SOME ASPECTS OF THE ECOLOGY OF THE HEDGEHOG

(Erinaceus Europaeus L.)

IN THE MANAWATU NEW ZEALAND

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1972

A THESIS PRESENTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN ZOOLOGY AT MASSEY UNIVERSITY.

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1972.

ABSTRACT

During the period from 1/1/70 to 24/6/71, 150 hedgehogs were marked and 356 resightings were recorded in a study area covering 16.28 hectares of pasture and trees. Population size and density are estimated and the seasonal changes in activity are described.

The sex ratio of the population and the apparent changes in this ratio due to behavioural dimorphism between sexes are discussed in relation to the body weights of the animals and to hibernation and breeding season. No detailed age structure is presented for the present population.

The breeding season and the number and size of the litters are discussed, as are the causes of mortality in the population. Dispersal of the population is seen as an important demographic parameter, and the sexual and seasonal influences upon movement are discussed.

Home ranges are investigated using two statistical methods; the convex polygon method and a probability ellipse method. The shape and size of individual's ranges are described using the first method, while the second method is used to describe synthesised ranges for males, females and juveniles. The nest site and food locations are discussed in terms of foci of activity, and seasonal changes in movements were investigated and an argument is advanced on the hedgehog's territorial behaviour and social structure.

PREFACE

When choosing a topic within the desired field of mammalian ecology, the length and economics of the study meant that certain restrictions had to be applied. Short studies of mammalian population ecology are usually complicated by the difficulties of catching enough individuals and the expense of traps. As hedgehogs are numerous in the Manawatu and are easily caught without traps, this species fulfills these two requirements. Further, the number of mammalian species within the region is limited and the majority of species have been or are being studied more intensively than this thesis allows. The exception to this was the hedgehog, the last ecological study in New Zealand having been carried out by Brockie (1958).

An appreciation of the critical assistance and patience of my supervisor, Dr R.A. Fordham is gratefully acknowledged.

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INTRODUCTION.

1.1 Review of previous work.

While there has been a great amount of popular writing about the hedgehog and some detailed laboratory studies of the species' physiology and behaviour, the amount of quantitative data available on the natural life of hedgehogs has been, until quite recently, rather fragmentary.

Herter (1963) and Burton (1969) distilled the knowledge obtained from many scientific studies and the observations of naturalists into two popular books.

In laboratory studies on the hedgehog, Eisentraut (1935), Adrian (1942), Proctor (1949), Bioerck, Johansson and Veige (1956), Kristoffersson and Suomalainen (1964), Kristoffersson and Soivio (1967a and 1967b), Kristoffersson and Broberg (1967), Sarajas (1967) and Clausen, Gunnar and Ersland (1968) have studied various aspects of species' physiology related to hibernation. In other laboratory studies Dimelow (1963) has described the general behaviour of captive hedgehogs, while Kristoffersson (1964) has recorded activity cycles in caged animals.

Field studies on the hedgehog have been largely restricted to investigations of various aspects of the breeding cycle. Mating behaviour has been observed by

Degerbol (1943), Haarlov (1943) and Morris, B. (1961), while studies on the actual breeding cycle have been carried out by Courrier (1927), Allanson (1934), and Allanson and Deanesly (1935), Deanesly (1935), Schuetz (1956) and Saure (1969).

A few, mostly limited, studies on the feeding ecology of hedgehogs have been carried out by Ch'eng Chao Lui (1937), Bull (1940), Cott (1951), Brockie (1957, 1959) and Dimelow (1963).

The fact that hedgehogs are vectors for several human diseases has resulted in a number of investigations of the pathogens and parasites carried by the species. In New Zealand, Brockie (1958) and Smith (1968) have made studies of the diseases carried out by the hedgehog, while in Europe McLauchlan and Henderson (1947), Webster (1957), Campbell and Smith (1966) and Foxall (1969) have described various ailments of the hedgehog. Little quantitative data exist however on the ecological effects of these diseases on natural hedgehog populations.

Field studies on the population ecology of hedgehogs are much more rare, the two major works of relevance to the present study being in the form of theses and associated published papers by Brockie (1958) on New Zealand hedgehogs, and Morris, P. (1968) on a British population. Both of these authors have some data on the movements of hedgehogs, although their results are presented in a two-dimensional frame and thus give little idea of the "anatomy" of the home range of the species. The larger movements involving population dispersal have been discussed by Wodzicki (1956) and Kruger (1969). Both studies describe the colonisation of new territory, the former in New Zealand and the latter in Finland.

Other works on hedgehogs which contain relevant ecological data are mentioned in the body of the present thesis.

1.2 Study area.

The study area chosen for the main part of this work was the grassed farmland of the Massey University Number Two Dairy Farm. This area is bordered on one side by the Manawatu river, is continuous with similar farmland on two sides, and is bordered on the fourth side by a large pine plantation some 150 meters deep. An intensive study area extended over 16.28 hectares, comprising 12.5 hectares of pasture, 3.78 hectares of trees (mostly *Pinus radiata* but with small areas of *Populus italica*, *Salix alba* and *Eucalyptus ficifolia*) plus some small areas of long tussocky grass, mostly *Festuca* species, and a small lagoon (plates 1, 2, 3 and 4).

This particular area was chosen as it is close to the university and yet largely undisturbed by humans, apart from a few farm staff. Further, the number of shelter belts and plantations around the area provide ample cover in which the hedgehogs can nest. A significant cause of interference however, both to myself and to the hedgehogs, was the periodic presence of a herd of dairy cows.

Data on breeding cycles were obtained from animals caught in the suburbs of Palmerston North and in the Massey University orchards. Most of these animals were caught during 1969 and none were taken from within one mile of the main study area.

Plate 1. Central Pine Plantation with the Deep Plantation in the background.

Plate 2. Typical summer pasture. Deep Pine Plantation in the background.

Plates 3 and 4. Typical nest sites within the Pine Plantations.

Plate 5. <u>Lush grass surrounding area of Pig Sty effluent</u>. <u>A rich food supply for the hedgehogs</u>.

1.3 General methods.

A map of the study area was drafted on aerial photographs from the town planning section of the Palmerston North City Council, and on measurements taken in the field, from which the scale was calculated. An error of closure of less than 0.5 per cent of the total perimeter was considered acceptable.

Observations of the area was made on at least two nights per week during the year February 1970 to February 1971, except for the winter months - July, August, September and October - when the scarcity of active hedgehogs made this programme unwarrented and the frequency of observation was halved. Infrequent observations were continued until July 1971.

These observations of the study area were made by walking over a grid system and spotlighting the animals with a six volt battery-lantern. The "lines" of the grid were dependant on the range of the lantern, ideally about 25 meters, and on the nature and height of the vegetation. To eliminate any possible bias caused by following a permanent route, the orientation of the "lines" was altered from that of the previous night. A minimum search-time of one hour was used, ensuring some standardisation of effort, and a system of staggered visits throughout the night was invented to allow for any changes in nocturnal activity. This latter was done by starting the search period at about the time when the previous night's search had finished. When visits were interrupted by the dawn, the next visit was made at dusk and the whole system repeated.

The positions of all animals found within the search area were located by means of numbered pegs, the co-ordinates of which were noted and transferred to maps. A system of marked fence posts was used as the origins for these co-ordinates and later, when many distances were memorised, the co-ordinates could be noted without having to measure about a peg.

Before the 24th March 1970 only those individuals found around the central pine plantations were marked, although after this date the area in which animals were marked was gradually extended and all animals caught were weighed, sexed and marked with paint for easy individual identification. Most animals were also ear-tagged with small metal fish tags as a more permanent check on identity.

Two types of paint were used in marking the hedgehogs' prickles; Dulux Superenamel and Mecca waterproof paint. Marks consisted of a series of simple designs painted on the spines on the hedgehog's back in one of six colours - red, white, blue, yellow, green and pink. The enamel was the more successful of the two types, the marks remaining clear throughout the study. The waterproof paint had to be replaced after three or four months, as it tended to wear off. A few animals apparently lost their spines more frequently than is usual, and retouching of the mark was necessary in these cases as well.

Generally these operations were carried out while the animal was anaethetised with chloroform, however it was later found to be possible to do all of these operations on most animals without having to anaethetise them. This was useful as it saved time, caused less disturbance to the animal and there was less chance of an accidental death from an overdose of chloroform.

Recaptured animals were weighed and their positions were noted.

Hedgehogs captured in the Massey University orchards and in Palmerston North were killed in the laboratory, weighed and measured; after dissection the various reproductive organs and accessory glands were weighed and preserved in Bouin's solution. The carcases were stored in a refrigerator at the University.

Meteorological data were obtained from a field station at the Department of Scientific and Industrial Research, a few hundred meters from the main study area.

2

POPULATION STRUCTURE.

2.1 Population size and density.

An estimate of the number of hedgehogs in an area at any one time is made extremely difficult by the nocturnal habit of the species which makes individuals difficult to locate, and in the present case, by the high turnover of individuals in the population.

In this study, 150 animals were marked 356 resightings were recorded between 1/1/70 and 24/6/71, giving a mean of 2.37 resightings per individual marked. Of those marked, 58 (38.7 per cent) were never resighted and only six were resighted more than ten times.

TABLE 1

ANIMALS RESIGHTED MORE THAN TEN TIMES

Individual	Date marked	Date last seen	Number of times resighted
SpotML817	11/1/70	22/12/70	19
StripBL831	6/4/70	24/6/71	16
Sp. MYWL820	20/3/70	30/11/70	15
Strip G	24/3/70	24/6/71	19
BB WL838	21/1/70	24/6/71	13
BB ML829	19/2/70	19/3/71	11

Excluding (a) the first three months of the study when large numbers of animals were still unmarked and recruitment through breeding complicated matters,

(b) the winter months June to September inclusive, when hibernation affected the numbers of hedgehogs observed, and

(c) all resightings, the number of hedgehogs seen per ten hours searching in the four months April, May, November and December averaged 33.5 - 2.6 per month. Assuming that the numbers of individuals entering and leaving the study area throughout the period were equal, this figure is probably a fair estimate of the number of individuals whose home range's lie wholly or partly within the study area. This density of two animals per hectare is an overestimate because of the peripheral individuals which spend some time out of the area, and at the same time is an underestimate on account of those animals present in the area but not observed during the month.

Previous estimates of the density of hedgehogs have been made in several places in Europe. Burton (1969) estimated an average density of 2.5 hedgehogs per hectare for the whole of Britain. In Germany, Zimmermann (quoted in Herter, 1963) gives an estimate of 40 to 50 individuals in a Saxon woodland comprising about 400 wooded[1] and 24 open hectares, an overall density of between 0.094 and 0.128 animals per hectare. If we ignore the wooded area as a normal foraging habitat for the hedgehogs, this is a density of between 1.66 and 2.08 animals per open hectare.

A Russian study, Kalabuchow (1928) gave a density of between five and 7.5 animals per hectare as the maximum reach in parts of the Ukraine, while Bibikov (1957) studying Erinaceus auritus, estimated a density of three animals per hectare in dairy country in Southern Russia.

In New Zealand, Brockie (1958) gave densities of at least 2.5 animals per hectare at Gwavas and Point Howard, while in the sand dune country at Paekakariki and Otaki, he estimated densities of at least five to 7.5 hedgehogs per hectare.

The density estimated in the present study is within the range expected from these earlier studies however it is hard to find any evidence for the commonly quoted assumption that densities in New Zealand are very much higher than those in Europe and Britain. The main evidence for this assumption comes from three road-mortality studies on the hedgehog, the

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[1] Misquoted as 4000 hectares in the English edition of Herter (1963).

first by Davies (1957) in Hampshire, the second by Morris (1968) in Surrey and the third by Brocke in New Zealand. This last study indicated very much higher road mortality indices in New Zealand; x50 and x32 respectively, however these data are difficult to reconcile with the actual densities estimated in this and previous studies.

The variation in the densities given may be explained in part by the differing methods of estimation, in part by the differences in the habitats from which the estimations were made, and in part by the differing patterns of dispersal in the various populations.

2.2 Seasonal Changes in Activity

Seasonal rhythms are apparent in the lives of almost all animals, hedgehogs being typical of those animals with a more or less distinct breeding season and a period of hibernation during the winter. These rhythms, involving the population in different levels of activity are expressed in changes in the number of animals observable.

Consideration of the apparent changes in the population size as estimated from the number of animals seen each night, standardised to a constant searching time of one hour, shows that considerable variation exists in the numbers of animals seen on nights separated by only a few days. For example 14 animals were observed per hour searched on 3/2/70 and only five animals per hour searched on 27/2/70. (Figure 1). No satisfactory reason can be given for these large variations.

Taken over the whole year however, a pattern of activity is apparent. From monthly means of between 8.5 and 9.3 animals per hour searched over January, February and March, the activity of the population steadily dropped until July which had a mean of only 1.6 animals per hour searched. This lack of activity did not alter significantly until mid-October and November, when the monthly mean was about five animals per hour searched. (Figure 1)

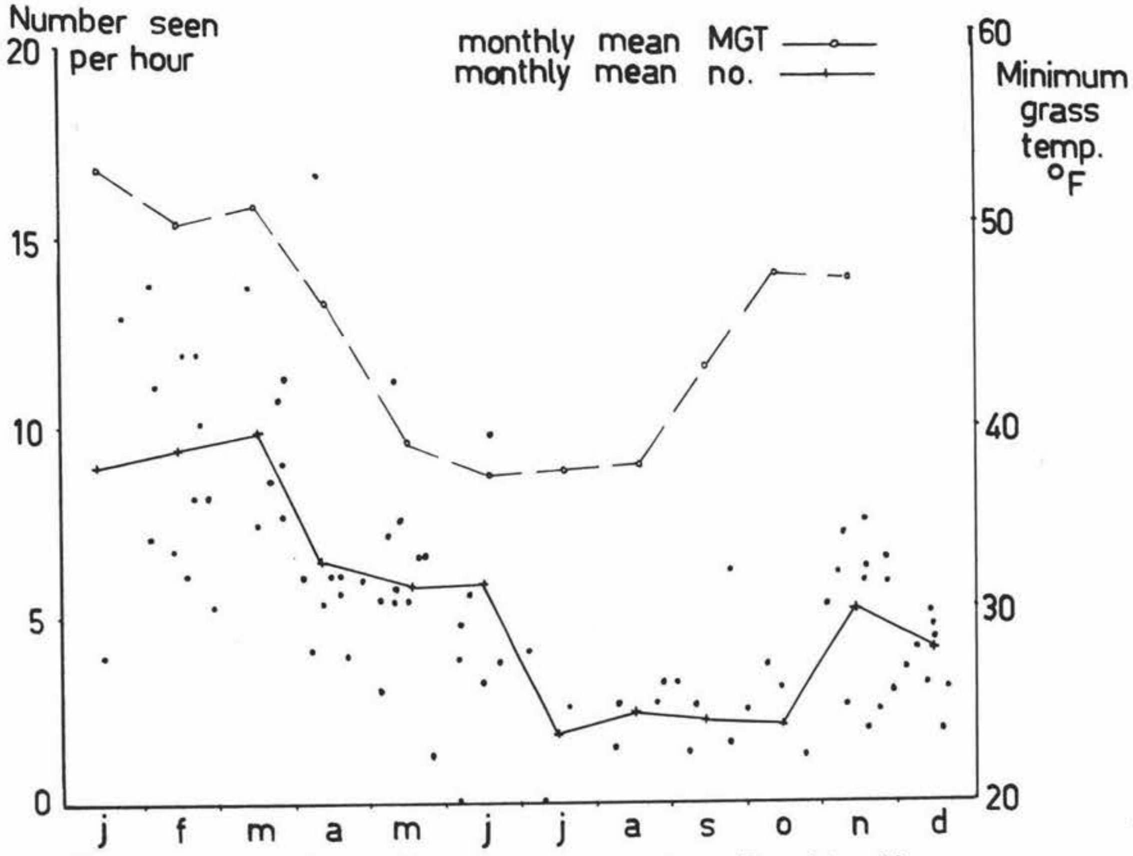


Figure 1. Seasonal Activity

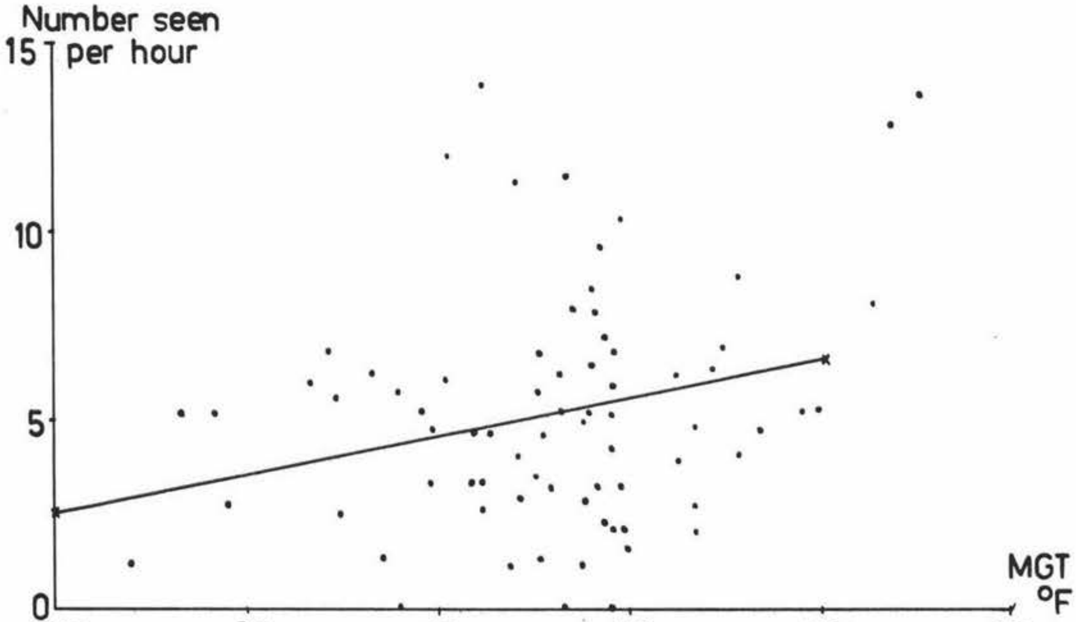


Figure 2. Regression of activity on MGT

These changes in the number of active individuals may be explained by a consideration of the hedgehog's seasonal behaviour patterns, which in turn can be correlated with climatic variables. Temperature seems to be the most important of these variables for over the range 20 to 65 degrees Fahrenheit there is a positive correlation between the number of animals seen per hour searched and the minimum grass temperature recorded during the night. The equation for the regression is $y = 0.513 + 0.104x$. (Figure 2).

It is clear however that hibernation behaviour is not controlled entirely by the minimum ambient temperature. From Figure 1, it can be seen that extensive hibernation did not occur until late June, even though the minimum grass temperature had reached winter values during May. The minimum grass temperature coinciding with some lessening in activity in the population is about 47 degrees Fahrenheit (8.5 degrees Celsius), although the majority of the animals did not enter full hibernation until a minimum grass temperature of about 37 degrees Fahrenheit (2.6 degrees Celsius) was reached. Arousal in late October coincided again with a minimum grass temperature of about 47 degrees Fahrenheit.

Previous work on the role that the ambient temperature plays in determining the limits of hibernation has shown that in the laboratory the critical temperature initiating behaviour which leads to hibernation is about 15 degrees Celsius (Proctor, 1949 and Herter, 1963) while the animal actually hibernates below temperatures of eight to ten degrees Celsius (Herter) or 12 degrees Celsius (Proctor). If the temperature rises above this latter range the animals may awaken and become active with no extra stimulus.

A comparison with the present field study shows some relationships with these laboratory experiments. Both the onset of hibernation and arousal from it are coincidental with a temperature quoted above, namely 8.5 degrees Celsius, although the temperature of initiation was true for only part of the population. The initiation of hibernation behaviour would seem to be controlled by more factors than the minimum ambient temperature alone. This is to be expected in New Zealand, where in contrast with Europe, the seasons are rather indistinct and thus the initiation of hibernation probably depends upon a complex of factors such as the minimum temperature, the day temperatures, food supplies and the condition of the individual animal.

In this study no decrease in nocturnal activity was found during the hottest months, December until March inclusive. Brockie (1958) showed in laboratory experiments that New Zealand hedgehogs were capable of torpor at temperatures exceeding 20 degrees Celsius, however the evidence of the present study suggests that if such an estivation does occur on hot days it is of limited duration and has no effect on nocturnal activity.

2.3 Body Weights

From 440 recordings of adult body weights comprising 219 males and 221 females, the mean weight of males was found to be 700 grams and that of females, 679 grams. The mean body weight of the whole adult population was 684 grams. The slight weight advantage shown by the males is not unexpected as most mammals tend to have heavier males.

Seasonal changes in body weights show some interesting sexual differences. From table 2, it can be seen that males gain weight over the autumn to a maximum monthly average of 785 grams in May, while females do not gain weight until June and then to a lesser extend than the males. A possible reason for this difference is that the females are often still rearing young during early autumn and are not able to reserve much food.

TABLE 2

MONTHLY MEAN BODY WEIGHTS FOR ADULT HEDGEHOGS

	Males			Females		
Month	Sample Size	Mean Weight	Standard Error	Sample Size	Mean Weight	Standard Error
Jan.	4	719	50.2	4	725	25.1
Feb.	9	628	37.6	13	621	35.3
Mar.	16	711	40.3	12	705	47.2
April	33	706	42.4	30	710	22.8
May	24	785	35.3	31	664	21.9
June	21	766	37.6	29	719	51.6
July	9	602	49.5	19	610	37.9
Aug.	6	608	47.1	7	706	58.6
Sept.	24	708	32.3	17	711	43.6
Oct.	17	676	30.4	5	620	57.8
Nov.	41	664	16.0	34	648	33.4
Dec.	14	689	38.7	20	709	16.7

During the winter both sexes lose condition; the males from an average of 785 grams in May to an average of only 602 grams in July - a loss of nearly 200 grams, and the females from a maximum weight of 719 grams on average in June to a minimum of 610 grams on average in July. Females appear to begin to recover this winter loss in weight slightly earlier than males.

It is probable that the winter monthly averages are not truely representative of the whole population as heavier animals tended not to come out of hibernation and become active during the winter and so the data are biased towards the lighter individuals in the population.

For the rest of the year the two sexes show little difference between their body weights. One interesting fluctuation in weight is the loss of condition shown by both sexes during February, 1970. It is likely that this was due to the lack of food during this dry part of the year, which in 1970 was the end of a very severe drought.

Most previous studies on hedgehogs have shown that they are typical of those hibernators which gain weight in the autumn. This increase in weight depends mainly on the deposition of fat in their bodies (Suomalainen, 1935; Eisentraut, 1956 and Kayser, 1961) and is used as a food reserve over the hibernating period. Data on body weights given by Herter (1933), Allanson (1934) and Saure (1969) for European populations conform to this general pattern although Brockie (1958) obtained from a New Zealand sample of 117 males and 89 females, much lower body weights during the summer than would be expected, although his limited autumn and winter data again conformed to the general pattern described above.

2.4 Sex Ratio

Counts of all juvenile animals seen in the two study areas showed that the sex ratio a few months after birth was unity. Of 50 juveniles found, 25 were males and 25 were females. Considering the whole population however, there was a slight excess of males; 181 males to 164 females, a males/female ratio of 1.103 : 1.

Sexual differences in seasonal behaviour and activity altered the apparent sex ratio of the population.

TABLE 3

MONTHLY APPARENT SEX RATIOS OF ALL ANIMALS SEEN

Month	Number of Males	Number of Females	Sex Ratio
Jan.	11	13	0.85
Feb.	21	33	0.63
Mar.	55	53	1.03
April	41	48	0.85
May	37	44	0.84
June	27	35	0.77
July	12	22	0.54
Aug.	6	8	0.75
Sept.	24	19	1.26
Oct.	19	9	2.10
Nov.	57	56	1.01
Dec.	25	39	0.64
Totals	335	379	0.90

As mentioned in section 2.2, the number of animals seen in the field dropped with the onset of hibernation towards the end of June. The apparent sex ratio also altered at this time and for the next two and one half months females were more active than males, the male : female ratio averaging 0.52 : 1 in July. This position was suddenly reversed during the middle of September and for the next two months males were the more active, the male : female ratio averaging 2.11 : 1 in October. (Table 3).

It is suggested that males are less common than females over winter because of sexual differences in hibernation behaviour, which in turn is thought to be due to sexual differences in the amount of autumn fat storage. It seems from the results in the previous section that males accumulate more fat during the autumn than do females and thus are capable of more sustained hibernation. That is the lighter individuals in the population must become active and feed over winter and the females being lighter than males on average are therefore more inclined to be active over the winter months.

The excess of males during the spring is thought to be due to the retiring nature of suckling females, as no females with young were observed at any time in the study area although many young, recently weaned animals were found.

The average sex ratio of 1.103 : 1 is consistent with the estimates given by most other sources. Brockie (1958) obtained from 206 New Zealand hedgehogs a ratio of 117 males to 89 females - 1.31 males to one female. In Europe most sources again favour the male; Allanson (1934) and Deanesly (1934) being the exception giving a sex ratio of one in a sample of 270. Herter (1938) found from 249 animals that there were 1.16 males per female, while a more recent and thorough study by Morris (1968) showed that the primary ratio was one to one, although males became progressively more common in the older age groups reaching a maximum of 2.6 males per female in animals over three years in age.

Morris also found that males predominated in the spring; 1.9 males to one female, although he found that the females were predominate in the autumn; 1.8 females to one male, in contrast with the present study which shows an apparent sex ratio of about one to one in the autumn and the females the predominant sex in the winter. This latter difference in behaviour is probably due to the British autumn being roughly equivalent to a New Zealand winter in terms of the temperature and thus in the effect upon the species' hibernating behaviour.

Some rather extreme sex ratios quoted in Burton (1969); "three to four males to every female" and a

"50 : 1 ratio", could possibly be explained by mistakes in sexing the animals. The same author also gives a sex ratio of two males to each female from counts of a long series of litters, however no reference or sample sizes are given in the text so these claims can not be evaluated.

2.5 Age Structure

No detailed age structure was worked out for the population under study, however some age and longevity statistics can be estimated from other known population parameters. While investigating the cottontail rabbit Petrides (1951) invented the statistic T, equaling the time for 99.5 per cent of a population to be replaced by its descendants.

$$T = \frac{\log 0.005}{\log (1 - j)} + 1$$

Where j equals the proportion of young animals in the population. For the present study, j has been calculated from the 80 observations made in February as 50 per cent. Thus T equals 8.6 years.

Another population statistic formulated by Petrides is the average longevity, L, of adult animals, that is the mean life span of animals surviving until their first breeding season.

$$L = \frac{100}{j}$$

In the present study, L is equal to two years.

Morris (1968) has carried out a more detailed analysis of the age structure of a population of British hedgehogs and calculated T to be 10.7 years and L to be 2.3 years.

The actual age structure of Morris's population, calculated from the number of incremental growth lines in the periosteal bone of the jaw (Morris, 1968), showed however that very few animals lived until their seventh year. From a sample of 244 animals he found the age structure shown in Table 4.

TABLE 4

AGE STRUCTURE OF BRITISH HEDGEHOGS FROM MORRIS (1968)

Nth Summer	Number of Animals
1st	36
2nd	90
3rd	61
4th	41
5th	8
6th	7
7th	1
	244

In New Zealand, Smith (1964) suggested that few wild individuals lived beyond 18 months, however in view of the life table worked out by Morris and the evidence of the present study, it seems that this figure is too low.

3

POPULATION DYNAMICS

3.1 Breeding Season

This phase of the hedgehog's annual life cycle can be delineated by a study of the following four topics:

(a) Weight changes in the male reproductive organs.

The hedgehog is one species which exhibits enormous hypertrophy of the accessory sex glands - the seminal vesicles, the prostates and Cowper's glands - at the start of the breeding season. In this study a massive increase in the total weight of the reproductive tract, including these accessory glands plus the testes and penis, began to occur in early September and tapered off during March, April and May. (Table 5).

TABLE 5

MONTHLY MEAN WEIGHTS FOR THE MALE HEDGEHOG'S REPRODUCTIVE TRACT, TESTES AND ACCESSORY GLANDS COMBINED.

Month	Sample Size	Mean Weight (grams)	Mean Weight Per 100gm Body Weight
Jan.	4	26.73	3.75
Feb.	6	19.04	2.75
Mar.	6	17.14	2.14
April	8	7.46	0.97
May	7	10.30	1.23
June	15	7.12	1.02
July	9	4.10	0.77
Aug.	2	2.91	0.53
Sept.	18	34.40	4.77
Oct.	10	23.78	3.61
Nov.	6	22.46	4.15
Dec.	4	28.85	3.71

(b) Field observations of mating and premating behaviour.

In the hedgehog, premating behaviour is quite a lengthy and conspicuous affair, often lasting several hours and not always ending in copulation. The display has been described in full by Haarlov (1943), Wall and Wall (1968) and Bell (1969) and it involves a pair of animals snuffling and snorting in a circular type of dance. In the present study it was occasionally seen to end in copulation, although the animals were usually disturbed by the light and stopped their dance.

This behaviour was first seen on 24/8/70[1], reached a peak over the period November, December and January when 30 such observations were made, and was last observed on 17/5/71[1]. Altogether 36 such displays were observed.

(c) Pregnancies observed in dissected females.

During the study 99 females were caught and dissected and 14 were found to be pregnant. The first pregnancy was discovered in an animal dissected on 7/11/70 and the last in an animal dissected on 21/6/69, although this latter animal was probably an exceptional case as no pregnancies were observed during the previous two months. It is probable that this late pregnancy would not have resulted in birth as the foetuses appeared as rather undifferentiated lumps of tissue suggesting that resorption was occurring. This phenomenon is known in the species, having been described by Morris, B. in 1960.

[1] Copulation was not observed on either of these occasions.

A seasonal grouping of these results shows that 22 per cent of females were pregnant during the spring, 35 per cent were pregnant during the summer, 4.5 per cent were pregnant during the autumn and 3.1 per cent were pregnant during the winter. (Table 6).

TABLE 6

SEASONAL CHANGES IN THE NUMBERS OF PREGNANCIES

Month	Number Dissected	Number Pregnant	% Pregnant
Jan.	2	1	50%
Feb.	10	3	30%
Mar.	6	1	16%
April	8	0	0
May	8	0	0
June	13	1	7.7%
July	17	0	0
Aug.	2	0	0
Sept.	8	0	0
Oct.	5	0	0
Nov.	10	5	50%
Dec.	8	3	37%

(d) The number of juveniles observed in the field.

The first weaned juvenile found after winter was a female weighing 150 grams and was caught during the day-time on 13/10/70. Newly found juveniles were most common

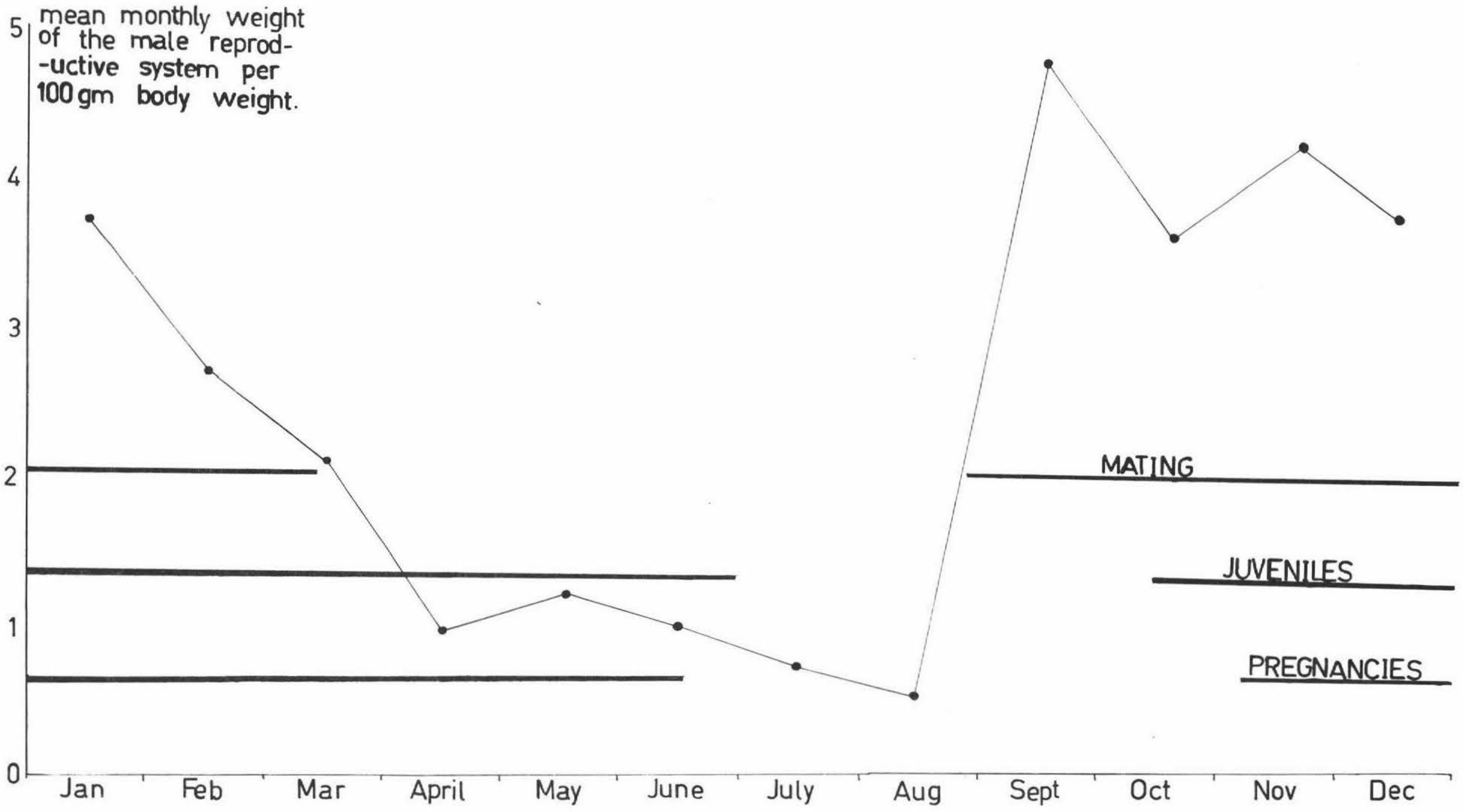


Figure 3. Seasonal changes in breeding parameters

during January and February and a few animals weighing less than 300 grams were found as late in the season as July.

The results of these four studies are presented graphically in figure 3. It appears that the male hedgehogs do not become sexually active until the beginning of September, although the first sexual displays were observed as early as 24/8/70. However it is probable that few pregnancies resulted from this early activity as the earliest pregnant female was not discovered until October. The first weaned juvenile animal was seen during October, so allowing for a six-week-long gestation period and a six-week-long weaning period (Herter, 1963), this individual must have been conceived during July.

Distinguishing the start of the breeding season is also complicated by the fact that hedgehogs pass through a succession of infertile dioestrous and pseudopregnancy cycles before fertile matings occur (Deanesly, 1934), hence the early mating displays observed in this study may have occurred during this infertile period and not given rise to any pregnancies.

The male hedgehogs retain their fertile condition until at least March although mating displays continued until May. From the data on pregnant females it is suggested that few conceptions occur after March.

Thus in New Zealand, the breeding season extends over the period from mid-August until at least March although like the hibernating period, the limits of the breeding season in New Zealand are somewhat blurred. During this seven-month-long season two and perhaps three litters are born. Unfortunately it was not possible to distinguish discrete periods of pregnancies because the sample numbers were too low and because mating was not clearly synchronised over the whole population.

In Europe the breeding season is said to last from April until August, a period of five months, when an average of two litters are reared (Deanesly, 1934; Morris, 1960; Herter, 1963 and Burton, 1969). In New Zealand, Brockie (1958) has also suggested that a third litter is reared, although he claims that few of the earliest litter survive.

3.2 Litter Size

Results for this study were obtained from two sources; two nests each containing five suckling hedgehogs were found during December 1970 and 14 more results were obtained from those pregnant females which were dissected. The mean litter size from both of these sources was 4.9, with a range of between two and six and a most common number of five.

In Britain, the average litter size does not appear to differ significantly from this New Zealand average. Deanesly (1934) found an average of five young per litter from ten observations, Morris (1961) averaged 4.6 young from 42 observations and Burton (1969) averaged five young per litter, no sample size being given. In Europe, Herter (1963) found an average of seven young per litter, again however this figure is not qualified by a sample size.

One interesting difference between British and German hedgehogs and those of New Zealand, is the greater range of the litter sizes in the former. Herter found a range of between two and seven young in his German litters[1] and Burton found a range of between two and nine young in his British litters, compared with the more compacted distribution of litter sizes found in the present study.

[1] It is hard to see how Herter got an average of seven from this range.

In general, litter sizes are related to the length of the breeding season and the number of litter produced during this period. In long breeding seasons several litters with few young are produced in contrast with short breeding seasons when fewer but larger litters are the norm. Other factors such as the rate of parental mortality may also affect the number of young born in each litter.

3.3 Mortality

The second major influence on the population's structure is mortality. In this study, seven deaths of marked animals were discovered, of these three were accidental deaths due to chloroform overdoses, two were found run over on the roads near the study area, one was found wandering in an apparently dazed condition during the daytime (it died the next day) and one was found dead from causes unknown in the study area.

For the four months April, May, November and December, the number of hedgehogs seen per ten hours searching averaged 38,38,27 and 29.5 respectively. Thus it seems that approximately 25 per cent of the population failed to survive the winter. The exact causes of these winter deaths can only be guessed as only one decomposed corpse was found in a winter nest outside the study area. Some flooding occurred during the winter and a few probably nest sites were innundated, so it appears likely that drowning caused a few of these deaths.

The main cause of mortality during the winter was, however, probably disease. Known causes of disease in hedgehogs include such factors as Brucella bronchisepta which was described as common in laboratory animals studied by Edwards (1949), abscesses possibly caused by interspecific fighting or by scratching flea bites, and heavy parasitism by the skin mite Caparina tripilis which as well as being the vector of several diseases, causes some irritation and stops the animal from rolling up completely, thus making defence against predators less effective. Frost (quoted in Wodzicki, 1950) found hedgehogs with fly blown ears because of irritation caused by cattle ticks.

It is suggested that a higher proportion of these winter deaths are females as they are the more active sex over winter, and are therefore more exposed to the harsher climate. This hypothesis, if true, would explain the gradual predominance of males in older age groups.

Summer mortality seems to be mainly caused by road deaths, although three animals were observed with large abscesses on their faces - one of these animals was known to have recovered and the other two disappeared.

Predators are less common in New Zealand than in Britain where foxes, badgers, polecats and some of the larger birds-of-prey such as magpies will kill hedgehogs. In New Zealand only wise dogs which have learnt how to unroll the hedgehog, and magpies are known predators, and together would have very little effect on the total numbers of hedgehogs.

In view of the number and size of litters produced each year it is likely that most of the juveniles die before they reach maturity. Brockie (1958) claims that few of the early litters produced in New Zealand survive and it is probable that few of those juveniles born late in the breeding season would survive the winter.

3.4 Dispersal

The third demographic parameter to be considered is population dispersal. This may take three forms; emigration, or movement out of the original home range area, immigration, or movement into the particular area of study, or mogration, involving a return to the previously vacated area. Although emigration and immigration are not biologically different, they will be distinguished in this study as emigration involved marked individuals while immigration involved unmarked new-comers to the study area.

Since the mean number of resightings permarked individual was only 2.37 (see section 2.1), and since many new adult animals were found during the whole period of the study, it is clear that the individuals in the population show a high degree of dispersal.

When these resightings were sorted according to sex it was found that females were resighted on average 3.71 times, while males were resighted on average only 2.08 times. Further, while six females were resighted more than ten times, no males were seen more than eight times (Table 1). Thus it appears that males are more liable to disperse than females, possibly because of the lack of restrictions imposed by rearing young.

Four animals were observed at considerable distances from the study area, of these, two were females found run-over on the main road about 1000 meters from the edge of the study area, and the other two consisted of one female and one male seen in the general area of the main road.

The degree of dispersal in this population alters with the season. Over winter; June, July and August, 24 sightings were recorded of which only three were previously unmarked individuals, while during the spring, 30 per cent of those animals found were immigrants. This spring dispersal is a common feature of many mammalian populations as the individuals seek out mates and compete for new feeding areas.

Generally it appears that a few animals, mostly females, are quite stable with respect to dispersal, while other individuals, both male and female, are much more nomadic and are therefore not attached to a given area for any length of time.

Dispersal has been suggested as a potentially important factor in the regulation of populations (Errington, 1956 and Liddicker, 1962). In the present study the large dispersing group had little effect on the density of the population as immigration and emigration were approximately equal. However because of the sexual differences in dispersing behaviour, females were more common than males in terms of the intensity of use of the study area.

Genetic polymorphism between dispersing and resident populations has been described in the two field voles, *Microtus pennsylvanicus* and *Microtus ochrogaster* by Myers and Krebs (1971), however apart from sex, no genetic differences were measured between the dispersing and resident hedgehogs in the present study.

This area of study provides ample new research material as in the present study no data is available as to the behaviour of the dispersing population. Radiotelemetry obviously offers the best method of describing the movements of these wide-ranging dispersing animals.

4

HOME RANGE

4.1 Introduction and Statistical Methods

The home range of an animal has been defined by Burt (1943) as the area over which the animal normally travels while engaged in its usual activities. However it has become more usual to widen the concept of home range to include the intensity of use of parts of the home range. Studies by Murie (1936, 1940 and 1944) on red foxes, coyotes and wolves, by Scott (1943 and 1947) on red foxes and by Adams and Davies (1967) on the Californian ground squirrel, confirm that for these species some parts of the home range had a higher intensity of use than other areas within the home range. In accepting Burt's definition it has been usual for most authors to exclude the occasional larger-than-usual "sallies outside the area".

Although the concept of land tenure in animal populations is a relatively simple one, it is not easy to put into practice, and the actual measurement of an animal's home range is a difficult exercise. Of the many methods described in the literature - most of which relate to trapping grids - two have been used in the present study:

(a) The convex polygon method. This involves the smallest convex polygon which contains all the points of capture. This method which gives a conservative concrete boundary for the home range has been used by Dalke and Sime (1938) and Mohr (1947).

(b) A probability ellipse method. This ellipse is based on the covariance matrix of the capture loci, (Jennrich and Turner, 1969 and Mazurkiewicz, 1971), and is based upon the following three assumptions;

(1) The animal prefers movement in one direction. This is clear from the shape of the polygons constructed by the first method.

(2) The probability of sighting an animal at a given place is governed by the relationships of a two-dimensional normal distribution.

(3) The extent of the home range is an elliptical curve enclosing a defined density of probability of capture of the individual.

In an arbitrary system of rectangular co-ordinates, the following data may be calculated;

x = abscissa of the geometrical centre of all sightings.

y = ordinate of the geometrical centre of all sightings.

Sxx = variance of the abscissae.

Sxy = covariance of the abscissae and ordinates.

Syy = variance of the ordinates.

If we now shift the co-ordinates so that

$x = 0$

and $y = 0$, then

$Sx'x' = Sxx \, Cos^2 a + 2Sxy \, Sin \, a \, Cos \, a + Syy Sin^2.$

and $Sx'y' = Sxy \, Cos^2 a - 1/2 \, (Sxx - Syy) \, Sin 2a.$

and $Sy'y' = Sxx \, sin^2 a - 2Sxy \, Sina Cosa + Syy \, Cos^2.$

where, $Sx'x'$, $Sy'y'$ and $Sx'y'$ are the variances and the covariance of the new system of co-ordinates and a is the angle between the old and the new abscissae.

Now if we let a be such that $Sx'y' = 0$, then we obtain

$Sx'y' = 0 = Sxy \, Cos \, 2a - 1/2 \, (Sxx - Syy) \, Sin \, 2a.$

and thus $tan \, 2a = 2 \, Sxy / \, (Sxx - Syy)$

Hence we can obtain the two variances under the new co-ordinates from the following equations:

$Sx'x' = Sxx + Sxy \, tan \, a$

and $Sy'y' = Syy - Sxy \, tan \, a.$

Now the area of the ellipses enclosing defined densities of probability of capture has been given by the statistic,

$$A = k\pi |S|^{1/2}$$

where $|S|$ is the determinant of the capture point covariance matrix -

$$S = \begin{vmatrix} Sx'x' & Sx'y' \\ Sy'x' & Sy'y' \end{vmatrix}$$

$$= Sx'x' \, Sy'y'$$

and k equals a number dependant on the probability of recapture. When k = 6, the ellipse encloses 95 per cent of an individual's utilisation of its habitat or when k = 9, 99 per cent of the utilisation is included. In the present study we shall use the ellipse including 95 per cent of the probability of capture.

Further, because of the small sample numbers of recaptures per individual, a weighted mean variance has been calculated thus;

$$S = \frac{(n_1 - 1)\,S_1 + (n_2 - 1)S_2 + + (n_r - 1)\,S_r}{(n_1 - 1) + (n_2 - 1) + + (n_r - 1)}$$

for the three classes, adult females, adult males and juveniles, and from these weighted variances a representative area of the home range has been calculated.

Similarly the mean areas of the three classes minimum polygons have been weighted by the number of captures within each class to make comparison of results more valid.

$$A = \frac{(n_1 - 1)\,a_1 + (n_2 - 1)a_2 + + (n_r - 1)a_r}{(n_1 - 1) + (n_2 - 1)\,1 + (n_r - 1)}$$

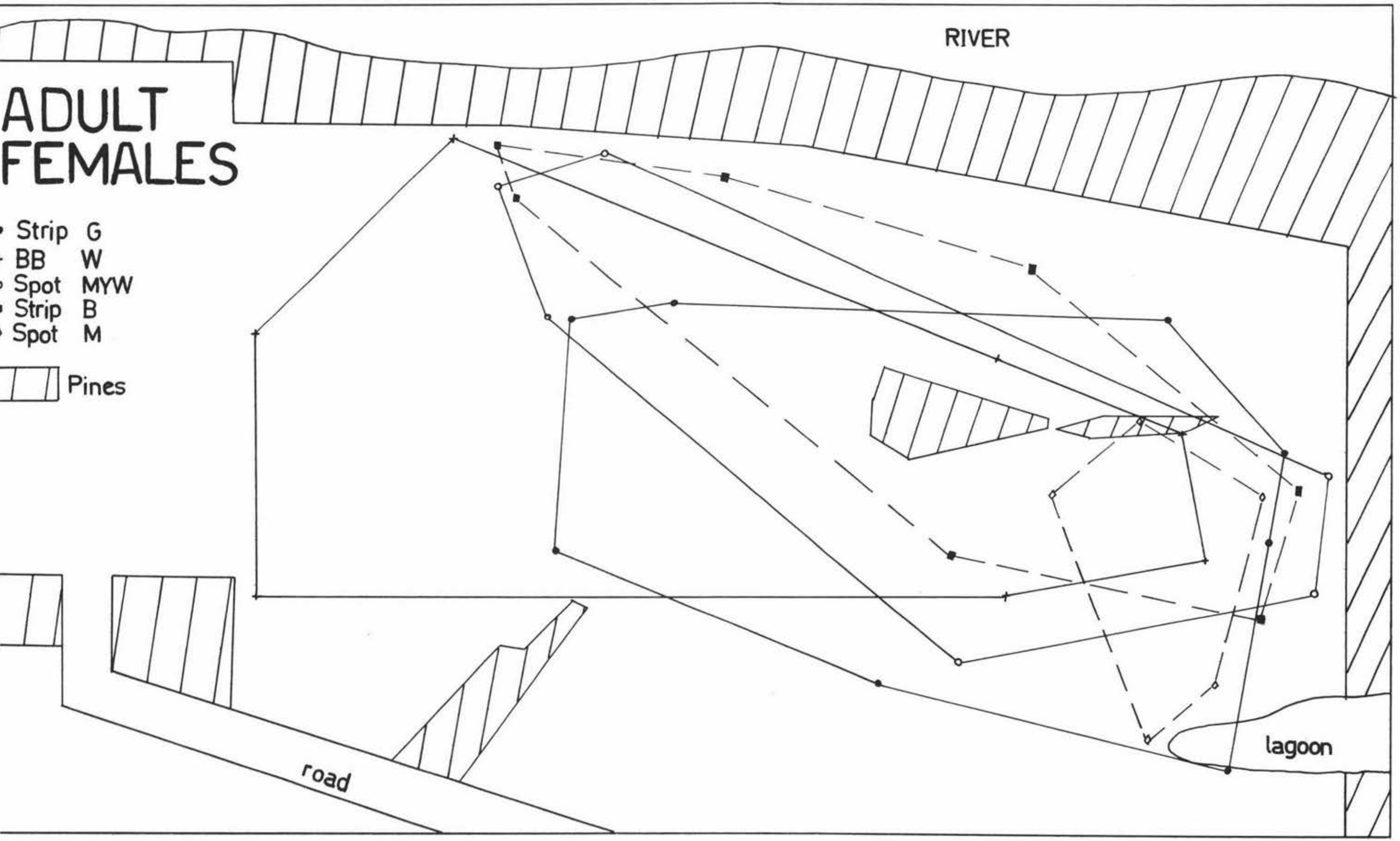
4.2 Results

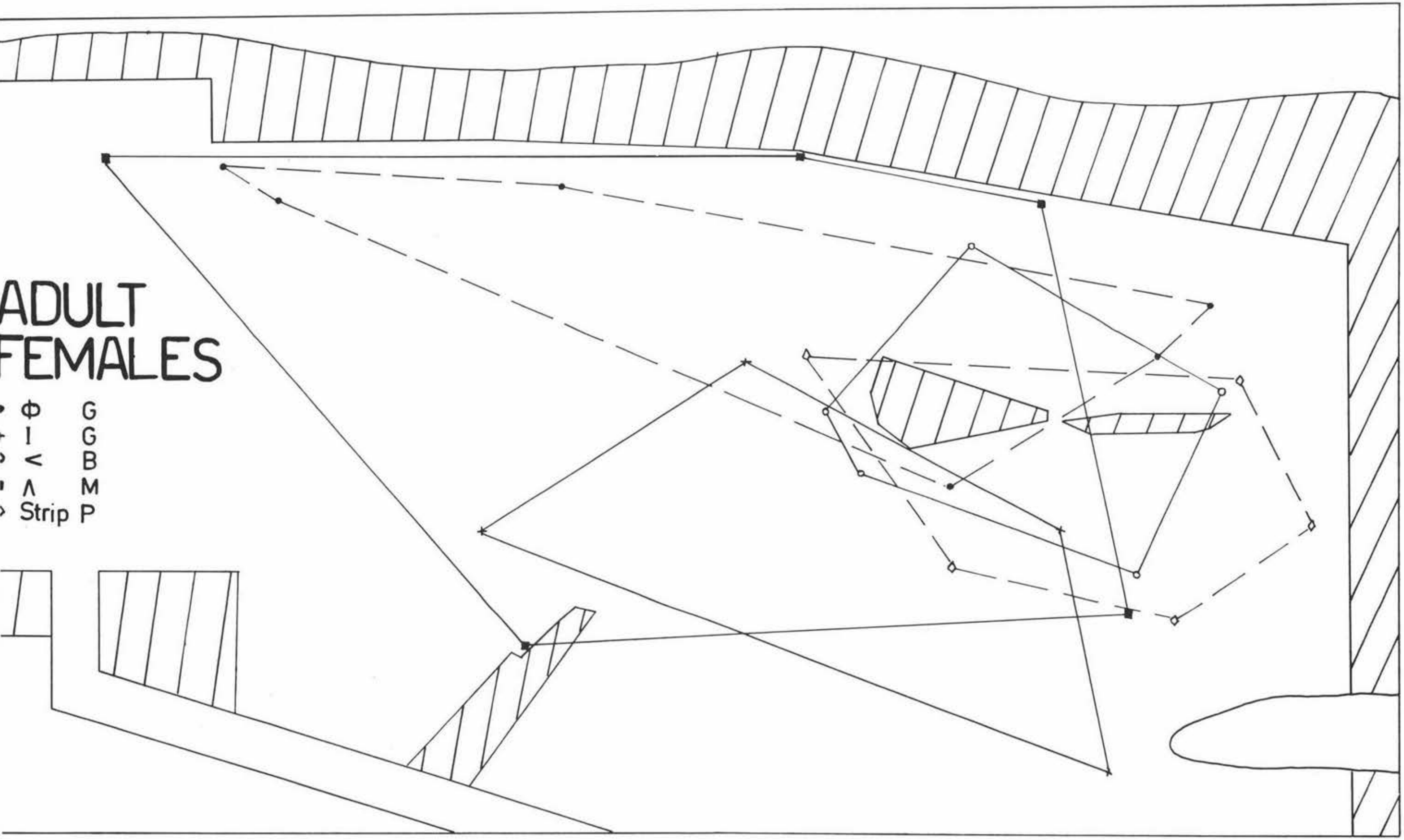
(a) Adult Females

Only those individuals sighted eight or more times are considered. The mean area of the minimum convex polygons, weighted as described in section 4.1, was 3.68 hectares and was obtained from ten animals. The actual sizes of the polygons ranged between 1.02 hectares for Spot M and 6.51 hectares for M. The weighted area of the representative ellipse was 12.90 hectares. (Table 7).

TABLE 7. HOME RANGE DATA FOR ADULT FEMALES

Individual	Number of Sightings	Area of the Minimum Convex Polygon
Strip G	20	5.04
Spot M	19	1.02
Strip B	17	3.94
Spot MYW	16	4.69
BB W	13	5.71
O G	10	2.87
I G	9	2.72
B	8	1.57
Strip P	8	1.97
M	8	6.51


ADULT
FEMALES
Strip G
BB W
Spot MYW
Strip B
Spot M
Pines
RIVER
lagoon
road


ADULT
FEMALES
Φ G
I G
< B
Λ M
Strip P

From figures four and five, it can be seen that most of the minimum convex polygons are orintated with their long axes parallel to the river, the exception being Spot M with its long axis at right angles to the river. Obviously the topography of the study area is one factor involved in this alignment, the river and the position of the pine plantations are the most probable factors causing the common orientation of the home ranges' long axes.

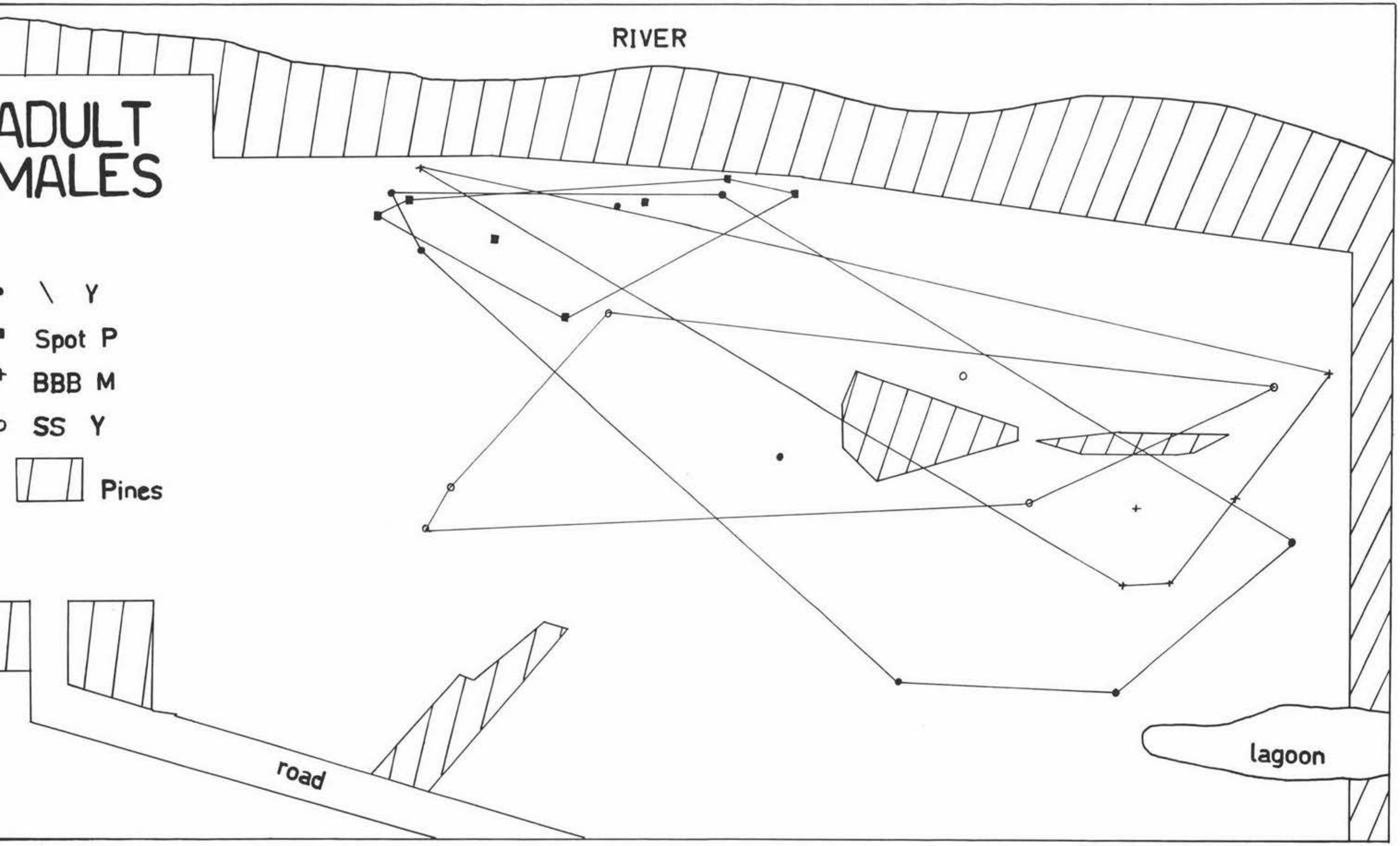
The polygons are clearly underestimations of the individual's true home ranges; the home range of such an animal as I G for example must be larger as the represented polgon in figure five includes no possible nest site.

(b) Adult Males

In the case of adult males, few individuals remained within the study area for any length of time and therefore the number of resightings of marked animals was low, only four being resighted more than four times. (Table 8)

TABLE 8. HOME RANGE DATA FOR ADULT MALES

Individual	Number of Sightings	Area of the Minimum Convex Polygon (Hectares)
/ Y	9	4.78
Spot P	7	0.76
SS Y	6	2.24
BBB M	5	2.35


ADULT
MALES
● \ Y
■ Spot P
+ BBB M
○ SS Y
Pines
RIVER
road
lagoon

The weighted mean area of the minimum convex polygons was 2.74 hectares, while the actual range of areas over the four individuals' home ranges was between 0.76 and 4.78 hectares. The weighted area of the representative ellipse was 7.04 hectares. As in the case of the females, all but one home range, that of / Y, were orientated with their long axes parallel to the river. Further, the smallest polygon, that of Spot P, was entirely pasture and thus could not contain the animal's nest site. (Figure 9).

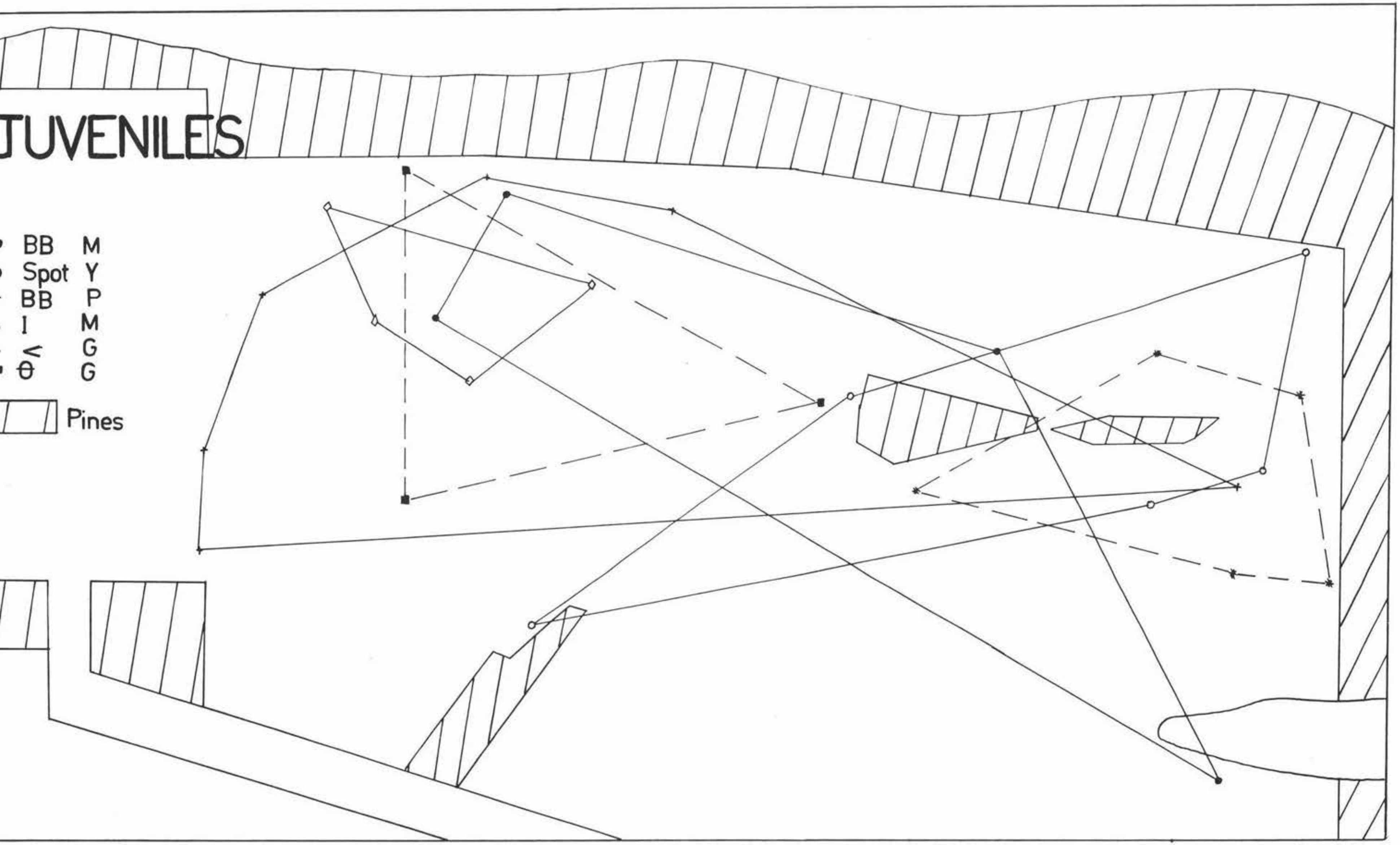
(c) Juveniles

Three juvenile females were resighted an average of nine times while three juvenile males were resighted an average of six times. The weighted mean area of the minimum convex polygons of all these animals is 2.70 hectares, with a real range of between 0.73 hectares for the male, I M, and 4.90 hectares for the male G. The weighted mean area of the representative ellipse is 10.93 hectares. (Table 9).

TABLE 9. HOME RANGE DATA FOR JUVENILES

Individual	Sex	Number of Sightings	Area of the Minimum Convex Polygon (Hectares)
BB M	Female	11	2.99
BB P	Female	10	1.38
Spot Y	Female	9	3.56
G	Male	9	4.90
θ G	Male	6	1.47
I M	Male	6	0.47

The orientation of the home ranges of the juveniles is not as unified as that for the adults, although there is still some alignment with the river. Two convex polygons do not include any possible nest site, those of I M and θ G so these are obviously underestimates of the real home range.


JUVENILES
BB M
Spot Y
BB P
I M
V G
Θ G
Pines

4.3 Discussion

Of the large number of animals marked in this study, only 20 could be said to be attached to a given area and thus fulfill Burt's definition. The largest part of the population appeared to be nomadic and even many of the more stable animals described in this chapter did not remain in the study area over the entire study period. Thus it must be stressed that the following discussion is relevant only to the non-dispersing part of the hedgehog population.

(i) Shape of the Home Range

From the cartographical minimum convex polgon representation of the home range, it is clear that the hedgehog utilises an area several times as long as it is wide, the best statistical model for this shape being an ellipse.

Such elongated home ranges are not uncommon among animals; Godfrey (1954), Mohr (1965) and Mazurkiewicz (1971) have demonstrated such shapes for the ranges of Clethrionomys glareolus while Jennrich and Turner (1969) have described the elongate home range of the lizard cnemidophorus tigris. Brockie (1958) has shown from a mark recapture study on the hedgehog in New Zealand that the animals preferred movement in one direction.

It is clear from the life style of some animals, the water vole Arvicola terrestris for example, that an elongate home range along the banks of a stream is the most useful area for the animal to utilise. However for other species such as the hedgehog it is not clear as to why an elongate rather than circular home range is a species characteristic.

(ii) Size of the Home Range

Once again the hedgehog is not typical of mammals with respect to the size of its home range in that females generally have larger home ranges than males, the difference being significant as F - tests performed on the weighted variances proved to be significant. In most other species the males have the larger home ranges. (Burt, 1940; Bakken, 1959 and Adams, 1959).

It is possible that these differences exist because the males were more nomadic than the females and were therefore not recaptured as many times; the 10 females being resighted on average 11.8 times while the four males were resighted on average only 5.8 times.

Generally the area utilised by an animal bears a relationship to the trophic position of the species, the metabolic rate and the body size (McNab, 1963), and to the amount of food present in the region. Hedgehogs, being insectivorous, can be expected to have a relatively large home range as compared with herbivoures of a similar size. Within the population it was not possible to compare body weights with home range sizes because the measurement of the home range was not accurate enough (due to the lack of data) and because it was difficult to decide on a weight for an individual since very large seasonal fluctuations in body weight occurred. SS Y, an adult male, for example weighed 560 grams on the 27/2/70 and 870 grams on the 12/5/70, an increase of 310 grams in 10 weeks.

(iii) The nest as a focus of Activity

The centre of activity of a home range may be defined as the geometric mean of the recapture sites, but in a biological sense it is more real to talk of foci of activity, a term first used by Carpenter (1940), as the areas of greatest use intensity are not necessarily around the geometric centre of the home range.

In the present study the most important focus of activity is the nest site which does not always occupy a central position in the home. This is because the possible nest sites are often on the edges of possible feeding sites. The position of the nest site may be moved several times each year. The adult female, Spot MYW, for example, occupied a nest in the north end of the central pine plantation from at least as early as 20/3/70 until some time in September when she moved to a new nest site along the south end of the trees along the Manawatu river. This move extended her known range only slightly but it did mean that the nest site was moved from a central position to a peripheral position in the estimated home range.

The nests discovered during the present work were all situated in pine plantations, generally within a thicket of grass or fallen branches and were constructed of pine needles. No nests within the study area were investigated fully as this would have involved their physical destruction, however four winter nests were found in the pines bordering the Massey orchards, and these were 'dissected' and found to be substantial structures consisting of a small hollow in the ground, some six inches in diameter and three or four inches deep, around and over this was a ball of pine needles and leaves about 12 inches in diameter and over all this was a mound of pine needles about two feet wide and about 18 inches high. This outer layer had a tunnel through the wall and the hedgehog itself was wrapped in the inner ball of material.

The nesting behaviour of the hedgehog has been studied in more detail by P. Morris (1968) and this work on British animals is confirmed by the unstable nesting and dispersive behaviour discovered in the New Zealand population studied in the present work.

(iv) Food Concentrations as foci of Activity

As the hedgehog's food supply is not likely to be evenly distributed over the region it is to be expected that the hedgehogs will themselves show an uneven use of their home ranges. During the present study the following three concentrations of food organisms resulted in the formation of focal areas for the hedgehogs.

(1) During mid-March, 1970, the effluent from nearby pig sties was spilled over the study area in two areas of pasture each covering about 100 square meters. These areas became heavily populated with the horse-tail maggot of the fly Eristalis tenax upon which large numbers of hedgehogs fed - on 24/3/70 for example, 21 animals were observed in the area over a space of two hours.

(2) Army worms, (Pseudolatia Separata), reached a density of two or three per square meter on the surface of the ground at night during the early part of May. Many hedgehogs were seen gorging themselves in such areas; one animal, X G an adult female, was accidently killed and was found to have eaten 178 army worms.

(3) At the end of November a small area of pasture which had been recently flooded, supported many slugs. On 1/12/70, nine hedgehogs were observed eating slugs within an area of about 300 square meters.

Converse to these focal areas, sterile areas such as the pine plantations were rarely seen to contain hedgehogs except for periods near dusk and dawn when the individuals seen were arising or returning to their nests. Within the pasture itself, the hedgehogs avoided, if possible, very long grass and very short grass and thus the grazing pattern of the herd of cows influenced the movements of the hedgehogs.

Individual hedgehogs that were followed meandered about the fields stopping at the larger clumps of grass and feeding. It was found that during the dry part of the summer, insects were ten times as plentiful by weight in the isolated tufts of fescue than between the tufts. Two foot square samples of pasture were dug out to a depth of about three inches on 6/3/70; the dry weight of the animals in the sample including the grass tuft was 0.335 grams while the dry weight of the animals taken from the sample between the tufts was only 0.034 grams.

(v) Seasonal Changes in Movement

Since the hedgehog hibernates during the winter, movements during this season will be different from those in other seasons. As mentioned in the first chapter, not all animals remain inactive for the whole winter and it was found that those individuals that did become active in the winter limited their movements to a fairly small area about the hibernation nest. Further, there was less dispersal in the population and thus less shifting of the nest site, a common occurrence during the rest of the year.

Similarly the few pregnant females observed over the spring and the early summer were also more restrictive in their movements, presumably because of the need to build a nest and subsequently care for the young.

During the latter part of the summer distances between resightings were generally much larger than those during the rest of the year and it is thought that this may have been due to the drought conditions making food supplies scarce and thus necessitating larger forays by the hedgehogs.

(vi) Territory and Social Structure

Perhaps the most widely accepted definition of the term territory is that given by Noble (1939) as, "any defended area". Defence of the area is by means of combat, threat, vocalisations, or any other behaviour which causes avoidance in other animals, but particularly in conspecifics. Noble's definition takes no account of function, and more rigid definitions exclude most moving defended areas such as the individual's approach distance.

In the case of the hedgehog population studied, no evidence of any behaviour associated with territorial defence was observed; no combat or threat behaviour was seen and the great overlap of home ranges and the amount of dispersal in the population tend to reinforce this view. Even nest sites did not appear to be defended as several nests were found within a few inches of one another - Hediger (1955) claims that captive hedgehogs will sleep in a huddle.

Under normal conditions of feeding some sort of individual distance (at least five meters) is maintained, and it is possible that the snuffling noises of active hedgehogs acts as a sign to warn conspecifics. However this distance was observed to break down at mating time and at the concentrations of food mentioned earlier in this chapter.

Leyhausen (1963) has shown with domestic cats that although several individuals may occupy the same area, the fact that each animal uses the travel pathways at different times of the day means that effective territories are enforced. It is possible that hedgehog populations are similarly integrated as it is known that at least some animals use regular paths for some part of their wanderings. However more complete studies would be needed to test this hypothesis.

Social hierachies apparently exist in the hedgehog, for Herter (1938) described a peck order that existed between four captive hedgehogs, two adult males and two adult females. Of these animals, one female was dominant and boxed and bit all the others. One male was dominated by all others. In the present study non-sexual meetings have been observed in the field although no actual combat was seen, the animals being content to sit nose-to-nose and snort at one another. It is possible that these meetings were for the purpose of establishing a social order.

It is not clear what function a social peck order would perform in wild hedgehogs as no territories exist and feeding is not a social act. The two possible reasons are the control of mating through social exclusion of dominated individuals or possibly the formation and maintenance of a stable home range is restricted to the dominant individuals, the dominated section of the population being forced to be nomadic. This hypothsis would necessitate the females being dominant which is the case with Herter's captives at least.

SUMMARY OF RESULTS

(1) 150 marked hedgehogs were resighted 356 times.

(2) The density was estimated as two animals per hectare.

(3) A minimum temperature of 8.5 degrees Celsius initiated hibernation behaviour as well as arousal from hibernation.

(4) Body weights of 440 adult hedgehogs were recorded. The mean weight of adult males was 700 grams and that of females was 679 grams.

(5) Both males and females gain weight over the autumn, males slightly earlier than females. Both sexes lose weight over winter, males more than females.

(6) The primary sex ratio is unity although males become successively more common in older age groups. The overall adult ratio is 1.103 males per female.

(7) Females are more active over winter and males are more active over spring.

(8) 99.5 per cent of the population is replaced by its ancestors in 8.6 years and the mean life span of animals surviving until their first year is 2 years.

(9) The seasonal hypertrophy of the reproductive organs, mating and premating behaviour, pregnancies, and the appearance of young animals are used to delineate the breeding season. This season extends from mid-August until at least March.

(10) The mean litter size from 16 observations was 4.9 with a range of between two and six.

(11) Seven marked animals were found dead and it was estimated that 25 per cent of the population died over winter.

(12) Most animals were nomadic and thus did not have a home range.

(13) The mean area of the minimum convex polygons of the ten females sighted eight or more times was 3.68 hectares. The weighted area of the representative ellipse was 12.90 hectares.

(14) Only four adult males were resighted more than four times and the weighted areas of the polygon and the ellipse were 2.74 and 7.04 hectares respectively.

(15) Six juvenile animals had a mean home range area of 2.70 hectares for the minimum convex polygon estimation and 10.93 hectares for the probability ellipse method.

(16) The home ranges described were elongated and most were orientated in the same direction.

(17) Several 'blooms' of insects attracted great numbers of hedgehogs.

(18) Hedgehogs appear to have no territories and little evidence of social hierachies were discovered.

REFERENCES

Adams, L. (1959) An Analysis of a Population of Snowshoe Hares in Northwestern Montana. Ecol. Monographs 29 : 141-170.

Adams, L and Davis, S.P. (1967) The Internal Anatomy of Home Range. Jour. Mamm., 48 : 529 - 536.

Adrian, E.D. (1942). Olfactory Reactions in the Brain of the Hedgehog. J. Physiol., 100 : 459-473.

Allanson, M. (1934). Seasonal Variation in the Reproductive Organs of the Male Hedgehog. Phil. Trans. B, 223 : 227 - 303.

Allanson, M. and Deanesly, R. (1935). The Reaction of Anoestrous Hedgehogs to Experimental Conditions. Proc. Roy. Soc. Lond. B, 116 (797) : 170 - 185.

Bell, R.E.S. (1969). Hedgehog's Courtship. Country-side (Bournemouth, 121 (3) : 132.

Bioerck, G.; Johansson, B. and Veige, S. (1956). Some Laboratory Data on Hedgehogs, Hibernating and Non-Hibernating. Acta Physiologica Scand., Stockholm, 37 (4) : 281-294.

Brockie, R.E. (1957) The Hedgehog Population and the Invertebrate Fauna of the West Coast Sand Dunes. Proc. N.Z. Ecol. Soc., 5 : 27-29.

-------------- (1958) The Ecology of the Hedgehog (Erinaceus europaeus) in Wellington, New Zealand. MSc Thesis, Victoria University.

-------------- (1959). Road Mortality in the Hedgehog in New Zealand. Proc. Zool. Soc. Lond., 134 : 505-508.

--------------- (1959). Observations on the Food of the Hedgehog in New Zealand. N.Z. J. Sci., 2 : 121-136.

Bull, P.C. (1940). Hedgehogs and Ground - Nesting Birds. The Orn. Soc. N.Z. Ann. Report, No.1.

Burt, W.H. (1940). Territorial Behaviour and Populations of Some Small Mammals in Southern Michigan. Miscl. Publ. Mus. Zool. Univ. Michigan, No. 45 : 1-58.

--------------- (1943). Territoriality and Home Range Concepts as Applied to Mammals. Jour. Mamm., 24 : 346 - 352.

Burton, M. (1947). Hedgehog deaths on the Road. Illus. Lond. News, 211 (5656) : 300.

---------------- (1957). Hedgehog Self-Annointing. Proc. Zool. Soc. Lond., 129 (3); 452 - 453.

---------------- (1969). The Hedgehog. Survival Books. Edited by C. Willcock.

Campbell, D.J. and Smith, T. (1966). A Pituitary Edenoma in a Hedgehog, Erinaceus europaeus. Endocrinology, 79 (4) : 842-4.

Carpenter, J.R. (1940). The Grassland Biome. Ecol. Monographs, 10 : 617-684.

Ch'eng Chao Lui, (1937). Notes on the Food of Chinese Hedgehogs. Jour. Mamm., 18 : 355-357.

Cott, H.B. (1951). The Palatability of the Eggs of Birds: Illustrated by Experiments on the food preferences of the Hedgehog. Proc. Zool. Soc. Lond., 121 : 1-43.

Courrier, C. (1927). Reproductive Cycle of the Hedgehog. Arch. de Biol., 37 : 173 - 334.

Crawford, S.C. (1933). The Habits and Characteristics of Nocturnal Animals. Quart. Rev. Biol., 9 : 201-214.

Dalk, P.D. and Sime, P.R. (1938). Home and Seasonal Ranges of the Eastern Cottontail in Connecticut. Trans. North Amer. Wildl. Conference, 3 : 659-669.

Davies, J.L. (1957). A Hedgehog Road Mortality Index. Proc. Zool. Soc. Lond., 128 : 606-608.

Deanesly, R. (1934). The Reproductive Processes of Certain Mammals. VI The Reproductive Cycle of the Female Hedgehog. Phil. Trans. B, 223 : 239 - 303.

Degerbol, K. (1943). Pairing and Pairing Fights of the Hedgehog. Videnski - Medd., 106 : 427-430.

Dimelow, E.J. (1963). The Behaviour of the Hedgehog (Erinaceus europaeus) in the routine of life in captivity. Proc. Zool. Soc. Lond., 141 (2) : 281 - 289.

------------- (1963). Observations on the feeding of the Hedgehog (Erinaceus europaeus L.). Proc. Zool. Soc. Lond., 141 (2) : 291 - 309.

Eisentraut. M. (1935). Die Entwicklung der Warmeregulation beim jungem Ygel. Eiol. Zeutrabl. 55 : 45 - 53.

-------------- (1956). Der Winterschlaf mit seinen okologischen und physiologischen Begleiterscheinungen - Jena.

Errington, P.L. (1956). Factors limiting higher Vertebrate Populations. Science, 124 : 304 - 307.

Foxall, A. (1969). Afflicted Hedgehogs. Countryside (Bournemouth), 21 (3) : 133.

Godfrey, G.K. (1954). Tracing Field Voles with a Geiger-Muller Counter. Ecol., 35 : 5-10.

Haarlov, N. (1943). Die Kopulation der Igel. Viddensk Middel Dansk. Naturhist Kobenhaun, 106 : 431-433.

Hayne, D.W. (1949). Calculation of Size of Home Range. Jour. Mamm., 30 : 1-17.

Hediger, H. (1955). Studies of the Psychology and Behaviour of Captive Animals in Zoos and Circuses. London.

Herter, K. (1933). Gefangenschaftsbeobachtungen an Europaischen Igeln, II. Z. Saugetierk, 8 : 195-218.

------------ (1938). Die Biology der Europaischen Igel. Monogr. Wildsauget., 5. Leipzig.

------------ (1952). Igel - Neue Brehmbucher. Monogr. Wildsauget., H. 71. Leipzig und Wittenberg.

------------ (1961). Uber Igel von Neuseeland. Zoologische Beitrage, 6 : 347 - 376.

------------ (1963). Hedgehogs. Phoenix House, London. I - V, 1 - 69, 40 figs.

Jefferies, D.J. and Pendlebury, J.B. (1968). Population Fluctuations of Stoats, Weasels and Hedgehogs in Recent Years. J. Zool. Lond., 156 : 513 - 549.

Jennrich, R.I. and Turner, F.B. (1969). Measurement of Non-Circular Home Range. Jol. Theor. Biol., 22 (2) : 227 - 237.

Jewell, P.A. (1965). The Concept of Home Range in Mammals. Symp. Zool. Soc. Lond., 18 : 85-107.

Kalabuchow, N.K. (1928). Uber die Nahrung des Igel im Nord-Kaukasus und in der Ukraine. Mitt. Nord-Kaukas Pflanzenschutzstation Rostow, 6 : 62-68.

Kayser, Ch. (1961). Mammalian Hibernation. I. Hibernation Versus Hypothe Bull. Mus. Comp. Zool. Harvard Univ., 124 : 1-29.

Knight, M. (1962). Hedgehogs. Animals of Britain 3. ed. L.H. Matthews. Sunday Times book publ.

Kristoffersson, R. (1964). An Apparatus for Recording General Activity of Hedgehogs. Ann. Acad. Sci. Fenn., A4 No.79 : 1-8.

Kristoffersson, R. and Suomalainen, P. (1964). Studies on the Physiology of the Hibernating Hedgehog. 2. Changes of Body Weight of Hibernating and Non-Hibernating Animals. Ann. Acad. Sci. Fenn., A4 No.76 : 1 - 11.

Kristoffersson, R. and Broberg, S. (1967). Glutamic Decarboxylase Activity in the Brains of Hibernating and Non-Hibernating Golden Hamsters and Hedgehogs. Ann. Acad. Sci. Fenn., A4 No. 119 : 1-8.

Kristoffersson, R. and Soivio, A. (1967). *Studies on the periodicity of Hibernation in the Hedgehog (Erinaceus europaeus). 2. Changes of Respiratory Rhythm, Heart Rate and Body Temperature at the Onset of Spontaneous and induced Arousals*. Ann. Zool. Fennici (Helsinki), 4 (4) : 595-597.

Kristoffersson, R. and Soivio, A. (1967). *A Comparative Long-term Study of Hibernation in Finnish and German Hedgehogs in a constant Ambient Temperature*. Ann. Acad. Sci. Fenn. A4 122 : 1-23.

Kruger, P. (1969). *Zur Rassenfrage der nordeuropaischen Igel*. Acta Zool. Fenn., 124.

Leyhausen, P. (1965). *Communal Organisation of Solitary Animals*. Symp. Zool. Soc. Lond., 14 : 249-263.

Lidicker, W.Z. (1962). *Emigration as a Possible Mechanism Permitting the Regulation of Population Density below Carrying Capacity*. Amer. Natur., 96 : 29-33.

Lindemann, W. (1951). *Zur Psychologie des Igels*. Z. Tierpsychol., 8 : 224.

Lord, R.D. (1960). *Litter Size and Latitude in North American Mammals*. Amer. Midl. Nat., 64 : 488-499.

Marples, M.J. and Smith, J.M.B. (1960). The Hedgehog as a Source of Human Ringworm. Nature, 188 (4753) : 867 - 868.

Mathias, P. (1929). Sur la biologie du herisson (Erinaceus europaeus L.) Bull. Soc. Zool. France, 45 (5) : 463-466.

Mazurkiewicz, M. (1971). Shape, Size and Distribution of Home Ranges of Clethrionomys glareolus (Schreber, 1780). Acta Theriol., 16 (1) : 23-60.

McCann, C. (1939). Number of young Hedgehogs have at Birth. Jour. Bombay Nat. Hist. Soc., 41 (1) : 171.

McLauchlan, J.D. and Henderson, W.M. (1947). The Occurrence of Foot and Mouth Disease in the Hedgehog under Natural Conditions. J. Hyg. Camb., 45 : 474-479.

McNab, B.K. (1963). Bioenergetics and the Determination of Home Range Size. Am. Nat. 894 : 133 - 140.

Mohr, C.O. (1947). Table of Equivalent Populations of North American Small Mammals. Amer. Midl. Nat., 37 : 223 - 249.

Morris B. (1961). Some Observations on the Breeding Season of the Hedgehog and the Rearing and Handling of the Young. Proc. Zool. Soc. Lond., 136 : 201-206.

Morris, P.A. (1968) Some Aspects of the Ecology of the Hedgehog (Erinaceus europaeus). Ph D Thesis. University of London.

----------------- (1968). Fieldwork on the Hedgehog. Bull. Mammal. Soc. (Lond.), 30 : 3-4.

----------------- (1970). A Method for Determining Absolute Age in the Hedgehog. J. Zool., 161 : 277 - 281.

----------------- (1971). Epiphyseal Fusion in the Forefoot as a Means of Age Determination in the Hedgehog (Erinaceus europaeus). J. Zool., 162 : 254 - 259.

Morrison, P. (1960). Some interelations Between Weight and Hibernation Function. Bull. Mus. Comp. Zool. Harv., 124 : 75.

Mountford, M.D. (1968). The Significance of Litter Size. J. Anim. Ecol., 37 : 363.

Murie, A. (1963). Following fox Trails. Miscl. Publ. Mus. Zool. Univ. Michigan, No.32 : 1-45.

Murie, A. (1940). Fauna of the National Parks of the United States: Ecology of the Coyote in the Yellowstone. U.S. Dept. of the Interior Nat. Park Service, Fauna Series, 4 : 1 - 206.

Murie, A. (1944). The wolves of Mount McKinley. U.S. Dept. of the Interior, Nat. Park Service, Fauna Series, 5 : xx + 238pp.

Noble A.K. (1939). The Role of Dominance in the Social life of Birds. Auk; 56 : 264 - 73.

Proctor, E. (1949). Temperature Changes in Hibernating Hedgehogs. Nature, 163 (4133) : 408.

Petrides, G.A. (1951). The Determination of Sex and Age Ratios in the Cottontail Rabbit. Amer. Midl. Nat., 46 : 312-36.

Sarajas, H.S.S. (1967). Blood Glucose Studies in Permanently Cannulated Hedgehogs during a Bout of Hibernation. Ann. Acad. Sci. Fenn., A (4), 120 : 1 - 11.

Saure, (1969). Histological Studies on the Sexual Cycle of the Male Hedgehog (Erinaceus europaeus L.) Aquilo Ser. Zoologica, 9 : 1 - 43.

Schuetz, H. (1956). Verhalten des Hodens und Nebenhodens beim Igel (Erinaceus europaeus et romanicus L.) waehrend des Anoestrus. Anat. Anz. Jena, 103 (1 - 4) : 66 - 78.

Scott, T.G. (1943). Some Food Coactions of the Northern Plains Red Fox. Ecol Monographs, 13 : 427 - 479.

Scott, (1947). *Comparative Analysis of Red Fox Feeding trends on two Central Iowa Areas*. Agric. Exper. Sta. Iowa State Col. Res Bull., 353 : 425-487.

Smith J.M.B. (1964) *Some Microbiological Aspects of the Short-eared European Hedgehog*, (*Erinaceus europaeus*), *in New Zealand*. Ph.D. Thesis. Dept. Microbiology. Univ. of Otago.

Smith, J.M.B. and Marples, M.J. (1965). *Dermatophyte Lesions in the Hedgehog as a Reservior of Penicillin* - Resistant Staphylococci. J. Hyg. Camb., 63 : 293.

Smith, J.M.B. (1968). *Diseases of Hedgehogs*. Vet. Bull., 38 (7) : 425 - 430.

Taber, R.D. (1956). *Marking of Animals*: Standard Methods and New Developments. Ecol., 37 : 681-685.

Turabian, K.L. (1969) *A Manual for Writers of Term Papers, Theses and Dissertations*. The University of Chicago Press.

Wall, N.E. and Wall, R.M. (1968). *Mating Hedgehogs*. Country-side (Near Aylesbury), 21 (2) : 69-70.

Webster, W.M. (1957). *Susceptibility of the Hedgehog* (*Erinaceus europaeus*) *to Infection with Leptospira pomona.* Nat., 180 : 1372.

Wodzicki, K.A. (1950). Introduced Mammals of New Zealand. Dept. of Scientific and Industrial Res., Bull. No. 98.