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## Some aspects of the biology of the hedgehog (*Erinaceus europaeus* L.) in the Manawatu, New Zealand

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In a study area of 16.3 ha of dairy pasture and pine plantations in the Manawatu region of the southern North Island, 150 hedgehogs were marked and 356 recaptures recorded between 1 January 1970 and 24 June 1971. Population density was estimated at between 1.1/ha in winter and 2.5/ha in summer and autumn. Only 11 females and 5 males were considered to be residents, and these used overlapping feeding ranges of similar extent. Concentrations of food organisms became foci of hedgehog activity. During winter, when an estimated 20% of the population died, movement was restricted to the vicinity of the nest site; the hedgehogs hibernated fitfully during July-October. The breeding season as such extended at least from November to March; some breeding activity was observed in most months, however. The average life span of adults was 1.97 years. The causes of 6 natural deaths and the incidence of abscesses and external parasites were noted.

### INTRODUCTION

The European hedgehog is the only representative of the Insectivora established in New Zealand; it was introduced from Britain in the latter part of the 19th century. It has subsequently spread over much of New Zealand, remaining in habitats generally similar to those occupied by its forbears, viz pasture, hedgerows, sand dunes, and suburban gardens, although it has colonised alpine tussock grassland in the South Island (Wodzicki 1950).

The Manawatu region was colonised by hedgehogs transferred from the South Island in 1910 (Ostler 1942), and they were recorded at Tokomaru, 8 km south of the present study area, in 1911 (Wodzicki 1950). They have since occupied all of the suitable habitats in the region, reaching high densities (more than 2.5/ha) in the coastal sand dunes (Wodzicki 1950, Brockie 1957).

The biology of European populations of hedgehogs has been described by many authors (see Poduschka 1969 for a review of the European literature), and as might be expected the New Zealand animals have diverged from these populations in some aspects of their biology. Wodzicki (1950) suggested that New Zealand hedgehogs have extended their breeding season at the expense of the time spent in hibernation. Similarly, Brockie (1959a, b, 1964, 1974) considered that the local animals depend less than European hedgehogs on insects as a main source of food, reach higher densities, show a higher proportion of genetically determined dental abnormalities, and carry fewer species of parasites (the hedgehog flea, *Archaeopsyllus erinacei*, is absent) than most European hedgehogs.

The aim of the present study was to examine a free-living population in order to obtain data for such comparisons with the European hedgehogs.

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## STUDY AREA

The 16.3 ha study area is situated between Massey University and the Manawatu River, which forms one boundary (ref. NZMS 1 sheet N149). In 1970–71 it comprised 12.5 ha of pasture and 3.8 ha of trees, mostly *Pinus radiata* but also some *Populus* sp., *Salix alba*, and *Eucalyptus ficifolia* (see Fig. 3). A large pine plantation marked a second boundary; the other two were set arbitrarily across continuous grassed farmland. A small lagoon and areas of long tussock were included.

## METHODS

Data were obtained from observations made on at least 2 nights each week (except during July–October, when the number of observations was halved) by walking along transects and searching for animals by torch-light. The transect spacing (about 50 m) was governed by the range of the torch and the nature of the vegetation. The transects were reoriented by 90° on each successive visit, and the minimum total search time of 1 h was staggered throughout the night. Climatic variables (minimum and maximum air temperatures, minimum grass temperatures, rainfall, and daylength) were obtained from a meteorological station located 500 m from the study area, and each search period was classified into 1 of 4 classes of weather (Table 1). A minimum grass temperature of 8°C was chosen to separate 'cold' from 'warm' because Herter (1963) has shown this temperature to be critical in the induction of hibernation.

Weather	Mean no. of hedgehogs/h searched $\pm$ S.E.
Fine and warm	7.04 $\pm$ 0.57
Fine and cold	5.05 $\pm$ 0.58
Wet and warm	4.24 $\pm$ 0.77
Wet and cold	2.90 $\pm$ 1.07

TABLE 1—Effect of weather on number of hedgehogs sighted, Manawatu, New Zealand, Jan. 1970–June 1971

Before 24 March 1970 only those hedgehogs found around the central pine plantations were examined, but subsequently all animals caught were weighed, sexed, and marked (by painting various colour codes on their spines) for individual recognition. Most were also ear-tagged with small, numbered, metal tags for permanent identification (animals with severe mite infestations, which caused 'cauliflower ears', could not be tagged). Initially all animals were anaesthetised with chloroform, but with experience it proved possible to dispense with this. All animals captured were inspected for ectoparasites. Additional information on breeding condition was gained from autopsies performed on hedgehogs caught in the suburbs of Palmerston North and in the Massey University orchards.

Population densities were estimated from the number of different animals seen each month, standardised between months to a 10 h search time. This method led to underestimation because of unseen hedgehogs and to overestimation because of emigration, but was preferable to Lincoln index estimates because the assumptions implicit in them were not fulfilled.

The location and movements of hedgehogs were determined by reference to maps drawn from aerial photographs and field measurements; as a check on the location of wide-ranging individuals the surrounding countryside was surveyed monthly. The feeding ranges of marked hedgehogs observed sufficiently often are represented (see Fig. 3) as the smallest convex polygons (Mohr 1947) containing all the points of capture.

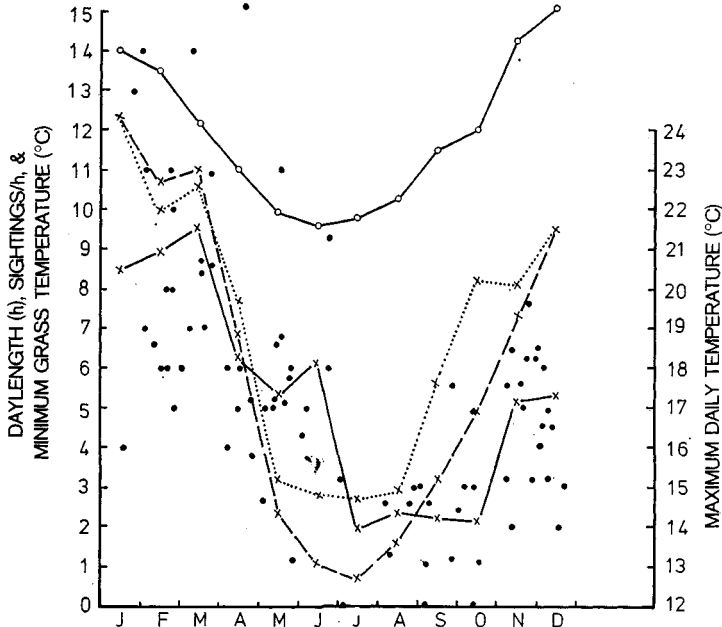


FIG. 1—Incidence of hedgehog sightings in the Manawatu, New Zealand, in relation to climatic variables (●, sightings/h for each observation period; x—x, mean monthly sightings/h; x—x, min. grass temp.; x...x, max. air temp.; o—o, daylength).

## RESULTS AND DISCUSSION

### POPULATION DENSITY AND SEASONAL ACTIVITY

Between January 1970 and June 1971, 150 hedgehogs were marked and 356 recaptures were recorded. It was estimated that  $40.8 \pm 2.9$  hedgehogs used the study area in every month except July–October, when only  $18.4 \pm 1.8$  hedgehogs were seen each month, part of the population presumably being in hibernation. These figures are equivalent to densities of 2.5/ha and 1.1/ha, and are comparable with the density of 2.5/ha for hedgehogs from Paekakariki (Brockie 1957), though much less than Campbell's (1973) estimates of up to 8/ha in March and nearly 4/ha over winter for a Canterbury pasture.

The frequency of sightings varied both seasonally and from day to day (Fig. 1), and though there were strong correlations between the number of sightings/h and both the minimum grass temperature and the maximum air temperature ( $r = 0.377$ ,  $r^* = 0.329$ ), the large variances about the two regression lines ( $y = 3.4 + 0.267x$ ,  $s = 13.5$ ;  $y = -3.5 + 0.469x^*$ ,  $s^* = 2.62$ ) suggest the influence of other factors. Rain accounted for some of this variability (Table 1): more hedgehogs were seen in fine than in wet weather, when many animals presumably remained in their nests.

It is also clear from Fig. 1 that whereas the various climatic variables are at minimum values between mid May and mid August, fewest hedgehogs were seen during July–October, and in fact there is no significant correlation between the pairs of data during this latter period. This casts some doubt on the postulated association between low temperatures and hibernation, suggesting that the cumulative effects of 2 months' low or rising temperatures are necessary before hibernation begins or ends.

In Europe hibernation lasts for some 5 months (Herter 1963), compared with 3 months' hibernation and continued activity of nearly half of the animals in the present study. This reinforces the view that the mild winters in the Manawatu do not rigidly enforce hibernation.

TABLE 2—Monthly mean adult body weights of hedgehogs, Manawatu, New Zealand, Jan. 1970–June 1971

	♂♂		♀♀	
	n	Mean wt. (g) ±S.E.	n	Mean Wt. (g) ±S.E.
Jan	4	719±26	4	725±25
Feb	9	628±38	13	622±35
Mar	16	718±32	12	705±55
Apr	33	731±27	30	710±23
May	24	789±34	31	664±33
Jun	21	739±49	29	753±28
Jul	9	603±49	19	648±40
Aug	6	608±47	7	706±58
Sep	24	709±32	17	711±44
Oct	17	676±30	5	620±58
Nov	41	674±16	34	674±20
Dec	14	689±29	20	696±25

TABLE 3—Monthly mean weights of hedgehog ♂ genitalia, Manawatu, New Zealand, Jan. 1970–June 1971

	n	Mean wt. (g) ±S.E.	Mean wt./100 g body weight
Jan	4	22.9±4.2	3.14
Feb	6	17.5±5.4	2.49
Mar	6	17.1±4.4	2.15
Apr	8	7.5±2.5	0.99
May	7	9.4±2.3	1.15
Jun	15	5.6±1.5	0.74
Jul	9	3.0±0.4	0.58
Aug	2	2.3±0.1	0.42
Sep	18	26.0±3.5	3.46
Oct	10	19.1±3.5	3.11
Nov	6	19.7±2.9	3.63
Dec	4	28.8±6.4	3.71

### BODY WEIGHT

In the course of the study, 218 adult males and 221 adult females were weighed; the overall mean weight for males was  $706 \pm 10$  g and for females was  $688 \pm 9.9$  g. Animals weighing under 400 g were considered to be juveniles, because the genitalia of those autopsied were never in breeding condition. The monthly mean weights of the sexes were significantly different only in May ( $t = 3.15$ ,  $P < 0.01$ ; Table 2).

A seasonal pattern of weight change was apparent also, males in particular gaining weight in autumn and both sexes losing weight during winter and February (Table 2). Abundance of food could not be responsible for the autumn weight increase, since the sexual difference in May would then be inexplicable. Rather, endogenous rhythms of fat deposition (*see* Kayser 1961), in which the males preceded the females in this population, must have been responsible. However, reduced food supply probably explains the loss of condition in February, when there was a severe drought in the Manawatu.

### BREEDING BIOLOGY

Abrupt increase in the average weight of male genital organs (Table 3), and particularly the seminal vesicles (Table 4), marked the onset of male fertility in September and its termination in February–March. During this period male/female encounters of two kinds were observed: brief, casual contacts which were never seen to result in any overt interaction, and sexual meetings. Encounters between males and receptive females were characterised by a display (*see* Haarlov 1943, Wall & Wall 1968) in which the couple, snuffling and snorting, performed a circular ‘dance’. This pre-copulatory behaviour was seen 36 times between 24 August and 17 May, most frequently during November–January, when 30 of the displays were observed. It was seen to end in copulation only twice, perhaps because of the disturbing influence of the observer’s light.

Of 99 females autopsied throughout the year, only 14 were pregnant. The earliest pregnancy was recorded on 7 November and the latest on 21 June; all pregnancies but the latest were discovered in the 36 females autopsied during November–March.

The first weaned juvenile found after winter was a female weighing 150 g, caught during daylight on 13 October. However, most independent juveniles were first seen during January–February, when 36 unmarked animals weighing less than 400 g were located. Two hedgehogs weighing less than 300 g were found as late as July. No dependent young were found in the study area, but elsewhere in the region 2 nests, each with 5 young, were

TABLE 4—Spring hypertrophy of hedgehog testes and accessory sex glands, Manawatu, New Zealand, 1970–71

	Wt. of seminal vesicles (g)	Wt. of testes (g)	Wt. of prostates (g)	Wt. of Cowper's glands (g)
Jun–Aug	0.74±0.16	1.84±0.20	0.29±0.06	0.35±0.07
Sep–Jan	13.32±1.87	4.21±0.29	2.96±0.51	2.90±0.44

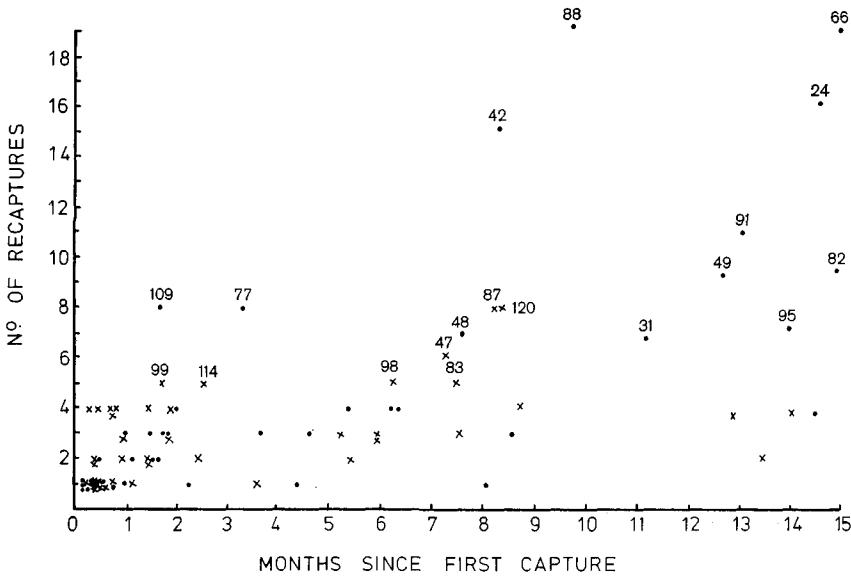


FIG. 2—Recapture data for 92 of 150 marked hedgehogs, Manawatu, New Zealand (x, ♂; •, ♀; numbers, codes for individual animals whose minimum ranges are indicated in Fig. 3).

found during December. One was in a hay-field and one in a shed; the young from the hay-field weighed on average  $38 \pm 0.9$  g. These 2 litters and the 14 pre-partum litters from the autopsied females gave a modal litter size of 5 (range 2–6). The sex ratio of 50 juveniles examined was exactly unity, and in the whole population there was a slight, but non-significant, excess of males (181:164).

Most breeding by Manawatu hedgehogs occurred during November–March, although, against the evidence of male fertility, unseasonal litters were produced. The onset of male fertility coincided with the first mating displays, but the females did not normally conceive until 2 months later, presumably having passed through the infertile, dioestrous, and pseudo-pregnancy cycles described by Deanesly (1934).

The termination of breeding was even less clear-cut, mating displays, small juveniles, and even one pregnancy being observed well into autumn. This late pregnancy was unusual in that the foetuses were being resorbed (see Morris 1961), and no pregnant animals were found during the preceding 2 months. The juvenile found in October was also exceptional; allowing 6 weeks for gestation and 6 weeks for weaning (Herter 1963), it must have been conceived in July.

This situation confirms Wodzicki's (1950) suggestion that New Zealand hedgehogs have extended their breeding season, though the 'core' period of 5 months remains equivalent to the April–August season in Europe (Herter 1963).

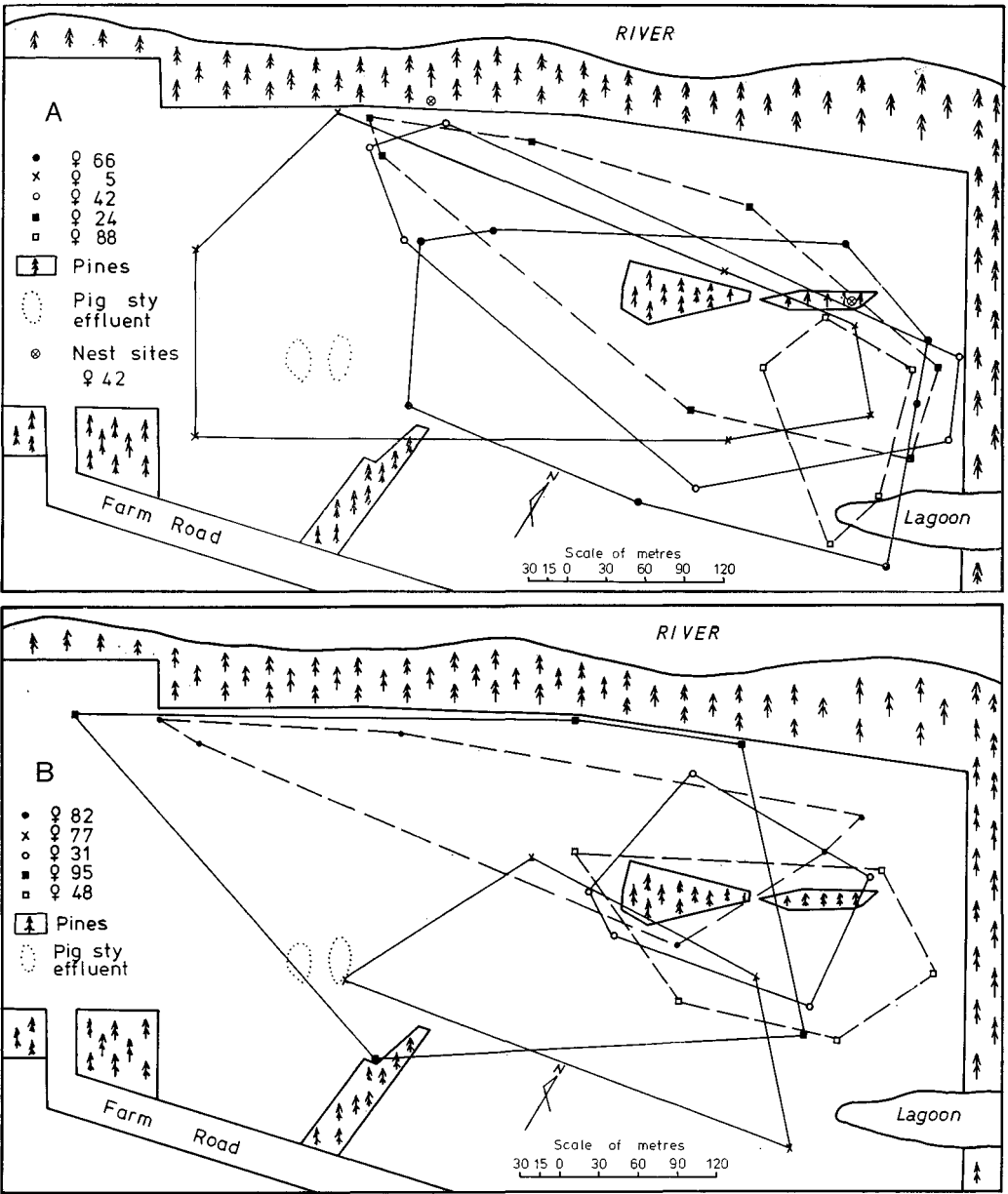
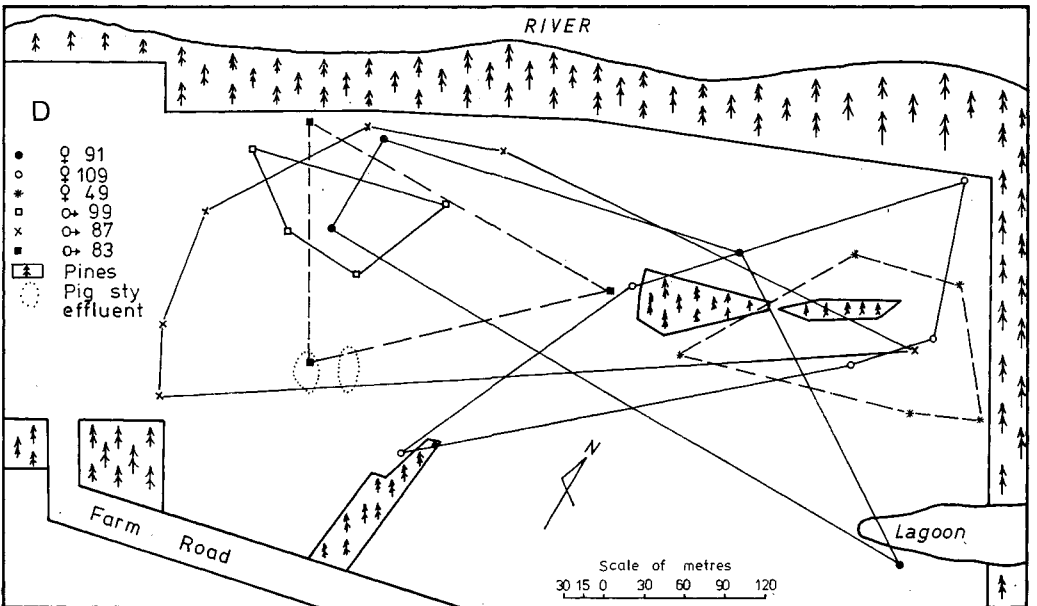
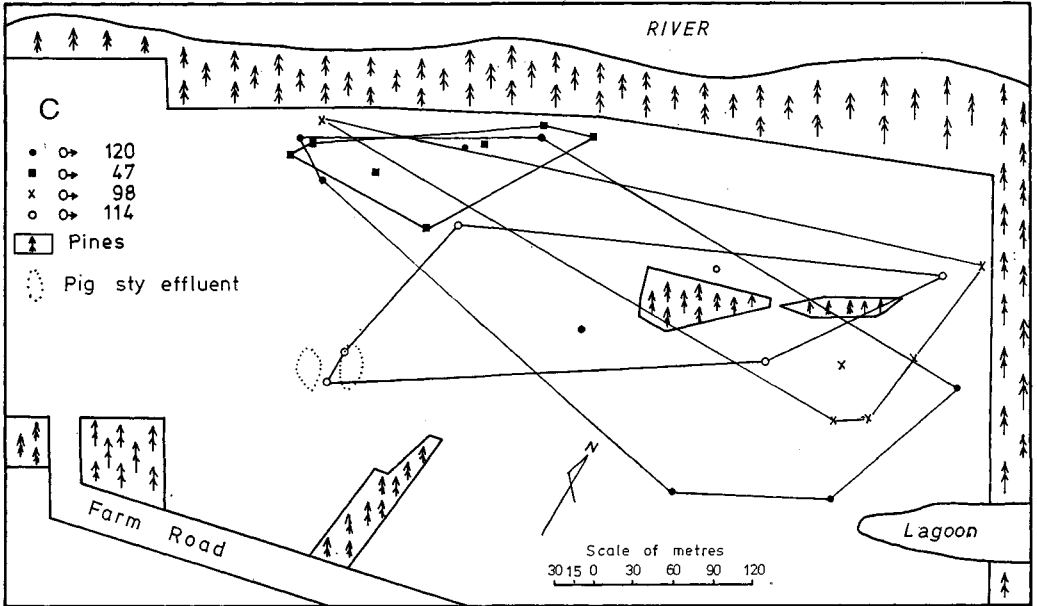


FIG. 3—Minimum ranges of resident hedgehogs, Manawatu, New Zealand, from capture/recapture locations: A, B (above) – adult ♀♀; C (opposite page, upper) – adult ♂♂; D (opposite page, lower) – juveniles.

**MORTALITY AND DISEASE**

Estimates of the number of hedgehogs using the study area dropped from an average of  $35.5 \pm 2.6$  in April–June to  $28.2 \pm 2.4$  in November–December, presumably because of winter mortality. Drowning during hibernation probably caused many deaths (although no bodies were found), since parts of the study area were flooded during winter.

No direct measure of age was made, but by dividing the sample taken over the breeding



season (taken as January–March) into juveniles and adults and applying the formulae derived by Petrides (1951), two statistics— $T$ , the time required for 99.5% of the population to be replaced by its descendants, and  $L$ , the average life span of animals surviving until their first breeding season—can be calculated.

$$T = \frac{\log 0.005}{\log (1-j)} + 1 = 8.5 \text{ years,}$$

where  $j$  is the proportion of juveniles in the sample (73/144);

$$L = 1/j = 1.97 \text{ years.}$$



Individual	No. of sightings	Date marked (1970)	Date last seen	Range (ha)
Adult ♀ No. 66	20	24 Mar	24 Jun 1971	5.0
88	20	11 Jan	22 Dec 1970	1.0
24	17	6 Apr	24 Jun 1971	3.9
42	16	20 Mar	20 Nov 1970	4.7
5	13	21 Jan	24 Jun 1971	5.7
82	10	24 Mar	24 Jun 1971	2.9
77	9	24 Mar	2 Jul 1970	2.7
31	8	15 Apr	19 Mar 1971	1.6
48	8	24 Apr	1 Dec 1970	2.0
95	8	26 Jan	25 Mar 1971	6.5
Mean	12.9			3.6
Adult ♂ No. 120	9	29 Sep	10 Jun 1971	4.8
47	7	24 Apr	30 Nov 1970	0.8
114	6	27 Feb	12 May 1970	2.2
98	5	8 Nov	17 May 1971	2.3
Mean	6.7			2.5
Juv. ♀ No. 91	11	19 Feb	19 Mar 1971	3.0
49	10	24 Apr	17 May 1971	1.4
109	9	11 Jan	3 Mar 1970	4.9
Juv. ♂ No. 87	9	24 Mar	1 Dec 1970	4.9
83	6	24 Mar	7 Nov 1970	1.5
99	6	4 May	24 Jun 1970	0.5
Mean	8.5			2.5
Adult mean	11.1			3.3
Total mean	10.3			2.9

TABLE 5—Feeding range areas and recapture data for resident hedgehogs, Manawatu, New Zealand

These statistics are probably overestimates; the calculation of  $j$  did not include unweaned juveniles, whose mortality rate will be higher than that of independent juveniles if hedgehogs resemble other mammals with regard to the distribution of juvenile mortality (Caughley 1966).

The bodies of 4 marked hedgehogs were recovered: 2 were killed on nearby roads, 1 was found *in extremis* and died the next day, and 1 was found dead in the study area. Apart from many uncounted road deaths, the deaths of 2 unmarked animals were recorded. One young hedgehog with 'fly-blown' ears was found *in extremis*, and an adult, located by its loud screams, was found staggering about tearing up grass; it died within an hour, possibly the victim of a plant toxin, since its stomach contained the sclerotia of an unidentified fungus.

Three marked animals were found with large facial abscesses, possibly infected lesions caused by mites; one is known to have recovered. The mange mite, *Caparinia tripilis*, was identified from 20% of the marked and autopsied hedgehogs, and caused scaly encrustations on the ears and skin which, when severe, inhibited rolling up. Unidentified fleas were found on 5 autopsied hedgehogs, but infestation rates could not be determined reliably because of the difficulty of searching captured animals in the field at night.

#### MOVEMENTS

The 150 marked hedgehogs were divided into residents (11 females, 5 males), which were recaptured at least 5 times over a period exceeding 6 months, and transients (60 females, 74 males), which were recaptured over shorter periods, never recaptured, or caught only irregularly over longer periods (Fig. 2). Altogether, the 71 females marked were recaptured on average  $3.70 \pm 0.24$  times, whereas the males were recaptured on average only  $2.08 \pm 0.18$  times. Fifty-eight hedgehogs (25 females) were never recaptured.

TABLE 6—Distances moved by transient hedgehogs, Manawatu, New Zealand

Individual	Date sighted in study area (1970)	No. times seen	Date last seen (1970)	Distance moved (m)
Adult ♀ No. 26	30 Apr	3	1 May	1130
„ ♀ No. 34	21 Apr	2	24 Apr	1500
„ ♂ No. 54	21 May	3	10 Jun	1500
„ ♂ No. 117	2 Sep	2	6 Sep	1050

The points of capture of the 16 residents, plus those of males 99 and 114 and females 77 and 109 (transients captured 5 or more times), were plotted; the minimum ranges inferred from this varied between 0.4 ha and 6.51 ha (Fig. 3, Table 5). There were no significant differences between adult males, adult females, and juveniles with respect to range area or to the distance between the furthest points of capture. The ranges are considered to be feeding ranges, since the polygons enclosing the points of capture of animals 43, 83, 87, and 99 contained no possible nest sites.

The transient animals were each recaptured on average 1.37 times. Excluding the newly caught juveniles, the number of unmarked adults caught each month (after March 1970, when a large number had been marked) averaged  $7.9 \pm 1.9$ , compared with the total number of previously marked adults caught each month of  $17.6 \pm 4.8$ . This near 1:2 proportion of transients was recorded in all months except July and August, when no new hedgehogs were found. It was thought that the study area might be too small to accommodate the hedgehogs' movements, but during the monthly surveys of the surrounding areas only 4 marked animals were discovered more than 500 m from the edge of the study area (Table 6).

One assumption made in the definition of resident and transient animals was that an animal marked and not recaptured had either moved from the area or died, and considering the low average life span suggested it is likely that many of the animals classed as transients had indeed died. The high proportion of transients to residents is therefore overstated.

The factors controlling the size of the resident population are not known, but since nest sites and food supplies form important foci of activity (Carpenter 1940), their availability is probably an important limiting factor. Nests located were in piles of pine needles and were of two types. Summer nests were flimsy structures and were probably temporary, since adult female 42 changed her nest site during September (Fig. 3), although she continued to use the same feeding range. Hibernation nests (*see* Morris 1970) were much more elaborate structures, and were apparently not abandoned until spring, as evidenced by the lack of transient animals seen during winter.

Concentrations of food became foci of hedgehog activity. During mid March 1970 the effluent from a pigsty spilled over 0.1 ha of pasture in two places (*see* Fig. 3) and became infested with the maggots of the shed fly, *Eristalis tenax*. Large numbers of hedgehogs – 21 on 24 March for example – were seen to be eating them. In early May the larvae of the armyworm moth, *Pseudaletia separata*, were present at an estimated density of 2–3/m<sup>2</sup> in some areas around the central pine plantations, and the hedgehogs gathered to feed. In late November an area which had recently been flooded supported a dense population of slugs of various species, and on 1 December 1970, 9 hedgehogs were observed feeding on these molluscs.

Conversely, unproductive areas such as the pine plantations were avoided by feeding animals. Within the pasture the hedgehogs avoided very long grass, so indirectly the grazing pattern of the herd of cows influenced hedgehog movements.

No evidence of social dominance or territorial behaviour was observed, although the high proportion of females among residents may indicate female dominance, as found by

Lindemann (1951) with caged hedgehogs. Neither was any evidence of the trail system, described by Lindemann (1951) for suburban German hedgehogs, discovered, possibly because the physical barriers characteristic of suburbia were absent.

#### CONCLUSIONS

Wodzicki's (1950) suggestion that the breeding season is lengthened at the expense of hibernation is confirmed for Manawatu animals, although the situation is more complex than this statement implies because the seasonal cycles of breeding and hibernation of the sexes are not synchronised. Males gain weight in autumn and attain breeding condition in spring about 2 months before females. A similar situation exists with respect to the limits to the hibernating season (to be described in a joint paper with R. E. Brockie). It is suggested that the length of the breeding season delays the females' autumnal fat storage and thus delays hibernation and subsequent breeding. This suggests that endogenous rhythms control hibernation, and indeed climatic factors did not correlate with winter activity in this study.

#### ACKNOWLEDGMENTS

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