the best known of which is ringworm. However, the incidence of this disease is very low in New Zealand, and only about 5% of all clinical cases caused by dermatophytes, in the Auckland area, between 1958 and November 1962, were caused by the hedgehog ringworm (English et al., 1964). The incidences of other diseases carried by hedgehogs are even lower. Few people come into actual contact with hedgehogs, and normal personal hygiene should prevent many of these diseases. The benefits from its destruction of pasture pests far outweigh these disadvantages.

Hedgehogs have often been accused of eating the eggs and young of chickens and ground-nesting birds. While this does happen, recorded instances are rare, and evidence is often circumstantial (Bull, 1940; Shout, 1954 and Axell, 1956). Knight (1962) and Otway (1965) found that the gape of a hedgehog's mouth was too small to enable it to eat fowl eggs. During the present study no egg shell was found in any hedgehog droppings or stomachs. That egg shell was always present in the droppings of any hedgehog which had eaten eggs in the laboratory was shown by Kruuk (1964) and Otway (1965) and confirmed during the present study. Further, several larks' nests, and two ducks' nests, were left completely undisturbed in the study area. The only lark's nest in the study area which was disturbed during this investigation had two of four eggs disappear completely. As an animal predator would probably have left some sign of its presence, and have taken all four eggs, it is at least possible that the two eggs were removed by a human predator. The small number of birds or eggs taken by a few hedgehogs in New Zealand are insignificant, compared with the beneficial effects of hedgehogs. Hedgehogs have been observed to eat dead birds on roads, and they are often killed near road corpses, which they have presumable been eating.

Hedgehogs have also been accused of milking cows, and of stealing fruit by impaling it on their spines. These accusations have been widely discussed in much popular British literature, but the most comprehensive account is given by Burton (1969), who has come to the conclusion that at best the accusations are unproven.

My general conclusions are, therefore, that although the hedgehog is not yet recognised as an economically significant animal it is far more beneficial than harmful, and as such should be left unmolested. Its destruction, as carried out in some farming districts, is rather pointless, as a high hedgehog population would assist in the destruction of grass grub and other pasture pests.

One qualification should be added to this conclusion. Hedgehogs can carry and transmit foot-and-mouth disease. Although this disease is often fatal to the hedgehog (McLauchlan and Henderson, 1947), those that recover may carry the disease for long periods. Any hedgehogs that contract the disease immediately before hibernation, may develop clinical foot-and-mouth disease on emergence. Should foot-and-mouth disease ever gain entry to New Zealand, hedgehogs could, by becoming a reservoir of infection, assist its spread and hinder its eradiction. Under these circumstances, the effect of the hedgehog on the economy of New Zealand could change significantly.

CHAPTER VIII

GENERAL DISCUSSION

I. INTRODUCTION

The primary objective of this study was to investigate the feeding behaviour of the European hedgehog (Erinaceus europaeus L.) in a pastoral environment. Because the use of irrigation is increasing in Canterbury it was intended to compare the population densities and feeding behaviour of hedgehogs between irrigated and non-irrigated pastures on comparable soil types. Changes in paddock utilisation by the farm manager concerned meant that the first part of the objective could not be accomplished, but modification of the study did permit a valid comparison of the diets of animals from the two areas. Animals were also fed under laboratory conditions to ascertain if this caused any changes in their feeding behaviour, and to determine the recovery rate of diagnostic parts of prey species.

It was not intended at this stage to investigate the changes in population density or feeding behaviour that would occur in a hedgehog population as a result of changes in the available food supply or cover, caused by ploughing or any other normal farming operations. Such a study can be accomplished more effectively once behavioural patterns in stable environments have been established.

II. CHOICE OF SUITABLE STUDY AREAS

The nature of the field study imposed restrictions on the management of the areas involved. It was essential that they would remain in pasture for the duration of the study, and that pasture growth could be controlled, both to maintain a suitable habitat and to allow accurate observation of hedgehog behaviour. These restrictions, and the inconvenience caused by using stakes to mark plots in the paddocks were the major factors involved in the decision to locate the study on areas controlled by Lincoln College. Preliminary observations and discussions with the farm managers had indicated that suitable irrigated and non-irrigated areas, with soil and pasture types representative of much of the pasture land of the Canterbury Plains, were available.

III. POPULATION DENSITY IN AN IRRIGATED PASTURE

Apart from this thesis, an 18 month study by Parkes (1972) and current work by Brockie (pers. comm.) no systematic attempts have been made to determine the population density of hedgehogs in natural habitats.

There is considerable controversy as to the best method of estimating an animal population in a given situation. Because hedgehog droppings were relatively easy to find in the study area, and because their use was consistent with the aim of minimum interference, an estimate based on dropping counts was attempted. However, estimates obtained by this method give no information on the composition of the population. The population estimates obtained from dropping counts were usually less than half the number of animals actually seen during spotlight searches. Reasons for this discrepancy were listed in

Chapter 4. The formula used to calculate the population assumed that the animals were active only in the study area, and that they were active each night. Each animal was therefore assumed to deposit an average of 22.4 droppings per week in the study area. However, allowance should be made for observations that hedgehogs invariably defecated in the vicinity of their nests on first emerging each night (Otway, 1965 and Brockie, pers. comm.) and that they were present in the study area for an average of only 3.3 of the eight hours that they were active each night. If hedgehogs defecated randomly throughout their period of activity a more realistic value would be 6.3 droppings per animal per week. Using this value, together with the sum of the droppings collected throughout the one year study period, a value of 45 was obtained for the mean annual population. This estimate corresponded with the winter minimum of 35 and the summer maximum of 64 obtained by capture-recapture methods. These values corresponded to population densities of 4.4 and 8.0 animals per hectare respectively. All values excluded nestlings.

Only one other estimate of the population density of hedgehogs in pastures has been completed. Parkes (1972) reported that two animals per hectare were present in an area in the Manawatu containing 12.5 ha of pasture and 3.8 ha of pine plantations. To date all hedgehog population studies have used spotlighting and/or radios. The capture-recapture method used in the present study involved locating hedgehogs by spotlight searches, and fixing their positions in relation to a grid of marked pegs, that was equivalent to a trapping grid. This method subjected the animals to considerably less interference than occurs with live trapping and avoided the problems associated with trap-prone and trap-shy animals. Searching was carried out during the period of maximum hedgehog activity.

Other advantages of using spotlighting to locate hedgehogs were that it was both rapid and effective in grazed pasture and needed only equipment which was cheap, reliable and readily operated by a lone observer. The chances of animals escaping detection by being in boundary hedges when the observer passed, or by crossing from unsearched to searched areas, in front of or behind the observer, could be reduced to an insignificant level by using an overlapping search pattern that permitted rechecking of searched areas.

The main disadvantages of the technique were the weight of the accumulators that had to be carried, and the difficulty of locating and tracking animals where pasture growth was uncontrolled. This latter difficulty may have resulted in the population being underestimated during periods of excessive pasture growth, and limited all-night observations to those occasions when pasture growth was such that the study area could be accurately checked within an hour. It also resulted in failure to track animals to their nests. Brockie's technique of locating nests by holding animals captive until daylight, and then releasing them (pers. comm.) had it been known at the time, would have eliminated the most serious of these failings without the need to use more sophisticated tracking equipment. Provided animals were not subjected to this disturbance more than was necessary to permit the estimation of the period of use of individual nests it is likely that this technique would cause less interference to a population than fitting the individuals with radio transmitters.

Use of radio transmitters, however, was the only method that would have allowed animals to be tracked under all conditions. Radiolocation has reached the degree of sophistication where the movements of radio-tagged animals have been plotted on maps, by computers, fed data from automatic scanners placed in fixed towers (Tester and Siniff, 1965; Mech, Tester and Warner, 1966 and Mech, 1967). Such projects, however, involved multidisciplinary teams of workers and considerable budgets, and were primarily concerned with refining radiolocation techniques. For a study where the feeding behaviour of an animal of minor economic significance was the primary aim, a system that was relatively cheap and simple to operate was all that could be justified.

Unless pasture growth was excessive it would be quicker and simpler to locate hedgehogs by spotlighting than by radiolocation. If animals established as resident within the study area were fitted with transmitters similar to those developed by Cockran and Lord (1963) the position of any resident not found by spotlighting could than be determined by subsequent radiotracking. This dual approach would also minimise the chance of animals with malfunctioning radios being overlooked. Nests could be located during daylight by radio-tracking. Hourly all-night spotlight searches could be augmented by regularly following selected animals throughout the night. A study organised in this manner would permit a more comprehensive population census, including determination of births, deaths, immigration and emigration, and would enable home ranges to be mapped.

Marking the animals in the population by spine clipping and spraying different areas of the back with aluminium paint was simple and effective, and caused no interference to the animals since they were readily identified from a distance of a few metres. The markings lasted more than 12 months and could be renewed when necessary. The aluminium paint also acted as a reflector. Although use of permanent markers such as eartags would have permitted identification of the mummified remains found in hay barns, animals could not have been identified in the field without handling if eartags alone were used. In retrospect, the ideal marking system would have been a combination of a permanent marker and that used.

The capture-recapture data was analysed by Jolly's (1965) stochastic model. This general model which was designed to fit the majority of capture-recapture problems involving an area within which the individuals of a population were free to move and mix with each other, was applicable to the present study. Jolly (1965) shows that the stochastic solution to capture-recapture problems is actually simpler than the deterministic. Since less realistic deterministic assumptions were originally introduced into capture-recapture problems in an attempt to simplify the theory, he concluded that they should no longer be retained, and that for capture-recapture problems, in general, purely deterministic models should be abandoned in favour of stochastic models. The basic assumptions of Jolly's model, that marked animals were individually recognisable, that all emigration was permanent, and that there was no back and forth migration were met. Jolly's (1965) model also had the advantages that it permitted grouping of data, which compensated in part for the comparatively small number of animals in the population and it was available as a computer programme (White, 1971 a and b). Because of the small number of animals involved population estimates would contain large uncertainties what ever model of data analysis was used.

After allowing for the differing areas involved a comparison of the relative numbers of animals observed in the irrigated and non-irrigated areas during the population and diet studies suggested that the former areas carried the higher population. The greater numbers of earthworms, slugs and subterranean larvae, all important food items in the diet of hedgehogs found in the irrigated area could account for this larger population. It follows, therefore, that home ranges of hedgehogs in the irrigated study area are probably smaller than those of animals in comparable, but non-irrigated areas.

IV. HOME RANGE AND MOVEMENT

Failure to locate nesting sites meant that the estimates of home range obtained in this thesis are incomplete. The 'home ranges' described (Figures 5-24) must be considered as minimum feeding ranges. The all-night count data, which showed that each animal resident in the study area, was present in that area for an average of only 3.3 hours per night, also confirmed that these feeding ranges were part of a larger home range.

The high degree of correlation between the size of the 'home range' and the number of captures showed that insufficient captures were made to obtain the full home range of any animal. More captures would have been necessary for a plot of size against number of captures to reach the asymptote proposed by

Haugen (1942) and Stickel (1954).

As the 'home ranges' obtained were known to be incomplete, it was considered that little advantage was to be gained by presenting them as other than simple convex polygons. The 'home ranges' were also represented as circles having the same areas as the convex polygons to allow ready visual comparison of their respective areas. The areas of the complete home ranges would be considerably larger.

Although the hedgehog home ranges as determined were incomplete, this study has provided some of the most detailed information yet available. Herter (1938) marked only four animals, and claimed merely that the home range was "small", yet one of the animals was recaptured a year later 3 km from its point of release. Kruuk (1964) reports only that hedgehogs resident in an area of open sand country made trips of several kilometres. Kruuk (cited by Morris, 1969) indicated that the longest distance observed was 4 km. Kruuk also marked and released 15 hedgehogs but recaptured none. Morris (1969) attempted to define hedgehog home ranges in parkland by radio-tracking individuals, but the method proved unsatisfactory. He reports that several animals retired immediately to their nests or soon escaped from their radio-harness. Morris (1969) fails to indicate whether the radios were fitted immediately before the attempts at tracking, or at some earlier time to allow the animals to become accustomed to them before recording their movements. As the animals' natural movements were likely to be upset, at least initially, by the addition of transmitters, a conditioning period should have been allowed. The reported behaviour would seem to suggest that this was not done. Morris (1969) provided all-night tracking information on only three animals. Two of these were followed on a single night, and the third over four consecutive nights. Morris himself realised that tracking for longer periods at different times of the year was required, and the only estimate he made was that in summer the animals could probably find sufficient food in a 300 m course of careful searching. The greatest distance between capture points for any resident hedgehog in the present study was 340 m.

Parkes (1972) estimated the home ranges of hedgehogs in a non-irrigated area of pasture and pine plantation by the minimum convex polygon method. He reported values of 3.7 hectares for 10 females sighted an average of 11.8 times and 2.7 hectares for four males sighted an average of 5.8 times. These values were greater than those obtained in the present irrigated study area, where the average number of captures was 21.4. The higher values obtained by Parkes (1972) were probably a function of the lower availability of food in a non-irrigated area. It is likely that the lower value he obtained for the home range of males was a function of a lower number of sightings. The topography of the area in which Parkes' study was located led to the animals utilising elongated home ranges which were oriented in a common direction. In most instances the individual nesting sites were located in a small pine plantation included within the home ranges. These circumstances enabled Parkes to calculate complete, and hence more realistic home range areas by the probability elipse method of Jennarich and Turner (1969). For the females and males discussed above he obtained values of 12.9 and 7.0

hectares respectively. As in the present study Parkes found that the individual home ranges overlapped considerably.

V. LABORATORY FEEDING BEHAVIOUR EXPERIMENTS

These experiments showed that captive hedgehogs, fed under laboratory conditions, exhibited a feeding rhythm similar to that observed in the field, during the present study and previously by both Herter (1938) and Burton (1969). By using only adults, it was hoped that habits developed over at least nine months of natural feeding would be strong enough to overcome possible interruptions to any natural rhythms resulting from the provision of an unaccustomed diet, and a lower energy requirement, caused by a warmer environment and the ready availability, without the need for searching, of an adequate food supply. The temperature and humidity were controlled because it had been shown (Otway, 1965) that an unacceptable mortality rate occurred when animals were kept under ambient laboratory conditions. The present study showed that it is possible to satisfactorily use hedgehogs for laboratory studies such as food recovery experiments.

Adult hedgehogs commenced feeding on average two hours after sunset, with feeding activity usually reaching a maximum between 8 p.m. and 9 p.m., and then declining. A small increase in activity was observed between 1 a.m. and 5 a.m. This feeding rhythm was similar to that reported for wild hedgehogs by both Herter (1938) and Burton (1969). The small increase in activity in the early morning was not observed during the all-night searches in the present study. It should not be assumed, however, that all the recorded observations necessarily correlated with actual feeding activity as other normal activities such as grooming and courting were frequently observed.

VI. HEDGEHOG FOODS AVAILABLE IN THE STUDY AREA

The major part of the present study involved the identification of broken and partly digested food remains in the stomach contents and droppings of hedgehogs. A reference collection of the various invertebrate prey species present in the study areas was prepared and became an invaluable aid for the identification of food remains and in the selection of diagnostic parts for the determination of hedgehog diet by the direct count method.

The reference collection also provided a qualitative estimate of the hypothetical food supply available to the animals, and confirmed that similar species were present in both irrigated and non-irrigated areas. As no attempt was being made to quantitatively measure the invertebrate populations, the arrangement of the comparatively small number of traps used in obtaining the reference collection was not randomised but was deliberately chosen to reveal if the plantation and hedges bounding the study areas were causing edge effects. If they involved major prey species, edge effects could influence the movements and feeding behaviour of the hedgehogs. Earwigs (Forficula auricularia), one of the major animal food items found in the hedgehog diet were present in greater numbers in the drier areas near the hedges. This distribution, however, did not appear to influence hedgehog feeding behaviour.

Dropping analyses showed that the species that formed the major animal food items in the hedgehog diet tended to be those that were present in the study area throughout the greater part of the year. Thus the hedgehog diet may reflect food availability rather than any food preferences. The only major species present in large numbers throughout the year that was ignored by the hedgehogs was the Argentine stem weevil (Hyperodes bonariensis). With larger prey species readily available, hedgehogs did not expend energy catching small insects of low nutritional value.

Although the present work is the most comprehensive study of the diet yet attempted it does not establish if food preferences existed or determine the extent of predation. To obtain this additional information a quantitative assessment of the available food species was required. To have undertaken this task, however, would have required a team effort, and was beyond the scope of a fixed term study by one investigator.

VII. HEDGEHOG DIET

The contents of the stomach, or less frequently of the entire gut, of captured animals are usually preferred to dropping analyses for determining the diet of small mammals. The reasons advanced in support of this preference are that it is difficult to locate the droppings of many small mammals, and that changes produced by digestion are less advanced in stomach contents.

Since hedgehog droppings were readily available in the pastures of the study area, their use provided an opportunity to examine, throughout a two year period, the diet of the animals actually involved in the concurrent population estimates and feeding range studies.

Because of the increasing importance of irrigation on the Canterbury Plains it was desirable to undertake a comparative study that would establish the effect of pasture irrigation on hedgehog diet. Soon after this comparative study commenced, unforseen changes in management practices on the Lincoln College town supply dairy farm resulted in pasture growth conditions which made it difficult to locate hedgehogs and impossible to find their droppings in the non-irrigated part of the study area. This area had to be abandoned as it was no longer suitable for population studies, and no suitable alternative non-irrigated area was available. The stomach contents of those hedgehogs subsequently caught in the abandoned area, and in comparable pastures surrounding it, were therefore used to determine the diet of hedgehogs from non-irrigated pastures. The advantages of comparing samples from this nearby area, which contained similar soil types, pasture species and available invertebrate food species to the irrigated study area, was considered to outweigh any disadvantages from comparing stomach content analyses with those of droppings.

The size and overlap of feeding ranges confirmed that collecting droppings from the Z-shaped transects was valid. Some part of both transects crossed 80% of these feeding ranges, while part of one of them crossed the remainder. That two thirds of the droppings collected during the entire trial period should have come from the transects was unexpected, as their area was only one quarter that of the 12 randomly sited plots. This discrepancy was not caused by a greater proportion of the transects being included within the observed feeding ranges, as the mean proportions of the area of the transects and plots included within each feeding range were essentially similar being 31% and 29%, respectively. If droppings were randomly distributed throughout the feeding area, seven eights of the droppings from the plots and none from the transects would have to have been overlooked or destroyed to yield the proportions actually collected. Irrigation was applied uniformly over the area, and the plots and transects were searched with equal care.

It is, therefore, concluded that droppings were not randomly distributed throughout the feeding ranges. This conclusion was supported by examination of the actual capture points shown in Figures 5-24, inclusive, as 1.6 times as many capture points lay along the two transects, as fell within the 12 random plots. This confirmed that hedgehogs did not make uniform use of all parts of their feeding ranges, and that some parts of the transects corresponded with areas of more intense usage. Morris (1969) has also concluded that all parts of the hedgehog home ranges were not used with equal intensity. Care was taken to confirm that the animals did not follow tracks made by the observer. The conclusion reached was compatible with field observations which showed that tracked animals tended to follow similar routes on successive nights.

The more important food species in the diet of hedgehogs in pastures were earwigs, lepidopteran larvae, beetles (especially grass grubs during their flight seasons), slugs, dung flies, earthworms, harvestmen, slaters, and spiders. The size of those deliberately eaten ranged from slaters at 0.8 cm to large earthworms at 12 cm. The diet was also characterised by the presence of small quantities of a comparatively large number of minor food species. In these circumstances none of the methods usually applied to data obtained from droppings or stomach contents is, if used alone, able to satisfactorily express the relative importance of all the individual food items in the diet. A combination of numerical and volumetric methods was used to overcome this problem. The major limitations of the direct count method were successfully overcome by the freeze-drying of the samples, (a new technique that was developed in the course of the study), the preparation of the reference collection, and the use of diagnostic parts.

It is recommended that in future studies of this type, combining the results of direct counting, corrected for recovery percentages, with mean weight and volume data for the species concerned would give the most reliable and comprehensive estimate of the relative importance of the various diet items. The wide range in recovery values of diagnostic parts, obtained in the food recovery experiments, clearly demonstrates the need to obtain this information, particularly in studies involving a large number of different food species. The reliability of recovery data will depend on the quantities of the different prey species used for each feed and on the extent of replication achieved. In the present study, the availability of invertebrates restricted experiments to droppings, and to the use of a single animal. Each prey species, was however, fed on at least four occasions. The low recovery rate of hard parts, which could be used to quantify the numbers of each food item eaten, from droppings for Lycosidae, Opilio opilio, Porcellio scaber, and Wiseana cervinata suggests that these species would also undergo considerable losses in analyses of stomach contents.

The number of samples analysed (230 droppings and 60 stomach contents) makes the present work the most comprehensive study of hedgehog diet that has yet been attempted. The only available studies of the diet of hedgehogs in pasture lands in New Zealand, those of Brockie (1958) and Wood (1970), each analysed only 10 samples. Although their results can be criticised on statistical grounds, and on their disregard for pasture content, soil type and food availability their results were generally consistent with those obtained in the present study. Both Brockie and Wood also examined the diet of hedgehogs in a number of other habitats.

Five systematic studies of the diet of wild hedgehogs have been carried out in other countries (Kalabukhov, 1928; Liu, 1937; Shilova-Krassova, 1952; Kruuk, 1964 and Yalden, 1969). The works of Kalabukhov and Liu concerned species or genera other than Erinaceus europaeus. Kruuk's study was carried out in the limited environment of a black-headed gull breeding colony during a three month breeding season. Insects occurred in 94% of the 33 droppings he analysed, but these were followed in importance by gull chicks, eggshells, snails and amphipods. None of these three works can reasonably be compared with the present study.

Shilova-Krassova (1952) examined 262 droppings from hedgehogs in pine and oak plantations in southeast Russia,and reported that beetle species formed the only important diet items. Only during the flight season of the May beetle

(*Melolontha hippocastani*) were hedgehogs found in the forested areas in appreciable numbers. The hedgehogs showed a definite preference for this pest, and during its flight season other species, which throughout the remainder of the year formed the major items in the diet, were ignored. Captive animals would consume about 100 May beetles per day. These observations form an interesting parallel with the place of grass grub beetles in hedgehog diet as found in the present study.

Yalden (1969) examined the stomach contents of 106 hedgehogs captured between April and October from 'estates' in various parts of England. Half of the samples were collected before the end of May, and 82% of them came from East Anglia. Carabid beetles formed the most important diet item (percentage occurrence), and these were followed in importance by earwigs, lepidopteran larvae, millipedes, earthworms, slugs, spiders and harvestmen. These results show a remarkable degree of correlation with those obtained in the present study. Yalden (pers. comm.) is currently extending this work.

The large number of droppings analysed in the present study allowed the data to be subdivided by season. The number of stomach contents obtained during the spring and summer of 1970-71 were also sufficient to allow breakdown by season and sex. Insufficient juveniles were captured to permit separate analysis.

Irrigation was not found to be a major factor affecting the diet of hedgehogs in pasture lands. An increase in the importance of earthworms and slugs from a combined total of 5% (relative volume) in the non-irrigated pastures to 12% in irrigated areas was the only difference that could be directly attributed to the use of irrigation. The major animal foods in the diet of hedgehogs from both areas were earwigs, beetles and lepidopteran larvae. These items provided over 60% of the animal food items in the diet. This dominance was caused by their relatively large size and their availability throughout the year. Food preference studies (Wood, 1970) have shown that of 11 food items investigated beetles were most preferred by hedgehogs. This observation correlates with the results of present study and with Shilova-Krassova (1952) and Yalden (1969). Wood's (1970) ranking of earwigs (sixth) is of doubtful statistical validity. In addition he failed to determine whether or not lepidopteran larvae were a component of hedgehog diet.

Seasonal variations in the hedgehog diet were related to changes in the availability of the species involved. The most obvious seasonal effect was the dominance of grass grub beetles during their flight season. The length of this flight season in the irrigated Lincoln pastures, as determined from the first and last appearances each year of the beetles in hedgehog droppings, was 35 ± 3 days in November-December, 1969, and 46 ± 3 days in the same months in 1970. The possible error in these values is a result of uncertainties in the age of droppings. It is doubtful if the degree of dominance found during the flight season could be explained solely by the increase in availability of this easily captured prey. It is likely that hedgehogs showed some preference for this species.

Although individual hedgehogs can consume large quantities of this pasture pest, the likely densities of prey and predator in affected pastures would be such that hedgehogs alone are unlikely to provide any effective measure of biological control. However, contemporaneous hedgehog predation, when added to other mortality factors such as irrigation, high stocking rates, intelligent management and starling predation can only increase the possibility of achieving effective biological control. Their presence in pastures should, therefore, be encouraged to the extent of providing shelter for nest sites where these are lacking. However, should foot-and-mouth disease be introduced into New Zealand, the hedgehog as a carrier of this disease, would need to be exterminated within affected areas.

CHAPTER IX

SUMMARY AND CONCLUSIONS

The feeding behaviour of a natural population of the European hedgehog (Erinaceus europaeus L.), resident in a pastoral environment was investigated. The sampling methods used were consistent with a policy of minimum interference.

1. By examining a large number of samples and by developing more effective techniques for sorting and identifying food remains, the difficulties usually associated with the direct count method were overcome and a comprehensive diet analysis obtained. Fragmentation during sorting was considerably reduced by freeze-drying the samples, while the preparation of a reference collection of available foods, and the use of diagnostic parts (those with the highest recovery rate for each species, as determined by feeding trials) simplified identification and enabled the quantities actually eaten to be calculated. As recovery rates vary widely they should be obtained in diet studies.

2. Earwigs, lepidopteran larvae, beetles, dung flies, slugs, earthworms, harvestmen and spiders were the more important invertebrate food items in the hedgehog diet. The sex of the animals and the irrigation of pastures did not significantly influence the diet. Seasonal

variations were related to changes in availability of prey species. Although hedgehogs consumed large numbers of grass grub beetles during their flight season it is unlikely that they provide any effective measure of biological control.

3. It is concluded that the most effective estimate of the relative importance of food items in small mammal diet is obtained by combining direct counting, corrected for recovery rates, with average volume and weight data for the available prey species.

4. The population density (excluding nestlings) in an irrigated pasture ranged from 4/ha (winter) to 8/ha (summer). The density is probably lower in similar but non-irrigated pastures.

5. The average minimum hedgehog feeding range in an irrigated pasture was 2.4 ha. Individual ranges overlapped considerably. All parts of the ranges were not used with equal intensity. Animals were active for an average of eight hours per night, and tended to use relatively fixed routes. Their maximum activity occurred between 9 p.m. and 11 p.m. Laboratory fed hedgehogs retained their natural feeding rhythms.

6. The presence of hedgehogs in pastures is beneficial. They do not interfere with stock or crops, destroy some insect pests, and are insignificant as predators on ground-nesting birds. Hedgehogs can, however, carry and transmit foot-and-mouth disease, and should this disease ever enter New Zealand, hedgehogs could assist its spread and hinder its eradiction. In a country as dependent on its livestock industry as New Zealand, this aspect alone justifies accumulation of basic information on the ecology of the hedgehog.

7. This work could be extended to investigate the effects on the population resulting from changes in food availability caused by normal farming operations such as ploughing. In future diet studies it would be desirable to compare the results of diet analysis with a reliable population census and a quantitative assessment of the available food supply, as this would determine any food preferences and the extent of any predation.

8. This study is the most comprehensive on the diet of hedgehogs in any environment. As it is the first such study it tends to be qualitative. Further studies could improve on this by quantitatively establishing the exact proportions of food species taken out of the area by hedgehogs.

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APPENDIX I

MISCELLANEA

I. BREEDING

It was impossible to obtain the breeding rate of the population studied at Lincoln, as the difficulties involved in locating nests and young could not be overcome. Despite assiduous searches of all possible nesting sites surrounding the study area, only one nest was ever located. However, notes were kept on relevant observations made during this study.

Of the 60 hedgehogs collected for stomach content analyses six of the 26 females were found to be pregnant. The breeding data for these six hedgehogs are shown in Table 17.

TABLE 17.

BREEDING DATA FOR SIX PREGNANT HEDGEHOGS COLLECTED FROM PASTURE LANDS.

HEDGEHOG	DATE	NUMBER OF EMBRYOS	SIZE OF EMBRYOS
S16	21/11/68	5	LARGE (> 30 mm)
S30	5/12/68	4	MEDIUM (10-30 mm)
S47	7/ 2/69	4	LARGE
S51	15/ 2/69	4	SMALL (< 10 mm)
S52	15/ 2/69	4	SMALL
S53	15/ 2/69	4	LARGE

From this table it seems that the most common number of embryos is four and that young may be born any time between November and March.

Copulation between two hedgehogs was first observed about 10 p.m. on 4/11/68 on a lawn on the Lincoln College campus. Two hedgehogs were seen circling around each other while making loud snuffling and snorting noises. After 10 minutes of circling the male was observed to mount the female from behind and hold her by the scruff of the neck with his teeth. The spines of the female were laid flat. The male remained mounted for 20 minutes, during which time six copulations took place. The first five of these were of about one minute duration while the sixth lasted for three minutes. The male, then, dismounted sideways, still holding the female by the neck, and pulled her over on her side. He held her in this position for five minutes, during which period she gave four spasms of convulsive action. The male then released the female and lay by her side occasionally nudging her and snuffling for about 20 minutes. The female lay curled up on her side after the male released her, and snorted when nudged by the male. The spines of the male remained flat throughout, while those of the female remained flat until she curled up, following release by the male, when her spines were erected. The entire mating ceremony lasted about one hour.

Both these animals were captured and kept in captivity, in a field cage, along with several other hedgehogs. The female appeared to be pregnant after about two weeks, but young were never seen. If the young were born alive they were presumably eaten by other hedgehogs, or alternatively the embryos may have been resorbed before birth.

Courting behaviour was observed several times in the population under study. One pair of hedgehogs (female 16 and male 17) was observed courting on 12/1/70, and just after they had mated a month later, on 16/2/70. On this second occasion the female was curled on her side and the male was nudging her. Semen was present on the female. Two females (26 and 50) were seen courting with different males; female 26 with male 54 on 14/12/70, and with male 33 on 18/10/71, female 50 with male 55 on 1/2/71, and with male 59 on 15/2/71. This latter male (59) had previously been observed after he had mated with female 29, on 14/12/70. On this occasion the female was curled on her side with the male nudging her. No semen was present. On 8/3/71, male 67 was noticed courting with female 68.

These observations suggest that hedgehogs are not monogamous, and do not mate for the season or for life. However, the courting ceremony was interrupted on each occasion, so mating may not have taken place. Hedgehogs were relatively easily disturbed while courting, but were completely imperturbed while mating.

During the 1971 February to March breeding period, five pregnant female hedgehogs were observed. A hedgehog was classified as pregnant if the nipples were visibly swollen, and embryos could be felt on palpating the hedgehog's abdomen with the finger tips. Hedgehogs 19, 23, 26 and 31 appeared to be pregnant when captured on 1/3/71, 22/2/71, 1/3/71 and 8/3/71, respectively. When captured four, four, one and five weeks later, respectively, they were no longer pregnant. These females may have produced live young, but, despite extensive searching, including attempts to trace nesting sites by using wet sand to reveal hedgehog tracks, no nest or young were found.

Hedgehog 26 was observed courting on 18/10/71, and had she been successfully mated at this time the pregnancy which may have terminated between 1/3/71 and 8/3/71 would have been her second of the season.

Hedgehog 50 was found to be pregnant on 8/3/71, and on 23/3/71, when she was followed to a nest in a hole under an upturned stump, on the western edge of block B. This hole was lined with dried grass and was almost certainly a nursery nest. These latter observations took place during an all-night count, when the hedgehog was observed to return to her nest at 5.40 a.m. Some light sticks were then placed across the entrance of this nest and they remained undisturbed for five days. This hedgehog probably had her young during this period, but a full-arm-stretch search of the nest failed to detect them. The nest was not dug up as this would have disturbed the young. This animal became active again on 28/3/71, but was not observed again until 6/4/71 when she was no longer pregnant.

The only other nest discovered near the study area was found on 20/3/71 by a Lincoln College employee, in a hole under some hay bales, in a tractor shed near block A. This nest contained one adult female, two live and one dead, less than one week old, young. All had disappeared by the time the author was notified the following day. The female had apparently shifted her young after they were disturbed. Although he noticed that this hedgehog was a marked animal, the employee could not recall the mark.

During this study five litters of newly born hedgehogs (all less than one week old) were brought to Lincoln College by members of the public. The first of these litters contained two males and three females, the second two males and one female. Neither litter was accompanied by the female. In spite of strenuous efforts to raise the young, including two-hourly feeding from eyedroppers, all eight animals died within a week. The third litter of, one male and two females was accompanied by the female, but she died shortly after capture. Again, efforts to raise the young failed. The fourth litter, contained two males and one female, which were accompanied by the female. Although she died soon after the young opened their eyes, all were successfully raised to eight weeks. While this litter was being weighed the female managed to get its head tightly wedged between a stainless steel bench and a concrete wall, causing injuries which proved fatal. One of the males from this litter died of pneumonia at 20 weeks. The remaining male was released at Lincoln College when 29 weeks of age. The fifth litter contained three males, accompanied by the female. This female also died suddenly at the time the young were opening their eyes. All three young were successfully raised, marked and released in Lincoln at six weeks. One of the three was sighted, alive and thriving, several times after release.

II. MORTALITY

It appears that many of the hedgehogs which foraged in the study area nested in nearby hay barns, at least during the winter, as several dead hedgehogs were found each winter when the hay was removed. In the winters of 1969, 1970 and 1971, six, seven and 11 dead hedgehogs, respectively, were found in hay barns. All these animals had been dead for some time, and were dried out and mummified, making it impossible to determine their sex, or any markings they may have carried.

Apart from the 24 hedgehogs found dead in the hay barns near the study area, only two other dead animals were found. The first of these was found on the southern boundary of block B on the first day of the study period. On 14/6/71 the second was also found near the southern boundary of block B. Only the spiny skin of this marked animal remained, but as it was impossible to determine which part of the skin was the head of the animal, its mark could not be determined. It was also possible that the skin may have been removed from the carcass while it was lying elsewhere.

The main cause of winter mortality appears to be respiratory diseases. Six adult hedgehogs (three male and three female) which died in field cages and two adults (one male and one female) which died in the laboratory were sent to the Department of Agriculture Veterinary Diagnostic Station in Lincoln. All were found to have died from pneumonia.

III. DISEASE IN THE STUDY AREA

About one third of the adult population of hedgehogs had some lesions on their face or undersurface. The severity of these lesions ranged from very minor to severe. Severely infected animals were almost entirely covered with crusty lesions, and some had lost all the hair from their undersurfaces. Juveniles were generally free of these lesions. The diseases causing these lesions were not investigated as these have been adequately covered by workers such as English, Smith and Rush-Munro (1964), English (1964 and 1967), Smith and Marples (1964), Smith and Robinson (1964) and Smith (1965 and 1968).

IV. CANNIBALISM

It has often been reported that hedgehogs are cannibalistic in habit. Observations made during the present study tend to confirm this. Prakash (1953) reported that when a group of captive hedgehogs were not fed for six days, five adults began to attack a juvenile while it was on the move. The adults chewed its hind limbs and finally succeeded in unrolling the victim and eating its abdomen. These animals belonged to the species _Hemiechinus auritus collaris_ Gray and Hardwicke. When an adult hedgehog of this species died of natural causes hedgehogs of the same species and the species _Parechinus micropus_ Blyth were observed eating the carcass. Prakash introduced a dead hedgehog, the abdomen of which was cut open, into the cage and found that most of the hedgehogs present readily ate the viscera.

During studies carried out in Otago in 1965, by Otway and Woodhouse, a six week old female hedgehog, was put in a store cage with four adults of each sex. Two days later the remains of this young hedgehog were found in the nest box. The adults had eaten the viscera and flesh, leaving only the skin, spines, and a few fragments of attached muscles. The limbs, tail and ears had been eaten and all the flesh had been removed from the snout. As the actual sequence of events was not observed, it was not known whether the young animal was killed by a hedgehog and eaten, or whether if first died of natural causes. No other species was responsible for the act as the cage was completely covered with fine-mesh chicken wire and the carcass was not flyblown. The adults could not have been unduly hungry, as they were fed daily.

Two young hedgehogs in a store cage were eaten in a similar manner by adults during the present study. Another adult hedgehog (S8) was found feeding on the carcass of a dead, flyblown, male hedgehog in a field near Lincoln. Both types of cannibalism are present among hedgehogs. That is, hedgehogs feed on dead companions, or may kill them before feeding on them.

APPENDIX II.

STATISTICAL DATA FOR THE HOME RANGES OF 20 HEDGEHOGS IN THE STUDY AREA BETWEEN 30/6/69 AND 29/11/71.

	ADULT MALES	ADULT FEMALES	JUVENILE MALES	JUVENILE FEMALES
n	7	7	3	3
ΣX	170,252	195,757	57,619	60,408
ΣX^2	4,979,652,584	6,297,998,921	1,254,154,341	1,317,469,416
$(\Sigma X)^2$	28,985,743,504	38,320,803,049	3,319,949,161	3,649,126,464
$\bar{X}$	24,321.71	27,965.29	19,206.33	20,136.00
$(\Sigma X)^2/n$	4,140,820,501	5,474,400,436	1,106,649,720	1,216,375,488
Σx^2	838,832,083	823,598,485	147,504,621	101,093,928

$t\ (A_{♂}\ A_{♀}) = 0.579$ NONE SIGNIFICANT

$t\ (J_{♂}\ J_{♀}) = 0.144$ AT THE 5% LEVEL

$t\ (A_{♂}\ J_{♂}) = 0.015$

$t\ (A_{♀}\ J_{♀}) = 0.015$

CALCULATED FROM THE "t" TEST TABLE IN SNEDECOR AND COCHRAN (1967).

APPENDIX III.

FEEDING FREQUENCY PER NIGHT FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR A PERIOD OF 107 DAYS.

NO. OF FEEDS PER NIGHT	FREQUENCY HH.A.	HH.B.	HH.C.	HH.D.
0	0	1	7	0
1	1	0	1	3
2	1	0	3	3
3	2	2	2	0
4	2	5	1	3
5	9	13	2	2
6	11	18	4	5
7	21	18	3	4
8	18	12	1	2
9	18	10	3	7
10	10	6	4	4
11	7	6	6	4
12	1	4	6	5
13	3	3	5	3
14	1	5	8	5
15		2	5	4
16		1	6	8
17		1	6	5
18			5	7
19			3	4
20			2	3
21			5	4
22			0	3
23			4	5
24			0	1
25			0	1
26			1	1
27				2
28				1
29				1
30				2
31				1
32				1
AVERAGE	7.84	8.01	12.31	14.71

APPENDIX IV.

TOTAL TIME SPENT FEEDING PER NIGHT BY 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

DURATION OF FEEDING*. (MINUTES)	FREQUENCY			
	HH.A.	HH.B.	HH.C.	HH.D.
0	0	1	7	0
3.3	2	0	3	4
6.7	2	4	4	4
10.0	4	7	2	5
13.3	6	7	6	4
16.7	6	8	5	3
20.0	6	13	7	5
23.3	6	12	10	7
26.7	11	14	7	9
30.0	20	12	9	8
33.3	7	7	11	11
36.7	9	8	6	13
40.0	11	6	5	10
43.3	3	1	5	6
46.7	9	0	2	6
50.0	3	1	1	2
53.3		0	0	1
56.7		2	2	1
60.0		0	0	1
63.3		0	1	0
66.7		1		1
70.0		2		1
73.3		0		0
76.7		0		0
80.0		0		1
83.3		1		0
86.7				1

* These fractional numbers arise because of direct conversion from centimetres on the event recorder tapes (3 cm = 10 minutes).

APPENDIX V.

FREQUENCY OF THE DURATION OF THE FIRST FEED EACH NIGHT OF 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

DURATION OF FEED (MINUTES)	FREQUENCY			
	HH.A.	HH.B.	HH.C.	HH.D.
0.3	1	5	7	5
0.7	1	8	1	3
1.0	1	5	3	3
1.3	3	3	7	5
1.7	1	4	3	6
2.0	1	3	4	5
2.3	3	6	6	6
2.7	1	3	4	7
3.0	3	4	5	6
3.3	4	5	11	9
3.7	5	4	3	7
4.0	5	5	2	2
4.3	5	7	6	8
4.7	5	4	5	5
5.0	6	5	3	3
5.3	5	4	2	2
5.7	8	7	4	3
6.0	10	8	3	4
6.3	5	6	3	5
6.7	9	0	0	2
7.0	4	1	3	1
7.3	3	1	1	0
7.7	3	1	2	1
8.0	4	0	0	1
8.3	1	1	1	0
8.7	3	0	0	0
9.0	1	1	1	0
9.3	2	0	1	2
9.7	0	0	2	1
10.0	1	1		0
10.3	0	0		0
10.7	0	1		0
11.0	0	0		2
11.3	0	0		
11.7	1	0		
12.0		1		
12.3		1		
12.7		0		
13.0		0		
13.3		1		
13.7		0		
14.0		0		
14.3		0		
14.7		1		

These fractional numbers arise because of direct conversion from centimetres on the event recorder tapes. (3 cm = 10 minutes).

APPENDIX VI.

FREQUENCY OF INDIVIDUAL FEEDS OF 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

DURATION OF FEED (MINUTES)	FREQUENCY			
	III.A.	III.B.	III.C.	III.D.
0.3	21	42	77	147
0.7	41	70	149	201
1.0	38	38	107	123
1.3	55	52	122	134
1.7	31	47	119	141
2.0	38	65	103	102
2.3	38	65	87	112
2.7	34	35	79	71
3.0	41	44	66	59
3.3	55	44	59	97
3.7	41	19	24	39
4.0	44	27	28	38
4.3	39	28	23	25
4.7	36	21	11	16
5.0	38	15	7	30
5.3	22	19	4	8
5.7	19	11	5	8
6.0	18	30	6	10
6.3	12	7	1	6
6.7	17	13	0	5
7.0	12	11	0	1
7.3	5	6	0	2
7.7	9	6	0	1
8.0	7	6	0	1
8.3	7	7	0	1
8.7	1	1	0	2
9.0	2	2	0	1
9.3	1	3	0	0
9.7	1	2	1	1
10.0	3	1		0
10.3	1	1		0
10.7	1	4		1
11.0	1	2		0
11.3	0	4		0
11.7	0	1		1
12.0	0	0		0
12.3	0	1		0
12.7	0	1		0
13.0	0	1		0
13.3	0	0		0
13.7	0	0		0
14.0	0	0		0
14.3	1	0		0
14.7		0		0
15.0		0		0
15.3		0		0
15.7		1		0
16.0		0		0
16.3		1		0
16.7				0
17.0				0
17.3				0
17.7				0
18.0				0
18.3				0
18.7				1
AVERAGE	3.34	3.03	1.78	1.89

These fractional numbers arise because of direct conversion from centimetres on the event recorder tapes (3 cm = 10 minutes)

APPENDIX VII.

AVERAGE NUMBER OF FEEDS IN ONE HOUR PERIODS THROUGHOUT THE NIGHT FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

TIME	AVERAGE NUMBER OF FEEDS PER HOUR			
OF DAY	HH.A.	HH.B.	HH.C.	HH.D.
6 P.M.				
	0.12	0.06	0.33	0.28
7 P.M.				
	1.18	1.08	2.28	1.79
8 P.M.				
	1.64	2.04	3.03	3.66
9 P.M.				
	1.06	1.51	1.91	2.14
10 P.M.				
	0.63	0.68	1.18	1.55
11 P.M.				
	0.48	0.40	0.81	1.18
12 P.M.				
	0.46	0.31	0.77	1.10
1 A.M.				
	0.39	0.54	0.71	0.93
2 A.M.				
	0.46	0.55	0.29	0.57
3 A.M.				
	0.54	0.34	0.33	0.75
4 A.M.				
	0.68	0.32	0.10	0.47
5 A.M.				
	0.17	0.08	0.05	0.19
6 A.M.				
	0.04	0.08	0.01	0.05
7 A.M.				

APPENDIX VIII.

AVERAGE TIME SPENT FEEDING IN ONE HOUR PERIODS THROUGHOUT THE NIGHT BY 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

TIME OF DAY	AVERAGE TIME SPENT FEEDING PER HOUR HH.A.	HH.B.	HH.C.	HH.D.
6 P.M.				
	0.62	0.26	1.36	1.34
7 P.M.				
	4.90	3.58	5.45	4.60
8 P.M.				
	5.59	6.29	6.47	7.65
9 P.M.				
	3.22	4.38	4.03	4.94
10 P.M.				
	2.16	2.17	2.55	3.02
11 P.M.				
	1.90	1.73	1.70	1.94
12 P.M.				
	1.84	1.05	1.72	1.87
1 A.M.				
	1.55	1.72	1.46	1.82
2 A.M.				
	1.64	2.10	0.65	1.14
3 A.M.				
	2.22	1.33	0.58	1.67
4 A.M.				
	2.58	1.25	0.18	1.16
5 A.M.				
	0.81	0.38	0.11	0.59
6 A.M.				
	0.15	0.29	0.06	0.09
7 A.M.				

APPENDIX IX.

CORRELATION BETWEEN AVERAGE NUMBER OF FEEDS (X) AND AVERAGE DURATION OF FEEDING (Y), IN ONE HOUR PERIODS THROUGHOUT THE NIGHT, FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

TIME OF DAY	HEDGEHOG A.					HEDGEHOG B.				
	X	X^2	Y	Y^2	XY	X	X^2	Y	Y^2	XY
6 P.M.	0.12	0.01	0.62	0.38	0.07	0.06	0.00	0.26	0.07	0.02
7 P.M.	1.18	1.39	4.90	24.01	5.78	1.08	1.17	3.58	12.82	3.87
8 P.M.	1.64	2.69	5.59	31.25	9.17	2.04	4.16	6.29	39.56	12.83
9 P.M.	1.06	1.12	3.22	10.37	3.41	1.51	2.28	4.38	19.18	6.61
10 P.M.	0.63	0.40	2.16	4.67	1.36	0.68	0.46	2.17	4.71	1.48
11 P.M.	0.48	0.23	1.90	3.61	0.91	0.40	0.16	1.73	2.99	0.69
12 P.M.	0.46	0.21	1.84	3.39	0.85	0.31	0.10	1.05	1.10	0.33
1 A.M.	0.39	0.15	1.55	2.40	0.60	0.54	0.29	1.72	2.96	0.93
2 A.M.	0.46	0.21	1.64	2.69	0.75	0.55	0.30	2.10	4.41	1.16
3 A.M.	0.54	0.29	2.22	4.93	1.20	0.34	0.12	1.33	1.77	0.45
4 A.M.	0.68	0.46	2.58	6.66	1.75	0.32	0.10	1.25	1.56	0.40
5 A.M.	0.17	0.03	0.81	0.66	0.14	0.08	0.00	0.38	0.14	0.03
6 A.M.	0.04	0.00	0.15	0.02	0.01	0.08	0.00	0.29	0.08	0.02
7 A.M.										

TIME OF DAY	HEDGEHOG C.					HEDGEHOG D.				
6 P.M.	0.33	0.11	1.36	1.85	0.45	0.28	0.08	1.34	1.80	0.38
7 P.M.	2.28	5.20	5.45	29.70	12.43	1.79	3.20	4.60	21.16	8.23
8 P.M.	3.03	9.18	6.47	41.86	19.60	3.66	13.40	7.65	58.52	28.00
9 P.M.	1.91	3.65	4.03	16.24	7.70	2.14	4.58	4.94	24.40	10.57
10 P.M.	1.18	1.39	2.55	6.50	3.01	1.55	2.40	3.02	9.12	4.68
11 P.M.	0.81	0.66	1.70	2.89	1.38	1.18	1.39	1.94	3.76	2.29
12 P.M.	0.77	0.59	1.72	2.96	1.32	1.10	1.21	1.87	3.50	2.06
1 A.M.	0.71	0.50	1.46	2.13	1.04	0.93	0.86	1.82	3.31	1.69
2 A.M.	0.29	0.08	0.65	0.42	0.19	0.57	0.32	1.14	1.30	0.65
3 A.M.	0.33	0.11	0.58	0.34	0.19	0.75	0.56	1.67	2.79	1.25
4 A.M.	0.10	0.01	0.18	0.03	0.02	0.47	0.22	1.16	1.35	0.55
5 A.M.	0.05	0.00	0.11	0.01	0.00	0.19	0.04	0.59	0.35	0.11
6 A.M.	0.01	0.00	0.06	0.00	0.00	0.05	0.00	0.09	0.01	0.00
7 A.M.										

APPENDIX X.

STATISTICAL DATA FOR THE FEEDING FREQUENCY PER NIGHT FOR 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

	HH.A.	HH.B.	HH.C.	HH.D.
n	105	107	93	104
ΣX	823	857	1145	1530
ΣX^2	7009	7915	17993	28186
$(\Sigma X)^2$	677329	734449	1311025	2340900
$\bar{X}$	7.84	8.01	12.31	14.71
X^2/n	6450.75	6864.00	14090.00	22508.65
Σx^2	558.25	1051.00	3903.00	5677.35
S^2	5.37	9.92	42.42	55.12

$t' (X_A X_B) = 0.450$

$t' (X_C X_D) = 2.418$

$t' (X_A X_D) = 9.020$***

$t' (X_B X_C) = 5.804$***

*** SIGNIDICANT AT THE 0.1% LEVEL AS CALCULATED FROM THE "t" TEST TABLE IN SNEDECOR AND COCHRAN. (1967).

APPENDIX XI.

STATISTICAL DATA FOR THE TOTAL TIME SPENT FEEDING PER NIGHT BY 4 HEDGEHOGS KEPT IN LABORATORY CAGES ~~FOR 107~~ DAYS.

	HH.A.	HH.B.	HH.C.	HH.D.
n	105	107	93	104
ΣX	2925.40	2687.00	2232.80	3123.30
ΣX^2	95121.00	87902.88	71629.48	119129.85
$(\Sigma X)^2$	8557965.16	7219969.00	4985395.84	9755002.89
$\bar{X}$	27.86	25.11	24.00	30.03
X^2/n	81504.43	67476.00	53600.00	93798.11
Σx^2	13616.57	20426.88	18029.48	25331.74
s^2	130.93	192.70	195.90	245.94

$t'\ (X_A X_B) = 1.574$

$t'\ (X_C X_D) = 2.853$**

$t'\ (X_A X_D) = 1.142$

$t'\ (X_B X_C) = 0.562$

** SIGNIFICANT AT THE 1.0% LEVEL AS CALCULATED FROM THE "t" TEST TABLE IN SNEDECOR AND COCHRAN. (1967).

APPENDIX XII.

STATISTICAL DATA FOR THE FREQUENCY OF THE DURATION OF THE FIRST FEED EACH NIGHT OF 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

	HH.A.	HH.B.	HH.C.	HH.D.
n	105	107	93	104
ΣX	549.91	429.86	332.81	373.32
ΣX^2	3361.59	2599.55	1683.55	1890.58
$(\Sigma X)^2$	302401.01	184779.62	110762.50	139367.82
$\bar{X}$	5.24	4.02	3.58	3.59
X^2/n	2880.01	1726.91	1190.99	1340.08
Σx^2	481.58	872.64	492.56	550.50
s^2	4.63	8.23	5.35	5.35

$t' \ (X_A X_B) = 3.506$***

$t' \ (X_C X_D) = 0.033$

$t' \ (X_A X_D) = 5.330$***

$t' \ (X_B X_C) = 1.193$

$t' \ (X_A X_C) = 5.204$***

$t' \ (X_B X_D) = 1.201$

*** SIGNIFICANT AT THE 0.1% LEVEL, AS CALCULATED FROM THE "t" TEST TABLE IN SNEDECOR AND COCHRAN (1967).

APPENDIX XIII.

STATISTICAL DATA FOR THE FREQUENCY OF INDIVIDUAL FEEDS OF 4 HEDGEHOGS KEPT IN LABORATORY CAGES FOR 107 DAYS.

	HH.A.	HH.B.	HH.C.	HH.D.
n	730	754	1078	1385
ΣX	2441.47	2282.88	1918.69	2618.04
ΣX^2	11481.39	11476.14	5013.56	8379.09
$(\Sigma X)^2$	5960775.76	5211541.09	3681371.32	6854133.44
$\bar{X}$	3.34	3.03	1.78	1.89
X^2/n	8165.45	6911.86	3415.00	4948.83
Σx^2	3315.94	4564.28	1598.56	3430.26
S^2	4.55	6.06	1.48	2.48

$t' (X_A X_B) = 2.651$

$t' (X_C X_D) = 1.943$

$t' (X_A X_D) = 16.264$***

$t' (X_B X_C) = 12.866$***

*** SIGNIFICANT AT THE 0.1% LEVEL, AS CALCULATED FROM THE "t" TEST TABLE IN SNEDECOR AND COCHRAN. (1967).

APPENDIX XIV.

LIST OF SPECIES CAUGHT IN THE STUDY AREA BETWEEN 1/9/69 AND 31/8/70 AND THEIR CLASSIFICATION.

Phylum Annelida
Class Oligochaeta
Order Opisthopora
Family Lumbricidae
Sp. Allolobophora caliginosa (Savigny). (All year).

Phylum Arthropoda
Subphylum Mandibulata
Class Crustacea
Subclass Malacostraca
Order Isopoda
Family Porcellionidae
Sp. Porcellio scaber L. (All year).

Order Amphipoda
Family Talitridae
Sp. Orchestria tenuis Dana. (Nov. - Jan.)

Class Collembola
Order Collembola
Family Poduridae
Sp. Hypogastrura rossi (Salmon). (Aug. - Jun.)

Family Entomobryidae
Sp. Entomobrya nivalis Schöffer. (Aug. - Jun.)

Class Insecta
Subclass Pterygota
Order Odonata
Suborder Zygoptera
Family Coenagrionidae
Sp. Xanthocnemis zealandica (McLachlan). (Dec.)

APPENDIX XIV continued.

Order Dermaptera

Suborder Forficulina

Family Forficulidae

Sp. Forficula auricularia L. (All year).

Order Orthoptera

Suborder Ensifera

Family Rhaphidophoridae

Sp. Pleioplecton sp. (Nov. - Jan.)

Family Tettigoniidae

Sp. Xiphidium semivittatum (Walker). (Jan.)

Family Gryllidae

Sp. Lissotracheles maoricus (Walker). (Nov. - May)

Suborder Caelifera

Family Acrididae

Sp. Phaulacridium marginale (Walker). (Jan.)

Order Hemiptera

Suborder Homoptera

Family Cicadellidae

Sp. Deltocephalus taedius (Kirkaldy). (Feb. - Apr.)

Sp. D. viridellus Evans. (Feb. - Apr.)

Family Aphididae

Sp. Lipaphis erysimi Kaltenbach. (Nov. - Feb.)

Sp. Macrosiphum euphorbiae (Thomas). (Nov. - Feb.)

Sp. Cinaria (Neochmosis) juniperina Cottier. (Oct. - Jan.)

Sp. Aulacorthum solani Kaltenbach. (Sep. - Dec.)

APPENDIX XIV continued.

Suborder Heteroptera

Family Nabidae

Sp. Nabis capsiformis (Germar.). (Jan. - Apr.)

Family Miridae

Sp. Calocoris norvegicus (Gemlin). (Feb.)

Sp. Eurystylus australis Poppius. (Jan. - Feb.)

Family Lygaeidae

Sp. Nysius huttoni White. (Dec. - Apr.)

Sp. Hudsona anceps White. (Nov.)

Order Neuroptera

Family Hemerobiidae

Sp. Micromus tasmaniae (Walker). (Oct. - Mar.)

Order Coleoptera

Suborder Adephaga

Family Carabidae

Sp. Megadromus antarcticus (Chaudoir). (Dec. - Mar.)

Sp. Laemostenus complanatus (Dejean). (Sep. - Apr.)

Sp. Metaglymma monilifer Bates. (Dec. - Mar.)

Sp. Clivinia rugithorax Putzeys. (Jan.)

Sp. Salenochilus sp. (Sep. and Mar.)

Sp. Notogonum feredayi (Bates). (Jan. - Feb.)

Sp. Scopodes elaphroides White. (Jan.)

Suborder Polyphaga

Family Hydrophilidae

Sp. Cercyon sp. (Dec.)

Family Staphylinidae

Sp. Atheta sp. (Dec.)

Sp. Leptacinus sp. (Sep. - Mar.)

APPENDIX XIV continued.

Family Elateridae

Sp. *Lacon variabilis* Candèze. (Sep. - Oct.)
Sp. *Conoderus exsul* (Sharp). (Nov.)
Sp. *Aeolus* sp. (Nov.)

Family Scarabaeidae

Sp. *Costelytra zealandica* (White). (Nov. - Dec.)
Sp. *Odontria striata* White. (Oct. - Dec.)
Sp. *O. varicolorata* Given. (Oct. - Jan.)
Sp. *Aphodius granarius* L. (Oct. - Nov.)

Family Nitidulidae

Sp. *Omosita colon* (L.) (Dec.)

Family Coccinellidae

Sp. *Coccinella undecimpunctata undecimpunctata* L. (Aug. - May)
Sp. *C. leorina* Fabricius. (Apr. - May).
Sp. *Adalia bipunctata* L. (Dec.)
Sp. *Rhizobius ventralis* Erichson. (Sep.)

Family Mycetophagidae

Sp. *Typhaea stercorea* L. (Nov.)

Family Colydiidae

Sp. *Enarsus rudis* Sharp. (Oct. and Mar.)

Family Tenebrionidae

Sp. *Enneboeus* sp. (Sep. - Apr.)

Family Cerambycidae

Sp. *Somatidia* (Ptinosoma) *convexa* Broun. (Sep. - May)

Family Curculionidae

Sp. *Hyperodes bonariensis* Kuschel. (All year).
Sp. *Irenimus carinalis* Broun. (Sep. - May)
Sp. *Otiorhynchus ovatus* (L.). (Oct. - Nov.)
Sp. *Listroderes obliquus* Klug. (Aug.)
Sp. *Epitimetes grisealis* Broun. (Oct. - May)

APPENDIX XIV continued.

Order Diptera

Suborder Nematocera

Family Tipulidae

Sp. Leptotarsus sp. (Sep. - Mar.)

Family Chironomidae

Sp. Chironomus zealandicus Hudson. (Oct.)

Suborder Brachycera

Family Syrphidae

Sp. Syrphus novae-zealandiae Macquart. (Sep. - Oct.)

Sp. Melanostoma fasciatum Macquart. (Oct.)

Family Heleomyzidae

Sp. Prosopantrum flavifrons (Tonnoir and Malloch). (Sep.)

Family Ephydridae

Sp. Hydrellia novae-zealandidae Harrison. (Dec. - Sep.)

Family Drosophilidae

Sp. Drosophila sp. (Dec. - Sep.)

Family Muscidae

Sp. Muscina stabulans Meigen. (Dec.)

Sp. Hylemyia cilicrura (Rondani). (Sep. - Jan.)

Family Calliphoridae

Sp. Calliphora erythrocephala. Meigen. (Sep. - Dec.)

Sp. C. laemica Wh. (Nov.)

Family Sarcophagidae

Sp. Sarcophaga milleri Johnston and Hardy. (All year).

APPENDIX XIV continued.

Order Lepidoptera

Suborder Monotrysia

Family Hepialidae

Sp. Wiseana cervinata Walker. (Oct. - Feb.)

Suborder Ditrysia

Family Coleophoridae

Sp. Coleophora alcyonipenella Kollar. (Nov. - Feb.)

Family Pyralidae

Sp. Crambus flexuosellus Dbld. (Dec.)

Family Noctuidae

Sp. Melanchra mutans Walker. (Sep. - Oct.)
Sp. Agrotis ypsilon (Walker). (Apr.)
Sp. Tmetolophota (Persectania) atristriga Walker. (Mar.)

Order Hymenoptera

Suborder Apocrita

Family Ichneumonidae

Sp. Diplazon laetatorius (Fabricius). (Jan.)

Family Brachonidae

Sp. Macrocentrus rubomaculatus (Cameron). (Dec.)

Family Psammocharidae

Sp. Salius wakefieldi Kby. (Jan.)
Sp. S. carbonarius Sm. (Dec.)
Sp. S. marginatus Sm. (Jan.)
Sp. S. monarchus Sm. (Dec.)

Family Vespidae

Sp. Vespula germanica (F.) (Apr.)

<u>APPENDIX XIV</u> continued.

Family Apidae

Sp. <u>Bombus terrestris</u> L. (Sep.)

Sp. <u>Apis mellifera</u> L. (Dec. - Jan.)

Phylum Arthropoda

Subphylum Mandibulata

Class Chilopoda

Order Craterostigmomorpha

Family Craterostigmidae

Sp. <u>Craterostigmus</u> sp. (Jan.)

Class Diplopoda

Sp. <u>Icosidesmus schenkeli</u> Carl. (Sep. - Feb.)

Sp. <u>Schedotrigona</u> sp. (Sep. - Nov.).

Phylum Arthropoda

Subphylum Chelicerata

Class Arachnida

Order Opiliones

Suborder Laniatores

Family Triaeonychidae

Sp. <u>Nuncia coriacea</u> Pocock. (Jan. - Feb.)

Suborder Palpatores

Family Phalangiidae

Sp. <u>Opilio opilio</u> L. (All year).

Order Araneae

Suborder Mygalomorpha

Family Ctenizidae

Sp. <u>Cantuaria</u> sp. (Jan.)

Family Dipluridae

Sp. <u>Aparua</u> sp. (Dec.)

APPENDIX XIV continued.

Suborder Araneomorpha

Family Gnaphosidae

Sp. Anzacia sp. (Feb.)

Sp. Megamyrmecion spp. (Nov.)

Family Lycosidae

Sp. Lycosa spp. (All year).

Family Toxopidae

Sp. Laestrygones sp. (Dec.)

Family Pisauridae

Sp. Dolomedes minor (Jan.)

Suborder Arachnomorpha

Family Linyphiidae

Sp. Meioneta sp. (Jan. - Feb.)

Sp. Mynoglenes incerta (Dec. - Jan.)

Sp. Lephtyphantes tenuis (Dec.)

Sp. L. trispathulatus (Jan.)

Family Micryphantidae

Sp. Aulacocyba subitanea (Sep. - Oct.)

Sp. Diplocephalus cristatus (Blackeo). (Oct.)

Family Epeiridae

Sp. Aranea pustulosa (Walckenaer). (Jan.)

Phylum Mollusca

Class Gastropoda

Subclass Pulmonata

Order Stylommatophora

Family Limacidae

Sp. Agriolimax spp. (All year).

APPENDIX XV.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

SPRING 1969

FOOD ITEM/DROPPING	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
GRASS	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CLOVER	1										1			1		1	1						1											1		1	1	1		
SEEDS	1		1						1	1	1	1								1		1								1							1		1	1
MISCELLANEOUS PLANTS	1	1	1	1		1	1		1	1	1	1	1	1	1	1		1		1									1				1				1		1	1
DIRT AND GRIT	1	1	1	1	1	1	1			1	1	1	1	1	1	1		1		1		1	1	1			1		1	1	1				1	1	1	1		1
EARWIGS					1			2	1	1	1	3	3	4	1	1	4	4		4	2	3	1	3	5	5	4	3	3	1	4	1		1	1	2	1	1	1	
LEPIDOPTERAN LARVAE		1	2	1	3			2	1		2	1	1	1	2	1	1				1		1					1						1		1	1	1		
HARVESTMEN																																				1				
<u>SARCOPHAGA</u> <u>MILLERI</u>																												1												
SLUGS		1	1	3		2	1				1	1			1	1		1		1			2				1	1	1		1	1	2	1	1	1	1	3		
UNKNOWN COLEOPTERA	1			1				1				1					1		1		1		1	1					1	1		1			1	1	1	1	1	1
EARTHWORMS	3	3	2	1		1	2																										1	1						
SPIDERS	1	1	1						1					1	1	1						1						1	1	1										
SLATERS									1	2			1	1														1	1	1		2	1		1		1		3	
GRASS GRUB BEETLES																																			2	2	3	1		4
HONEY BEES																					2		1										1		1				1	
<u>MEGADROMUS ANTARCTICUS</u>																											1									1				
ORIBATID MITES									1																										1		1			
PORINA MOTHS																			4										1								1	1		
<u>SALIUS</u> SP.																																								
<u>ODONTRIA</u> <u>STRIATA</u>								1																																
THRIPS																																								1
UNKNOWN LARVAE																														1										
BLOWFLIES																				1																				

APPENDIX XV continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

FOOD ITEM/DROPPING	SPRING 1969 41	42	43	44	45	46	47	48	49	50	SUMMER 1969/70 51	52	53	54	55	56	57	58	59	60	61
GRASS	1	1	1	1	1	1	1	1	1	1	1	1		1		1	1	1	1	1	1
CLOVER				1	1		1	1		1			1		1		1			1	1
SEEDS	1	1	1	1	1		1		1	1		1				2					2
MISCELLANEOUS PLANTS	1	1	1					1	1					1							1
DIRT AND GRIT	1	1				1				1	1		1			1				1	1
EARWIGS	1			1			1	1	1	2	1	4	1		1	4	4	4			1
LEPIDOPTERAN LARVAE	1	1	1					2	1			1					1	1	4	5	1
HARVESTMEN												1				1	1	1			1
SARCOPHAGA MILLERI									1						1				1		1
SLUGS		1						1	1												
UNKNOWN COLEOPTERA			1	1					1				1								
EARTHWORMS																					2
SPIDERS									1												
SLATERS		1											1			1	1	1	1		
GRASS GRUB BEETLES	4	4	4	4	4	5	4	2	3	1	4	1	4	5	3	1					
HONEY BEES					1																1
MEGADROMUS ANTARCTICUS	1																1	1			
ORIBATID MITES									1												
PORINA MOTHS	1	1																			
SALIUS SP.																					1
ODONTRIA STRIATA																					
THRIPS																					
UNKNOWN LARVAE																					
BLOWFLIES												1									

FOOD ITEM/DROPPING	AUTUMN 1970 62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
GRASS	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CLOVER	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1			1		1	1	
SEEDS		1	1			1					1	1	1		1					1			1	
MISCELLANEOUS PLANTS																			1					1
DIRT AND GRIT		1		1	1				1			1	1	1		1	1	1	1	1		1	1	1
EARWIGS	3	3				3		1	4		1	3		1			1	1	2		4			4
LEPIDOPTERAN LARVAE		1					1	3	1		1	1			1					1		2	3	1
HARVESTMEN		1	1		1	1	3	1			1	1				1		1	1	2			1	1
SARCOPHAGA MILLERI	1	1	1	1				1		1	1	1		1	1	1	1			1		1	1	1
SLUGS												1				1		1		1			1	1
UNKNOWN COLEOPTERA																			1		1			
EARTHWORMS	1	1		1	2		2						1	2	1			1						
SPIDERS						1		1	1			1	1				1					1		
SLATERS						1				1						1			2	1				
GRASS GRUB BEETLES																								
HONEY BEES																	1							
MEGADROMUS ANTARCTICUS								1																
ORIBATID MITES																								
PORINA MOTHS																								
SALIUS SP.																								
ODONTRIA STRIATA																								
THRIPS																								
UNKNOWN LARVAE															1									
BLOWFLIES																								

APPENDIX XV continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

AUTUMN 1970

FOOD ITEM/DROPPING	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122
GRASS		1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1
CLOVER		1	1		1	1			1	1	1	1	1	1	1			1	1		1	1						1	1				1		1	1	1
SEEDS	2	1			1															1	3					1					1					1	
MISCELLANEOUS PLANTS																	1				1													1			
DIRT AND GRIT	1	1	1	1		1	1	1			1	1			1		1	1		1				1					1				1				1
EARWIGS	1	4	2	3	3	1	3	4	3	2	1	2	1	1	1	1	3		2	1	2	1	1			1	1	1	1	1	3		1	1		1	
LEPIDOPTERAN LARVAE	1			1			1	1				1		3				1	1			1				1	1	4								1	
HARVESTMEN	1			1	1			1	1	1	1	1	2	1	2		1	1	1	1	1		1	1	5	1								1		1	
SARCOPHAGA MILLERI	3			1	1	1			1	1		1		1	1		1	1	1			1	2	1		1		1		1		1			1	1	1
SLUGS												1					1		1				2	3		1	1				1	1					
UNKNOWN COLEOPTERA					1					1									1															1			
EARTHWORMS		1	2								2		2																2	1		1			2		
SPIDERS			1	1						1											1									1						1	
SLATERS					1	2				1		1				3			1					1										2			
GRASS GRUB BEETLES																																					
HONEY BEES																																					
MEGADROMUS ANTARCTICUS																										1											
ORIBATID MITES										1																											
PORINA MOTHS																																					
SALIUS SP.															1																						
ODONTRIA STRIATA											1																										
THRIPS																																					
UNKNOWN LARVAE							1					1																									
BLOWFLIES																																					

APPENDIX XV continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

AUTUMN 1970

FOOD ITEM/DROPPING	123	124	125	126	127	128	129	130	131	132	133	134	135
GRASS	1	1	1	1	1	1	1	1	1	1	1	1	1
CLOVER	1				1	1	1	1	1	1	1	1	1
SEEDS													
MISCELLANEOUS PLANTS							1						
DIRT AND GRIT	1	1	1	1		1	1				1		1
EARWIGS								1			1		
LEPIDOPTERAN LARVAE	1	1		1			4	1	1		1		
HARVESTMEN	1	1			1						1		
<u>SARCOPHAGA</u> <u>MILLERI</u>					1		1	1			1		
SLUGS	1	1								4			5
UNKNOWN COLEOPTERA			1										
EARTHWORMS	2	1	1			1				2		2	
SPIDERS			1										
SLATERS													
GRASS GRUB BEETLES													
HONEY BEES													
<u>MEGADROMUS ANTARCTICUS</u>													
ORIBATID MITES													
PORINA MOTHS													
<u>SALIUS</u> SP.													
<u>ODONTRIA</u> <u>STRIATA</u>													
THRIPS													
UNKNOWN LARVAE													
BLOWFLIES													

WINTER 1970

FOOD ITEM/DROPPING	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156
GRASS	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CLOVER	1	1	1	1		1	1					1	1	1	1	1	1		1	1	1
SEEDS		1						1													
MISCELLANEOUS PLANTS								1													
DIRT AND GRIT				1					1	1	1		1		1			1			
EARWIGS			1								1	3	1								
LEPIDOPTERAN LARVAE													1			1	1			3	
HARVESTMEN											1					1	1				
<u>SARCOPHAGA</u> <u>MILLERI</u>	1	1	1	1																	
SLUGS		1			5	4			3		1	1					1				
UNKNOWN COLEOPTERA						1						1		1							
EARTHWORMS							1	1	2	1					2			2	1	1	
SPIDERS												1									
SLATERS												1									
GRASS GRUB BEETLES																					
HONEY BEES																					
<u>MEGADROMUS ANTARCTICUS</u>																					
ORIBATID MITES																					
PORINA MOTHS																					
<u>SALIUS</u> SP.																					
<u>ODONTRIA</u> <u>STRIATA</u>																					1
THRIPS																					1
UNKNOWN LARVAE																					
BLOWFLIES																					

APPENDIX XV continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

	WINTER 1970																SPRING 1970																	
FOOD ITEM/DROPPING	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190
GRASS	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1		1	1	1	1
CLOVER		1	1	1	1	1		1	1	1		1		1	1		1	1	1	1	1	1	1											
SEEDS					1	1						1								1				1			1		1					
MISCELLANEOUS PLANTS					1							1																						
DIRT AND GRIT				1	1	1			1	1	1	1	1	1	1		1		1		1										1	1	1	
EARWIGS			1			1					5		1			3	1		1		1			1		1		1			1	2	2	3
LEPIDOPTERAN LARVAE	4	1		1	4	1		1	1	1			1		1		1				1													1
HARVESTMEN																												1				1	1	1
SARCOPHAGA MILLERI																				1														
SLUGS			1	1			4							2	1	1	2		2	2	1	4										1		
UNKNOWN COLEOPTERA	1		1		1									1		1			1		1		1	1	1	1	1	1	1		1	1	1	
EARTHWORMS									2	2		1		2				1	1															
SPIDERS								1								1											1	1						
SLATERS															2		2						3	1		1								1
GRASS GRUB BEETLES																								4	4	3	4	4	4	5	4	2	2	1
HONEY BEES																																		
MEGADROMUS ANTARCTICUS												1																						
ORIBATID MITES							1																											
PORINA MOTHS																																		
SALIUS SP.																																		
ODONTRIA STRIATA																																		
THRIPS						1																												
UNKNOWN LARVAE																																		
BLOWFLIES																																		

APPENDIX XV continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

	SUMMER 1970/71					AUTUMN 1971																												
FOOD ITEM/DROPPING	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224
GRASS	1	2	2	1	1		1	1	1		1	1	1	3	3	2	3	1	2	1	1	1	1	1	1	1	3	2	2	2	1	2	2	1
CLOVER	1	1											1		1	1	1		1	1		1					1	1	1		1	1	1	1
SEEDS	1		1						2													2	2									1	2	2
MISCELLANEOUS PLANTS																																		
DIRT AND GRIT		1			1	1			1				1			1		1			1		1		1			1			1	1		
EARWIGS	1	1	1			4	4	3	1		2											4		3	2	2							1	2
LEPIDOPTERAN LARVAE		2	2	3				1	3	5	1	3	4		1		1	1	1	1	1	1	2	1	1		1				1			1
HARVESTMEN		1	1		1	1	1	1			1	1			1			1	1	1		1	1	1	1				1	1		1	1	1
SARCOPHAGA MILLERI			1	1					1		1	1	1			1		1		1	1			1	1	1	1	1	1	1	1	1	1	1
SLUGS	2																																	
UNKNOWN COLEOPTERA				1																	1										1			
EARTHWORMS									1																									
SPIDERS	1											1			1	1			1			1			1	1								
SLATERS			1																															
GRASS GRUB BEETLES																																		
HONEY BEES				1																														
MEGADROMUS ANTARCTICUS																																		
ORIBATID MITES	1													1																				
PORINA MOTHS																																		
SALIUS SP.												1				1	1																	
ODONTRIA STRIATA						1																												
THRIPS														1																				
UNKNOWN LARVAE																																		
BLOWFLIES																								1										

APPENDIX XV continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 24 FOOD ITEMS.

	AUTUMN 1971			WINTER 1971				
FOOD ITEM/DROPPING	225	226	227	228	229	230	NUMBER OF OCCURRENCES	PERCENTAGE FREQUENCY OF OCCURRENCE
GRASS	3	1	1	1	1	1	218	95
CLOVER	1	1		1	1	1	124	54
SEEDS							57	25
MISCELLANEOUS PLANTS							39	17
DIRT AND GRIT	1				1		115	50
EARWIGS	1	1					126	55
LEPIDOPTERAN LARVAE	1	1	2	1		1	106	46
HARVESTMEN	1						75	33
<u>SARCOPHAGA MILLERI</u>							73	32
SLUGS			1	1	4	2	69	30
UNKNOWN COLEOPTERA							52	23
EARTHWORMS				1	1	1	50	22
SPIDERS							39	17
SLATERS							39	17
GRASS GRUB BEETLES							32	14
HONEY BEES							9	4
<u>MEGADROMUS ANTARCTICUS</u>							8	3
ORIBATID MITES							8	3
PORINA MOTHS							6	3
<u>SALIUS</u> SP.							5	2
<u>ODONTRIA STRIATA</u>							4	2
THRIPS							4	2
UNKNOWN LARVAE							4	2
BLOWFLIES							3	1

APPENDIX XVI.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

SPRING 1969

FOOD ITEM/DROPPING	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
EARWIGS					5			8	5	4	1	9	17	75	2	1	35	12		17	3	3	1	3	3	13	51	10	6	2	19	1		1	6	9	3
LEPIDOPTERAN LARVAE		1	8	1	12			9	4		16	4	1	3	4	1	1				2		1					3						1		1	1
HARVESTMEN																																				1	
SARCOPHAGA MILLERI																												1									
SLUGS		1	3	3		5	3				6	2			1	1		1		1			2				3	2	1		2	1	2	1	3	5	3
UNKNOWN COLEOPTERA	1			1				1				3					1		1		1		1	1					1	2		1			1	1	2
SPIDERS	1	1	1						2					2	1	1						1						1	1	1							
SLATERS									9	13			3	12														1	1	1		6	1		11		4
GRASS GRUB BEETLES																																			17	8	34
HONEY BEES																					3		1										1		1		
MEGADROMUS ANTARCTICUS																											1									1	
ORIBATID MITES									1																										11		1
PORINA MOTHS																			12										2								2
SALIUS SP.																																					
ODONTRA STRIATA								1																													
THRIPS																																					
UNKNOWN LARVAE																														8							
BLOWFLIES																				1																	

APPENDIX XVI continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

SPRING 1969

FOOD ITEM/DROPPING	38	39	40	41	42	43	44	45	46	47	48	49	50
EARWIGS	3	2		4			1			3	1	4	3
LEPIDOPTERAN LARVAE	1			9	2	1					17	5	
HARVESTMEN													
SARCOPHAGA MILLERI												1	
SLUGS	8				1						1	2	
UNKNOWN COLEOPTERA	2	1	1			1	1					2	
SPIDERS												1	
SLATERS		12			1								
GRASS GRUB BEETLES	3		33	70	14	13	32	8	15	16	21	25	1
HONEY BEES		1						1					
MEGADROMUS ANTARCTICUS				1									
ORIBATID MITES												3	
PORINA MOTHS	1			1	1								
SALIUS SP.													
ODONTRA STRIATA													
THRIPS			1										
UNKNOWN LARVAE													
BLOWFLIES													

SUMMER 1969/70

FOOD ITEM/DROPPING	51	52	53	54	55	56	57	58	59	60	61
EARWIGS	1	12	3		5	16	18	25			1
LEPIDOPTERAN LARVAE		1					3	1	48	50	3
HARVESTMEN		1				1	1	3			4
SARCOPHAGA MILLERI					1				2		1
SLUGS											
UNKNOWN COLEOPTERA			1								
SPIDERS											
SLATERS			1			1	4	3	1		
GRASS GRUB BEETLES	29	3	14	4	8	1					
HONEY BEES											1
MEGADROMUS ANTARCTICUS							1	1			
ORIBATID MITES											
PORINA MOTHS											
SALIUS SP.											1
ODONTRA STRIATA											
THRIPS											
UNKNOWN LARVAE											
BLOWFLIES		1									

AUTUMN 1970

FOOD ITEM/DROPPING	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
EARWIGS	3	5				13		6	24		2	7		2			3	3	9		8
LEPIDOPTERAN LARVAE		1					1	12	4		1	2			2					3	
HARVESTMEN		1	1		2	2	5	2			3	3				1		2	1	8	
SARCOPHAGA MILLERI	1	1	1	1				3		2	3	1		1	3	2	1			7	
SLUGS												1				1		3		6	
UNKNOWN COLEOPTERA																			1		1
SPIDERS						1		1	1			1	1				1				
SLATERS						8				6						1			12	7	
GRASS GRUB BEETLES																					
HONEY BEES																	1				
MEGADROMUS ANTARCTICUS								1													
ORIBATID MITES																					
PORINA MOTHS																					
SALIUS SP.																					
ODONTRA STRIATA																					
THRIPS																					
UNKNOWN LARVAE															1						
BLOWFLIES																					

APPENDIX XVI continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

AUTUMN 1970

FOOD ITEM/DROPPING	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
EARWIGS			11	1	6	3	7	14	3	9	9	3	8	2	10	2	4	2	1	8		8	2	3	1	5			2	1	1	1	1	12		2	3	
LEPIDOPTERAN LARVAE	3	11	2	1			1			6	1				2		9				2	2			1				5	1	7							
HARVESTMEN		1	1	1			3	1			1	1	1	1	1	4	1	4		2	3	2	1	1		1	1	16	1								1	
SARCOPHAGA MILLERI	1	4	1	8			1	3	1			1	2		1		1	1		1	3	2			1	6	1		3		1		1		1			1
SLUGS		4	1												1					2		2				6	9		1	1				6	2			
UNKNOWN COLEOPTERA								1					1									1															1	
SPIDERS	1					1	1						1											1									1					
SLATERS								4	11				7		9				8			2					3										13	
GRASS GRUB BEETLES																																						
HONEY BEES																																						
MEGADROMUS ANTARCTICUS																													1									
ORIBATID MITES													2																									
PORINA MOTHS																																						
SALIUS SP.																		1																				
ODONTRA STRIATA														1																								
THRIPS																																						
UNKNOWN LARVAE										1					1																							
BLOWFLIES																																						

APPENDIX XVI continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

AUTUMN 1970

FOOD ITEM/DROPPING	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
EARWIGS	3									1			1		
LEPIDOPTERAN LARVAE	1		1	2		1			9	2	1		1		
HARVESTMEN	1		1	1			2						1		
SARCOPHAGA MILLERI	3	1					1		1	1			1		
SLUGS			1	1								8			8
UNKNOWN COLEOPTERA					1										
SPIDERS	1				1										
SLATERS															
GRASS GRUB BEETLES															
HONEY BEES															
MEGADROMUS ANTARCTICUS															
ORIBATID MITES															
PORINA MOTHS															
SALIUS SP.															
ODONTRA STRIATA															
THRIPS															
UNKNOWN LARVAE															
BLOWFLIES															

WINTER 1970

FOOD ITEM/DROPPING	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154
EARWIGS			1								1	4	1						
LEPIDOPTERAN LARVAE													2			1	2		
HARVESTMEN											1					1	1		
SARCOPHAGA MILLERI	1	1	1	1															
SLUGS		2			7	6			2		2	2					1		
UNKNOWN COLEOPTERA						1						1		1					
SPIDERS												1							
SLATERS												2							
GRASS GRUB BEETLES																			
HONEY BEES																			
MEGADROMUS ANTARCTICUS																			
ORIBATID MITES																			
PORINA MOTHS																			
SALIUS SP.																			
ODONTRA STRIATA																			
THRIPS																			
UNKNOWN LARVAE																			
BLOWFLIES																			

APPENDIX XVI continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

	WINTER 1970																		SPRING 1970															
FOOD ITEM/DROPPING	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188
EARWIGS					2			1					18		1			4	2		2		1			2		3		2			1	8
LEPIDOPTERAN LARVAE	4		6	2		2	11	3		3	2	2			1		2		1				2											
HARVESTMEN																														1				1
SARCOPHAGA MILLERI																						1												
SLUGS					2	1			6							3	1	1	4		3	3	2	8										1
UNKNOWN COLEOPTERA			1		1		1									2		1			1		1		1	2	1	1	1	1	1		1	1
SPIDERS										1								1											1	1				
SLATERS																	7		13						11	1		1						
GRASS GRUB BEETLES																										19	12	13	7	28	34	41	18	15
HONEY BEES																																		
MEGADROMUS ANTARCTICUS														1																				
ORIBATID MITES									1																									
PORINA MOTHS																																		
SALIUS SP.																																		
ODONTRA STRIATA		1																																
THRIPS		2						3																										
UNKNOWN LARVAE																																		
BLOWFLIES																																		

APPENDIX XVI continued.

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

	SUMMER 1970/71							AUTUMN 1971																										
FOOD ITEM/DROPPING	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222
EARWIGS	12	12	1	2	3			13	12	8	2		3											15		6	4	4						
LEPIDOPTERAN LARVAE		2		7	8	15				3	7	14	1	9	7		2		1	1	2	1	3	1	6	1	1		1				1	
HARVESTMEN	1	2		2	2		2	2	3	3			1	2			1			1	4	1		2	2	1	1				1	1		1
SARCOPHAGA MILLERI					1	1					1		1	3	1			1		1		2	1			2	1	1	1	2	2	1	1	1
SLUGS			4																															
UNKNOWN COLEOPTERA	1					1																	1										1	
SPIDERS			1											1			1	2			1			1			1	1						
SLATERS		2			4																													
GRASS GRUB BEETLES	9	4																																
HONEY BEES						1																												
MEGADROMUS ANTARCTICUS																																		
ORIBATID MITES			1													1																		
PORINA MOTHS																																		
SALIUS SP.														1				1	1															
ODONTRA STRIATA								1																										
THRIPS																1																		
UNKNOWN LARVAE																																		
BLOWFLIES																										1								

ANALYSES OF 230 DROPPINGS OF HEDGEHOGS FROM PASTURE LANDS, SHOWING THE DIRECT COUNTS OF 18 ANIMAL FOOD ITEMS.

	AUTUMN 1971					WINTER 1971			
FOOD ITEM/DROPPING	223	224	225	226	227	228	229	230	TOTAL NUMBER OF ANIMALS
EARWIGS	2	5	1	2					823
LEPIDOPTERAN LARVAE		2	1	2	4	2		1	465
HARVESTMEN	1	3	1						144
<u>SARCOPHAGA</u> <u>MILLERI</u>	2	2							121
SLUGS					3	2	8	4	206
UNKNOWN COLEOPTERA									60
SPIDERS									42
SLATERS									217
GRASS GRUB BEETLES									569
HONEY BEES									11
<u>MEGADROMUS</u> <u>ANTARCTICUS</u>									8
ORIBATID MITES									21
PORINA MOTHS									19
<u>SALIUS</u> SP.									5
<u>ODONTRA</u> <u>STRIATA</u>									4
THRIPS									7
UNKNOWN LARVAE									11
BLOWFLIES									3

APPENDIX XVII.

ANALYSES OF THE STOMACH CONTENTS OF 60 HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 25 FOOD ITEMS.

	SPRING 1970															SUMMER 1970-71																								
FOOD ITEM/HEDGEHOG	S1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
GRASS	2	1	1	2	1				1	1	1	1	1	1		2	1	2	1	3	2	1	1	1	2	1	1	1	1	1		2	2	1		1	1	1	1	1
CLOVER	1		1						1	1								1						1																
SEEDS		1	1												1				1		1	1	1	1		1	1	1	1	1				1		1				
MISCELLANEOUS PLANTS									1					1	1	1	1	1	1			1		1								1								
DIRT AND GRIT		1		1		1			1	1	1	1		1	1			1						1	1			1	1											
EARWIGS	1	2				1	1		1	4	4		1	1	1	1	1	2	1	1	2	4	1	1	1	1	1	3	4	4		1	1	1						
LEPIDOPTERAN LARVAE	2	1		2	4				3		1		1			2	1	1			1	1			1	1		1		1		2	2	2	5	4	4	2	1	1
HARVESTMEN																1	2	1	1	1	1	1		1	1	1	1	1	1	1	1			1			1	1	2	2
SARCOPHAGA MILLERI																												1											1	2
SLUGS		1			1		4			1			1	1	1	1		1		1			1			1				1										
UNKNOWN COLEOPTERA	1	1	1	1					1				1	2		1		1	2		1	1	1	1	1	1		1	1	1				1				2	1	
EARTHWORMS		1	1	1								1									1																			1
SPIDERS	1	1	1						1		1			1		1	1	1		1	1	1	1	1		1										1	1	1		1
SLATERS														1				1		1									1											
GRASS GRUB BEETLES		1			1				1					1	2	1	2	1				1																		
HONEY BEES			1						1						1			1			1	1		1		1					1		1	1			1			
MEGADROMUS ANTARCTICUS									1					2			1	1		1	1	1	1			1	1	1												
ORIBATID MITES				1										1		1													1	1						1				
PORINA MOTHS			1								1		3													1			1		1									
ODONTRIA STRIATA	1	1							1		1		1	1				1				1			1															
THRIPS				1	1								1																1											
WETAS															1							1	1																	
METAGLYMMA MONILIFER	1	2	3						1				1																											
CENTIPEDES											1																													
LAEMOSTENUS COMPLANATUS															1																									

APPENDIX XVII continued.

ANALYSES OF THE STOMACH CONTENTS OF 60 HEDGEHOGS FROM PASTURE LANDS, SHOWING THE OCCURRENCE AND RELATIVE VOLUMES OF 25 FOOD ITEMS.

	SUMMER 1970-71.																				NUMBER OF OCCURRENCES		PERCENTAGE FREQUENCY OF OCCURRENCE	
FOOD ITEM/HEDGEHOG	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	LINCOLN	KAIKOURA	LINCOLN	KAIKOURA
GRASS	1	2	1	1	1	1		2	1	1	1	1	1	1	1	1	1	1	1	1	39	14	65	23
CLOVER												1		1	1						6	3	10	5
SEEDS		1	1	1	1						1	1	1	1			1				19	5	32	8
MISCELLANEOUS PLANTS	1	1	1	1		1		1	1	1				1	1			1	1	1	14	9	23	15
DIRT AND GRIT	3	2	1	1		1		1	1	1	1	1	1	1		1	1	1	1		18	12	30	20
EARWIGS				1		1				1	1	1	1		1	1		1	1		29	9	48	15
LEPIDOPTERAN LARVAE	1			2	3		1	1	1	2	1	1	1	1	1				1	1	28	11	47	18
HARVESTMEN	1			1				2	1	1	1			1				1			22	6	37	10
SARCOPHAGA MILLERI	2		3	1	1										1					1	8	1	13	2
SLUGS		1			1		2						1		1		1				15	4	25	6
UNKNOWN COLEOPTERA						1				1	1	1	1	1	1	1	1				22	9	37	15
EARTHWORMS										1	1		1	1	1		1		1		6	6	10	12
SPIDERS		1								1	1	1	1	1	1	1		1			10	8	33	13
SLATERS																		1			4	1	6	2
GRASS GRUB BEETLES						1				2	4	4	3	4	4	4	4	4	4	4	9	12	15	20
HONEY BEES			1							1											13	1	22	2
MEGADROMUS ANTARCTICUS																					11	-	18	-
ORIBATID MITES				1																	7	-	12	-
PORINA MOTHS																					6	-	10	-
ODONTRIA STRIATA																					9	1	15	2
THRIPS																					4	-	6	-
WETAS				1		1	1														4	2	6	3
METAGLYMMA MONILIFER																					5	-	8	-
CENTIPEDES																		1			1	1	2	2
LAEMOSTENUS COMPLANATUS								1													1	1	2	2

APPENDIX XVIII.

ANALYSES OF THE STOMACH CONTENTS OF 60 HEDGEHOGS FROM PASTURE LANDS SHOWING THE DIRECT COUNTS OF 19 ANIMAL FOOD ITEMS.

FOOD ITEM/HEDGEHOG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
EARWIGS	3	10				3	1		8	8	47		5	9	2	2	2	9	6	4	19	47	4	4	2	17	1	11	27	21
LEPIDOPTERAN LARVAE	10	4		7	23				22		1		1			11	3	6			2	3			1	11		4		4
HARVESTMEN																1	4	1	3	1	4	2		2	1	4	1	3	2	1
SARCOPHAGA MILLERI																												1		
SLUGS		3			2		4			1			1	1	1	1		3		4			2			5				1
UNKNOWN COLEOPTERA	5	9	2	1					3				2	27		6		2	6		2	2	3	4	2	2		2	2	2
SPIDERS	3	1	2						2		2			1		1	1	1		1	1	2	1	1		1				
SLATERS														4				5		1									4	
GRASS GRUB BEETLES		4			1				3					2	5	4	3	4				5								
HONEY BEES			1						7						1			3			1	1		2		1				
MEGADROMUS ANTARCTICUS									2					11			1	1		1	7	6	1			1	1	1		
ORIBATID MITES				1										1		8													2	5
PORINA MOTHS			1								10		22													1			2	
ODONTRIA STRIATA	1	1							1		4		3	1				1				3			1					
THRIPS				1	1								1																1	
WETAS															1							2	1							
METAGLYMMA MONILIFER	3	11	6						1				2																	
CENTIPEDES											2																			
LAEMOSTENUS COMPLANATUS															2															

APPENDIX XVIII continued.

ANALYSES OF THE STOMACH CONTENTS OF 60 HEDGEHOGS FROM PASTURE LANDS SHOWING THE DIRECT COUNTS OF 19 FOOD ITEMS.

FOOD ITEM/ HEDGEHOGS	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	TOTAL NUMBER OF ANIMALS LINCOLN	KAIKOURA
EARWIGS		2	2	1										1		1				1	1	1	1		1	1		3	2		278	12
LEPIDOPTERAN LARVAE		6	2	3	46	1	16	2	2	1	5			3	19		1	1	1	7	1	4	1	10	4				8	1	217	39
HARVESTMEN	1			1			1	1	3	2	6			1				2	1	1	1			1				1			46	7
SARCOPHAGA MILLERI				1					1	2	8		66	1	6										1						86	1
SLUGS												2			1		2						1				1			2	32	6
UNKNOWN COLEOPTERA				1				2	1							1				2	1	2	3	2	1	1	1				88	14
SPIDERS						1	1	1		1		1								1	1	2	1	1	1	1		1			26	9
SLATERS																												1			14	1
GRASS GRUB BEETLES																1				4	128	122	9	101	74	150	284	73	175	125	31	1244
HONEY BEES	1		1	1			1						3							1											25	-
MEGADROMUS ANTARCTICUS																															33	-
ORIBATID MITES						1								1																	19	-
PORINA MOTHS	1																														37	-
ODONTRIA STRIATA																												1			16	1
THRIPS																															4	-
WETAS														1		1	1														5	2
METAGLYMMA MONILIFER																															23	-
CENTIPEDES																												1			2	1
LAEMOSTENUS COMPLANATUS																		1													2	1