BIOLOGY AND ECOLOGY OF THE SHIP RAT *RATTUS RATTUS RATTUS* (L.) IN MANAWATU (N.Z.) FORESTS

A thesis presented in partial
fulfilment of the requirements for
the degree of Master of Science in Zoology
at Massey University

John Gordon Innes

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Ship rat, "frugivorus" morph
(Half natural size)

ABSTRACT

Ship rats in Manawatu lowland forest were studied by snap and cage trapping for one year, and by tracking. The results are very similar to those of previous New Zealand studies. Rat density was low. Only 3.9 rats per 100 trap nights were trapped at Tiritea and the estimated mean density at Keeble's Bush was 2.8 rats per hectare. Although males with mature sperm were trapped all year round, pregnant females were trapped from mid-September to mid-April, except for one in June. The mean number of embryos per female was 4.95 and females produced up to four litters each. Annual mortality calculated from cage grid disappearances was 96% for both sexes combined, although the factors causing mortality were unknown. Four ectoparasite species and two stomach nematode species were identified. Large numbers of nematodes (up to 84) per stomach did not significantly reduce the weight of rats of a given length.

The stomach analysis of 178 ship rats showed that arthropods (mostly wetas) occurred in 88% of stomachs. Predominantly animal foods were eaten overall, but plant foods predominated in autumn and winter. Feathers were in few stomachs (5%) but their appearance in rats trapped only during the nesting season suggests that rat predation could be strategically severe at this time. Kiekie and kawakawa fruits were the commonest plant diet items. Rat damage to fruits and leaves of species found in the study areas is described in the thesis, and an index of palatability is given. An exclosure study in Keeble's Bush suggested that rats did not remove significant numbers of fallen titoki and tawa fruits. No plant species seems likely to have its regeneration endangered directly because of ship rat damage to its seeds. Some seeds are dispersed by rats.

A technique for tracking rats is described. Five toe-clipped ship rats were tracked for seven months on smoked kymograph paper inserted in special tunnels. Twenty tunnels, of which ten were on sloping branches in trees, were used in the .22 ha study area. Smoked paper was an ideal tracking surface, and rats were tracked at up to 16 locations in one night. Baiting the platforms significantly increased the rate of tracking and did not cause rats to leave their home ranges. Concurrent cage trapping produced inadequate data for home range determination and was insensitive in detecting changes in home range areas. All five rats were to some extent trap shy. Cage trapping is considered to be an inadequate technique for determining rat movement and perhaps population density. Tracking-

revealed home ranges were stable, and one was seemingly exclusive to the ranges of other rats. Smoked paper tracking has considerable promise as a technique in population ecology.

ACKNOWLEDGEMENTS

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* Taken by Massey Central Photographic Unit.

SECTION 1 - INTRODUCTION AND METHODS

CHAPTER 1

There can be little doubt that the ship rat is a pest in New Zealand forests. The actual extent of its impact by predation or competition on native bats, birds, reptiles and invertebrates will never be known with accuracy; first, because the period of its major impact was probably eighty to one hundred years ago, and second because many other factors were operating simultaneously to reduce animal populations.

The little doubt that remains concerns the possibility that the ship rat merely filled the niche vacated by the kiore, an earlier introduced rat which was once widespread in New Zealand forests.

1.1 Introductory Description

The ship rat is one of three species of the genus Rattus (family Muridae) in New Zealand. These are the Polynesian rat or kiore Rattus exulans Peale; the Norway, water or brown rat Rattus norvegicus Berk.; and the ship, bush, black or roof rat Rattus rattus rattus (L.) All three species were introduced.

Distinguishing characters are listed by Best (1968) and Atkinson (1973). The ship rat (see frontispiece) is the medium sized rat of the three. It weighs on average approximately 140g. The ears are thin and hairless and when pushed forwards always cover the eyes. The tail is in nearly all cases longer than the body. Females normally have two pectoral pairs of mammae and three inguinal pairs (total = 10) although the second pectoral teat is variable, sometimes being doubled on one side and sometimes on both (Best, 1968; the present study). The belly fur is either pure white or grey, rather than white with grey bases.

The ship rat in New Zealand exhibits a pelage polymorphism producing three colour morphs. These are: 'rattus' morph = black back, grey belly; 'frugivorus' morph = grey/brown back, white belly; 'alexandrinus' morph = grey/brown back, grey belly. While early workers gave these morphs subspecific rating, later observers noted that interbreeding between them occurred (see Best, 1968). Johnson (1962) concluded that the three were not true subspecies and that the trinomial Rattus rattus rattus (L.) should be applied to all three colour morphs. Feldman (1926) and Tomich and Kami (1966) described the genetics of coat colour inheritance. Tomich (1968) considered coat colours by themselves were of neutral selective value and that their distributional pattern had arisen through pleiotropic action

of the coat colour genes whose major adaptive significance in local environments was physiological.

In the South Island, New Zealand, all three morphs occur. In the North Island, however, only the 'rattus' and 'frugivorus' morphs have been found. (Daniel, 1972; the present study).

1.2 Spread and Distribution

R. rattus rattus was originally distributed in the Indo-Malayan region, extending into Southern China (Southern, 1964). With the trading and exploring activities of man, this rat has spread throughout the world where it is now a major pest, both because of the diseases it carries and the food it eats (Hinton, 1918; Walker et al., 1964).

There is no record of exactly when R. rattus rattus arrived in New Zealand. After an extensive review of the available evidence Atkinson (1973) concluded that ship rats may have reached New Zealand "at the time of Cook's voyages or soon afterwards". Furthermore, he concluded it probable that the major spread of ship rats to their present distribution did not occur in the North Island until after 1860, and in the South Island until after 1890. Today R. rattus rattus occurs throughout the three main islands, and on many offshore islands as well (Atkinson, in press). The species is common in urban areas (see e.g. Best, 1968) and is by far the most widespread rat in both indigenous and exotic conifer forest.

Ship rats seem to prefer mature forest. Moors (1975) found more ship rat tracks in mature forest at Kowhai Bush, Kaikoura, than in other habitat types. In the present study 290 trap nights on grass or in scrub at the bush edge produced only one rat (= .35 rats/100 trap nights c.f. 4.0 rats/100 trap nights inside the forest).

R. rattus rattus is largely arboreal. Daniel (1972) captured 27 ship rats in live traps set in trees in the Orongorongo Valley. Twenty-four of these were also captured on the ground, indicating that the great majority of this sample were not living entirely in the canopy. Most ship rats probably nest in trees but descend to the ground to feed. They are very agile climbers.

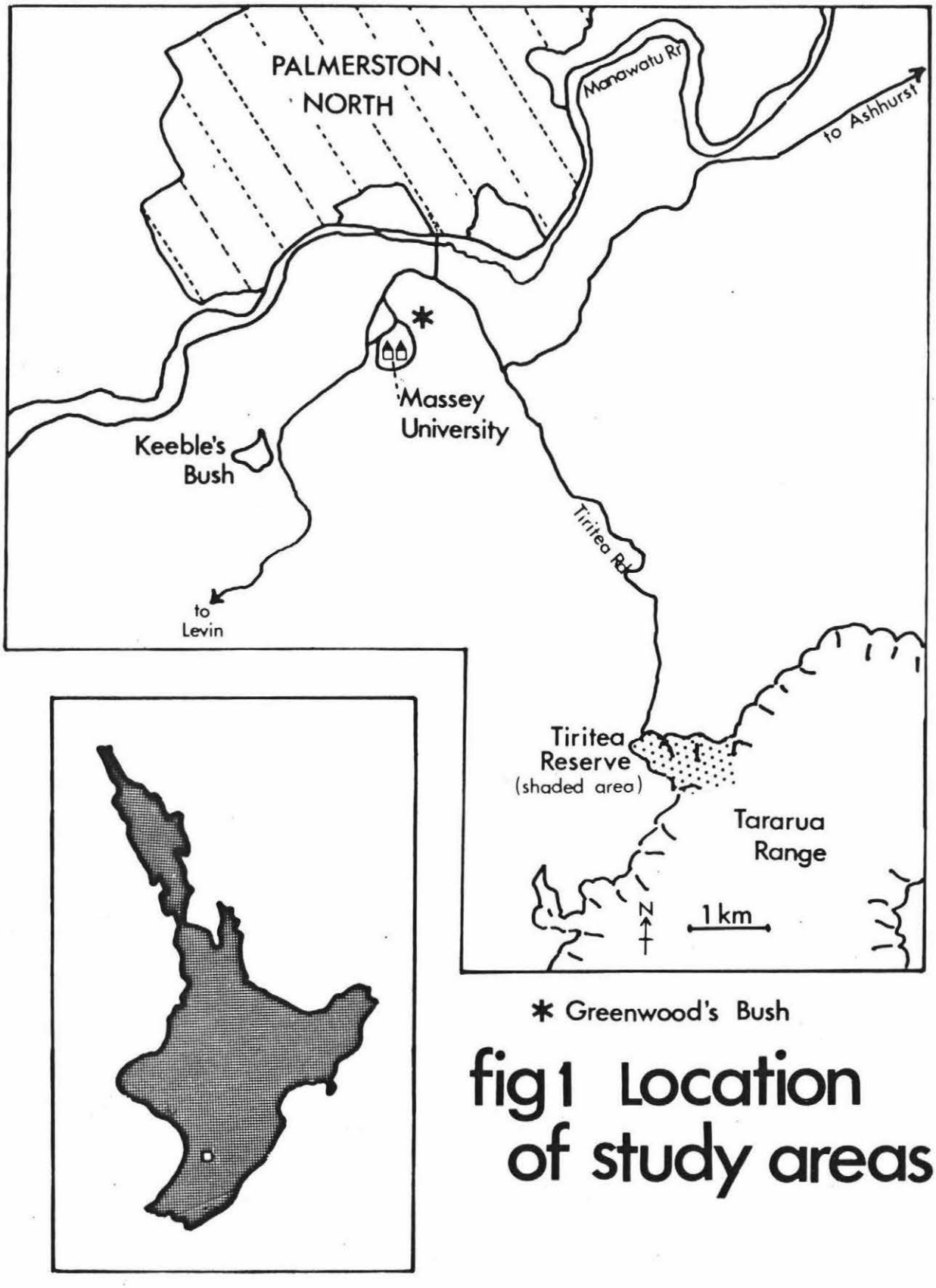


fig 1 Location of study areas

CHAPTER 2: DESCRIPTION OF STUDY AREAS

The locations of the three study areas are shown in Fig. 1.

2.1 Tiritea (Snap trapping)

The Tiritea reserve is a water supply catchment near the North western extremity of the Tararua Range, some 10km E. of Palmerston North. During this study the forest to the west and southwest of the main water storage dam (N.Z.M.S. 1, N149, Ref. Area 160250) was sampled by snap trapping. The range here is low; no part of the study area exceeded 450m. Mean annual rainfall for the ten years prior to 1976, as recorded at the water treatment station within the reserve, was 1284mm, but in 1976 a total of 1616mm was recorded. This is the highest figure ever measured. The winter months June, July and August accounted for 39% of this total.

Esler (1969) described the vegetation of the entire reserve. In my study area tawa Beilschmiedia tawa forms the great majority of the canopy. Remnant podocarps (especially rimu Dacrydium cupressinum; miro Podocarpus ferrugineus and totara Podocarpus totara) are scattered but nowhere common. As a result of high deer numbers in the 1950s the ridges are at present commonly devoid of understorey except for the unpalatable horopito Pseudowintera axillaris, peppertree P. colorata and crown fern Blechnum discolor (Plate 1). In contrast, the sides of ridges, in places very steep, hold dense pockets of supplejack Rhipogonum scandens and kiekie Freycinetia baueriana subsp. banksii (Plate 2). Here also, mature pigeonwood Hedycarya arborea, mahoe Melicytus ramiflorus, rewarewa Knightia excelsa and pukatea Laurelia novaezelandiae occasionally contribute to the canopy. Nikau Rhopalostylis sapida is localised but widespread. On the bush edge, and in regrown forest along Tiritea Road the following species are present: kawakawa Macropiper excelsum; rangiora Brachyglottis repandra; five-finger Neopanax arboreum; pate Schefflera digitata; tarata Pittosporum eugenioides and karamu Coprosma lucida. Kiekie and Collospermum hastatum are common epiphytes on tawa and other canopy trees.

Mammals other than the roof rat present in the study area are red deer Cervus elaphus, mice Mus musculus, possums Trichosurus vulpecula, hedgehogs Erinaceous europaeus, stoats Mustela erminea, weasels Mustela nivalis and feral cats Felis catus. Ferrets Mustela putoria are probably present but were not observed.

Native bird species seen at Tiritea include wood pigeon Hemiphaga n. novaeseelandiae bellbird Anthornis m. melanura, morepork Ninox n. novaeseelandiae, kingfisher Halcyon sancta, tui Prosthemadera n.

Plate 1: Tiritea, ridge top

Plate 2: Tiritea, side of ridge

novaeseelandiae, whitehead Mohoua albicilla, grey warbler Gerygone igata, waxeye Zosterops t. laberalis and fantail Rhipidura fuliginosa placabilis. The introduced species, blackbird Turdus m. merula and thrush Turdus philomelos were quite common on the bush edge but only blackbirds were found further than 400m into the bush.

This reserve was chosen as a study area because of its proximity to Palmerston North, its reasonably traversible ridges and its limited access for members of the general public.

2.2 Keeble's Bush (Cage trapping)

Keeble's Bush was described by Esler (1962), and Atkinson and Greenwood (1972). Esler reckoned it to be the finest Manawatu bush remnant. It covers 12.5 ha and is situated 2km southwest of Massey University, Palmerston North (N.Z.M.S. 1, N149, Ref. 091295). The Maungatungaroa Stream meanders through the bush and provides one geographical border to the present study area, which covers 2.4 ha in the southeast corner of the bush and is nearly all flat. Keeble's is surrounded on all sides by pasture, although pasture formed only one of the boundaries of the study area. Rainfall records at D.S.I.R. Station 19, two kilometers away, show that the mean annual rainfall for the ten years prior to 1976 was 944mm. During 1976 1216mm was recorded. This is the largest total recorded since 1947 when measurements began. The winter months June, July and August accounted for 43% of this total.

All Manawatu forest remnants are in a state of structural flux but Keeble's is at present distinctly three layered. The upper layer consists of emergent podocarps, particularly kahikatea Podocarpus dacrydioides and rimu. The middle layer, eight to twelve metres high, forms the bulk of the canopy. Titoki Alectryon excelsus, tawa and mahoe are major components. Young titoki and mahoe, ferns and sedges, and kawakawa are especially common in the third layer. This understorey is unusually diverse and luxuriant due to the complete absence of browsing mammals.

Lianes - supplejack; Calystegium tuguriorum; Muehlenbeckia australis and Tetrapathaea tetrandra - are widespread and sometimes produce dense aerial thickets on the subcanopy. The epiphytes Collospermum hastatum and Astelia solandri are common on the larger trees.

Opossums, hedgehogs, roof rats and mice were the only mammals observed in the bush although it is likely that cats and mustelids are also present. Native birds observed in the study area were fantails, grey warblers, waxeyes and kingfishers. Blackbirds, thrushes and several

Plate 3: Keeble's Bush interior

Plate 4: Greenwood's Bush from the south

passerines especially goldfinches Carduelis carduelis and greenfinches Carduelis chloris, were also common.

A severe storm in 1936 and droughts during the 1969-70 and 1972-73 summers killed many trees (Atkinson and Greenwood, 1972). Decaying logs are found throughout Keeble's.

As a study area, it was ideal because of its proximity to Massey University. Also, it is a Trust scientific reserve and has reduced access for the public.

2.3 Greenwood's Bush (Tracking)

Greenwood's Bush is a .22 ha private bush on the southern outskirts of Palmerston North (N.Z.M.S. 1, N149, Ref. 115318). Many trees have been hand planted by Mr. R.L. Greenwood although with just a few exceptions they are the species typical of Manawatu remnant forest. No tree is at present taller than about 10m and self seeded mahoe and tarata are the predominant species. Karaka Corynocarpus laevigatus, tree lucerne Lupinus arboreum and red beech Nothofagus fusca also contribute significantly to the canopy, which is sufficiently continuous to allow the arboreal roof rats to travel from tree to tree through it. There are no large epiphytes suitable as nest sites for roof rats. The best available rainfall data is from D.S.I.R. Station 19 (Section 2.2) one kilometre away. Virtually all of the bush slopes gently to the west.

Pasture surrounds two sides of the bush. A third side is bordered partly by uncut and partly by cut grass. A developed section (part garden, part lawn) containing a house makes the fourth boundary. I do not consider that the proximity of Mr. Greenwood's house or nearby human activity was at all disturbing to the roof rats living in the bush. The area was rarely visited other than by myself and virtually never at night when rats are active.

This bush is frequented by cats from nearby houses, and attracts many birds, mostly introduced species. Blackbirds and thrushes, together with the native fantails and grey warblers, usually nest there each year. A morepork was seen in the bush, and a weasel was observed on the nearby section.

Tracking began here initially to trace the movement of rats around known nest sites, and later became a method to determine accurately the home ranges of the ship rats present in the bush.

CHAPTER 3: METHODS

3.1 Snap Trapping

Snap traps were used at Tiritea principally to obtain year round samples of dead rats for autopsy. Although most were the wooden based "Woodstream Corps" type shown in Plate 5, some metal selfset traps were also used. A piece of wire mesh was added to all traps (Plate 5) to stop rats approaching the bait over the set mechanism, and all were sensitized to release at the minimum pressure. The traps were tied down to prevent possums, stoats or wounded rats dragging them away.

Forty-five traps, baited with peanut butter, were set in a line for as many consecutive nights as were apparently needed to trap the area out. Normally this meant trapping until no rats were caught for two consecutive nights, but traplines were sometimes closed when sufficient rats for a month's sample had already been taken or when time was limiting. All traps were then sprung but left in position until the beginning of the next month's sample period when they were rebaited until, again, no rats were caught. The line was then immediately transferred to a new area. During the year long period March 1976 to February 1977, 13 different areas were trapped for a total of 7153 trap-nights. The history of each trapline is presented in Appendix 1.

The following information was taken off trapped rats: Date and place of capture; morph ("frugivorus" or "rattus"); sex; weight; body length; tail length; ear length; reproductive condition (testes scrotal or abdominal, vagina perforate or non-perforate); presence of parasites; unusual features. The number of unsuccessfully sprung traps, and the number of traps containing non-target species was also noted.

3.2 Live Trapping

Live (cage) traps can supply information on rat movement and population levels. In this study 35 traps were laid in an incomplete 6 x 6 rectangular grid in the southeast corner of Keeble's Bush. Each trap (Plate 6) measured 35 x 15 x 13cm. A metal or canvas roof for waterproofing and a weight of spring to close the door faster had been added to the commercially retailed unit. Peanut butter on a piece of carrot was used as bait. Wood wool at the rear of the cage supplied insulation for the trapped rat. Traps were spaced 30m $\pm$ 1m apart in positions most cryptic to passers-by.

The traps were set for three consecutive nights per fortnight from May 1976 to April 1977 for a total of 2415 trap-nights. They were set

Plate 5: Snap trap

Plate 6: Cage trap

baited for the first night, then cleared and rebaited during each morning of the next three days. On the third day traps were sprung and left closed until the beginning of the next trapping period. Captured rats were handled in a sleeve of wire and canvas without anaesthetic (Emlen, 1944).

At each capture the following information was taken: Location (trap number); identification (tag number); sex; weight; morph ("frugivorus" or "rattus") reproductive condition (testes scrotal or abdominal, for males; for females, vagina perforate or non-perforate). Note was made of each rat's behaviour upon release, and when possible fleas were collected for identification. The size of nipples, occurrence of lactation or presence of large embryos by palpation was not noted in this study for two reasons. First, I felt that the observations relied at the outset on an experienced observer and second, I wished to keep manipulation of the rat and its time in the sleeve to a minimum.

Rats not previously captured were tagged in the base of one ear with a numbered fish fingering tag. None of the recaptured rats had lost a tag and a duplicate marking system, such as toe clipping therefore proved unnecessary.

3.3 Tracking

Tracking platforms recorded the footprints of free-ranging ship rats in Greenwood's Bush. A tracking platform consisted of an 18 x 30cm base board with a malthoid tunnel attached to keep rain off the smoked paper (Fig. 2). A removable hardboard sheet, also 18 x 30cm, held a piece of smoked paper measuring 14.5 x 25cm under two metal strips.

Smoked (physiologist's Kymograph) paper was prepared in the laboratory by rotating the paper on a drum over burning benzene. Carbon particles adhered to the white paper and provided a stable surface which was sensitive even to whisker traces. The smoked paper was inserted onto its hardboard sheet in the laboratory and transported to the study area in a specially made slotted carrying box, which kept papers separate. Unmarked sheets were exchanged for labelled tracked sheets in the field. Tracked sheets were rendered permanent in the laboratory with 'Spraykote' clear plastic spray paint.

The tracks of individual rats were made recognizable by clipping certain toes under ethyl chloride freezing anaesthetic. Initially rear toes only were clipped, but at later cage captures a front toe on all rats but one was clipped also. This was necessary because rats often marked

(above) in position

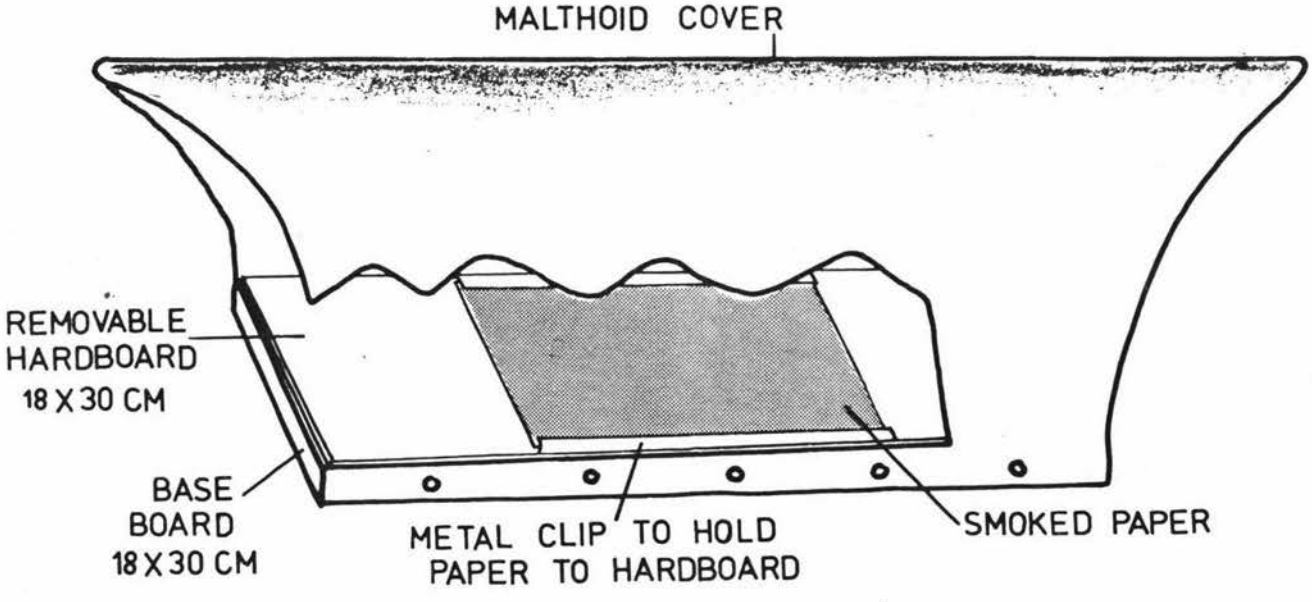


FIG. 2 tracking platform

the smoked paper with their front feet only, entering and leaving a platform at the same end. No more than two toes per rat was clipped. The toe clipping method has been described by Twigg (1975).

Initial cage capture is obviously necessary to toe-clip each rat. An irregular cage trapping programme commenced in mid-May 1976. By early September all rats subsequently found to be present in the study area had been captured at least once. From 7 October 1976 to 22 January 1977 a regular cage trapping programme was run to give information on home ranges. Ten traps (as described in 3.2) were set for three consecutive nights per fortnight. After one month they were wired open but unbaited between baited sessions in an attempt to reduce trap shyness. Seven were wired to branches of trees and three were on the ground. They were baited with peanut butter on carrot and checked early the following morning.

Ten tracking platforms were wired to branches of trees three weeks before they were actually first used in August 1976, to allow the rats to become accustomed to them. For a more direct comparison with the home ranges calculated from cage traps, they were put on flattish branches as close as possible to the cages without interfering with cage access. (Because flattish branches only could be used, the spacing of all aerial devices was irregular.) The platforms were set (supplied with smoked paper) for three consecutive nights per week, one unbaited week alternating with a baited week. Platforms were baited by smearing a very small amount of peanut butter on the hardboard sheet inside the malthoid tunnel on either side of the smoked paper.

A further ten tracking platforms, located on the ground, were added in late November 1976. These were set, always baited, coincident with the baited set period of the tree platforms and cage traps, i.e. for three consecutive nights fortnightly. They served two functions:
(a) They gave an indication of the extent to which rats used the forest floor as well as the trees.
(b) They were placed at locations midway between tree platforms, especially on apparent home range interfaces, to provide information on range boundaries additional to that already revealed by the tree platforms.

At the conclusion of the trapping and tracking programmes, rats were selectively cage trapped and killed to investigate the effect of their removal on the home ranges of those remaining. The last rat was killed on the first of April 1977. The location of the ground and tree platforms and the cage traps, and a description of the land surrounding the study area is shown in Fig. 3.

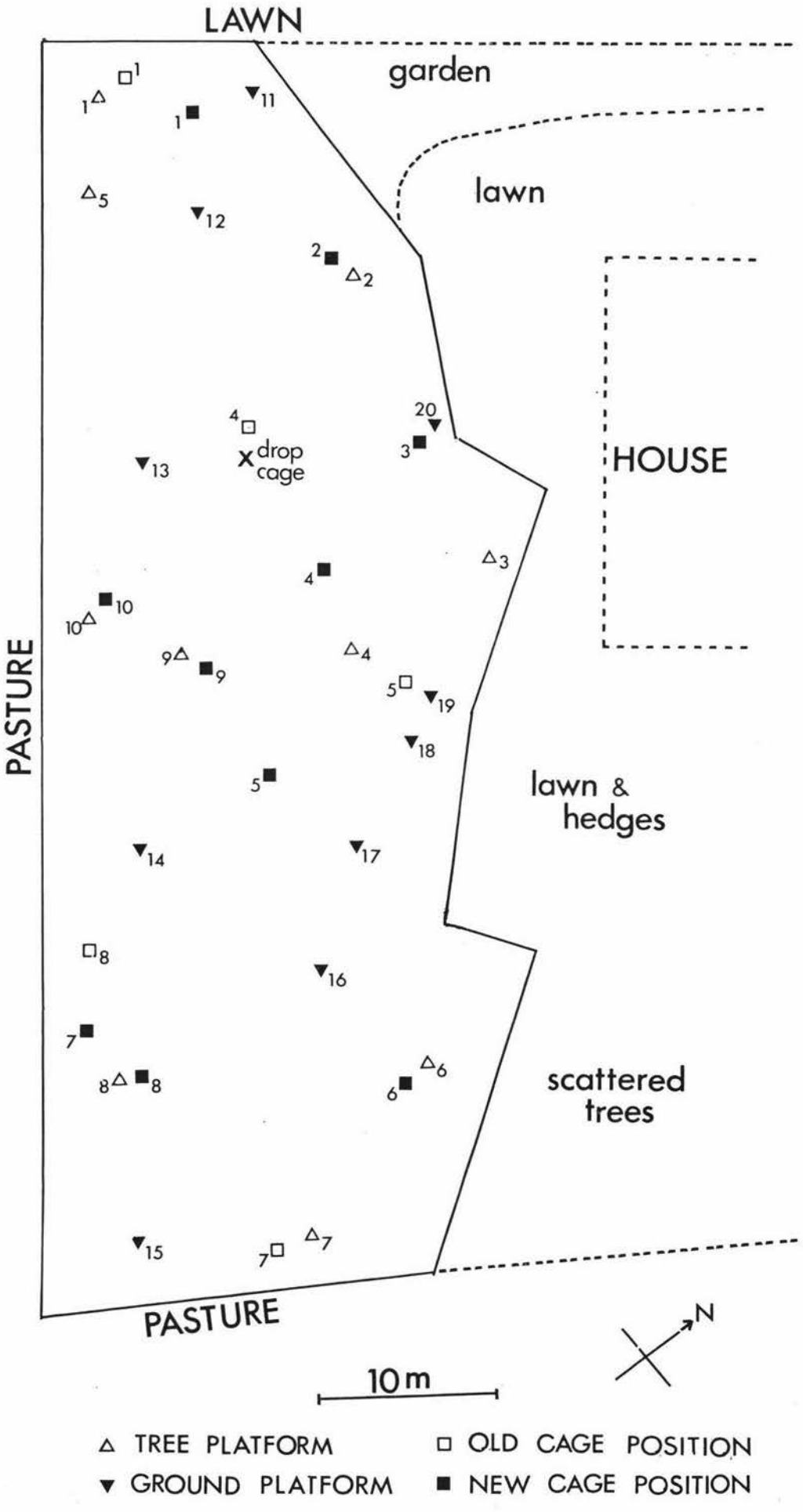


FIG. 3 Greenwood's Bush

3.4 Autopsy

Although some rats were examined fresh, the great majority were frozen and later thawed. Each stomach was removed and placed in 70% alcohol for subsequent analysis of stomach contents. If female, the uterine horns were removed and counts of embryos or uterine scars, if any, were made. If male, a smear of cauda epididymus was taken for microscopic examination to establish the presence or absence of mature spermatozoa. The correlation of smear results with the presence of macroscopically visible tubules within the cauda epididymus, as suggested by Jackson (1962), was noted. Rats were then refrozen.

The information for each animal was added to that obtained from the initial description after trapping (Section 4.1) and presented on an autopsy data sheet.

SECTION 2 - RESULTS

CHAPTER 4: SNAP TRAPPING

4.1 Trap Success

A total of 7153 trap-nights in the Tiritea reserve yielded 278 ship rats i.e. 3.89 per 100 trap-nights. Daniel (1972) snap trapped 2.13 ship rats per 100 trap-nights in his study in the Orongorongo Valley.

Because the trap lines were set for varying periods of time, monthly trap returns are best compared by looking at the number of rats taken per 100 trap-nights for the first three nights of each line. Fig. 4 shows that return was high from late autumn through winter to early spring, and low for the remaining six months of the year. Best (1968) obtained similar results. The low return for July could have been caused by exceptionally wet weather inhibiting the smell of the bait, or an initially low population in the area trapped during that month.

This supports Best's (1968) conclusion that should trapping be used as a control method in New Zealand forests, winter and early spring would give the greatest return for the trapping effort.

The factors affecting rodent trapline success are complex (Mystokowska and Sidorowicz, 1961; Hansson, 1967; Pettigrew and Sadleir, 1970; Fowle and Edwards, 1970). In the 13 areas snap trapped in this study no clear pattern emerged of change in capture success with time (see Appendix 1). During several trapping periods, e.g. December, the peak number of captures occurred several nights after the line was first set. Others, e.g. April II and August, continued to have constantly high nightly success for many nights and in fact the number of rats captured per night showed no sign of abating. In October, by contrast, many rats were caught on the first night, but only one during the next six consecutive nights.

During no month did the nightly number of removed animals decline from the beginning of the trapping period until the end. Hence in most areas the sampled population did not fulfil the assumptions necessary for population estimation by removal methods, even if the area sampled by the trap line could have been estimated (Grodzinksi et al., 1966; Flowerdew, 1976). In August, however, the number of rats captured on successive nights increased during the final nights of the trapping session only, perhaps due to immigration. A regression line to estimate the total population within the (unknown) trapped area by Haynes' (1949) removal

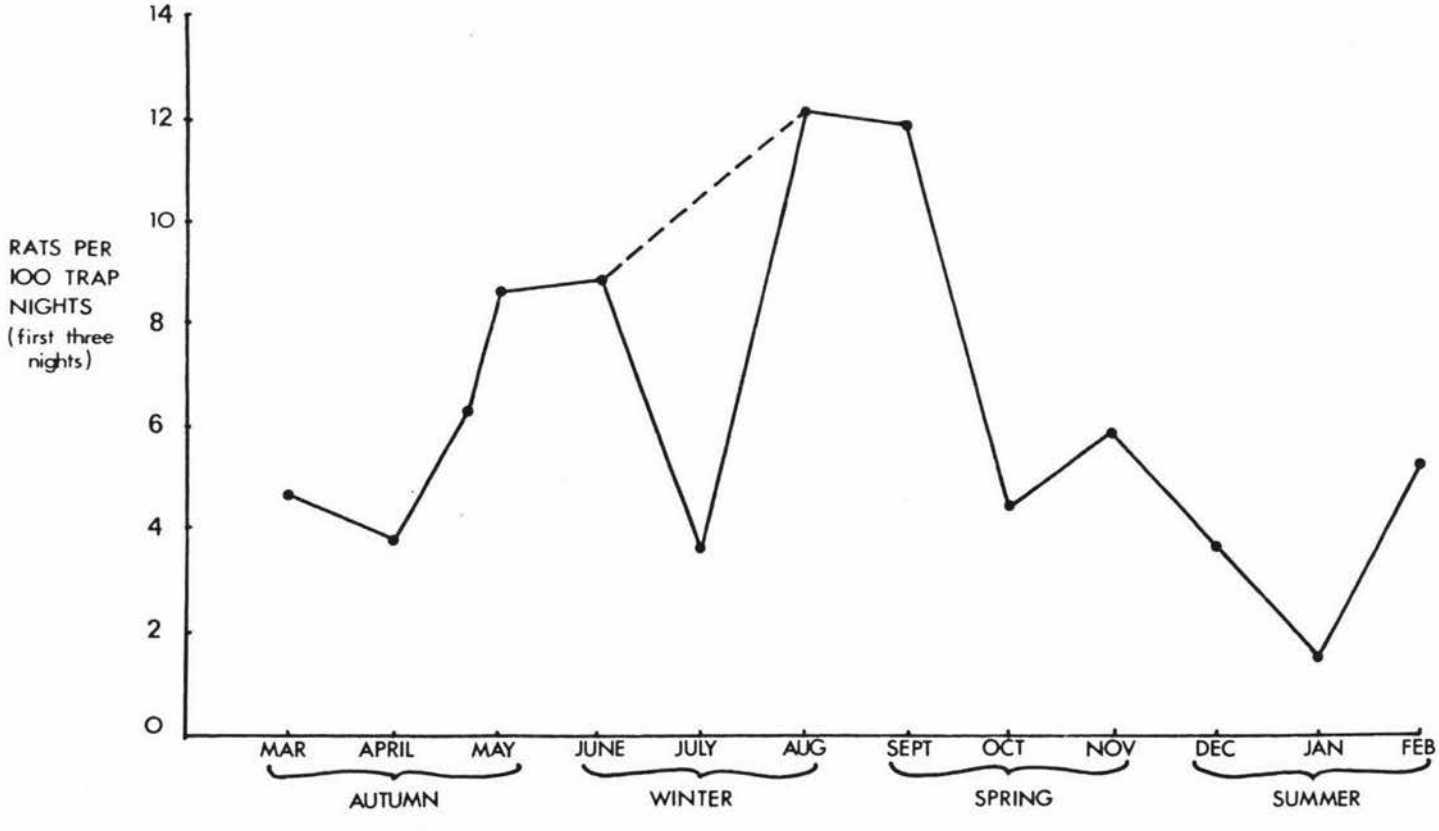


FIG. 4 Snap trap return through the year

method can be prepared (Fig. 5) using the early figures only (Flowerdew, 1976). Although the number of rats caught was small (34), the August results can provide a useful indication of the extent to which that trapline had trapped that area out. Fig. 5 shows that the estimated population of the (unknown) area sampled by the August trapline is 33.2. This is close to the 34 rats actually trapped in the first trapping session of that month.

This is not a density figure, as the actual area sampled by the trapline is unknown.

Some workers (e.g. Miller, in press) have used a number of rodents trapped in a three consecutive night trapping session, repeated at regular intervals in the same area, as a relative index of population levels. The impact of such sampling on the rodent population in the present study can roughly be assessed by expressing the number of rats trapped in the first three nights of a trapline session as a percentage of all rats eventually taken by each trapline. One necessary assumption is that each trapline did in fact trap its sampling area out. Considering the similarity between the estimated and trapped population levels for August, and the fact that the number of rats trapped per night reduced to one or none in all but one of the traplines, further discussion seems justified.

Table 1 shows the percentage of the total ship rat catch which was taken in the first three nights, for each trapline. These percentages must be regarded as approximate, first since it is unlikely that each area was absolutely trapped out and second because some of the rats trapped later in a trapline session were probably immigrants. On average, however 42% (S.D. = 14.7%) of rats eventually caught were captured in the first three nights. If such a capture success was repeated at regular (three month) intervals, immigration would need to be considerable to bring the population back to 'natural' levels, especially in winter when breeding may be non existent. Such a technique could still be a useful indicator of gross changes in population numbers. It would be most suitable for species such as the mouse, which has a high potential rate of increase.

Only during the April II trapline did recolonization of a trapped area appear to be significant (see Appendix 1). In this case, however, it is possible that the population was never completely removed from the sampled area during the first of the two trapping sessions. The time between samples in each area was relatively short ($\bar{x}$ = 14.1 days), allowing little time for recolonization to occur.

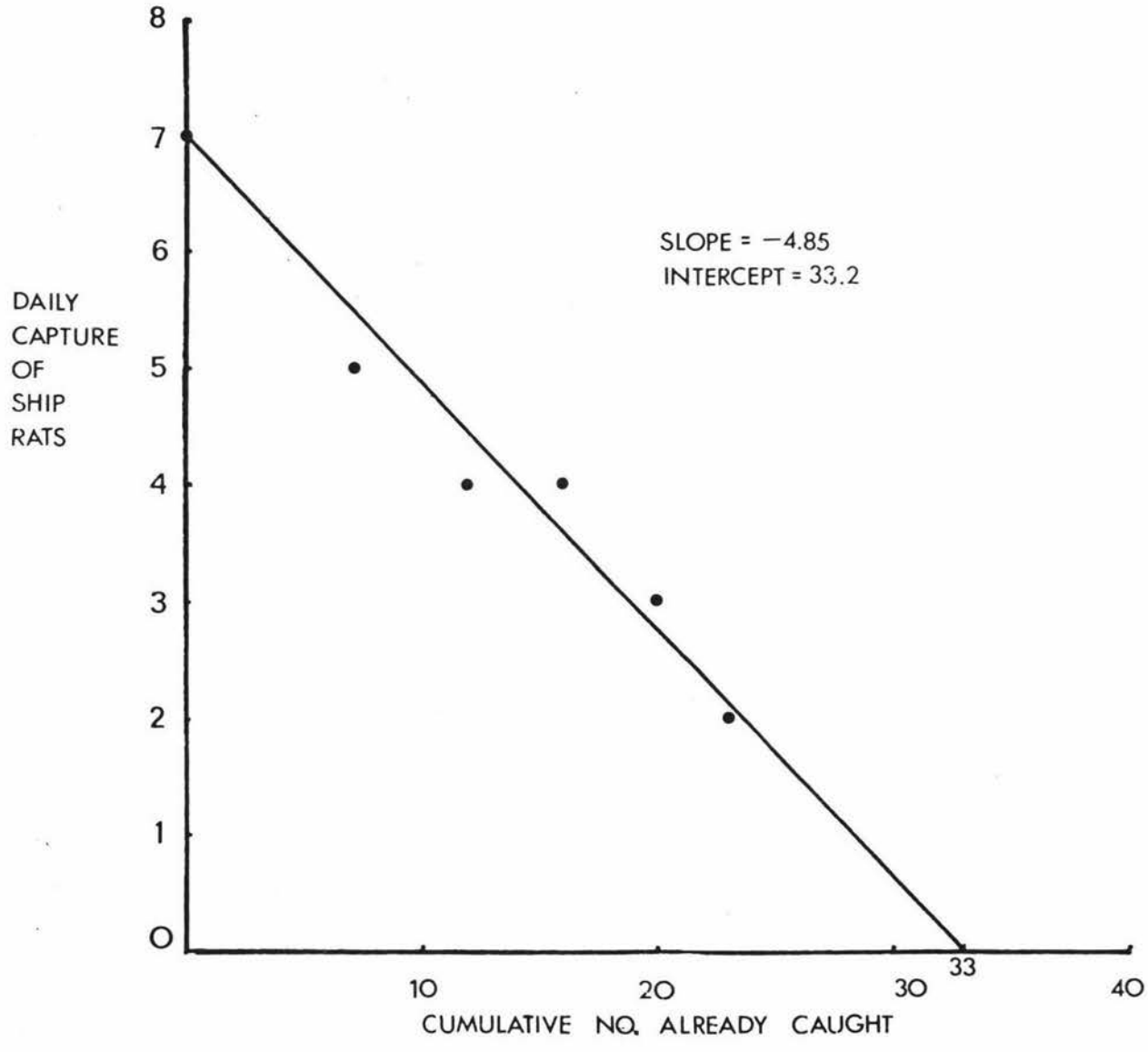


fig. 5 Removal method population estimation

First three nights in:	March	April I	April II	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Total rats	15	12	43	19	23	10	38	30	10	19	24	23	1
Rats in first three nights	6	5	*	9	12	5	16	16	6	8	5	2	*
As a %	40	42		47	52	50	42	53	60	42	21	9	

* Excluded since area not trapped out

Table 1: Percentage catch for each trapline taken in first three nights of trapping

Only 11.7% (278/2374) of sprung traps held rats. Non-target catches constituted 3.4% of sprung traps. The non target catch was 69 mice, six thrushes, four blackbirds and two hedgehogs. Fur left on sprung traps suggests that the majority of sprung traps were set off by possums.

4.2 Weight, Size and Condition of Rats

Male ship rats trapped at Tiritea were significantly heavier than females ($d = 3.643$, $p < .001$). Table 2 compares the weights of Tiritea rats with those from the Orongorongo Valley (Daniel, 1972) and from two forest areas in the South Island (Best, 1968). Tiritea females were significantly lighter than South Island females ($d = 2.25$, $p < .05$ for Waimangaroa) and significantly heavier than Orongorongo Valley females ($d = 2.18$, $p < .05$). Tiritea males were significantly lighter than South Island males ($d = 4.18$, $p < .001$ for Banks Peninsula).

Such comparisons are meaningful only if the age class structures of the sampled populations are similar.

Male rats from Tiritea had a significantly greater head and body length ($d = 3.632$, $p < .001$) and hind foot length ($d = 5.077$, $p < .001$) than females. Tail length and ear length were not significantly different between the sexes (Table 3).

Watson (1956) found that three of a sample of 91 New Zealand ship rats had a tail : head + body ratio of less than one. In the present study only one rat out of 307 had a shorter tail than body. The mean tail : head + body ratio was significantly greater for Tiritea females than males (see Table 4) because of the difference between sexes in head + body length already presented.

A quantitative estimate of the condition of rats was not taken. Most rats were in excellent looking condition. No rat looked in very poor condition (see Chapter 10 for effect of parasites).

The majority of females had the normal number of nipples, i.e. two pectoral pairs and three inguinal pairs. Thirty-seven per cent, however, showed variation in the second pectoral teat. Sometimes it was doubled on one side, or less often, on both. The percentages in each of these groups was:

	Left Doubled	Right Doubled	Both Doubled	Normal	
(n = 131)	18.2%	11.4%	7.6%	62.8%	(The present study)
(n = 157)	23%	13%	25%	39%	(Best, 1968)

Present study Tiritea (1976)			Orongorongo Valley Daniel (1972)			Waimangaroa Best (1968)			Banks Peninsula Best (1968)		
$\bar{x}$ (g)	S.D.(g)	n	$\bar{x}$ (g)	S.D.(g)	n	$\bar{x}$ (g)	S.D.(g)	n	$\bar{x}$ (g)	S.D.(g)	n
140.0	38.5	170	145.6	30.2	69	162.0	28.3	44	160.1	27.4	53
125.0	29.3	131	115.4	26.6	55	134.7	23.3	45	137.5	26.5	75

Table 2: Ship rat weights

Head and body length				Hind foot length				Tail length				Ear length			
$\bar{x}$ (mm)	S.D.(mm)	S.E.(mm)	n	$\bar{x}$ (mm)	S.D.(mm)	S.E.(mm)	n	$\bar{x}$ (mm)	S.D.(mm)	S.E.(mm)	n	$\bar{x}$ (mm)	S.D.(mm)	S.E.(mm)	n
174.0	19.2	1.5	172	32.7	1.8	.14	172	192.6	20.7	1.6	172	18.3	1.9	.15	171
165.8	19.8	1.7	133	31.7	1.5	.13	133	194.0	21.1	1.8	130	18.2	1.9	.17	132

Table 3: Ship rat length measurements

$\bar{x}$	S.D.	S.E.	n
1.11	.067	.0052	165
1.17	.073	.0065	128

Table 4: Tail: head + body length ratio

Eight rats (2.6%) had tails broken off short. Eleven males had torn ears. The mean weight of these was 155g (S.D. = 16.9g) which is significantly heavier than the male population mean weight ($d = 2.55$, $p < .02$). Female rats with torn ears ($n = 7$, $\bar{x} = 127g$, S.D. = 32.7) were not significantly heavier than the female population mean weight ($d = .158$). Such damage may have social significance. For example, this could mean that the heavier males fought more often or more fiercely than most males in the population.

4.3 Sex Ratio

Three rats could not be sexed as they were eaten in the traps. Of the remaining 304, 43% were females. The imbalance between sexes is statistically significant at the 5% level of probability.

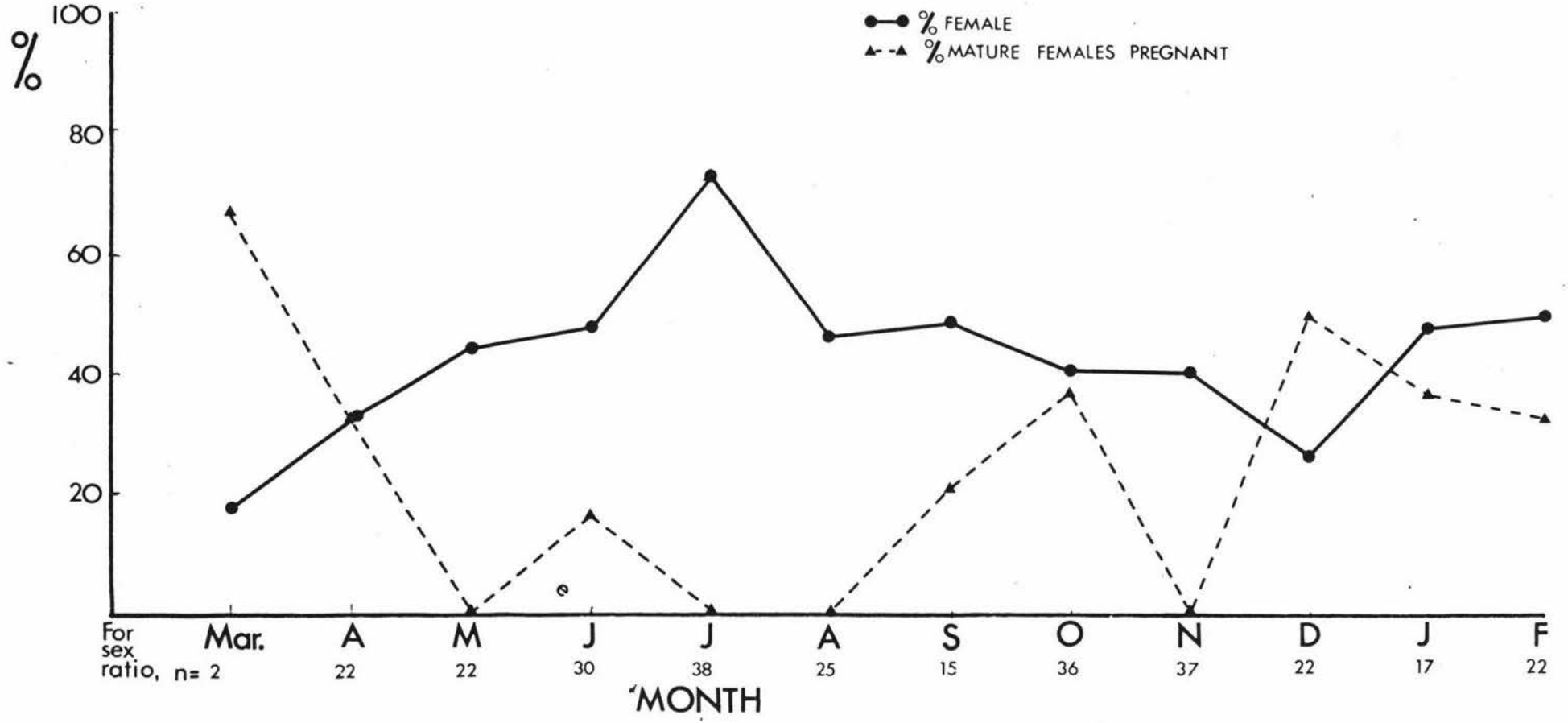
Monthly sex ratios are shown in Fig. 6. Males were more frequently trapped in all but the winter months. Despite the fact that Bentley and Taylor (1965) showed that weight was an unreliable age indicator, Best (1966) used weight-based age classes to show that there was a predominance of females in the older age groups. He concluded tentatively that males had a higher mortality rate than females. In the present study rats were not aged. It is possible that the monthly variation in sex ratio is an age effect caused by different mortality rates between the sexes. Another hypothesis is that females were easier to trap during winter when breeding had ceased and their movements lengthened (Fig. 4). Howell (1954) found that female cotton rats Sigmodon hispidus had greatly reduced home ranges when breeding. As a corollary it is possible that a bias existed towards trapping non-breeding females since traps were always set on the ground while most ship rats probably nest and breed in epiphytes. This can only be checked if another sampling method - one which samples rats spending much of their time in trees as well as those feeding frequently on the forest floor - is used.

Furthermore, studies of ship rat movement have revealed that males move further than females (Spencer and Davis, 1950; Watson, 1951; Jackson and Strecker, 1962; Best, 1966; Daniel, 1972). Greater movement by males increases their chances of finding a trap (Stickel, 1948; King, 1975) and may cause an overestimation of the actual male : female ratio, especially if the trapping period is short and traps are widely spaced.

4.4 Occurrence of Pelage Forms

Only 'rattus' and 'frugivorus' morphs were captured in the present study. Morph ratios of ship rats trapped throughout New Zealand are shown

FIG. 6 The sex ratio (% female)



	NORTH ISLAND				SOUTH ISLAND	
	Present study Tiritea (1976)	Orongorongo Valley Daniel (1972)	Tongariro and Egmont National Parks Skipworth (unpub. data)	Waimangaroa Best (1968)	Banks Peninsula Best (1968)	Westland, Fiordland and Nelson Lakes National Parks Skipworth (unpub. data)
% 'rattus'	11	13	18	35	21	39
% 'frugivorus'	89	87	82	6	6	1
% 'alexandrinus'	-	-	-	59	73	60
	n = 307	n = 280	n = 93	n = 114	n = 162	n = 114

Table 5: Morph ratios

in Table 5. No rat with a pelage intermediate between the normal morph colours was captured in this study, although Best (1968) reported a 'rattus'-'alexandrinus' intermediate and an 'alexandrinus'-'frugivorus' intermediate from the South Island. Tomich and Kami (1966) also found intermediates in a population of R. rattus rattus in Hawaii. In all these cases the aberrant colouring could be explained by soiling of a normal pelage. However, breeding experiments have produced genetically-based colours which differ from the three morphs most commonly found (in Matthews, 1952). The researchers hypothesized such colours were culled out in wild populations before they came to the attention of field workers.

Descriptions given by Best (1968) are accurate for rats captured in the present study. Best noted that the ventral 'rattus' morph pelage may have white hairs on the "throat, feet, tip of the tail and some vibrissae". Two rats ('rattus' morph) in the present study had distinct white fur patches approx. 1cm long on the ventral midline under the belly.

CHAPTER 5: BREEDING AND MORTALITY

5.1 Duration of Breeding Season

5.1.1 Males

The commonest criterion of maturity of male rodents is the enlargement of the testes and their subsequent movement from the abdomen to the scrotum. Jackson (1962) favoured the presence of macroscopically visible tubules in the cauda epididymus as a criterion because 17% of the rats he examined had scrotal testes but no sperm. Only 8% of his sample lacked epididymal tubules but had sperm in the cauda epididymus. The autopsies of 172 male ship rats from Tiritea showed that all scrotal males except three possessed tubules, and only one non-scrotal male possessed tubules. Furthermore, the correlation between presence of tubules and sperm was absolute.

Only two rats were trapped in a state of change between non-breeding and breeding condition. These were trapped at the onset of the breeding season (in August) and had sperm in the testes but not in the cauda epididymus; nor did they possess macroscopically visible tubules, although the testes were scrotal.

The lightest male with scrotal testes weighed 89g. The monthly percentages of males of this weight or heavier with scrotal testes are shown in Fig. 7. Males with mature sperm were trapped all year round.

5.1.2 Females

Perforation of the vagina occurs about a month before ovulation in female ship rats (Daniel, 1972). Since pregnancy can only occur after ovulation, the lightest female which was pregnant or had uterine scars (122g) was used to gauge the monthly percentages of pregnant females. Fig. 7 shows the percentage of females $\geq$ 122g which were pregnant when trapped, for each month.

The breeding season was defined as the period in which pregnant rats were trapped. The last pregnant female of the 1975/76 summer was trapped in mid-April 1976. One pregnant rat was trapped in June and breeding resumed for the 1976/77 summer in mid-September. Excluding the single June pregnancy, the breeding season covered seven months of the year of trapping. The sample size for each month is small, and it would be interesting to know how representative of the population was the single winter pregnancy. Winter breeding was recorded by Daniel (1972) in the

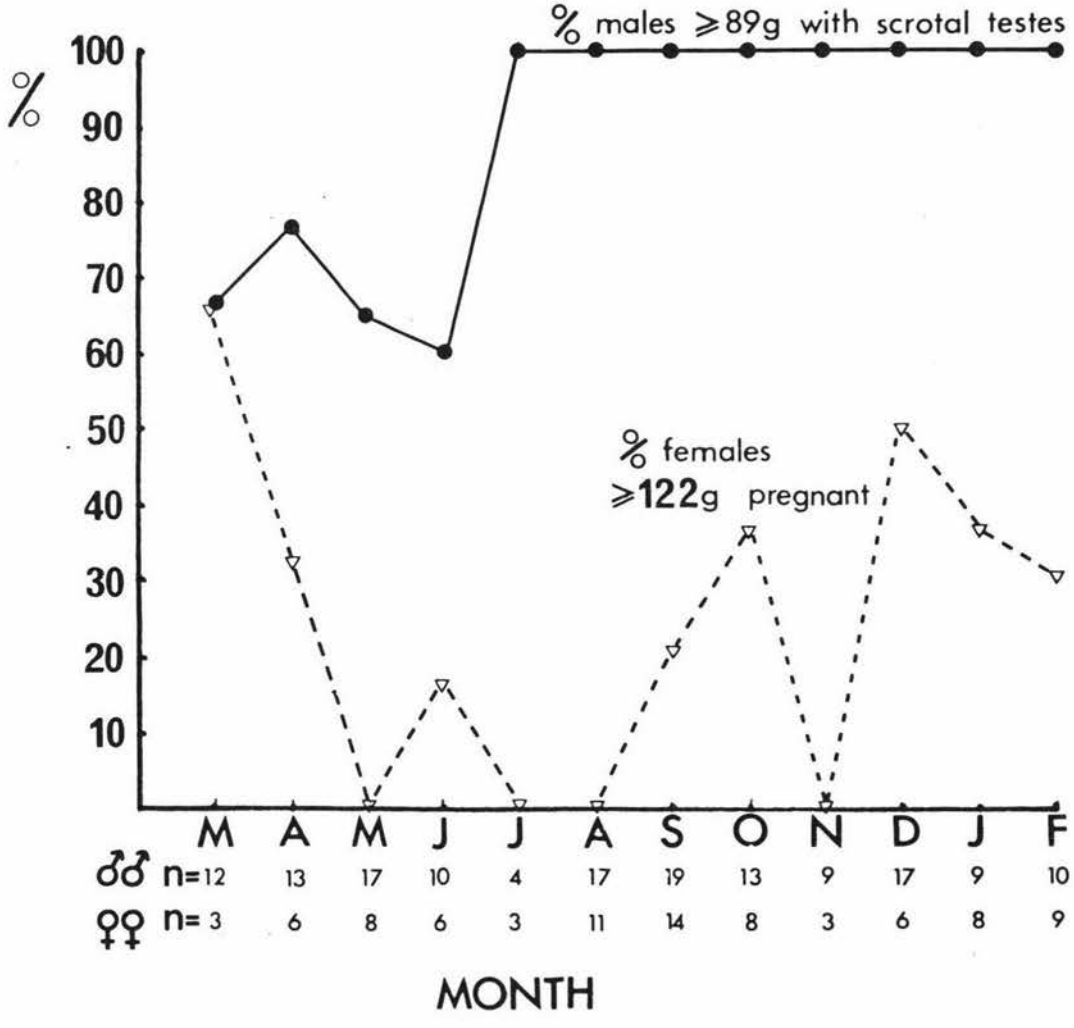


FIG. 7 % scrotal males and pregnant females per month

Orongorongo Valley (North Island) in 1969, but not in the previous three years, while Best (1972) found no breeding from May to September inclusive in his study in two South Island localities.

Twin summer breeding peaks were recorded by both Daniel (1972) and Best (1973). Best showed that immature rats and young adults had peaks of abundance at the same interval as the breeding peaks but later, indicating that the bimodal form was not an artefact of small sample size. The sharp initial peak of breeding, followed by a broader peak, in the present study is in agreement with Best's (1968) explanation that females will vary in the duration of the period between first and second pregnancies. Consequently the high degree of synchrony that females show in the initial October peak is followed by a period of little or no breeding (November) and then a less synchronized number of pregnancies (December to February).

Since male ship rats were in breeding condition all year round, it seems that females were responsible for the seasonality of breeding at Tiritea.

5.2 Female Productivity

5.2.1 Litter size

The mean number of embryos per pregnant female was 4.95 (n = 19, S.D. = 1.31). The mode was shared by 4, 5 and 6 (three each) embryos per female. This calculation excludes embryos which were being resorbed, i.e. were much smaller than other embryos in the uterus. The sample size was too small to estimate the extent of resorption.

5.2.2 Fertility

The number of litters born in a season to an average female can be calculated from other data (Emlen and Davis, 1948). Assuming that the population incidence of pregnancy is equal to the frequency of occurrence of pregnancy in the average female of that population, the equation for the incidence of pregnancy in the population is: $Fp = \frac{Ip.t}{d}$

where Fp = frequency of pregnancy (litters per season)
Ip = incidence of pregnancy (% visibly pregnant)
t = length of breeding season
d = duration of visible pregnancy

After Best (1972), the duration of visible pregnancy was taken to be equal to that of Rattus norvegicus, i.e. 18 days (Emlen and Davis, 1948). To obtain a figure for an "entire" breeding season I have added the data for March and April 1976 onto that of February 1977. Excluding the single winter pregnancy, pregnant females were trapped between

11th September and 18th April, i.e. 219 days. During this period 57 females ≥122g (the minimum weight at which a female was pregnant) were trapped. Nineteen (33%) of these were pregnant. Ip is therefore .33 and Fp is 4.06 litters per breeding season.

The fertility of the average female rat equals the product of the observed litter size and the calculated frequency of pregnancy.

Fertility = 4.95 x 4.06

= 20.1 young per breeding season.

This is slightly fewer than the 24.8 and 29.3 young per year calculated by Best (1972) and Daniel (1972) respectively using the same method as above.

5.2.3 Uterine Scars

Uterine scars are pigmented areas of uterine tissue marking the sites of previous placental attachment (Martin et al., 1976). The total number of young which implant in the uterus of a female during her lifetime can usefully be estimated by counting the scars. Such counts are estimates only since some scars may be difficult to see or may overlap each other. Forty six females from Tiritea had uterine scars. In three cases the scars could not be counted accurately because of scar overlap. Scar numbers did not supply a clearcut picture of the timing of breeding although they generally supported the evidence from observed pregnancies. Monthly sample sizes were small.

At the end of the 1975/76 breeding season, during May and June, 15 mature (≥122g) females were captured. Six of these had scars of three litters, four had scars of four litters and one had scars from one litter. Two had not bred at all and one was pregnant when captured. Twenty four mature females were captured in August and September, the first months of the 1976/77 breeding season. Fourteen had no scars. These were mostly just heavier than 122g. Females heavier than 150g were either pregnant (in September) or had some uterine scars. Most of these had scars indicating two litters, although one had 24 scars which may have corresponded to four or five litters. It is interesting that only a small majority of females in this sample entered the 1976/77 breeding season without having previously bred. This is probably because of the short (four months) gap between the two seasons rather than winter breeding. The short gap would allow some rats which began breeding late in the 1975/76 season to resume breeding again in the 1976/77 season. Daniel (1972) calculated that mean longevity for adult female ship rats was 4.5

months from initial capture in a cage trap. Since it is likely that the rats in his study survived for some time after the trapping period in which they were last captured, this figure should be regarded as a minimum.

Most (five out of seven) mature females trapped in October or November had scars of one or two litters, although two had scars of three. This is the expected result from the graph of observed pregnancies (Fig. 6). By January and February the pattern was much less clear. Females with histories of two, three or four litters were equally represented. One female had only five scars (one litter) and another weighing 141g had not bred at all. Those with uterine scars indicating four litters must have entered the breeding season already having borne one litter.

5.3 Mortality

Following the method of Davis (1964), the disappearance of tagged rats from cage capture records at Keeble's Bush was used to estimate annual mortality. The initial captures of all rats were grouped at a time taken as t = 0. In each monthly sample after t = 0 (i.e. t = 1, 2, 3 ..... k) the number of rats present was graphed against time. Use of the natural logarithm of the number present in each sample enabled the regression to approximate a straight line represented by the equation $\log_e N_t = 3.58 - .65t$ (Appendix 2). The annual disappearance rate was then estimated by letting t = 12 (months). Then:

$$\log_e N_{12} = 3.58 - 7.8$$
$$= -4.22$$

$$\therefore N_{12} \text{ (no. present)} = e^{-4.22}$$
$$= \frac{1}{e^{4.22}}$$
$$= .0147$$

$$\therefore \text{Annual disappearance rate after initial capture} = \frac{36 - .0147}{36} \times 100$$
$$= 99.95\%$$

The calculated high sample trappability (Section 6.1) and the few rats snap-trapped at the end of cage trapping (Section 6.3.2) suggest that when a rat disappeared from cage trapping records it was no longer alive on the cage grid. Rats which disappeared may have died or emigrated, although there were no long distance movements within the grid suggestive that any rats were emigrating. It is important to note, however, that disappearance from the capture records was not caused only by death, and the disappearance rate calculated above is probably an over-estimation of the actual mortality rate.

Furthermore, both adult and juvenile males and females were included in the calculation because the samples in separated age or sex categories were small. Daniel (1972) calculated annual disappearance rates of 99.4% for adult male ship rats and 92.8% for adult females, and Caughley (1977) considered that higher juvenile than adult mortality rates was characteristic of mammal populations. In the present study, these groups have been combined to calculate a figure which must be considered as an estimate only of annual mortality based on monthly disappearance after initial cage capture.

Feral cats, stoats and moreporks have been reported as predators of rats in New Zealand (Daniel, 1972), although the significance of predation as a mortality factor is unknown. Tracking at Greenwood's Bush indicated that ship rats forage in all weather; even during nights of heavy rain. Some may die from exposure to wind and rain. At Tiritea ship rats were often caught and killed in gin traps set for possums by commercial trappers. Other than this, however, no dead rats were recovered by me and the causes of mortality remained very difficult to pinpoint.

CHAPTER 6 - LIVE TRAPPING

6.1 Numbers caught and retrappability

At Keeble's Bush 51 ship rats were recaptured a total of 83 times. Thirty individuals (59%) were never retrapped after their initial capture. The recapture frequency for all rats is shown in Table 6. Two rats, ♀ 31 and ♂89, were recaptured five times each. Female 31 was captured at three non-linear points, and ♂89 at five non-linear points. The data are unsuitable for home range calculations because of the small number of recaptures involved and the long time needed to obtain them (see Section 7.5).

Table 7 shows that 66% of recaptures occurred within one month of the previous capture. While this suggests that some rats did not avoid recapture, these recaptures were of only 13 individuals (25% of total). In the only other major live-trapping programme undertaken in New Zealand with ship rats, Daniel (1972) did not recapture 53% of rats after their initial capture. In Cyprus Watson (1951) did not recapture 44% of 118 rats; in Hawaii, Tamarin and Malecha (1971) did not recapture 51% of 205 ship rats. Such loss of individuals could be due to death, emigration or trap-shyness. For the present study, trappability of the grid population of trappable rats was calculated using the method of Krebs (1966). The number of individuals caught in a trapping period is divided by the number known to be alive in that period. The results (Table 8) show a reasonably high mean (fortnightly) sample trappability (.68). The monthly mean trappability in Daniel's (1972) study over the period July 1966 to July 1968 was .69. My monthly mean trappability (Table 8) is higher than Daniel's because in the present study a monthly sample consists of two fortnightly samples pooled; i.e. six trapping nights per month instead of Daniel's three per month.

Such a high trappability indicates that the rats were not very trap-shy. However, in Greenwood's Bush, concurrent tracking showed that all five resident rats were to some extent trap-shy. At various times, each was in the study area for at least three months without being captured in the cage traps. Female 49 was not cage-trapped for nine months but in fact was present in the study area throughout that time. Mean fortnightly sample trappability at Greenwood's was .24; much lower than at Keeble's. It would be very interesting to know whether the 30 rats captured only once at Keeble's died, emigrated or became trap shy. These rats, which each have an individual trappability of 1.0, are largely responsible for the high

Number of times recaptured	Number of rats	% of total
0	30	59
1	17	33
2	1	2
3	1	2
4	-	-
5	2	4
TOTAL	51	100%

Table 6: Frequency of recapture of ship rats at Keeble's Bush

Time since previous capture (months)	Number of recaptures	% of total recaptures
Up to 1	21	66
2	8	25
3	2	6
4	-	-
5	-	-
6	-	-
7	1	3
TOTAL	32	100%

Table 7: Time between ship rat recaptures

	Month	A No. of untagged rats captured	B No. of rats recaptured	C Rats known alive	Sample trappability per fortnight = $\frac{A + B}{C}$	Sample trappability per month
1976	May	17	-	17	-	-
	June	12	5	20	.50 .62	.85
	July	4	5	12	.50 .50	.75
	August	5	2	10	.33 .62	.70
	September	2	3	6	.25 .80	.83
	October*	1	2	4	.66 .50 .33	.75
	November	1	2	3	1.0 1.0	1.0
	December	2	0	2	1.0 1.0	1.0
	January	0	0	0	-	-
	February	0	0	0	- -	-
1977	March	5	0	5	- 1.0	1.0
	April	2	0	3	.75 .66	.66
					$\bar{x}$ = .68 S.D. = .25	$\bar{x}$ = .84 S.D. = .13

* Three sessions in October

Table 8: Sample trappability of the cage trapped population

mean sample trappability.

At the conclusion of the live trapping study, snap traps were set at 15m intervals through the study area for two consecutive nights (138 trap nights). Four rats were captured. One had been first cage-trapped three days previous to being snap-trapped. The remaining rats were untagged. Two of these weighed 70g and 75g respectively and may have just entered the trappable population since no rat lighter than 70g was ever cage-trapped. The other untagged rat weighed 190g and was trapped at an inner grid trap site. It may have recently immigrated there or been trap shy throughout the study. These results also suggest that there were few cage trap-shy tagged rats in the study area.

6.2 Distances moved

The mean distances moved between successive captures, based on only 13 male movements and nine female movements, were 37.9m for males and 35.7m for females. The difference is not significant. Maximum distances moved were 67m for males and 45m for females. These distances are smaller than in most ship rat studies. For example, Strecker (1962) found that 60% of male recaptures and 70% of female recaptures on Ponape Island were within 37m of the previous capture point. In the Orongorongo Valley, 68% of males and 79% of females moved less than 61m (Daniel, 1972). It is unlikely that the fixed trap spacing in all these studies allows an accurate measurement of actual movements.(see Section 7.6).

6.3 Population estimation

6.3.1 Methods

It is impossible that the population at Keeble's Bush was sampled randomly. The traps were in fixed non-random locations and some adults may have been trap-shy. Random sampling is a basic assumption of all capture-mark-recapture estimation techniques, such as the Jolly/Seber method (Caughley, 1977). For this reason, direct enumeration or "minimum number known to be alive" (MNA) was used to determine the population density.

Hilborn *et al.* (1975) simulated by computer the capture-recapture process to investigate the influence of several population parameters on the reliability of the MNA enumeration. They generalized: "the MNA is quite insensitive to population size, but more sensitive to survival between sampling periods and variance in trappability. The MNA is very sensitive to trappabilities lower than 0.5 and differential trappabilities of marked and unmarked individuals". To estimate survival between monthly

sampling periods in the present study, the two fortnightly sampling sessions were pooled to give monthly data, and data for males and females were pooled also since recaptures were few. A rat was considered to have survived to a given month if it was captured during that month or any later month. The mean monthly survival rate was 32% (S.D. = 20%). Under the simulated conditions in the study of Hilborn et al., such a low survival rate would cause a 25% under-estimate of the actual population. Individual trappability, in contrast with Kreb's (1966) sample trappability, is defined by Hilborn et al. as the number of times the individual was captured divided by the number of times the individual was exposed to capture during this period. At Keeble's the variance of individual trappability was .03 (n = 51) and the mean sample trappability was .68. According to Hilborn et al. these figures are favourable and should not cause underestimation of the actual population by an amount greater than 10%. The differential trappability, if any, between marked and unmarked ship rats at Keeble's was unknown.

All the above factors reduce the estimated population level. The simulated conditions of Hilborn et al. (1975), in their estimation of the effect of low survival between samples on MNA, were quite similar to the actual conditions in the present study. For example, they made sample trappability equal 0.6, and variance of individual trappability equal 0.1. For this reason a correction factor of + 25% was added to the calculated MNA values in the present study to obtain a final estimation closer to the actual population present.

Following the method of Dice (1938), enumeration figures were converted into density values by adding to the grid area a border strip of half the mean distance moved between successive captures. This proposes that the traps were sampling an area of 3.12ha.

6.3.2 Results and discussion

Both MNA and corrected MNA density figures for May 1976 to March 1977 are shown in Table 9. The corrected MNA figures are graphed in Fig. 8. The population peaked at 8 rats/ha in June; no rats were trapped in January or February. The mean monthly density was 2.8 rats/ha.

Daniel (1972, p. 319) obtained similar results with similar techniques in the Orongorongo Valley, but a striking difference exists between the two studies in the timing of the population peak. In Daniel's three year study, the population peaked in November 1966 and February 1968, and was lowest during May, June or July of each year, i.e. the

Month	Rats known alive	MNA/ha	Corrected MNA/ha
May	17	5.4	6.7
June	20	6.4	8.0
July	12	3.8	4.7
August	10	3.2	4.0
September	6	1.9	2.4
October	4	1.3	1.6
November	3	1.0	1.2
December	2	.6	.7
January	0	0	0
February	0	0	0
March	5	1.6	2.0
April	3	excluded	excluded
		$\bar{x}$ = 2.2/ha	$\bar{x}$ = 2.8/ha
		S.D. = 2.1	S.D. = 2.7

Table 9: Population density

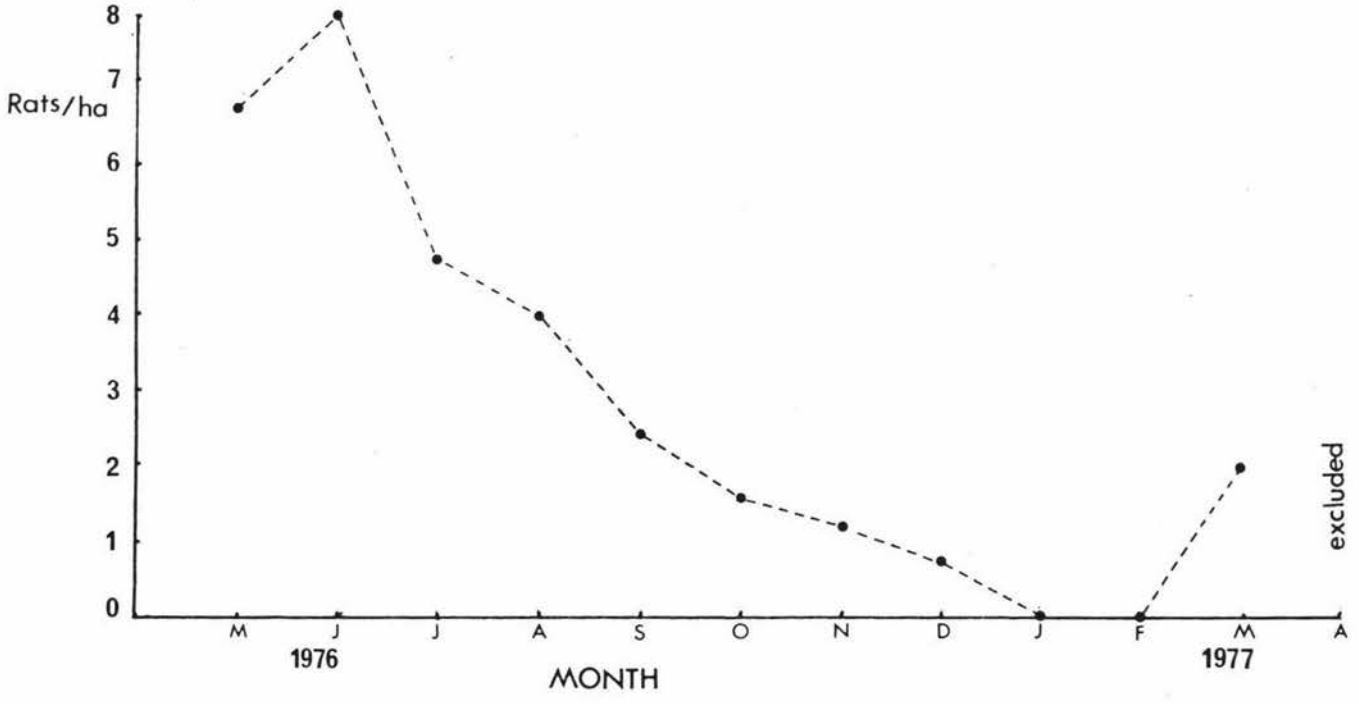


FIG. 8 Population density at Keeble's Bush (corrected mna./ha)

months of high population at Keeble's. One explanation of this is that when sampling began at Keeble's the population was already falling from a peak in the previous summer. It is likely that the population is under-estimated for May 1976 since trapping would not have captured all the rats present in the study area in just two trapping sessions. However, the decline continued until well into the breeding season, suggesting either cumulative trap shyness or a high mortality rate caused perhaps by an exceptionally wet winter.

In the tropics ship rats reach much higher densities. In Hawaii, for example, Tomich (1970) and Tamarin and Malecha (1971) calculated maximum densities of 25/ha and 64/ha respectively.

6.4 Behaviour on release

The majority of rats, when released from the holding sleeve, disappeared into plant cover within 10m of the release point. Four individuals (6%) went down tunnels and three (4%) remained high in the trees without moving before I left. Eleven (16%) ran away through the trees. Three rats did unusual things when released. One climbed a tree and bit off several twigs, sucking what seemed to be dew droplets off the leaves, then dropping the leaves. Another rat ran up a titoki tree and began to eat titoki seeds, dropping the damaged remains. A third rat became unusually "tame". It followed me as I walked away and ate peanut butter from my finger several times. When I left, it remained on the ground near the trapping point, apparently in normal health.

CHAPTER 7: SMOKED PAPER TRACKING

7.1 Introduction

Smoked paper tracking seems to provide a practical method of gathering data for home range determination while overcoming the major drawbacks of the cage trapping method (see Section 7.5). Its initial importance, therefore, is to assess some of the biases present in the cage trapping technique and to reveal and implications of these biases on the studies completed in the past.

Smoked paper as a tracking device was first suggested by Mayer (1957) who employed it to assay the use of tunnels by ground squirrels. Justice (1961) studied the home ranges of toe-clipped Mus musculus using smoked paper, and it has since been adopted by Sheppe (1965), Wise (1967) and Metzgar (1973a and b) with other rodents. Marten (1972) tracked Peromyscus maniculatus with smoked paper to determine population numbers. Batzli (1968) studied the dispersion of three woodland mouse species by smoked paper tracking. Sealander et al. (1968) and Bailey (1968) employed it in experiments on trap shyness in Mus musculus and Clethrionomys glareolus respectively. After Justice (1961) described the advantages of tracking as a means of obtaining data, later researchers devised tracking media other than smoked paper. Bovet (1968) studied the homing of deer mice Peromyscus maniculatus on snow. Brown (1969) used a tracking surface consisting of a fine suspension of talcum powder held in a water repellant silicone solution to follow movements of Apodemus sylvaticus in woodland. Bider (1968) and Sarrazin and Bider (1973) estimated animal activity by tracking on a sand transect, while both Lord et al. (1970) and King and Edgar (1977) used tracking boards where the animal walked over marking fluid and transferred it, as footprints, to a piece of paper.

7.2 The Smoked Paper Tracking Technique

All toe-clipped footprints could be readily identified after a little practice. An example of the effect of toe clipping on the resultant print is shown in Fig. 9. At its first cage trapping each rat had one rear toe only clipped. This caused problems when many tracks were unidentifiable because unclipped front feet only appeared on the paper. At subsequent recaptures each rat had a second toe clipped. In all cases but ♀ 49 this was off a front foot. The proportion of papers with unidentifiable prints changed from 26% (46 out of 176) prior to 13/11/76 to only 5% (22 out of 422) after this date. Most unidentifiable tracks after 13/11/76 were probably due to ♀ 49, which was the only rat

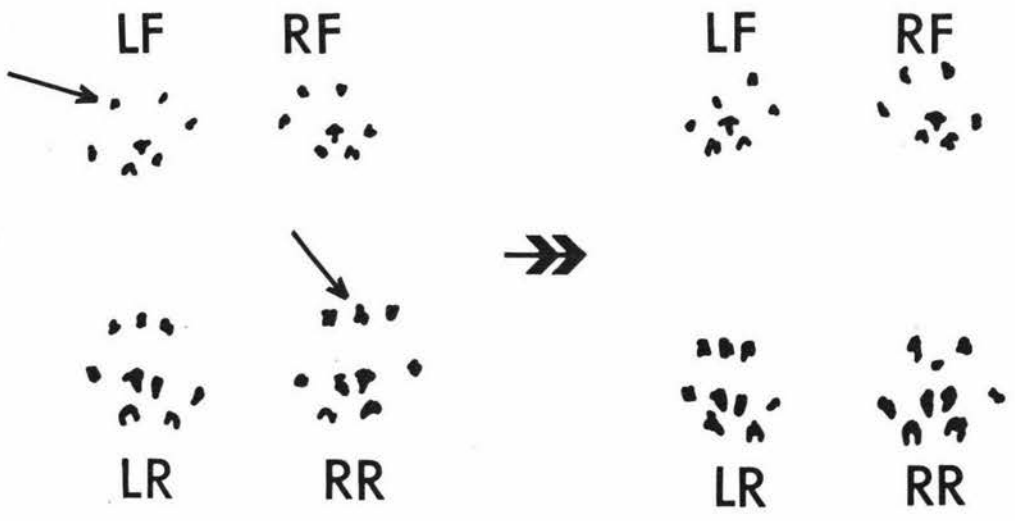


fig. 9 THE PRINTS (ACTUAL SIZE) OF ♂30 BEFORE AND AFTER TOE-CLIPPING

having two clipped rear toes rather than one front and one rear.

The smoked paper was very sensitive to tracking. Insect tracks often appeared on it over the summer and rat whisker traces showed up easily (see Appendix 3). After six weeks of tracking the paper size was increased from 15 x 15cm to 26.5 x 12.5cm. This made no difference to the proportion of identifiable tracks. Poor weather rarely affected track legibility. Only the steepest sloping platforms in heavy rain were prone to having drops of water obscure tracks. Similarly, there were no problems with rats skidding on steep platforms. Only one tree platform was steep enough to cause some skidding but the rat concerned was still nearly always identifiable.

Strips of smoked paper stapled onto the top of the malthoid cover of each tree tracking platform showed that the rats commonly climbed on top of the platforms. Most often, but not always, they tracked inside the platform as well. If the platforms were baited rats always tracked inside. The angled metal roof used by Moors (1975) to cover his tracking paper and chemicals would probably be a distinct improvement on the flatter traversible malthoid one used in the present study.

In summary, smoked paper proved to be an ideal tracking surface. It was stable and easily prepared. A device to burn benzene from a transportable gas cylinder would not be difficult to design for use in the field. The paper was very sensitive to touch when smoked, and needed careful handling in the bush to avoid scratching by twigs or leaves, but this was never a significant problem. In the present study smoked papers were transported from the lab to the field in a specially slotted box. While this was very efficient for the few (20) platforms involved, a study on a larger scale would need another method of carrying greater lengths of smoked paper.

7.3 Rat Response and the Effect of Bait

From 23/8/76 to 22/1/77 tracking platforms were baited with peanut butter each alternate week to see if baited home ranges were significantly larger than unbaited home ranges. Over this period 78% (279 out of 360) of baited platforms were tracked and 19% (57 out of 300) of unbaited platforms were tracked. That is, baited platforms were 4x as effective as unbaited platforms in obtaining tracks over the same time period. During unbaited weekly sessions the number of platforms tracked per night often declined from the first night to the third. The total number of trackings for the first, second and third nights of unbaited sessions from

23/8/76 to 22/1/77 was 29, 18 and 10 respectively. During baited sessions the total normally rose, i.e. 89, 92 and 98 trackings for the three nights over the same time period. It seemed that rats gradually ceased visiting platforms after the bait supply ceased, and that the unbaited records were the result of the end of this gradual reduction. To test this, unbaited papers were left out for the period between a normal baited session and a normally timed unbaited session especially added to the end of the programme. Results are shown below:

	20/1/77									29/1/77
Day	1	2	3	4	5	6	7	8	9	10
No. Platforms Tracked	9	10	10	6	4	2	4	3	1	0
	'Normal' baited session							'Normal' unbaited session		

It seems that the hypothesis is correct. If so, unbaited platforms probably depend on the fortnightly baited sessions to record any tracking at all. I concluded that none of the platforms were on runways and each rat could therefore go about its activities bypassing all of them. On the basis of this result ground platforms were used baited only.

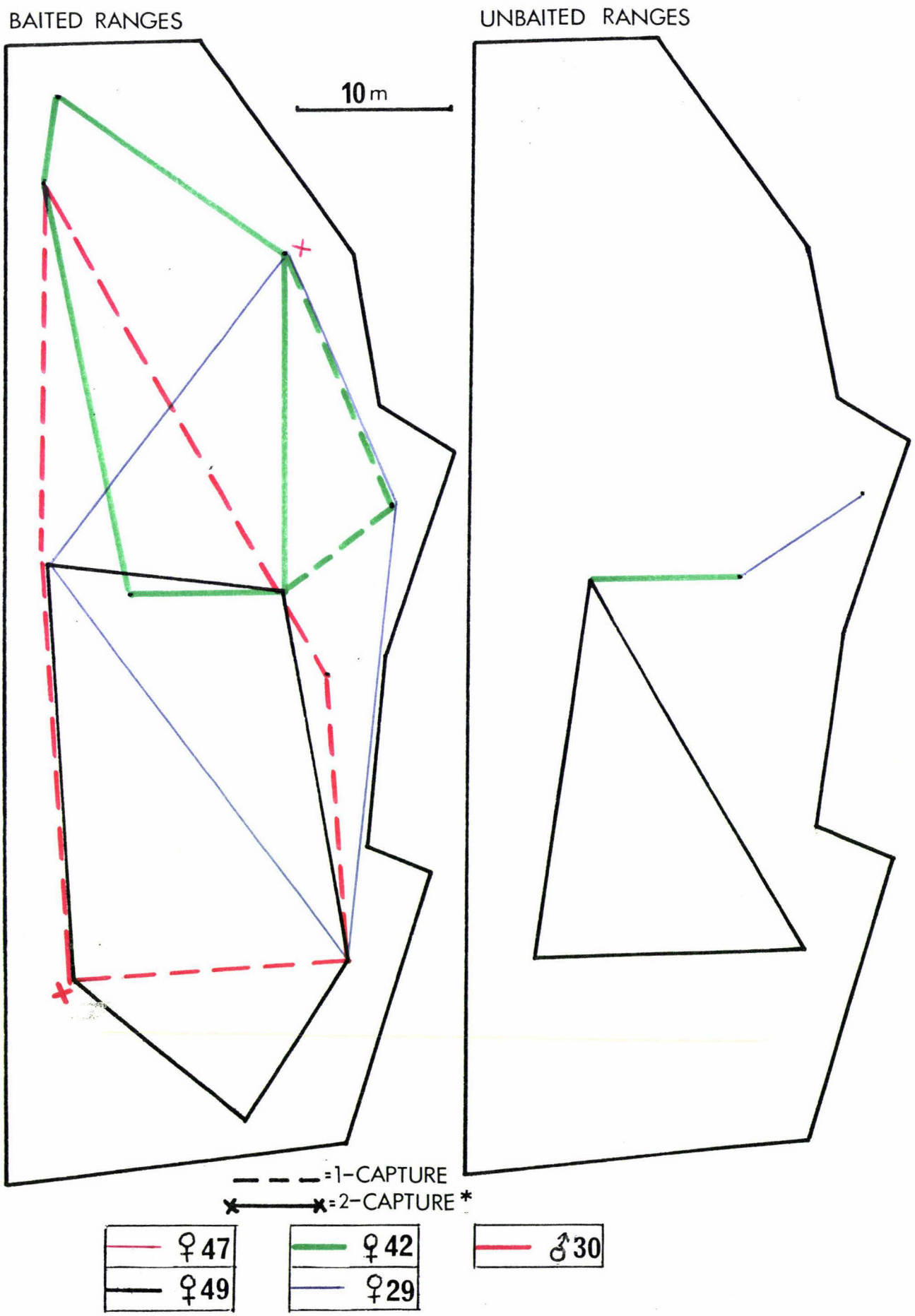
Since the number of marked papers per unbaited session did not decrease over the whole tracking period it is clear that the rats never learned that bait was available only fortnightly, for three days.

One disadvantage of baiting platforms is that once the first rat to visit any platform has removed the bait there is much less incentive for a second rat to track there also. This could account for differences in the tracking rates of different individuals. Because of this 'competition' for baits, activity patterns such as how early a rat begins its nightly foraging become important, since only early foraging individuals may be recorded at a platform. Two factors reduce this bias. First, as discussed earlier rats did visit platforms even though they were unbaited. Six per cent (40 out of 656) of all tracked papers had tracks of at least two individuals on them. One was tracked by four individuals. Second, if the data is taken over a sufficiently long period the chances of tracking less active rats are increased.

Bailey (1969) did not bait his tracking devices when he studied the

Fig. 10: Baited and unbaited tracking-revealed ranges compared, prior to 22/12/76.

FIG. 10



*EACH RAT TRACKED AT LEAST TWICE PER LOCATION

movements of voles and mice since "bait may introduce an additional element of bias". Brown (1969) and Metzgar (1973a and b) also relied on the curiosity and exploration of the study rodent. Sheppe (1965) found that both baiting and a new shelter design increased tracking, but exploratory movement still provided sufficient data without encouragement from the researcher. Clearly, in the present study, exploration by ship rats was insufficient to supply usable amounts of home range information, without baiting. It is important, however, that baiting did not induce bias. Stickel (1948) found that individuals of Peromyscus leucopus would not leave their home ranges to get bait. At Greenwood's Bush unbaited ranges were in the same places as baited ranges (Fig.10), although over the same time period much less data came from unbaited platforms. Two ship rats (♂30 and ♀47) were never tracked at an unbaited platform. Baiting some platforms but not others to attract rats out of their home ranges was never attempted. During removal trapping when baited cage traps were used, however, only the rat shown by tracking to frequent that area was ever caught. It is likely that bait acts in exactly the same way as a point source of natural food e.g. a fruiting tree. If a rat regularly visits a fruiting tree then that tree can be regarded as part of its home range, albeit perhaps temporarily. I concluded that baiting was not an unnatural cause of extension of ship rat home ranges in Greenwood's Bush.

7.4 Home Ranges Revealed by Tracking

In a review of the study of mammal movements, Sanderson (1966) stated that "the size and shape of an animal's home range probably have little or no significance in themselves" (page 219) and later that "Emphasis will have to be shifted from the movements themselves to the reasons for the movements" (page 231). In this thesis I have attempted to take such a functional approach.

7.4.1 Criteria of "Home Range"

In the most commonly used definition, Burt (1943) defined home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young". To exclude occasional or dispersal movements outside this area requires some definition of such a movement. Past researchers have used a distance criterion. If the animal travelled to an isolated point, and did so infrequently, then that point was not included in the home range. Such movements have been recorded in the chipmunk Eutamias (Martinsen, 1968); the pocket mouse Perognathus formosus (Maza et al., 1973). Harvey and Barbour (1965) quantified this

distance so that in their study if a recapture point was further than one quarter of the range length from any other point of recapture then it was excluded from the individual's home range.

No work known to me, however, pays any attention to the frequency the study individual is identified by an observer at each point in its range as a qualification for the inclusion of that point in the home range. The frequency of use seems to be a more reliable indicator of areas of "normal" usage than the distance criterion, assuming that the study method allows the differences between commonly and rarely used areas to become apparent. For example, if recapture (by whatever means) is infrequent, the researcher should not ignore these data; yet since he has not demonstrated regular usage of the locations constituting the range it is arguable whether he has demonstrated that the area is a home range, by Burt's definition. Furthermore, if the researcher has a set grid of devices which capture an animal only once in several places, twice in others, three, four and so on times in further places, it is similarly arguable whether the points where *capture occurred only once (I term these "1-capture points") should be included in discussions on home range. It is difficult to apply Burt's (1943) definition to the present study since at 1-capture points I had no way of telling whether the activities of the rats were "normal". Burt's definition was finally taken to embrace the concept of a rat localized more or less within a certain area, but as Brant (1962) concluded, "It would be difficult at this time to salvage enough of the home range concept (Burt, 1943) to use it to interpret the movements of small mammals quantitatively".

In the present study the two main parameters adopted for the interpretation of the home range data were:

(a) The number of times each rat was tracked at a given location before that location was included in the rat's home range.

(b) The length of time over which the tracking data was drawn.

While it is theoretically feasible to exclude from a calculation of home range the locations where a rat was tracked only once, some allowance needs to be made for the insensitivity of the tracking technique. Considering that a rat is probably present in an area on some occasions without being tracked there, a 1-capture point may represent a greater use of the area than just one visit. This was proved true for cage trapping data on R. rattus rattus in this study area (see Section 7.5)

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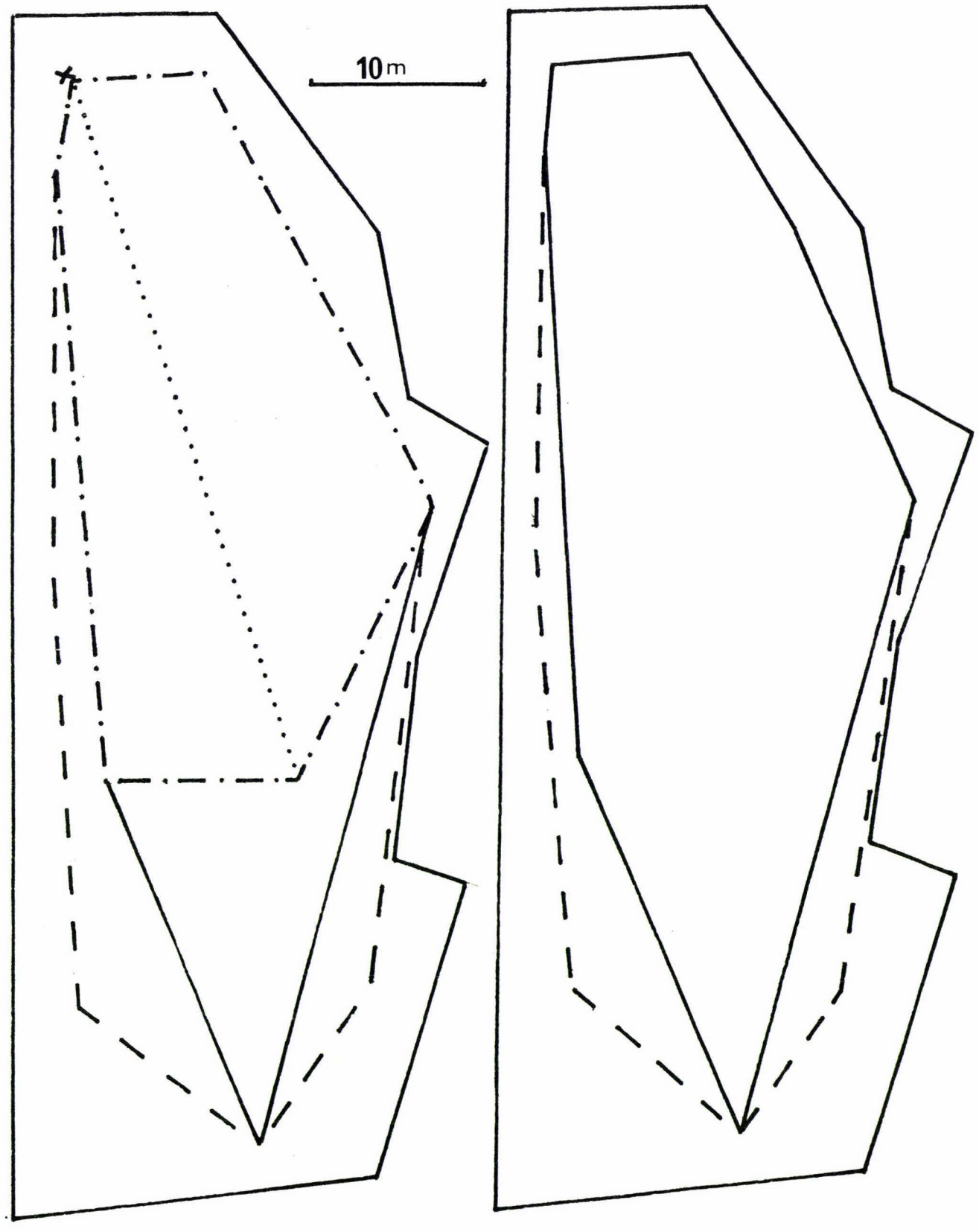
* 'Capture' here embraces identification by tracking and other non-detaining methods.

Fig. 11a: The effect of altering the number of trackings per location which I accept as indicating the home range boundary, for ♂30 from 22/12/76 to 23/1/77.

Fig. 11b: Tracking-revealed home range of ♂30 from 22/12/76 to 23/1/77, i.e. showing 1-capture and 2-capture ranges.

FIG. IIa

FIG. IIb



when recaptures were few. Although such data are presented, their information content is small since no indication of the regularity of usage of each location is available, and the relationship between the recorded home range and actual home range is doubtful.

Fig.11(a) shows that over the period 22/12/76 to 23/1/77 when ♂30 was resident in Greenwood's Bush, the minimum area home ranges (Stickel, 1954; Jennrich and Turner, 1969) decrease as I increase the number of trackings per location which I accept as indicating regular or "normal" (Burt, 1943) usage. In this thesis unless otherwise specified all home range diagrams will be drawn as minimum area ranges with a solid line joining points where the rat was tracked at least twice (i.e. 2-capture points), and a dotted line joining 1-capture points, i.e. Fig. 11 (b).

Each home range calculation should have an appropriate time qualification (Sanderson, 1966; Martinsen, 1968).

Three time periods were distinguished in the present study:
(a) From when tracking commenced to 19/12/77 when the nest of ♂ 30 blew down in a gale. After this date there was a dramatic increase in ♂30's range, i.e. 23/6/76 to 18/12/76 inclusive.
(b) From the end of the above period to the time when the first rats were selectively removed from the study area, i.e. 22/12/76 to 22/1/77 inclusive.
(c) The period of selective removal of rats, i.e. 16/2/77 to 1/4/77 inclusive.

Many researchers have calculated home ranges for only those individuals captured at three or more locations (Hayne, 1950; Williams, 1955; Miller, 1958; Getz, 1961; Metzgar, 1973a). Others have used five or more locations (Bleich et al., 1975), six or more (Howell, 1954), seven or more (Buckner, 1957) or ten or more (Blair, 1942 and 1951; Van Vleck, 1969). The criterion is normally chosen such that the apparent home range size does not increase with successive captures. Each range is then supposedly close to the actual range size and the true average range size can be calculated. Frequency of use rather than the number of locations visited was the major criterion in the present study, and no limitations relating to the number of locations were imposed.

7.4.2 Results and Discussion

The home ranges of the five ship rats resident at Greenwood's Bush are shown in Figs. 12 to 14. Home range size was latently variable since size increased as ship rats were removed from the study area (i.e. as

Fig. 12a: Tracking-revealed home ranges from 23/8/76 to 18/12/76 incl.

Fig. 12b: Tracking-revealed home ranges from 22/12/76 to 22/1/77 incl. i.e. after the expansion of ♂30's range, but before rat removal began.

FIG. 12a

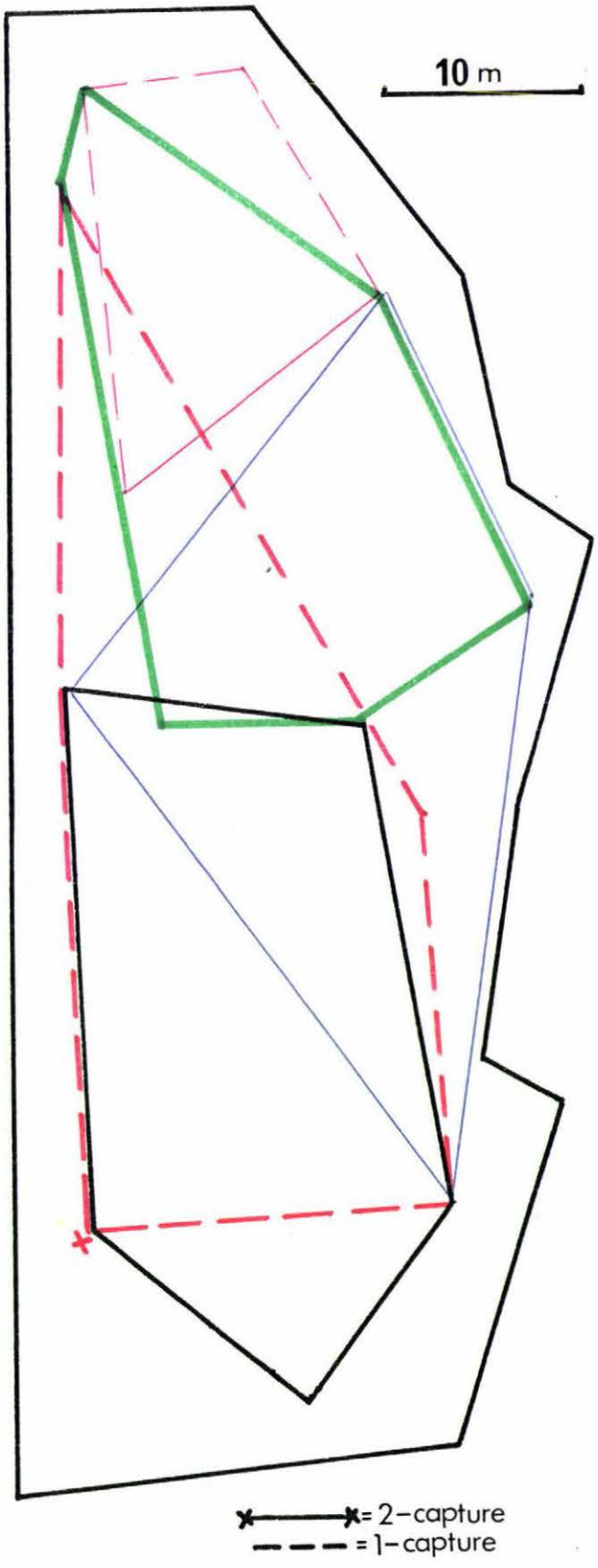


FIG. 12b

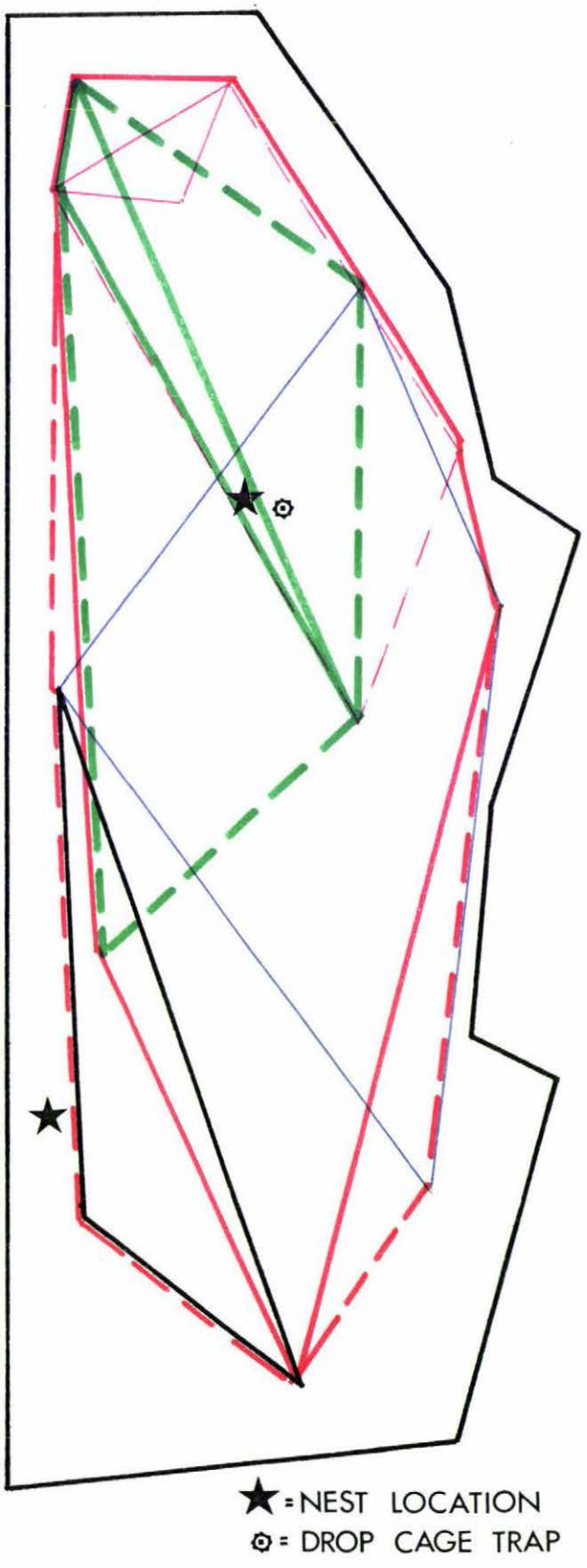


Fig. 13a: Tracking-revealed home ranges of ♂30 and ♀s42 and 49, 16/2/77 to 25/2/77 incl., i.e. after ♀s47 and 29 killed.

Fig. 13b: Tracking-revealed home ranges of ♀s 42 and 49, 4/3/77 to 12/3/77 incl., i.e. after ♂ 30 killed.

FIG. 13a

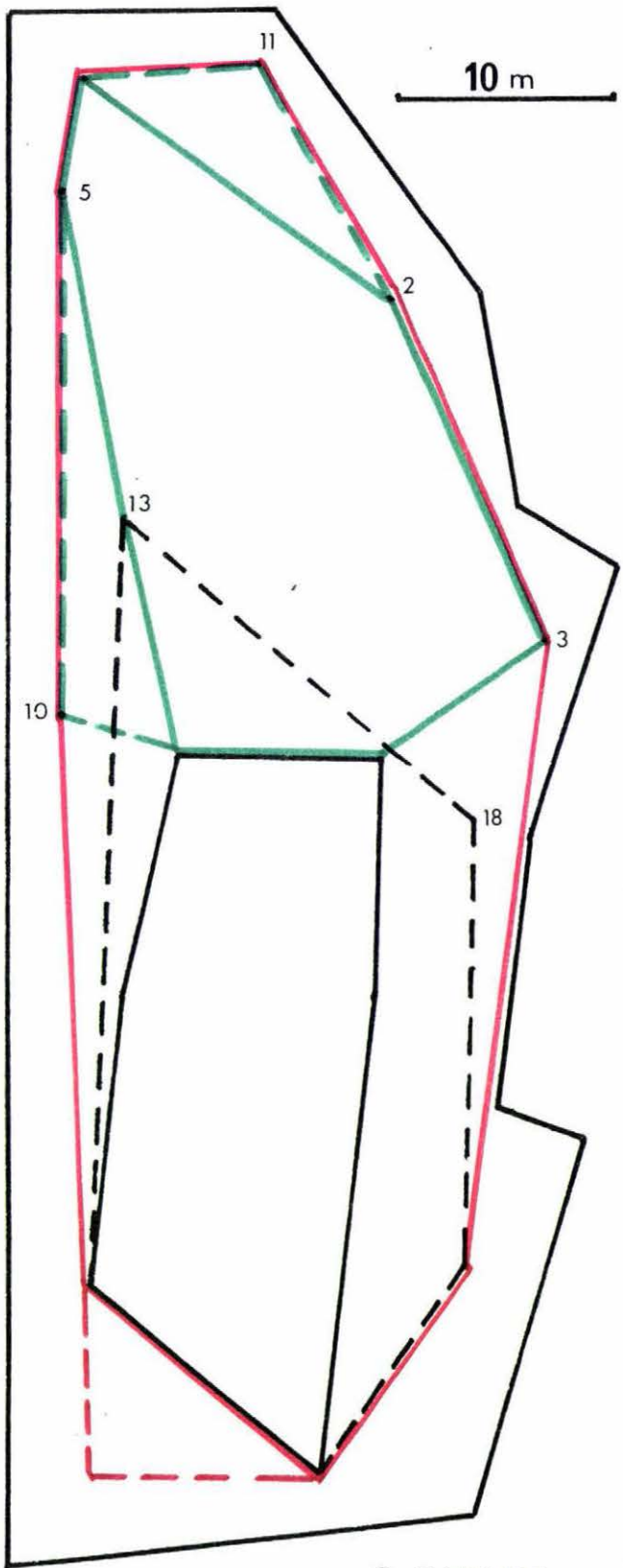
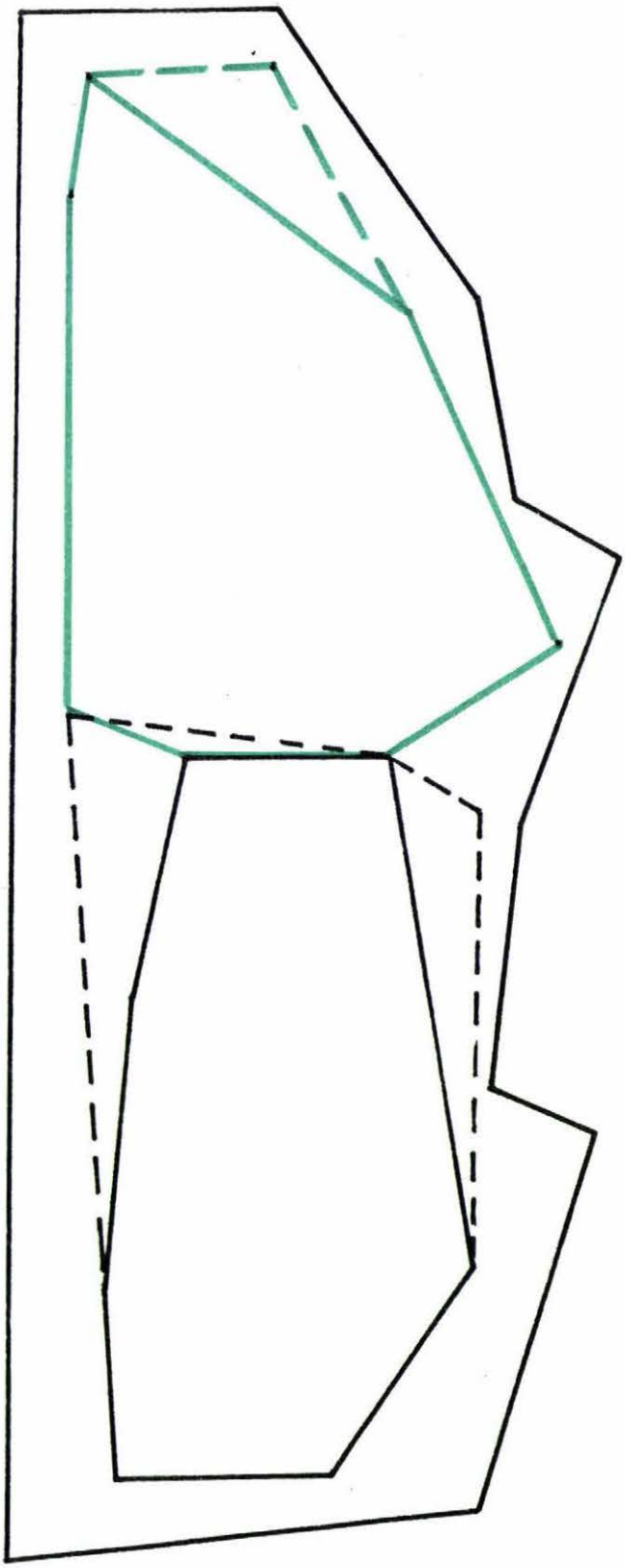


FIG. 13b



= 2– CAPTURE
= 1– CAPTURE

♀ 42
♀ 49
♂ 30

Fig. 14a: Tracking-revealed home ranges of ♀ 49 and untagged male from 16/3/77 to 18/3/77, i.e. after ♀ 42 killed.

Fig. 14b: Tracking-revealed home range of ♀ 49 alone, from 23/3/77 to 1/4/77, i.e. after untagged male killed.

fig. 14a

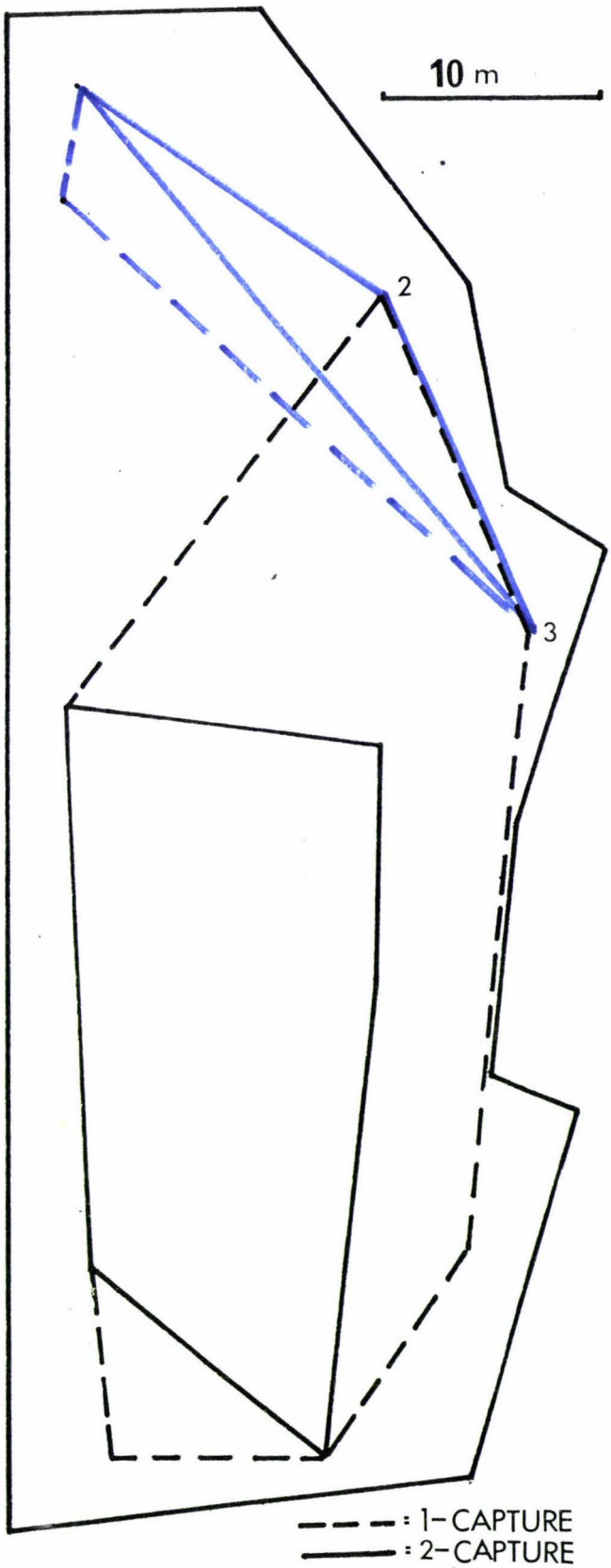
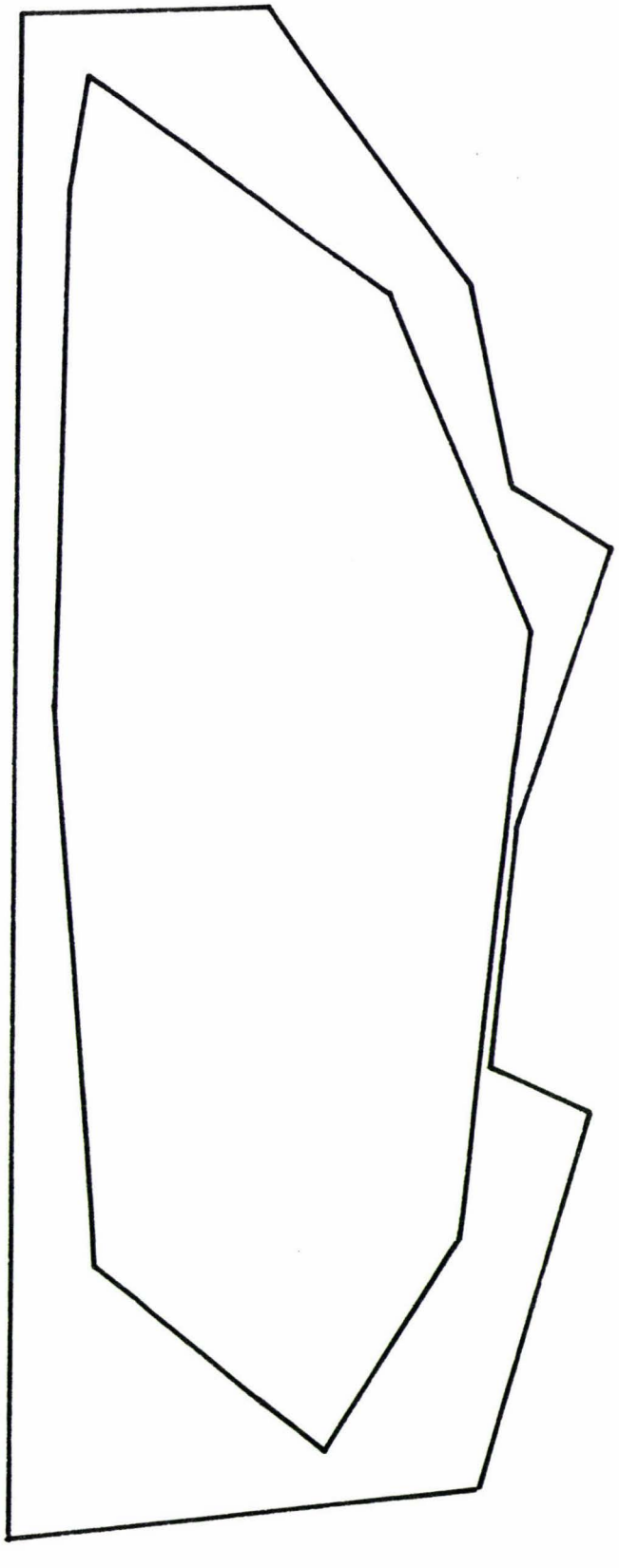


fig. 14b



= ♀ 49
= UNTAGGED MALE

density decreased). Home range shape was irregular and certainly did not conform to such a well known shape as a circle, rectangle or ellipse as other workers have assumed (e.g. Jorgenson, 1968). Such non-conformity was caused mostly by the study area being small, with sharp boundaries. Also, an examination of the study area at the conclusion of the study showed that tracking-revealed home range boundaries correlated quite closely with gaps or dips in the bush canopy. While the reasons for the shapes and sizes or changes in shapes and sizes of ship rat home ranges may be of zoological significance, the shape and size per se have much less significance in the present study. A descriptive rather than statistical (Hayne, 1949; Dice and Clark, 1953; Harrison, 1958; Calhoun and Casby, 1958) approach seemed useful.

The detected home ranges were stable throughout the study period except for the expansion of ♂30's range after 19/12/76 when wind destroyed its nest. Home ranges in Fig. 12b are generally smaller than those in Fig. 12a, probably because of the shorter time period (one month instead of four) involved. The ranges of ♀s 42 and 49 increased following the removal of ♀s 29 and 47 (Fig. 13a). Both remaining females soon tracked at stations never previously tracked by them, but commonly tracked by the removed rats, i.e. after two nights ♀49 was tracked at platform 16, and after three nights, at platform 13. Female 42 tracked at platform 10 after eight nights and at platform 11 after ten nights.

The removal of ♂30 triggered no obvious changes in the ranges of ♀s 42 and 49 (Fig. 13b). This is not surprising since little scope for change was available. The general expansion of both 2-capture ranges could be due either to the removal of the male or, more likely, to the previous removal of female rats. The male's range was freely overlapping with those of ♀s 42 and 49 and it is unlikely that it posed a hinderance to their range expansion.

Female 42 was captured and killed on 15/3/77. Female 49, the last remaining tagged rat, tracked at platform 3 on 17/3/77 and at platform 2 on 18/3/77 (see Fig. 14a). This rat had never previously visited these platforms. Although the 2-capture range has not increased in size, the 1-capture range has enlarged considerably. The untagged male referred to was tracked in the study area on these three nights only. It was captured and killed on 19/3/77. Its effect on the expansion of ♀49's range is difficult to decipher. It is probably not a coincidence that the two rats tracked predominantly at opposite ends of the study area. During the six nights tracking after the removal of the untagged male, ♀49 tracked

over most of the study area (Fig. 14b).

Two of the five rats were perhaps absent from the study area occasionally. Female 47 was cage-trapped on 16/8/76, and was not seen again until 13/11/76 when it was both tracked and cage-trapped. After this it tracked and was trapped only sporadically. Male 30 was neither tracked nor trapped between 25/5/76 and 8/10/76, nor between 30/10/76 and 10/12/76. Its home range in Fig. 12a is only a 1-capture range, and it seems unlikely that it was present in the study area during the long periods given above without being recorded there. After 10/12/76 it tracked regularly and prolifically.

Ten baited platforms were placed irregularly throughout the gardens, scattered trees and hedges on the developed section bordering the study area to see if any rats incorporated this area in their home ranges. Only ♀ 47 was tracked during five consecutive nights, commencing 4/2/77. It tracked consistently on two platforms in the narrow garden at the north-western section boundary, up to 20m from the native bush. This extension was adjacent to its bush home range. Presumably each rat found its nutritional requirements within its home range area. Prior to the beginning of rat removal, the smallest 1-capture home range was 249 sq.m, and the mean was 502 sq.m (excluding ♀ 47) (Table 10).

The minimum area home ranges shown in Fig. 12a appear to overlap considerably. Presenting the same data by joining adjacent points of capture suggests that the ranges were largely exclusive (Fig. 15). If such an interpretation is correct, ♀ s 49, 29 and 47 had mostly exclusive home ranges throughout the study. Female 42's range overlapped with that of females 29 and 47 but never with that of ♀ 49. The only intrusion ♀ 49 made into ♀ 42's range was on 18/2/77 to platform 13 (Fig. 13a). On this night ♀ 42 was tracked only at the distant platforms 2, 3 and 5; ♂30 tracked platform 13 on the same night. Perhaps ♀ 49 only made the movement into a new environment because ♂ 30 was present, or perhaps because ♀ 42 was elsewhere. Howell (1954) found that female cotton rats had exclusive home ranges although males' home ranges broadly overlapped with those of other males and females. The data of Daniel (1972; page 325) suggest that the ranges of male ship rats in the Orongorongo Valley overlapped considerably whereas females' home ranges did not. If home ranges in the present study were partly or periodically overlapping then there should be occasional trackings of, say, ♀ 42 well inside ♀ 49's range. In fact it would be surprising if two rats such as ♀ 42 and ♀ 49 should have the bulk of their ranges in such obviously separated areas, yet overlap much at the border. Fig. 18 (Section 7.6) shows that both

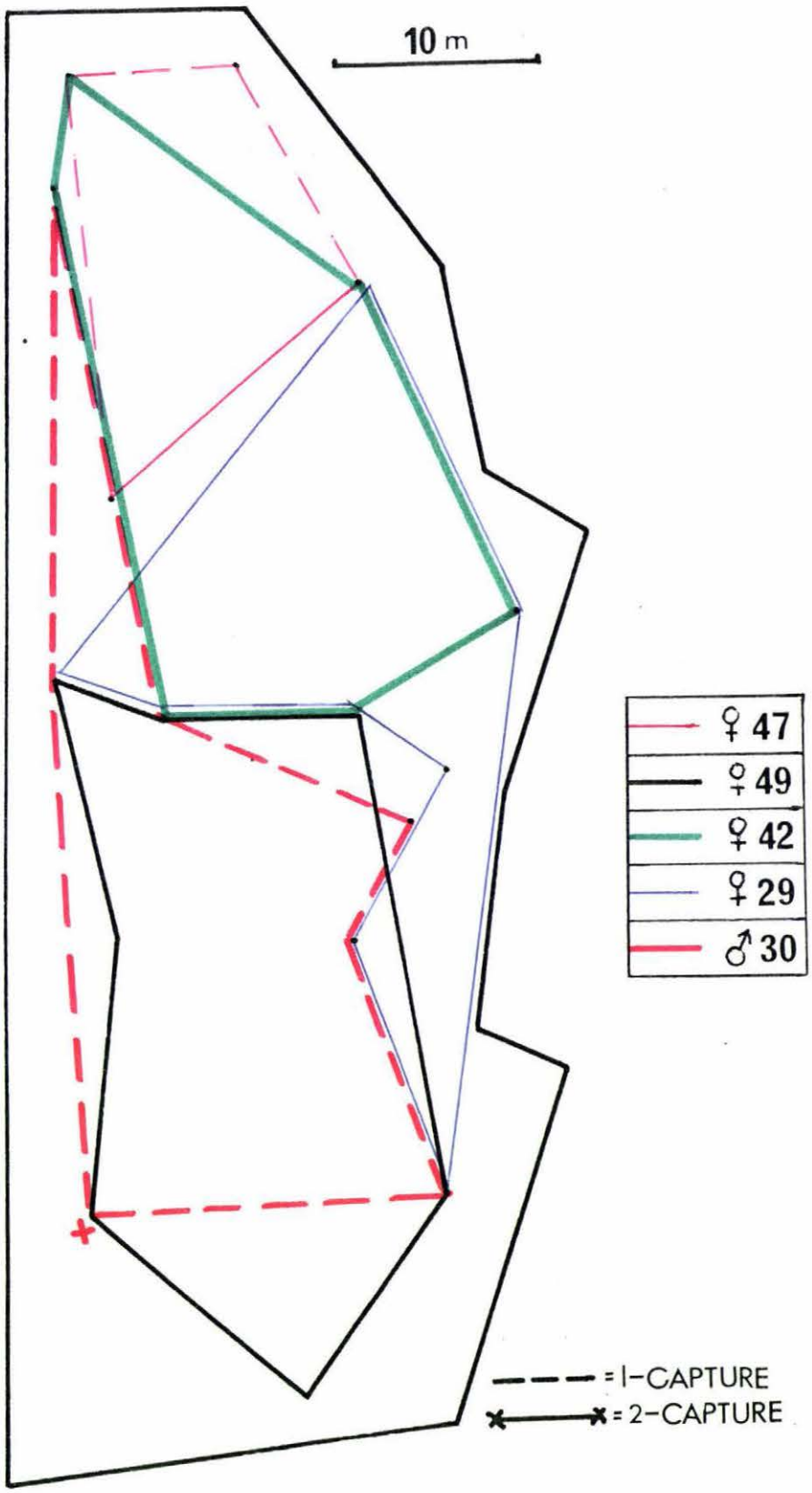


FIG. 15 Tracking-revealed home ranges calculated by joining adjacent points of capture, 23/8/77 to 18/12/77 incl.

spent some time at the border platforms, yet only twice during the entire tracking study did they track at the same platform on the same night. This perhaps indicates an avoidance response to the scent of the first visitor by the second. As far as I could tell, the two home ranges were spatially almost exclusive.

As rats were removed from the study area, the home ranges of those remaining expanded. The shortest time within which range expansion was detected was two nights after a removal. We can infer from this that the mechanism used by rats to mark their home range boundaries is a short lived one. Olfaction is an especially important communication method in nocturnal rodents (Ewer, 1968) and others (Hanney, 1975). Ewer (1971) considered that in ship rats smell appeared "to be more important than sight in individual recognition." In her studies of a free living colony of ship rats in Ghana she observed smell marking done by rubbing various parts of the body against the object to be marked (most frequently a tree branch); she concluded that R. rattus rattus had no specialised glandular areas used for scent marking. However, Rudd (1966) found staining from mid ventral glands in individuals of nine Malaysian species of Rattus including Rattus rattus jalorensis. Eibl-Eibesfeldt, 1953 (in Ewer, 1971) reported R. rattus rattus using urine drip trails as a scent marking device. Although no observations of scent marking methods were made in the present study, it seems likely that scent was used to mark home range boundaries.

Female 49 was the only female with a range almost exclusive to other females. Perhaps it was the dominant female, since prior to 19/12/76 it seemed to have exclusive access to ♂ 30, the only male. However, there was no reorganisation of the females' home ranges after 19/12/76 when ♂ 30 expanded its home range to overlap with them. Throughout her ship rat colony observations in Ghana, Ewer (1971) found that there were normally two or more high ranking females showing mutual tolerance but each prepared to attack any subordinates. When numbers were low, however, a single dominant female sometimes appeared. There were always several males in Ewer's colony. The single male at Greenwood's Bush was perhaps the most unusual feature of the rat population there. Despite ♂ 30 having scrotal testes at least from October 1976 to March 1977, no new litters appeared during that time. Also, no females were pregnant when finally captured and killed. Examination of the uterine horns of these females showed that only ♀ s 47 and 49 had given birth in the past. Both had six uterine scars. One of these, probably ♀ 47, could have been the mother of a

litter of six which was seen at the nest in front of the observation hide (near platform 4) in April 1976. The two lighter rats ♀29 and ♀42, which had no uterine scars when killed, may have been from this litter.

Whether ♀49 had her litter in the bush or before she arrived there is unknown. The fate of this litter and also the rest of ♀47's litter is also unknown. The density of ship rats at Greenwood's Bush was 22.7 rats per hectare. This figure is high compared to the only other New Zealand figures available. Daniel (1972) found that the number of ship rats known to be alive in his study area in the Orongorongo Valley varied from 1.2 - 3.7 per hectare in spring to 0.7 - 2.5 per hectare in autumn, although estimated rat density had been much greater in some earlier years (e.g. 37 - 49 per hectare in 1951). It is possible that Greenwood's Bush held its carrying capacity of rats and that some individuals of the litter/s produced in the bush were forced to emigrate. Only one rat disappeared within the study period. Female 33 was captured in a cage trap on 26/5/76 but was never tracked nor trapped after this date.

7.5 Cage Trapping and Tracking Compared

Cage trapping has been by far the most common method used to provide home range information on small mammals in past studies, despite the technique having several well known disadvantages. First, the capture of the animal prevents its further movement until it has been released, which may introduce a so-called "trap inhibition" bias (Hayne, 1950; Davis, 1953). This causes underestimation of the actual distances moved, and also home range areas based on those distances. Second, there may be a strong positive or negative learned reaction towards the trapping experience, which may cause animals to seek out or avoid traps when they encounter them next (Crawley, 1972; the present study). Third, with continual trapping there may be considerable fatigue or loss of life among animals that have been in traps on successive nights.

Kikkawa (1964) has described in some detail the factors such as those above which could violate the basic assumption that all individuals in the study population, whether marked or unmarked, have the same probability of being captured in any sample. This assumption is common to many formulae used for estimating population size from trapping data (e.g.

Jolly/Seber method).

Tracking data taken at the same time as cage trapping data can be used as a comparison to check the validity of the conclusions of the cage trapping studies.

Prior to the irregular trapping involved in rat removal at the end of the study, 603 cage trap nights were expended for 20 captures (3.3 rats/100 trap nights). This covers the period 11/5/76 to 22/1/77. From when tracking began, to the same date (i.e. 23/8/76 to 22/1/77), 810 tracking platform nights resulted in 400 trackings (49.3 trackings/100 tracking platform nights).

Cage trap-revealed home ranges and tracking-revealed home ranges up to 22/1/77 are shown in Figs.16a and b. The main points to note are:
(1) The tracking-revealed home ranges are much larger than the trap-revealed ranges for all individuals.
(2) No 2-capture home ranges were obtained with cage traps, and in one case (♀49), no 1-capture home range was available either.

The average number of cage trap recaptures per rat from 11/5/76 to 22/1/77 was 3.0. The average number of tracking "recaptures" over the shorter period 23/8/76 to 22/1/77 was 47.8. The latter are locational data only of course. The small number of recaptures by cage traps causes two major problems. First, the relationship between the apparent and actual home ranges must be doubtful. Simultaneous tracking has shown that in this study, cage-revealed 1-capture ranges were on average 18% of the area of tracking-revealed 1-capture ranges*. Home range areas are shown in Table 10. Second, cage traps give no indication of the intensity of use of various parts of each home range, or the relationships between the changes in home range boundaries. This is compounded by the long time needed to get sufficient recaptures to show any home range at all. Burt's (1943) definition of home range demands sufficient data to recognize whether the individual's movements in the study area are "normal". The relatively large amount of data supplied by tracking permits the recognition of unusual movements outside the home range area. When only three or four recaptures are available, such recognition is much more difficult. The home range obtained from few recaptures over a large period of time, no matter how it is calculated, may be of little biological significance.

Tracking was a sensitive technique, whereas cage trapping was not. After ♂30's nest was destroyed by wind, the rapid extension of its move-

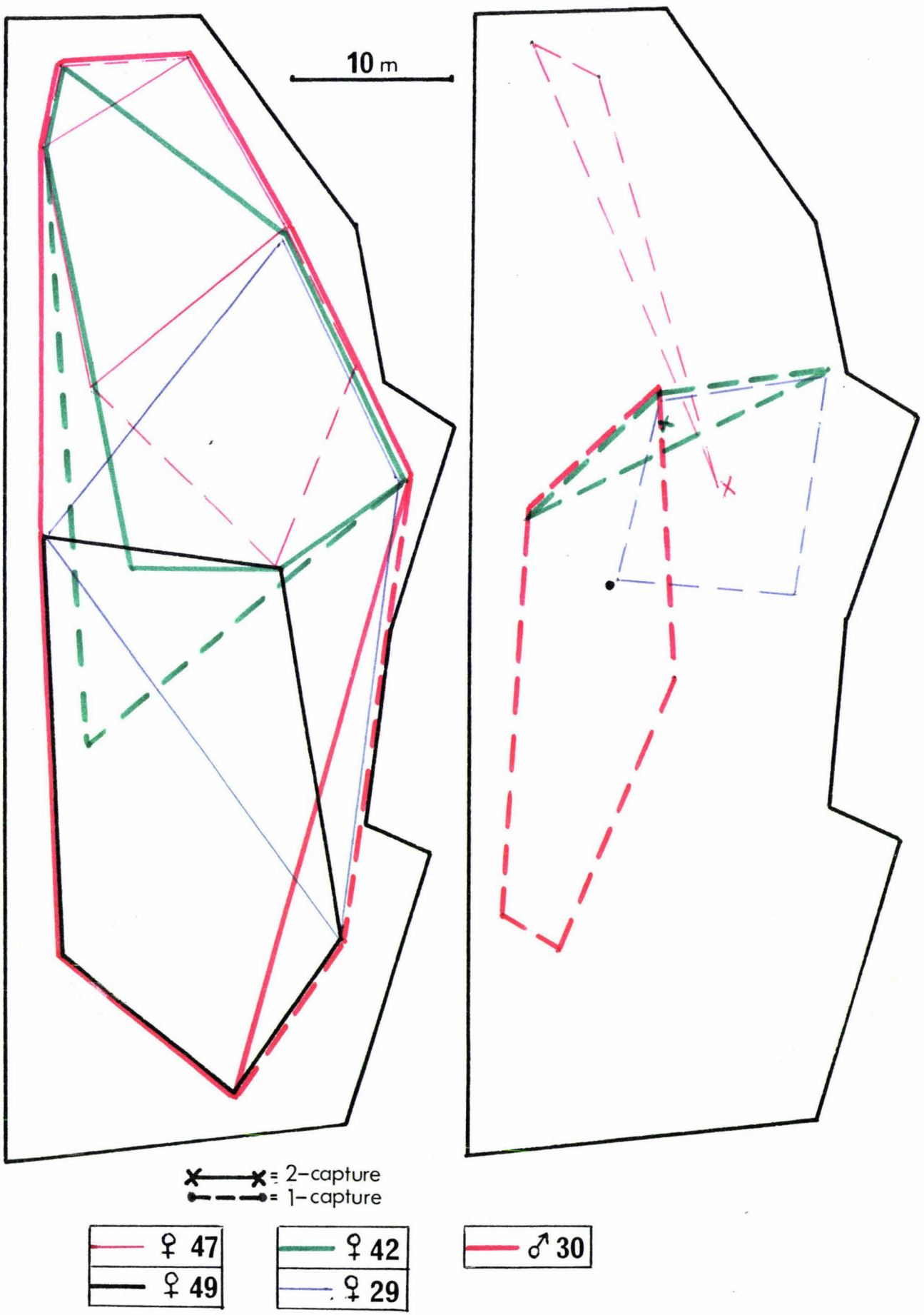
* This excludes ♀2747 which had part of its home range outside the study area.

Fig. 16a: Tracking-revealed home ranges from 23/8/76 to 23/1/77

Fig. 16b: Cage trapping-revealed home ranges from 11/5/76 to 23/1/77

FIG. 16a

FIG. 16b



	♂ 30	♀ 42	♀ 49	♀ 29	♀ 47	
Tracking	1011m^2	307	249	441	*	$\bar{x}$ = 502m^2
Trapping	221	50	-	140	*	$\bar{x}$ = 103m^2

* Excluded since part of the home range was out of the study area.

Note: Total study area = .21 ha.

Table 10: Area of 1-capture ranges prior to 23/1/77

ments to include four tracking platforms at the northwestern end of the study area was detected three nights later on the first subsequent night of tracking. However, ♂30 was not cage trapped in any location showing an increase in its home range until 45 nights later (after 110 trap-nights).

The total number of tracking and trapping records for each rat prior to 23/1/77 is shown below:

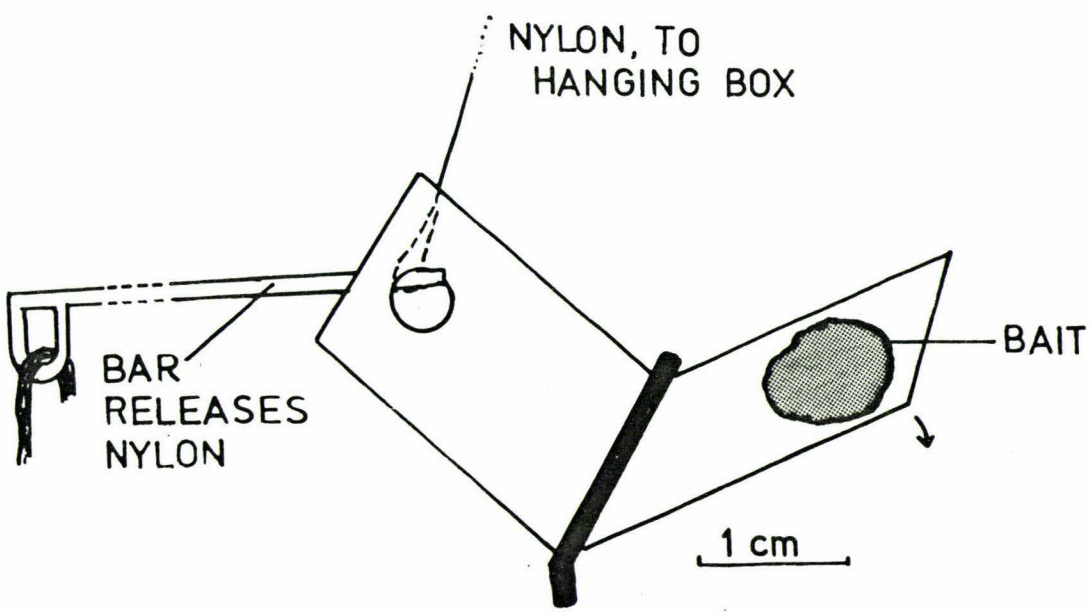
	♀29	♂30	♀47	♀42	♀49
Tracking	120	48	14	74	83
Trapping	4	5	4	5	1

With the possible exception of ♀47, all rats were to some extent trap shy. Female 49 was cage trapped on 17/6/76, but not again until 1/4/77. Tracking showed that it had in fact been present in the study area throughout that time. Small amounts of peanut butter placed at intervals up to cage traps showed that rats would approach to under the door of a trap without entering and being caught. All rats consistently tracked within two metres of set cage traps but would not enter and be caught. Female 42 was cage trapped on 1/6/76 and 7/6/76 but not for five months afterwards. A new live trap was designed (Fig.17) and used for the first time on 13/11/76. Female 42 was captured in the new trap on that night, and on two subsequent occasions. Again tracking showed that this rat had consistently been present in the study area.

The initial trapping experience can be so disturbing to rats that they will wear their noses literally to the bone overnight in repeated attempts to push between the cage bars. Perhaps the use of mesh, rather than bar, cages and more frequent checking of traps could ease the stress involved in capture and hence reduce trap shyness.

Individual rats were tracked at up to 16 locations in one night. Tracking therefore not only supplies more data faster than cage trapping but also types of data not available using cage traps. (See Section 7.6). Its major advantage, however, is that the rat is not detained. While no rats died in cage traps in this study, 8 of 51 cage trapped ship rats at Keeble's Bush died in traps. Most died during a very cold night or after several successive captures. Also, the recapture rate at Greenwood's was better than average in ship rat studies. At Keeble's Bush 59% of 51 cage-trapped rats were never recaptured. Since the animal remains largely

(above) in position



DETAILS OF MECHANISM

fig 17 New live trap

undisturbed when being tracked, it is hoped that the tracking results are genuine indicators of normal movement, and are not in any way alterations from status quo caused by the technique. This difference (between tracking and trapping) is especially important when tracing the movements of an animal such as R. rattus rattus which seems likely to become trap shy easily.

One disadvantage of tracking is that no information can be obtained on the weight and reproductive condition of the rat. It is, however, easier to gain a complete picture of reproductive condition if dead rats are used, especially in the case of females. Snap trap lines can be used in conjunction with tracking grids to trap, say, an area surrounding the tracking study area to check for dispersing rats. As in the present study cage traps can be used in the same study area as the tracking devices for the duration of the tracking study. The cage trapped rats then supply periodic weight and reproductive information. It is difficult to be sure how much trapping interferes with the normal activity of the animal. If accurate estimations of home range areas or distances moved by rats are required then the accumulation of reproductive data may need to be given second priority lest it results in diminishing accuracy of those estimations.

The techniques employed must be selected on the basis of the precise aims of the study.

There is some evidence that at times rats were "tracking platform shy" although they would enter cage traps. ♂ 30 was cage trapped on 25/5/76. Although tracking began on 23/8/76, the next record of ♂ 30 was when it was cage trapped again on 9/10/76. During the first subsequent tracking night (14/10/76) ♂ 30 was tracked at platform 8, and two nights later it was both tracked and trapped. After this it was not tracked again until 11/12/76, but during this period of apparent absence it was cage trapped (on 29/10/76). Since cage capture stops further movement of the trapped rat, perhaps ♂ 30 entered the cage trap first by chance and was prevented from tracking on those nights.

7.6 Ship Rat Activity

During the period when both ground and tree platforms were set, and all tagged rats were present in the study area (i.e. 25/11/76 to 22/1/77), 87% of smoked papers in trees and 36% of smoked papers on the ground were tracked. Hedgehogs caused problems early in the study by erasing rat prints as they explored the ground platforms. Thirty-six per cent should therefore be regarded as a minimum. Rats were about 2-1/2 times more active

in trees during the above period. Individual rats differed in their contribution to this generalization:

Number of Ground Trackings as a % Total Trackings, 25/11/76 to 22/1/77.

♀47	♂30	♀29	♀49	♀42
60% (9/15)	42% (22/52)	27% (25/94)	(16% (5/31)	4% (1/25)

During this period a majority of ♀47's tracking was on the ground, whereas a small minority of ♀42's tracking was on the ground. Rats seem to differ in their home range location through the height dimension as well as in length and breadth.

Over the six night's tracking between 23/3/77 and 1/4/77, ♀49 moved on average a theoretical minimum of 133m (S.D. = 13.7m). This assumes that it travelled in straight lines between platforms in the order which keeps the figure at a theoretical minimum. No allowance is made for the fact that some platforms are in trees while others are on the ground and movement up and down is also, therefore, involved. Considering further that the trees are discontinuous and tangled, the true movement may have been nearer 400m average. Daniel (1972) measured the distances moved between successive captures of ship rats in the Orongorongo Valley using cage traps, and found that 67.8% of the males and 78.6% of the females moved less than 61m. Maximum distances moved were 190m for males and 117m for females. Best (1968), also using cage traps, found that 81% of male recaptures and 100% of female recaptures were within 40m of the last capture. The maximum distance between recaptures for males was 120m, while the maximum for females was 40m. At Keeble's Bush during the present study the mean distances moved between successive captures were 37.9m for males and 35.7m for females. Maximum distances moved were 67m for males and 45m for females.

During the present tracking study, the maximum recorded distance between trackings was 63m. Both ♂30 and ♀49 travelled this distance in one night. It is close to the 70m maximum traversible distance in this study area (i.e. the diagonal of the study area). Although the other rats moved comparatively shorter distances, each was recorded moving the maximum distance across its home range in one night. This distance, for ♀s 29, 42 and 47 was 42m, 33m and 31m respectively. All the rats often tracked their entire recorded range in one night.

Cage trap-revealed range lengths were on average 50% of their tracking counterparts. The implications of these results for those of Best (1968) and Daniel (1972) are that the actual distances moved by rats in their studies were probably greater than their quoted figures. Furthermore the route each rat takes between cage captures can never be known while cage traps only are used for recapture. The distance a rat moves could be considerably larger than the distance along the straight line between the two points.

Since both ♀49 and ♂30 eventually had home ranges the size of the study area, it seems possible that their home ranges may have been larger had the study area been larger. If:

(a) This was true

(b) They were to continue to traverse all of their home ranges in one night, and

(c) They were not abnormally active,

we can tentatively conclude that ship rats may commonly move further than 400m in a single night within their home ranges, i.e. non-dispersal movements. The two large movements (> 100m) which Daniel (1972) observed in male ship rats may be dispersal movements, although the distinction in his study between these and the movements of four males and four females with a range length greater than 90m seems arbitrary.

Not all tracking platforms within each home range were visited equally by the ship rats. On the assumption that tracking accurately reflects the use of each area, such use for different areas of each home range can be compared. Fig. 18 shows as an example the use of tracking platforms by ♀ 49 and ♀ 42 after ♀29 and ♀ 47 were killed. Both rats tracked more away from the interface of their ranges, indicating either that they were competing for baits there or that both avoided the area to some extent. They tracked at the same platform on the same night twice only during the entire tracking study, although their combined total number of trackings at the interface platforms (4 and 9) was 65.

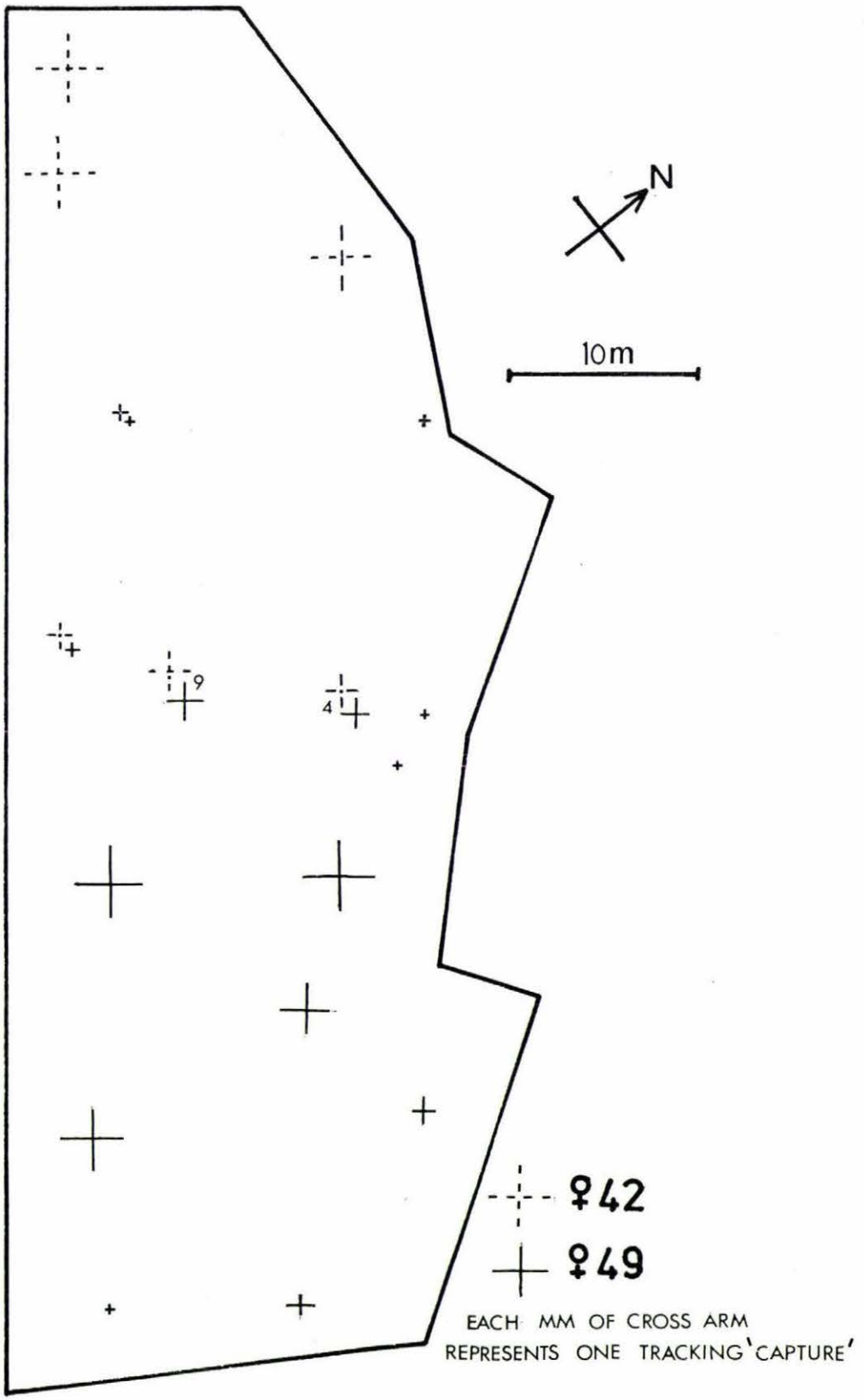


fig 18 Intensity of use of areas within the home ranges, revealed by tracking.
16/2/77 to 12/3/77 (12 baited nights)

The rats used different areas within their home ranges on different nights. Fig. 19 shows the nightly travels of ♀ 49 after all other rats had been removed. This rat tracked most often at the platforms which were within its old home range (i.e. Platforms 4, 9, 14, 8), but visited others in the surrounding bush in combinations which varied nightly.

Accurate notes on weather and its effect on rat activity were not kept. It is noteworthy, however, that during nights of heavy rain the rats still marked average numbers of tracking sheets. Since the baits were under cover, this is evidence that reduced catches in snap and cage traps during such nights are probably due to rain restricting the smell of the bait in some way, rather than the activity of the rats.

There were no trees in Greenwood's Bush large enough to carry perching epiphytes such as kiekie. Ship rats probably usually nest in such epiphytes (Daniel, 1972). In Greenwood's the rats built their own nests in the upper branches of several trees where the leaves were densest. Their construction is described in Chapter 9. An observation hide built approx. 1.5m from one nest apparently caused the occupants to desert the nest for ten days, and shortly after, forever. Within that time, attempts at observation of rat activity at night with red torch light failed because the rats were extremely sensitive to noise. Even the small click of the torch seemed to scare them. On five occasions a rat was seen to leave or have left a nest in the evening - certainly before dark. Rats shaken from a nest never returned within half an hour. They ran with amazing agility through the interlaced top branches of the taller trees, but eventually stopped and remained still in locations often difficult to see into. Rapid escapes from each nest occurred along set routes which were avoided only when several rats left a nest at once.

The locations of the two nests in use prior to 19/12/76 are shown in Fig.10b. After cage capture on 13/11/76 and 9/1/77, ♀ 42 disappeared into the nest by the drop cage trap. Similarly, ♀ 47 entered that nest on 22/12/76. It seems most likely that ♀ 29 nested there also. Note that in Fig. 10b (Section 4.2) the home ranges of all three rats overlap at this point. ♀ 47 and ♀ 29 tended to track in opposite directions from the nest although 42 overlapped with both of them. The nest was central in the home range of 42 but was definitely not for the other two. Up to 18/12/76, two rats could be shaken from a nest approx. 8m up a totara tree near the southern corner of the study area. In that time ♂ 30 and ♀ 49 had overlapping home ranges in which most tracking occurred at platform 8, near the nest. Note that in Fig.10a (Section 7.4.2) the only location

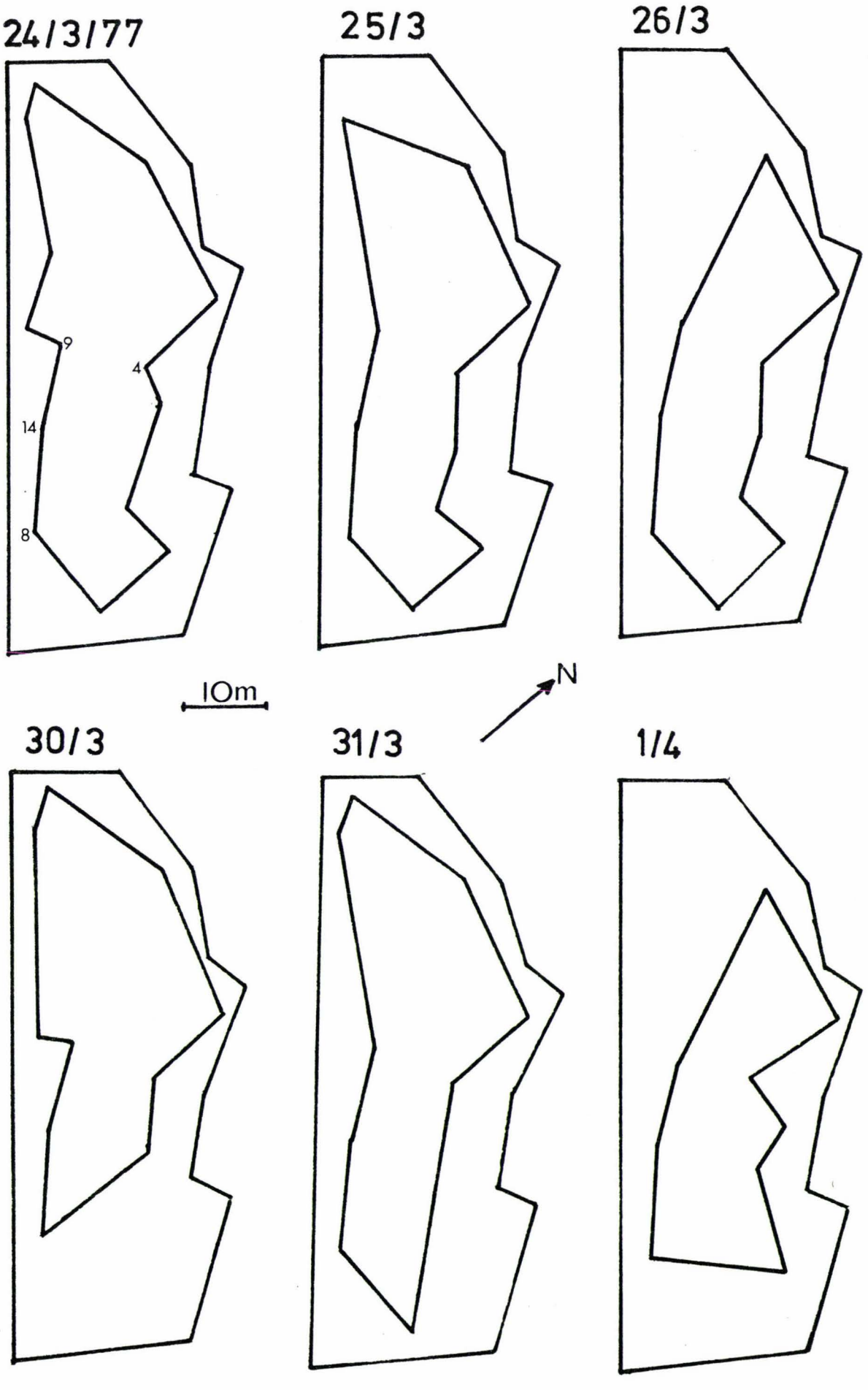


fig 19 Nightly tracking of ♀49

where ♂30 tracked more than once was platform 8, where it tracked three times. Presumably ♂30 and ♀49 nested together in this nest. It lies outside their home ranges as revealed by minimum area calculations. After the nest was destroyed by wind, no new nest location for either rat was ever discovered.

CHAPTER 8: ARBOREAL NESTS

Although rodents as a group are well known nesters (Hanney, 1975; Gunderson, 1976), nests of R. rattus rattus are generally hard to find. Kingsley (1895) and White (1897) described arboreal nests which were probably of ship rats. All the nests described by them were roughly made from materials near at hand. The base consisted of interlaced twigs and the walls were composed of leaves or ponga fibres. Best (1968) described two ship rat nests, based on birds' nests and built of leaves.

In the present study nine nests were examined - eight from Greenwood's and one from Keeble's. None were found at Tiritea. The rats there probably nest in epiphytes. Of the nests examined three were largely intact but the rest were decrepit. The nests were taken from a variety of tree and vine species. All, however, were between three and approx. eight metres off the ground, and most were in dense foliage which was difficult to see into. Broadleafs such as titoki and mahoe were the commonest nest building material. The nests in trees were always made in the centre of the tree, directly above the trunk (see Plate 7).

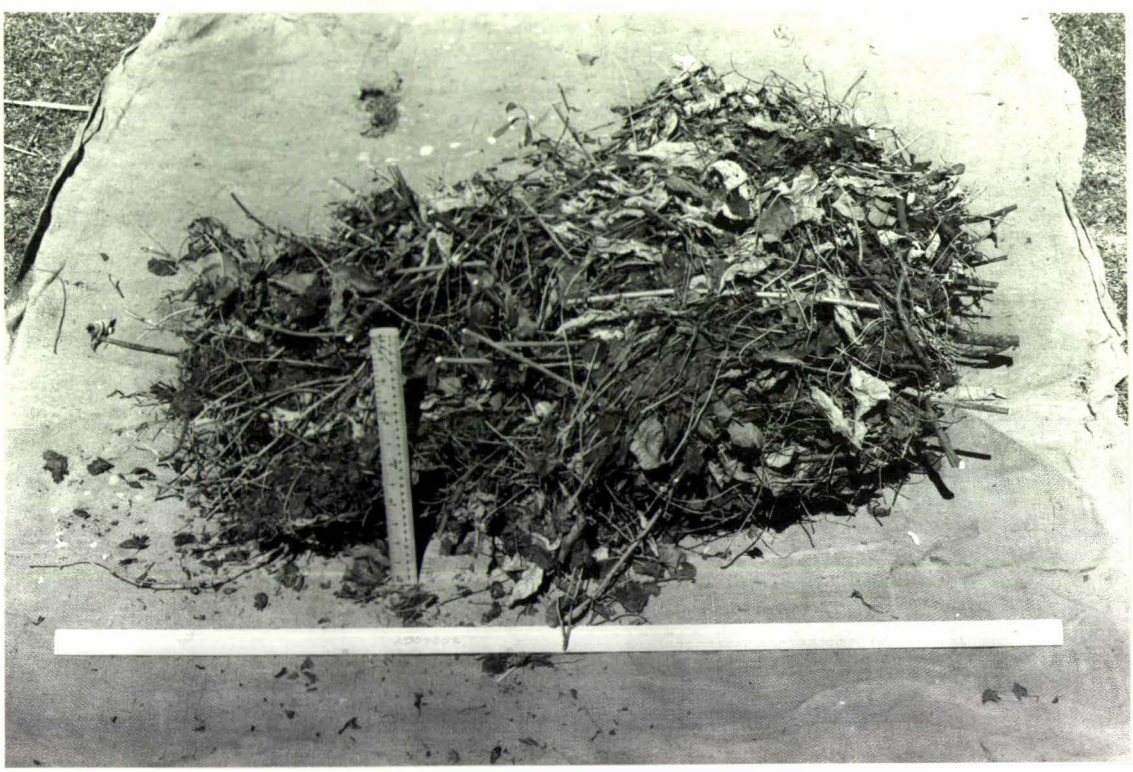
8.1 Nest Structure

The following general description applied to all nests. The base consisted of thick (up to 4mm) twigs roughly interwoven to form a platform. Thinner twigs, mostly 10-15cm long but up to 32cm, with leaves attached, were laid tangentially (the nests were approx. circular) and loosely woven to form walls. Some were partly bitten through, then folded in up to four places. All nest material was taken from within five metres of the nest with a characteristic clean oblique bite. Some of the largest ones were first bitten, and then broken off. I observed caged ship rats carrying large twigs in their teeth. Ewer (1971) reported the same in wild ship rats in Ghana. No observations of actual nest building have been reported in the literature. Although the nests appear roughly made, they are well-knit, stable structures. The actual nesting cavity is lined with softer individual leaves and twigs split lengthwise. No twigs protruded into the nesting cavity.

Since there was commonly 10-15cm of nest material above the nesting cavity, the cavity was probably waterproof in most showers. However no nest that I know of lasted longer than 2-1/2 months. Wind and rain erode a nest away and cause it to rot so that complete renewal, perhaps in the same place, is periodically necessary. One nest in a rewarewa at

Plate 7: Rat-built nest in red beech (comb = 12.5cm long)

Plate 8: Large rat nest containing three nesting cavities
(Rules measure 1m and 30cm long)



Greenwood's was destroyed by shaking, but the rats rebuilt it shortly afterwards (R.M. Greenwood, pers. comm.).

New green material was constantly added to nests in use. Consequently, the size of a nest always steadily increased. The largest nest taken from Greenwood's is shown in Plate 8. It was one metre long and contained three nesting cavities. Its construction incorporated thousands of twigs. The average nest, however, was an approximate sphere of about 35cm diameter.

The single nest from Keeble's Bush was unusual because it was made almost entirely of leaves rather than twigs. The leaves, when laid flat on each other, seemed to stick together in blocks. The twig nests from Greenwood's were also made in blocks rather than as whole units. Several nests did not have distinct entrance or exit holes. Presumably the rats pushed in and out between the blocks of nest material.

Caged wild ship rats housed in boxes measuring 30cm cubed and filled with wood wool, built nests functionally identical to those at Greenwood's. A narrow tunnel connected the nest cavity to the box entrance. The nest cavity was the same constant size as those in arboreal nests, namely 16cm long, 13cm wide and 9cm high. The top of the nest was used as a feeding platform (see 8.2). Faeces and urine were deposited in one place, away from the nest cavity. In one nest box faeces were voided in one corner and urine in another.

Feathers and the remains of insects were recovered from some nests. But few food scraps were recovered from a litter trap placed beneath one nest, which suggests that the ship rats did not carry a lot of food back to the nest.

8.2 Feeding Platforms

Rats at Greenwood's Bush built a second type of structure which I term a 'feeding platform' (Plate 9). It was smaller and less elaborate than a nest, consisting of twigs and leaves arranged to form a platform approximately 20cm across. Birds' nests were sometimes used as bases. In these cases one or two leaves or twigs were always added to the nest bowl. Feeding platforms, like nests, were sometimes built without the advantage of a bird nest base, as in Plate 9.

They commonly contained some faeces and food remains. The food remains are discussed briefly in Chapter 10.3.

Plate 9: Feeding platform
(Lens cap measures 5cm diameter)

CHAPTER 9 - PARASITES AND DISEASES

9.1 Ectoparasites

Four species of ectoparasite were isolated from ship rats in the Manawatu.

The flea Pygiopsylla hoplia was identified on rats from both Keeble's Bush and Tiritea. Another flea species, Nosopsyllus fasciatus was found on one individual at Greenwood's Bush. At Keeble's, fleas were often noted crawling to the tips of the fur of live rats in the holding sleeve and jumping off. A noticeable temperature increase and the release of a 'frightened' musky odour by the rat normally preceded this. Presumably the fleas were abandoning the rat when it emitted signs of serious distress.

A Sarcoptid burrowing mite, Notoedris muris, infected rats from both Tiritea and Keeble's Bush. Lesions produced by the rat on nose, tail, ears, testes and occasionally feet indicate the presence of this mite. At Tiritea, 33 males (19.1% of males) and nine females (6.8% of females) showed signs of infection, although since only the lesions are macroscopically visible the true percentage infections were probably higher than this. The mean weight of infected males was 160g, which was significantly heavier than the male population mean weight ($d = 4.20$, $p < .001$). The mean weight of infected females was 130g, which was not significantly heavier than the female population mean weight ($d = .64$). These differences may be due to the infection lesions being visible only among heavier, and perhaps older, individuals. Differences may exist between males and females, and between old and young rats, in their production of visible lesions in response to a given infection of mites. Such differences may be effected by stress, physiology, growth or behaviour differences between these groups of rats. The mite is transferred to clean animals by contact. Its life cycle is described by Leech and Spence (1951).

The Anopluran Polyplax spinulosa occurred on five ship rats from Tiritea.

All of the above parasites have been previously identified by Gibson (1972) on R. rattus rattus in New Zealand.

9.2 Endoparasites

The stomach only of each rat was examined for endoparasites. Sixty six per cent of the 191 rats examined from Tiritea carried the spiruroid

nematodes Mastophorus muris or Physaloptera sp., or both. The population infection and mean number of nematodes per stomach for the four seasons is shown below:

Autumn	Winter	Spring	Summer
31/53 = 58.5%	28/45 = 62.7%	28/47 = 59.6%	40/46 = 86.9%
$\bar{x}$ = 13.6	$\bar{x}$ = 3.5	$\bar{x}$ = 3.2	$\bar{x}$ = 6.4
S.D. = 20.0	S.D. = 5.5	S.D. = 5.6	S.D. = 6.4

Although the greatest mean number of nematodes per stomach occurred in autumn, the highest population infection was in summer when insects, the most likely intermediate host, were readily available as diet. Approximately 15 native cockroaches Celatoblatta vulgaris from ship rat nests at Greenwood's Bush, where nematodes also occurred in rats, were dissected by Dr W.A.G. Charleston in a search for nematode eggs. None were found.

The maximum number of nematodes found in a rat's stomach was 84. To test whether rats with large numbers of nematodes in their stomachs weighed less for a given body length, a regression diagram of weight versus length was drawn. Points representing rats with 20-40, and 40, nematodes were scattered evenly through the other points in the diagram. Some rats with severe nematode infections were among the heaviest for a given length, of all rats. I concluded that the presence of severe nematode infections did not significantly reduce the weight of rats for a given length. Both Gibson (1972) and Daniel (1973) have previously identified Mastophorus muris in ship rats in New Zealand.

9.3 Diseases

The serovar ballum of Leptospira interrogans was isolated from mature ship rats from Tiritea and Keeble's Bush by Mr S. Hathaway, Department of Veterinary Pathology, Massey University. This serovar accounts for < 1% of human infections of leptospirosis in New Zealand.

CHAPTER 10 - FOOD AND FEEDING

10.1 Introduction

The spread of the ship rat in New Zealand was approximately coincidental with declines in the populations of bellbirds Anthornis melanura, robins Petroica australis, saddlebacks Philesturnus carunculatus, stitchbirds Notiomystis cincta, native thrush Turnagra capensis, yellowhead Mohoua ochrecephala, South Island kokako Callaeas cinerea cinerea and red and yellow crowned parakeets Cyanoramphus n. novae-zelandiae and C. a. auriceps (Atkinson, 1973). Other factors, such as habitat destruction and the spread of mustelids, no doubt were also important in reducing the numbers of native birds. Buller (1888) linked the reduction in native bird numbers in bush areas with the increase in bush rats living there. Stead, 1927 (cited in Best, 1969), blamed R. rattus rattus for the reduction in fantail numbers on Banks Peninsula. After tracking predators on access routes to South Island robin nests, and making daily observations of nests, Flack and Lloyd (in press) and Moors (in press) concluded that ship rats were important predators of robin eggs and nestlings, and occasionally adults. Both Best (1969) and Daniel (1973) found feathers in a small percentage of stonachs from ship rats trapped in New Zealand mainland forests. Five of a sample of 115 ship rat stomachs (4.1%) taken from National Parks in the South Island during 1975 and 1976 contained feathers. No feathers were found in a similar North Island sample (J.P. Skipworth, unpublished data). This does not, of course, prove that the birds were killed by the rodents. Sir R.A. Falla (pers. comm. in Atkinson, in press) noted a ship rat predation on a shining cuckoo Chalcites lucidus chick at Wellington.

The most striking recent example of the effect on native birdlife of invading ship rats occurred when ship rats reached Big South Cape Island, off Stewart Island. Rats, first recorded in 1955, erupted to plague proportions by 1964 and remained in high numbers for at least three years. Bird species eliminated were the snipe Coenocorypha aucklandica iredalei wren Xenicus longipes variabilis, robin Petroica australis rakiura and fernbird Bowdleria punctata stewartiana. The one known colony of the Stewart Island bat Mystacina tuberculata robusta was severely reduced and later disappeared. The number of saddlebacks, parakeets and bellbirds also declined, although tuis, silvereyes, grey warblers and hedge sparrows Prunella modularis showed correspondingly large increases (Atkinson and Bell, 1973).

There is no published account of ship rats preying on New Zealand herpetofauna, although the other three rodent species in this country have been reported doing so (Whitaker, in press; Crook, 1973).

Both Best (1969) and Daniel (1973) found that invertebrates, specially arthropods, were important foods in the spring and summer for ship rats taken from mainland forest areas of both islands. Wetas were the most frequently occurring invertebrate diet item in both studies. Best, who trapped on Banks Peninsula and at Waimangaroa in the South Island, found that cave wetas were most common in the autumn/winter months while tree wetas occurred in stomachs most frequently in the summer months. Native slugs occurred in 21% of stomachs from these areas. In the Orongorongo Valley native land snails Wainuia urnula were eaten by ship rats (Daniel, 1973). Both Daniel and Best showed that moths, beetles, cicadas, diptera, ants and spiders were eaten, while cockroaches, stick insects or myriapods were found in one or other study. The large endemic weevil Hadramphus stilbocarpae Kuschel is thought to have been exterminated on Big South Cape Island by the ship rat (Watt, 1975). Ramsay (in press) has summarised the evidence for ship rat predation on invertebrates, both in New Zealand and overseas.

Less information is available about rat damage to New Zealand plants. Beveridge (1964) observed that ship rats destroyed large quantities of podocarp seed, especially rimu, but did not estimate how important this destruction was compared to that of other seed-destroying agents. He noted that seed germination of rimu and kahikatea was prolific following a good seed year despite the presence of seed-destroying animals. By the stomach analyses of 266 South Island rats, Best (1969) found that large volumes of plant material (especially fruits) were eaten in the winter, spring and autumn, but less in summer. He considered the variation due to seasonal availability of fruits. Daniel (1973) described the characteristic damage inflicted by rats on 26 species of New Zealand plants, and dissected 173 Orongorongo Valley ship rat stomachs to confirm Best's conclusions that in New Zealand as well as overseas the ship rat is an opportunistic feeder.

In the present study, 192 stomachs were analysed to obtain diet information from the Manawatu. More than 100 feeding trials, most with plant foods, were first completed to learn what foods might be expected to appear in the stomachs. Food remains collected from feeding platforms and nests at Greenwood's Bush were examined also. Finally, the disappearance of known numbers of fruits of Alectryon excelsus and Beilschmiedia tawa was traced in an exclosure system at Keeble's Bush to determine whether a known

population of ship rats (or other granivores) was likely to inhibit the regeneration of these species by eating nearly all the available seeds.

10.2 Feeding Trials

Six ship rats were live-trapped at Tiritea and transferred to 1m x .5m x .3m cages in a laboratory. A nest box measuring $30cm^3$ was exterior to each cage; a small tunnel connected each nest box and its cage. I checked for hoarded food after each trial by chasing the rat out of its nest box into the cage while I sorted through the nesting material (wood wool). Although leaves were often carried into the nest box to line the nest, the hoarding of trial fruits or animals caused few problems in estimating the amount of food consumed rather than merely taken for hoarding. Commercial rat pellets (approx. 20g per rat per night) were supplied to each cage daily and water was available ad libitum. On the evening of a feeding trial, the trial food/s rather than pellets were placed in the cage; the food remains were examined the next morning. A rat was never used for feeding trials on two consecutive nights so that each rat being used in a trial emerged to face the trial food having had a standard meal of pellets during the previous night.

Although usually only one trial food was placed in each cage, two or more foods were sometimes given to establish food preferences. Commercial pellets provided a useful palatability baseline. In Table 11, 'P' foods were preferred by rats to commercial pellets whereas 'E' foods were eaten only if the commercial pellets were not available. 'N' foods were never eaten, whether pellets were available or not. Unlike other types of trial food, leaves were supplied to a rat using the 'cafeteria method' (i.e. several species at once) because leaves were not very palatable and a choice of species gave the rat a better chance of getting a meal.

The mean weight of food eaten in one night by a ship rat was 21g ($S.D._{\bar{x}}$ = 7.8g), measured during 12 feeding trials involving different (plant and animal) preferred foods. Approximately this weight of 'P' foods (Table 11) was commonly eaten in one night, but lesser weights of 'E' foods were consumed.

Table 11 shows that fruits of karamu, karaka, kawakawa, mahoe and the native passion vine, and the female flowers of five-finger (one trial only) were preferred plant foods of ship rats. Fruits of titoki, tawa, pigeonwood, supplejack, nikau and puriri were eaten but not in preference to commercial pellets nor in amounts approaching 20g per night. The leaves of most species were not eaten; exceptions were mahoe and five-finger. Hangehange and tarata leaves were not eaten in normal feeding trials but

Species	Part of Plant	Palatability	Seed Destroyed	No. of Trials
Alectryon excelsus	ripe capsules	E	Yes	9
	leaves	N		4
Beilschmiedia tawa	unripe berries	E	Yes	6
	ripe berries	E	Usu. No	7
	germinating berries	E	Yes	1
	leaves	N		4
Brachyglottis repanda	leaves	*N, N		1,2
Coprosma lucida	unripe drupes	N	No	2
	ripe drupes	P	?	2
	leaves	*N, N		1,1
Corynocarpus laevigatus	unripe drupes	P	No	3
	ripe drupes	P	Yes	2
Geniostoma ligustrifolium	leaves	*E, N		2,2
Hebe (prob. stricta)	leaves	*N, N		1,2
Hedycarya arborea	unripe drupes	N	No	3
	ripe drupes	E	No	7
	overripe drupes	E	Yes	1
	leaves	N		2
Macropiper excelsum	berries	P	?	4
	leaves	*N, N		2,2
	flowers	P		2
Melicytus ramiflorus	berries	P	?	4
	leaves	*E, E		1,3
Metrosideros robusta	leaves	N		3
Neopanax arboreum	female flowers	P		1
	male flowers	N		1
	leaves	*E, E		2,2
	fruits	N	No	2
Pittosporum eugenioides	leaves	*E, N		1,2
Rhabdothamnus solandri	leaves	N		2
Rhipogonum scandens	berries	E	Yes	8
	leaves	N		4
Rhopalostylis sapida	drupes	E	Yes	3
Schefflera digitata	leaves	N		3
Tetrapathaea tetranda	berries	P	Yes	2
Vitex lucens	unripe drupes	N	No	1
	ripe drupes	E	No	1
"Jew's ear" fungus	fleshy thallus	N		2

* Trial rat starved for two previous nights.

P = preferred food

E = eaten but not preferred

N = never eaten

Table 11: Plant feeding trial results

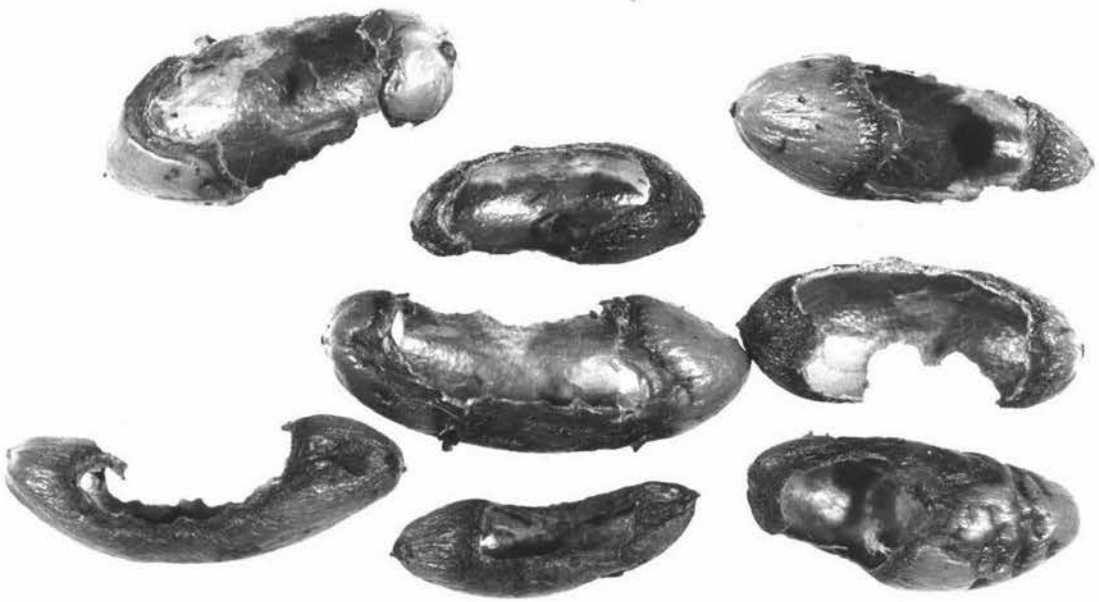
were eaten after the rats were starved for two nights previous to the feeding trial. Up to 12 mahoe leaves and 11 hangehange leaves were eaten by one rat in a night - lesser quantities of the other two species were taken.

Fewer trials with animal material were accomplished; the results are shown in Table 12. All animal material seemed to be preferred food since either all that was available or amounts totalling about 21g were eaten. The damage to Helix aspersa, the introduced garden snail, was the same as that described by Daniel (1973) as inflicted by ship rats on Wainuia urnula. The remains of mice and ship rats which had been eaten in snap traps showed very similar features to the remains of mice presented in feeding trials. Characteristically, ship rats ate the flesh and viscera of mice, neatly cleaning all flesh off the skin and larger bones. Limbs were everted as the skin was rolled back and the flesh underneath eaten. Ship rat feeding damage to dead thrushes was also characteristic. A hole was torn in the skin of the bird (usually on the breast), scattering feathers in the process. Muscles, especially the flight muscles, were then eaten. The eyes and brain were also commonly eaten, but the viscera was never touched. This damage was identical to that noticed on snap-trapped thrushes and blackbirds in the forest, and suggests that animals were eaten in snap traps primarily by ship rats.

Like the animal foods, plant foods were consumed leaving characteristic remains, the description of which may be useful for the identification of similar damage in the future. Both the palatability and the type of damage of a species were fairly constant during the trials, and occasionally fruits with the same damage appeared in the forest, indicating that in some cases, at least, the trials were producing typically damaged fruits. The palatability and type of damage to the fruit of a species often varied depending on the age of the fruit. Ship rats ate the kernels of unripe (green) tawa berries but the fleshy mesocarp was never eaten. In contrast, rats ate the mesocarp of ripe (blue-black) tawa but normally did not eat the kernels (Plates 10 and 11). In the only trial, older (sprouting) tawa berries which lacked a fleshy mesocarp did have their kernels eaten. Unripe karaka drupes were not destroyed although the fleshy mesocarp was eaten. When the drupes became ripe, rats ate both the mesocarp and kernels. Unripe puriri, mahoe, karamu and kawakawa were not palatable to ship rats, but the fleshy mesocarp of puriri and the whole fruits of the other three species were eaten when the fruits ripened. Rats did not eat the fleshy mesocarp of nikau or supplejack fruits but removed it before eating the

Plate 10: Rat damage to unripe tawa berries

Plate 11: Rat damage to ripe tawa berries



Species	Damage	No. of Trials
Garden snail Helix aspersa	Shell smashed at spiral and animal removed.	5
Mouse (dead) Mus musculus	Entire flesh eaten. Skin and bones picked clean. Limbs everted.	5
Thrush (dead) Turdus philomelos	Flesh eaten, especially flight muscles. Also brain and eyes.	6
Weta (alive) Hemideina thoracica	Killed by repeated bites at head. Whole body eaten except antennae, four rear legs and abdominal exoskeleton.	1
Large green cockchafer (dead) Chlorochiton longicornis	Whole body eaten except for elytra	2
Four old blackbird eggs in nest	Eggs eaten and nest floor 'snuffled' (see Moors, in Press).	1

Table 12: Animal feeding trial results

kernels. Pigeonwood, which is a drupe like nikau, showed the reverse damage, i.e. ripe pigeonwood drupes had the mesocarp eaten but not the kernels, although teeth marks could easily be seen on the testa. Unripe pigeonwood drupes were not eaten at all. In a single trial with overripe (soft kernel) drupes, both the mesocarp and kernel were taken. The titoki fruit consists of a brown capsule containing a black seed in a scarlet aril. Rat-opened capsules (Plate 12) had rough irregular edges compared to the smooth more regular edges of naturally opened capsules (Plate 13). Sometimes the testa of the seed was gnawed open and the hard kernel removed. This type of damage has been illustrated by Daniel (1973) for hinau and miro nuts and is probably the most characteristic damage caused by ship rats. Another example of such hollowing out is shown in Plate 14, the remains of passion flower fruits fed to rats. Leaves eaten by rats have nibbled margins. Hangehange and tarata leaves are shown in Plate 15.

These results agree broadly with those of Daniel (1973).

10.3 Collected Food Remains

Food remains were collected from three nests and four feeding platforms at Greenwood's Bush. Not many food items were taken back to these structures to be eaten, but the results do add to the variety of foods eaten by ship rats in New Zealand forest. Bare endocarps of karaka, the pods and seeds of tree lucerne and empty capsules of Pittosporum virgatum were the only plant items found. Neither L. arboreus or P. virgatum is a native of Manawatu. Insect parts found were of wetas, ground beetles, a bumblebee and a female case moth. Almost the entire plumage of a waxeye remained at one nest. Another nest and one feeding platform held feathers also, but in these cases the bird could not be identified.

When they became ripe, passion flower fruits were collected from a trellis just outside the bush. Their eaten out remains were dropped to form a large pile beneath a bird's nest near the trellis which was used as a feeding platform.

10.4 Stomach Analysis

10.4.1 Methods

The stomach of 192 rats were examined for diet contents. Fourteen of these were excluded from the results because they were either empty or more than half filled with nematodes. Of the remaining 178 stomachs, 15 came from each month except July, when only 15 rats were trapped and two were subsequently excluded. The stomachs to be analysed were selected from a month's total using a table of random numbers.

Plate 12: Rat-opened titoki capsules

Plate 13: Naturally opened titoki capsules

Plate 14: Rat damage to passion flower fruits

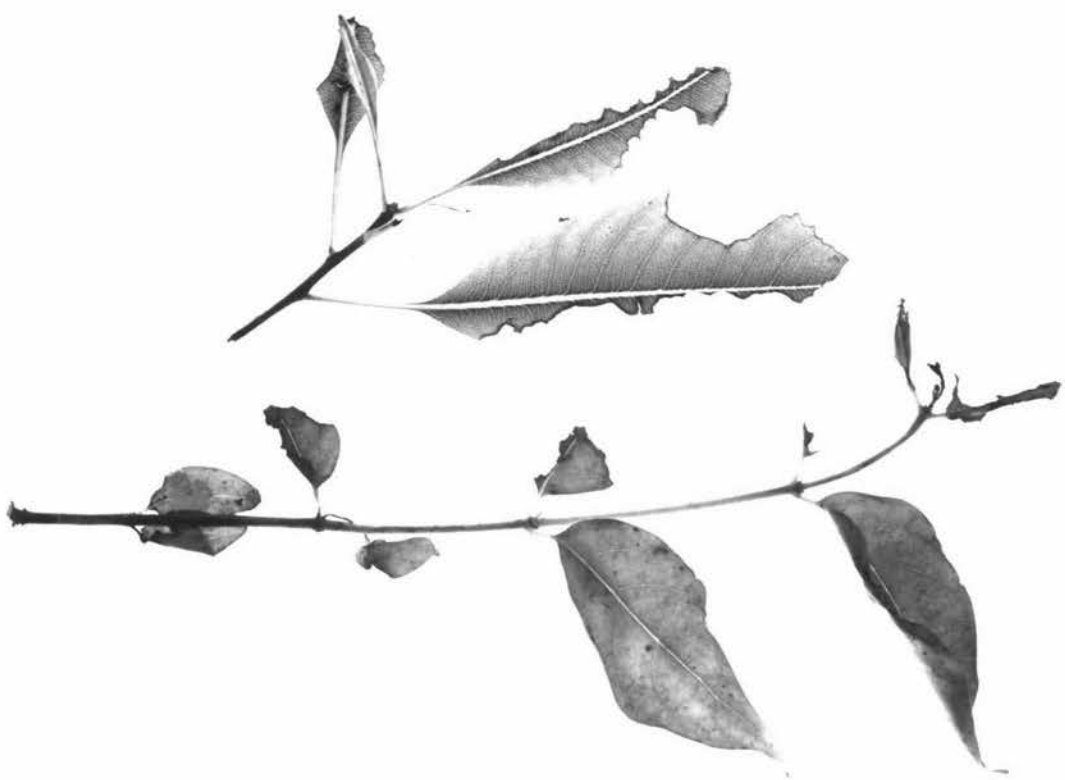


Plate 15: Rat-nibbled tarata (above) and hange hange leaves

They were opened and examined for distinct layers of material which may correspond to the remains of different plant diet items. Each layer was sampled for the presence of starch grains which could identify the plant species eaten. The sample was ground with several drops of water in a mortar to release the grains. A drop of the ground mixture was placed on a microscope slide and a drop of the following stain was added: (Based on Johansen, 1940) Dissolve 2g of KI in 10 ml of water, and dissolve 0.2g of iodine in the KI solution. Then add a further 90 ml of water. All stomach contents were then tipped into a Petri dish for examination under a binocular microscope. After approximately one half of the stomachs had been processed, I discovered that washing the contents on fine mesh stretched over a bunsen tripod removed all of the cloudiness from the Petri dish and improved my ability to find arthropod parts and other diet remains such as cuticles, quickly. Subsequently, all stomachs were washed prior to examination under a binocular microscope.

Samples taken for starch grain analysis were taken prior to washing because the identification of a seed species by its starch grains depends on the sample being pure. There is considerable variation within a species in grain shape and size (the principal identificatory characters), and the property which makes a certain species' grains distinctive can normally be claimed to be present only when many grains have been examined. It is therefore important that meals of different diet items do not mix in the rat's stomach. To test this, consecutive meals of different recognizable foods were fed to six laboratory mice and one ship rat. The rodents were killed and their stomachs examined. The meals appeared as distinct layers in the stomachs and pure samples of each meal item could be recovered easily. It is also important that the starch grains are not digested in the stomach or damaged by alcohol immersion or freezing. According to Rowett (1974), some starch is hydrolyzed to dextrin and maltose in the mouth and oesaphagus of rats by salivary amylase. However the digestion is very slow and most passes through the stomach to be hydrolyzed by pancreatic amylase in the small intestine. My observations confirm this. Starch grains taken from the stomachs of rodents which had been fed trial seeds were the same as those taken directly from the seeds. Grains were not damaged by freezing or immersion in alcohol.

The stain described above remains usable for at least four months if stored, and stains starch blue-black in several seconds. It was used to differentiate the pulped seeds of four species common at Tiritea: tawa, kawakawa, supplejack and pigeonwood. Titoki, totara, mahoe, karamu and

horopito were found to be unsuitable for starch grain detection because starch was either not present at all or present only in very small amounts.

Kawakawa and kiekie seeds were readily identified since they often remained complete in the stomachs. Preparations of the fruit cuticle of other likely diet species were made. Nikau kernel viewed through a microscope was found to possess characteristic perforated pipe-like structures, and supplejack pericarp possessed javelin-shaped siliceous raphides. The latter were found to occur also in kiekie seeds as bundles of raphides. In supplejack, raphides were never gathered together in bundles.

Arthropod parts were identified by comparison with a reference collection taken from the study area. Since only two groups of arthropods (wetas and caterpillars) occurred in many stomachs, arthropods were classed as weta, lepidopteran larva or other arthropod. The methods of Day (1966) were suitable for identifying fur found in stomachs; no attempt was made to identify feathers to the species of origin since they were small and few.

Two methods were used to quantify the information arising from stomach analysis. (a) The percentage frequency of occurrence of each diet item was calculated. This is the number of stomachs in which a certain item occurred, expressed as a percentage of the total number of stomachs examined.

(b) A visual estimate was made for each stomach of whether plant or animal material composed the majority of the volume of contents. Stomachs were sorted into three categories: majority plant, majority animal or equal volumes of each. This method provides an indication of seasonal changes occurring in the proportions of plant and animal matter. The major disadvantage of method (a) is that frequency of occurrence need not necessarily correspond accurately to the contribution by volume of a diet item (Hansson, 1970). A quantification by frequency of occurrence tends to overestimate prey which occurs in small quantities and prey that is not readily digested, and tends to underestimate the importance of prey which occurs in large quantities or is easily digested leaving few recognizable remains.

10.4.2 Results

Animal foods predominated in the stomachs on both percentage frequency of occurrency and majority of volume criteria for the year of sampling. Ninety five per cent of stomachs (n = 178) contained animal matter and 78% contained plant matter. Table 13 shows that during the year March 1976 to February 1977 101 stomachs contained a majority of animal matter and 60 contained a majority of plant matter. However during the autumn and winter months of March to August, plant foods predominated.

	Spring n = 45	Summer n = 45	Autumn n = 45	Winter n = 43	Total:
Majority animal	29	41	16	15	101
Majority plant	11	3	24	22	60
Equal volumes	5	1	5	6	17

Table 13: The number of stomachs containing a majority of animal or plant matter, for each season

	Spring n = 45	Summer n = 45	Autumn n = 45	Winter n = 43
Weta	55%	87%	58%	59%
Unidentified arthropod	27%	13%	24%	26%
Lepidopteran larva	13%	29%	22%	14%
Kiekie	69%	-	-	67%
Kawakawa	-	20%	58%	2%

Table 14: The seasonal frequency of occurrence of major ship rat diet items

The percentage frequency of occurrence of each diet item is shown in Fig. 20, and the seasonal percentage frequency of occurrence of the major diet items is shown in Table 14. By far the most frequent item was weta, which was found in 76% of all stomachs and in the majority of stomachs of each season; its frequency peaked in summer. Kiekie seeds or bundles of raphides indicating masticated seeds occurred in 40% of stomachs but only during winter and spring. Unidentified arthropods, mostly small pieces of exoskeleton, were in 26% of stomachs and were found throughout the year. The next most common animal food, caterpillars of unknown species, occurred in 23% of stomachs and in every season. Kawakawa was confirmed as a preferred food by being found in 24% of stomachs and throughout three seasons. Few other plant items were identified. Pigeonwood and supplejack were eaten, and the remains of unidentified fruit were found in 24% of the stomachs. Unknown fruit A, which was in 14.5% of the stomachs, was identified by characteristic sclereids or stone cells, similar to those which can be scraped off the hard endocarp of pigeonwood. It occurred only from January to July. As the feeding trials predicted, green leaves were eaten by few rats. The category 'other arthropods' comprised beetles, ants, spiders, moths, centipedes and nymphal cicadas. Feathers, which were in 5% of stomachs, and eggshell (2% of stomachs) were eaten from September to December, except for one record of feathers from June and one of eggshell from February. A check of the dates and locations of the trappings of rats which had bird remains in their guts showed that it was most unlikely that the birds were taken from snap traps. The almost exclusive restriction to spring of birds in the diet suggests either that the birds were more prone to predation when they were nesting, or that their mortality was higher then and the rats were eating dead birds. The eggshell fragments which occurred on the three occasions were all pale blue; perhaps they were remains of thrush or blackbird eggs. No flecks of black or brown which may have given further identificatory clues were on the fragments. Flesh was found in nine stomachs, all but one of which was also taken from rats trapped from September to December. Feeding trials (Section 10.2) showed that rats eat the major muscles of birds by preference. Perhaps the flesh found in stomachs, identified by its texture, came from this source.

Rat hair ingested during grooming and peanut butter, the bait used in this study, were found in large numbers of stomachs. Peanut butter was easily recognized by its colour, texture, smell, starch grains and location in the stomach.

Surprisingly, no tawa or mahoe was identified in any stomach although

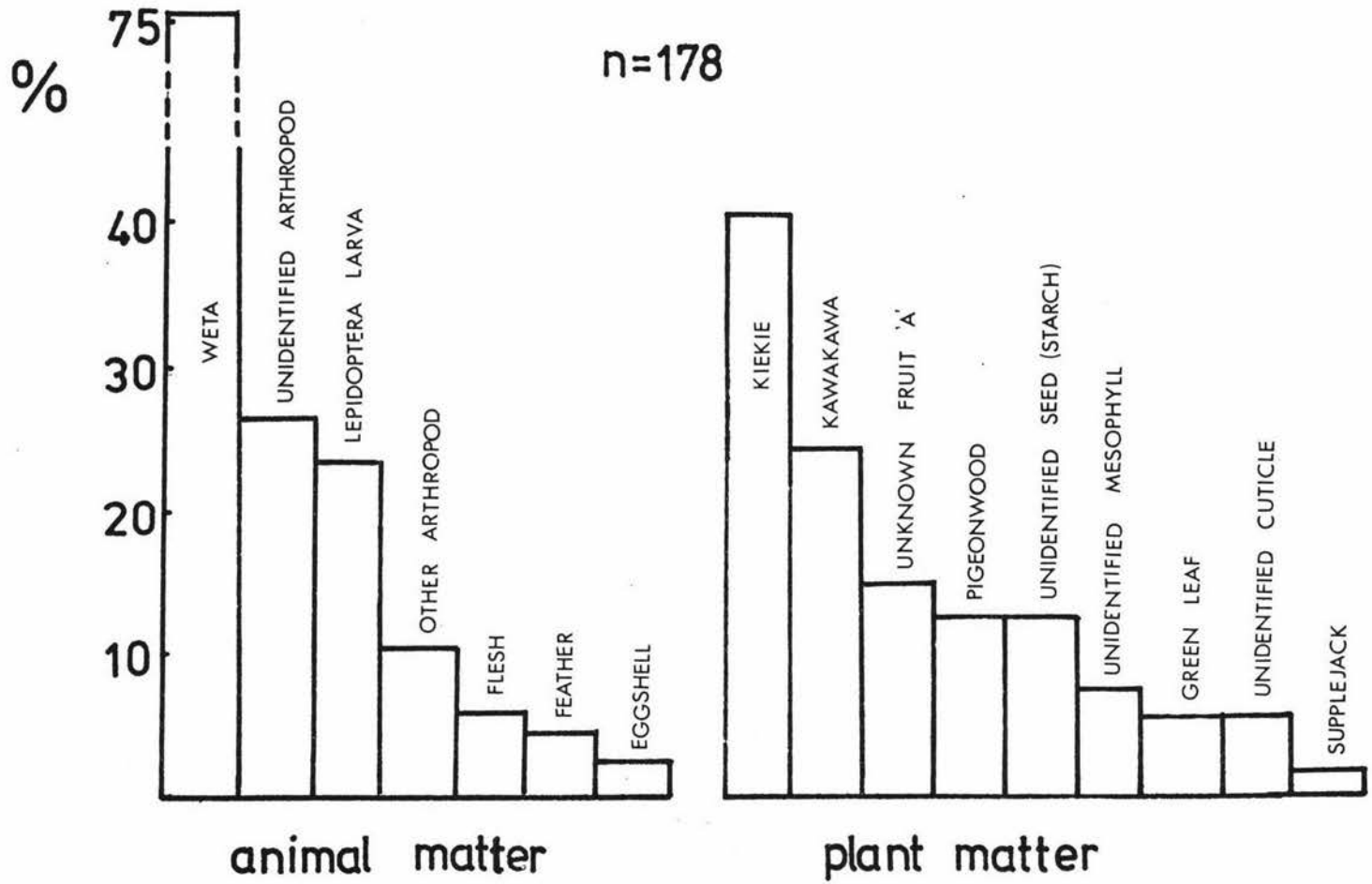


fig 20 Frequency of occurrence of ship rat diet items

both species were palatable to rats in feeding trials and fruited heavily at Tiritea. Nikau was also eaten in feeding trials but was not identified in any stomach.

10.5 Granivore Exclusion Trials

10.5.1 Introduction and Methods

Both Best (1969) and Daniel (1973) found a predominance of plant matter in ship rat stomachs. The berries of supplejack and the passion flower, and podocarp seeds, contributed most to the volume of plant matter in Best's study, while Daniel found that the most frequent single item of plant food was finely ground unidentified pericarp or endosperm material. Beveridge (1964) established that ship rats in Pureora and Pouakani podocarp forests destroyed almost all of the fallen seed of several podocarp species. In the present study, 78% of the 178 stomachs analysed contained plant matter, the great majority of which came from fruits. Not all the seeds of such diet species are destroyed when the fruit is eaten, however (see Table 11).

It is difficult to gain experimental evidence concerning the impact of forest rodents on the seed crop of a diet species when other agents such as birds are also removing seeds. At Keeble's Bush, exclosures with different mesh sizes restricted the access of some granivorous species to known number of seeds. The aim of this short experiment was to determine the relative importance of the ship rat as a destroyer of fallen seed. Eight exclosures were placed within the cage grid described in Section 3.2 so that the rate of seed removal could be ascribed to a known rat population density. All exclosures were further than 30m (the trap spacing) from the grid edge to avoid the "edge effect" where animals from outside the grid may be transient visitors to the outer cage traps and the exclosures. Four exclosures had walls of two inch mesh to permit the entry of rats and mice but exclude possums and hedgehogs. Two were walled with half inch mesh cut at ground level to make holes measuring 4.5 x 2.5cm diameter which allowed mice to pass but excluded rats, possums and hedgehogs. The remaining two had no walls and permitted the entry of all granivores. The exclosures measured 1m x 1m x 30cm. They were covered with camouflage-painted fabric to prevent the entry of freshly fallen seeds during the experiment, and placed under fruiting titoki trees (Plate 16). The presence of mice throughout the bush was confirmed by smoked paper tracking before a location was chosen for the two exclosures which permitted mouse entry but excluded rats. All exclosures were left in position for several weeks before the addition of any trial fruits, to allow the granivores time to

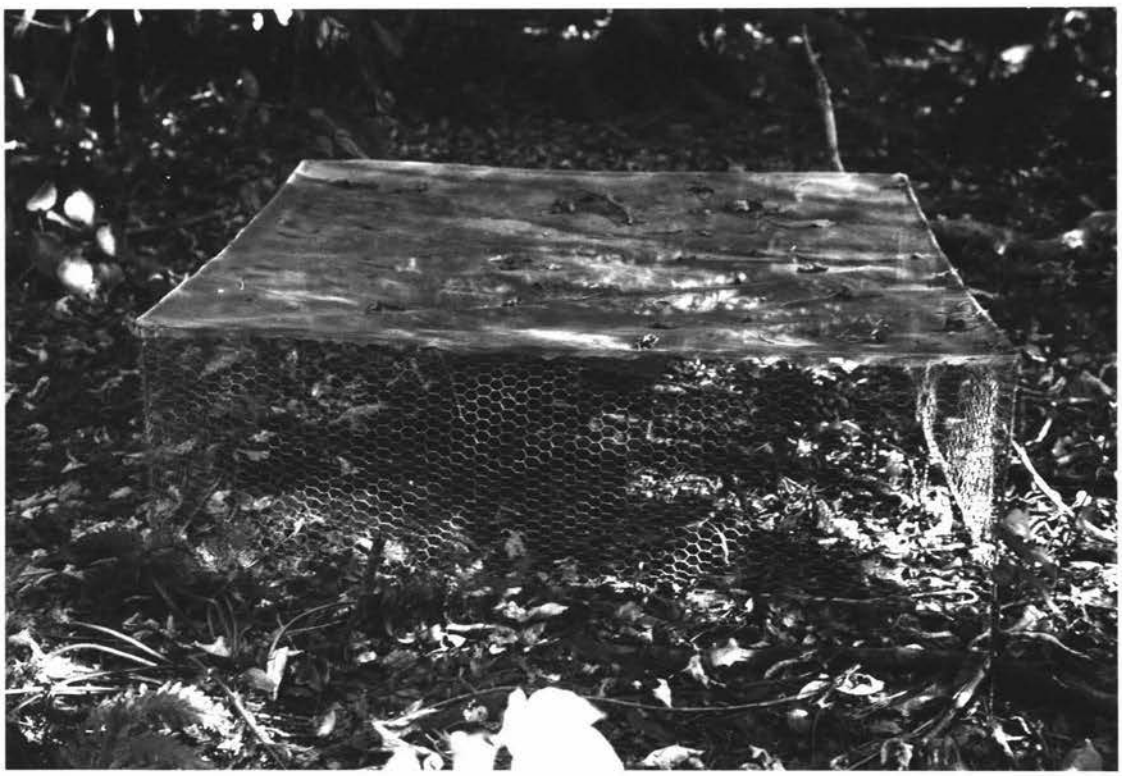


Plate 16: Exclosure permitting the entry of mice only

Plate 17: Device to record prints of mammals visiting an exclosure

become accustomed to them. A piece of smoked paper under a waterproof malthoid cover (Plate 17) was placed under the centre of each exclosure in an attempt to check which species of granivore, if any, visited there. The paper measured 15cm x 15cm for six of the exclosures, and 30cm x 15cm for the two which allowed in possums and hedgehogs. The paper was not baited.

It is important that the density of trial seeds in such an experiment is similar to the density of seeds outside the exclosure, so that animals are not encouraged to enter the exclosure by the unusually high seed density there. In the present study, 100 throws of a yard square quadrat revealed (after conversion) that the mean density of titoki fruits was nine per square meter. In some areas there were 80+ fruits per square yard quadrat. I decided to put twenty titoki under each exclosure. This was a compromise between a figure close to nine per square meter and a figure large enough to considerably reduce the importance of chance losses of fruits.

Titoki and tawa were chosen as trial fruits because they were available naturally, and in quite large numbers, in Keeble's Bush at the time of the experiment. Also, although neither were preferred foods, they were eaten by ship rats in feeding trials and the resultant damage was observed on fruits in the study area. The titoki fruits were scattered around the central smoked paper device in each exclosure and counted daily for a week. After a further five days, the procedure was repeated with fifteen tawa fruits per exclosure. The smoked paper was renewed when obscured by footprints or splashed by raindrops.

10.5.2 Results

No granivore removed significant numbers of titoki fruits (seeds plus arils) from any exclosure (Table 15a). The disappearance of a few fruits from each may have been due to granivores which left no tracks or, more likely, to my inability to locate them among the wind-tossed leaf litter under the exclosure.

Although rats, mice and hedgehogs did not eat the tawa drupes, possums removed all 15 drupes from the two exclosures permitting their entry, on the first night of the trial (Table 15b). While these results indicate that possums could impede tawa regeneration by eating all the fallen fruits, possums are inquisitive animals and may have been unnaturally attracted to the exclosures. Exclosure experiments risk the animals being scared off or attracted to the exclosures and this applied to the present study. The appearance of rat tracks under exclosure 1 (Table 15b) proves that the

	TITOKI Exclosure permits entry of	Prints recorded during 7 days	Initial Seed No.	Final Seed No.
1	Mice	-	20	18
2	Mice	Mouse	20	19
3	Mice, rats	Rat	20	17
4	Mice, rats	-	20	19
5	Mice, rats	Mouse	20	19
6	Mice, rats	-	20	18
7	Mice, rats, possums, hedgehogs	-	20	18
8	Mice, rats, possums, hedgehogs	-	20	15

Table 15a

	TAWA Exclosure permits entry of	Prints recorded during 7 days	Initial Seed No.	Final Seed No.
1	Mice	Mouse(2), rat	15	14
2	Mice	-	15	15
3	Mice, rats	Mouse, rat(2)	15	15
4	Mice, rats	-	15	15
5	Mice, rats	-	15	15
6	Mice, rats	Unid prints	15	12
7	Mice, rats, possums, hedgehogs	Possum(2), hedgehog	15	0
8	Mice, rats, possums, hedgehogs	Possum(2), hedgehog	15	0

Table 15b

Note: (2) signifies that a second piece of smoked paper was also tracked.

Table 15: Results of granivore exclusion trials

mesh size chosen to exclude rats was too large. Obviously, another problem is obtaining a mesh size which will permit the entry of mice, yet exclude rats. If the mesh is made too small rats would be excluded but entry could be so difficult for mice that they would not attempt it. The stomach analysis of 17 mice from Keeble's Bush showed that they ate almost entirely insects (Moore, 1977) and are unlikely competitors of ship rats for tree fruits.

SECTION 3 - DISCUSSION AND CONCLUSIONS

CHAPTER 11

This research has in general supported the results of Best (1969; 1972) and Daniel (1972; 1973) who have completed major studies of the ship rat in New Zealand forests.

Although they seem to be widespread in forests, only 3.9 rats per 100 trap nights were trapped at Tiritea for an effort of 7153 trap nights in 13 areas. The mean monthly population density at Keeble's Bush was 2.8 rats per hectare, although the calculated peak density was eight per hectare in June. Only 'rattus' and 'frugivorus' morphs were trapped, and in very similar proportions to those determined by Daniel (1972). The 'alexandrinus' morph which is the most frequent in the South Island is apparently not found in the North Island.

Although males with mature sperm can be trapped all year round, females breed for six or seven months of the year, normally during October to April. Occasionally pregnant rats are trapped in winter. Daniel (in press) suggested that "both the length of the breeding season and the overwinter survival of the rat population are directly controlled by the size of the autumn seed and fruit crop". He found that the size of the autumn hinau crop was significantly correlated with both the maximum winter and maximum spring rat densities. There are, on average, five young per litter. Up to four litters per female are produced each breeding season to yield an annual production per female of up to 20 young. While production per female is high, mortality must also be high. Factors causing mortality were unknown in the present study; Daniel (1972) considered that feral cats were important predators. The annual mortality of 96% calculated from cage grid disappearances is likely to be an overestimation of the actual mortality rate.

The rats do not normally move large distances; the maximum straight line movement between two recapture points in Keeble's Bush was 67m, although tracking at Greenwood's Bush showed that rats may move 400m within their home ranges in one night. Home range areas could not be calculated from cage trap data at Keeble's Bush, but tracking-revealed ranges known in detail at Greenwood's Bush were on average five times the area of cage trap-revealed ranges there. Tracked ranges measured, on average, .05 ha (.12 acres). Ship rats are superb climbers and normally nest in epiphytes such as kiekie. At Greenwood's Bush, in the absence of such epiphytes, the rats built nests of interlaced leaves

and twigs resembling rough sparrows' nests. Some food was taken to 'feeding platforms' in trees.

The diet of this rat in New Zealand forests has given it pest status and is therefore of special interest. In the Manawatu, as elsewhere in New Zealand, ship rats ate arthropods, fruits and occasionally birds or bird eggs. Furthermore, predominantly plant foods were eaten in winter and predominantly animal foods in other seasons, although both Best (1969) and Daniel (1973) found that plant food predominance extended into autumn. The reason for such a difference may be that palatable fruits were scarce at Tiritea in autumn. There was, for example, little hinau or miro fruit available since by far the majority of the Tiritea canopy is tawa. Perhaps for this reason, 88% of the 178 stomachs examined at Tiritea contained arthropods, whereas only 53% of the 173 stomachs examined by Daniel (1973) contained animal matter of any description.

After 100 years of rat predation it is unlikely that the animal groups worst affected initially will be present in significant numbers now. Large arthropods and low-nesting or fearless birds could be in this category. The animals appearing in significant numbers of rat stomachs at present will be those species which have managed to remain or become common despite not only rats but also mustelids and feral cats. They must also have adjusted to habitat changes such as those induced by introduced herbivores and those that are a consequence of milling. It is possible that after 100 years a balance has been achieved between predator and prey in some situations, although the general instability of New Zealand forests plus lack of knowledge of the development of such an equilibrium would make it a dangerous assumption. Wetas occurred in 76% of stomachs of rats examined from Tiritea; only Hemideina thoracica was identified although other species may have been present. Wetas were also the most frequent animal diet item in the studies of Best (1969) and Daniel (1973). Lepidopteran larvae (23% of stomachs) were the only other frequent invertebrate group in Tiritea stomachs and may have consisted of several species. To determine whether ship rat predation on these invertebrates is significant requires further detailed study.

The low (4-5%) frequencies of occurrence of feathers in rat stomachs from Tiritea (the present study) and North Island National Parks (J.P. Skipworth, unpublished data) are similar to the findings of previously published information. Eggshell fragments, probably thrush or blackbird, were reported for the first time in stomachs from Tiritea,

although Moors (in press) and Flack and Lloyd (in press) found ship rats to be important predators of robin eggs. Since rats ate only the muscles and brains of dead birds fed to them in feeding trials, it is possible that bird flesh was eaten without the inclusion of tell-tale feathers and that the frequency of occurrence of birds in the diet was higher than acknowledged. While, as Best (1969) and Daniel (1973) concluded, birds were not a frequent item of ship rat diet overall, the impact of a rat population on certain bird populations at nesting time could be severe. Certainly, while bird numbers may not be declining further from rat predation at present, the strategic removal of any rats from forest before nesting time may well increase bird numbers in the forest. It would be very interesting to know whether some trapping in winter (when return per trapping effort is high) of rodents and mustelids would significantly increase bird nesting success and hence total numbers.

What effect have ship rats had on plants? Although rats can digest little or no cellulose (Rowett, 1974) they may eat leaves if other food is unavailable (e.g. on Big South Cape Island, Daniel, 1973). Starving the rats increased the number of species whose leaves they would eat, in feeding trials in the present study, but rats do not appear to be significant leaf eaters in forests. However, they may eat sufficient fruit of forest trees to either prevent regeneration of the tree species or pose a competitive threat to fruit-eating birds. Rats in a population with a calculated density of two rats per hectare did not destroy any tawa or titoki fruits placed under exclosures, although tawa drupes and titoki capsules showing characteristic rat damage were found in the study area. Exclosure experiments are difficult because of the unavoidable biases involved, and information on seed removal would, I think, be better gained by studying open cast seed and performing feeding trials. Neither titoki nor tawa were preferred fruit species of ship rats, and there is no evidence for significant rat damage to them. The species whose regeneration is likely to be affected will have seeds which (1) are palatable (to rats), (2) are destroyed when eaten and (3) are not quickly distributed by other agents.

Of the six species of seed labelled in Table 11 as "preferred" diet, three - kawakawa, kiekie and mahoe - are not ground up when eaten. Both kawakawa and kiekie seeds have hard seed coats and probably remain viable after passing through the rat gut. Mahoe seeds are of similar size, but although they were eaten in feeding trials they did not appear in any examined stomachs. Both karamu and passion flower seeds

are larger but since neither appeared in stomachs (although they, also, were preferred foods in feeding trials) it was not possible to determine if they are destroyed by ship rats. It seems likely that their seeds would be dispersed by birds or possums. The sixth preferred species, karaka, is both destroyed and dispersed by ship rats. Rats nesting in a rewarewa at Greenwood's Bush dropped viable kernels of karaka from the nest and many karaka seedlings appeared below the tree. Among the species examined, therefore, there is no obvious candidate for having regeneration inhibited by ship rats. Beveridge (1964) noted that germination of podocarp species was still prolific despite severe ship rat damage to fallen seed.

The second possible ship rat damage, that of severe competition for food with fruit-eating birds, is a subtle one and would involve a complex study, especially in the light of other factors which may reduce the condition or limit the number of birds. Perhaps, as Campbell (in press) noted, the greatest affects of rats on vegetation dynamics may be indirect ones occurring when "other herbivores are present to consume the seedlings that germinate from the seed that is not eaten by rats, and when rats combine with other predators to reduce the numbers of birds that act as seed dispersing agents".

It would be dangerous to draw definitive conclusions on dominance, home range and breeding from tracking at Greenwood's Bush. Certainly, when ♀ 49 shared its range with ♂30, the only male, it was the only female with a seemingly exclusive home range, indicating that sexual activity confers dominance and dominance in turn confers territory. This picture is confused by two factors. First, no breeding was known to occur after 23/8/76, although all of the females were mature and the male had scrotal testes. Second, when the range of the male increased to include those of the other females, no female's home range altered. If ♀49's territory was conferred by dominance, then it retained that dominance although it had lost seemingly exclusive access to the male. Many possibilities exist for social organization, based on the evidence from the present study. For example, ship rats in forest may have a matriarchal society where the sexually active females hold territories. The males may be polygamous or monogamous. A study of the social organization in forest would make an interesting comparison to the work of Ewer (1971) who studied ship rats which nested and fed around buildings.

Known occupants of single nests at Greenwood's Bush included an adult (female?) and six young, and two adults (♀49 and ♂30). The juveniles were estimated to weigh about 50-70g, and it is interesting that they were still in the nest. This evidence also suggests that the male leaves the nest when the offspring are still young. Females 29, 42 and 47 also probably shared a nest. The fact that ♀49 was the only female to nest alone and the only (apparently) sexually active female suggests that sexually active pairs nest alone.

The small sample size, and especially the single male, involved in the study at Greenwoods is a factor preventing firm conclusions, and extrapolation to larger forest situations.

Immigration seemed to be fairly constant at Greenwood's Bush. One untagged immigrant male rat appeared on 12/3/77. It was killed four nights later; the last tagged rat was killed on 1/4/77. However, ship rats were tracked in Greenwood's again in October, 1977. The nearest source of immigrants would be Bledisloe Park, a bush remnant 400m from the study area.

Smoked paper tracking was a very successful technique for supplying not only the information normally obtained using cage traps, but also information unobtainable with cage traps. Its efficacy in situations other than home range determination or population estimation was demonstrated by its use in identifying granivores visiting exclosures. In the present study, the concurrent use of tracking and trapping meant that tracking could be used to check the efficiency of the trapping technique. From the comparison, the following conclusions can be drawn:

(1) All of the rats in the study area were trap-shy, since they repeatedly encountered traps but did not enter them. This fact points against the use of grid cage trapping to determine the density of a population of Rattus rattus rattus, since a disappearance from capture records caused by trap shyness must be assumed to be a disappearance caused by mortality. Therefore the population density calculated for the grid area will be underestimated, and the mortality rate will be overestimated. To estimate the extent of the difference between the calculated and actual population densities, a large scale study involving both trapping and tracking would seem to be the most effective approach.

(2) Cage trap-revealed 1-capture home ranges were about one fifth of the area of the actual ranges. Since the trap-revealed ranges are only 1-capture ranges, and since the time needed to obtain them was

considerable, they show neither the dynamic aspects of home ranges such as boundary changes, nor long term aspects such as an accurate outline of the range boundary and its relationship to those of neighbouring rats. Cage traps are quite inadequate for supplying accurate information about rat movement.

The following conclusions can be drawn from the tracking data obtained in the present study:

(1) Ship rats did have stable home ranges, some of which seemed to be exclusive to some other rats.

(2) The presence of bait did not induce rats to leave their home ranges.

(3) The removal of a rat effected the prompt expansion of the adjacent home ranges of other rats to include the vacated area, i.e. home range size was inversely related to ship rat density.

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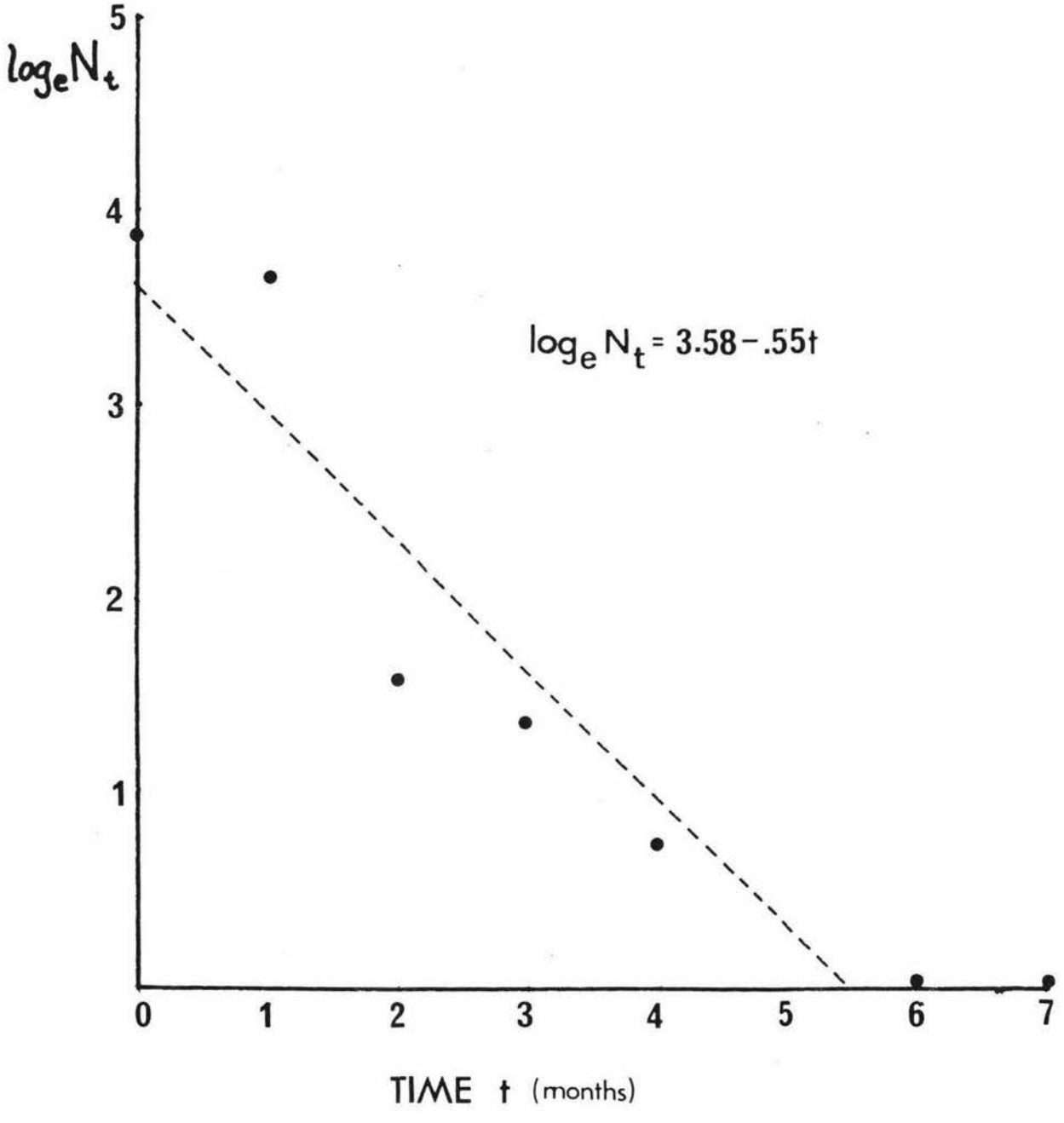
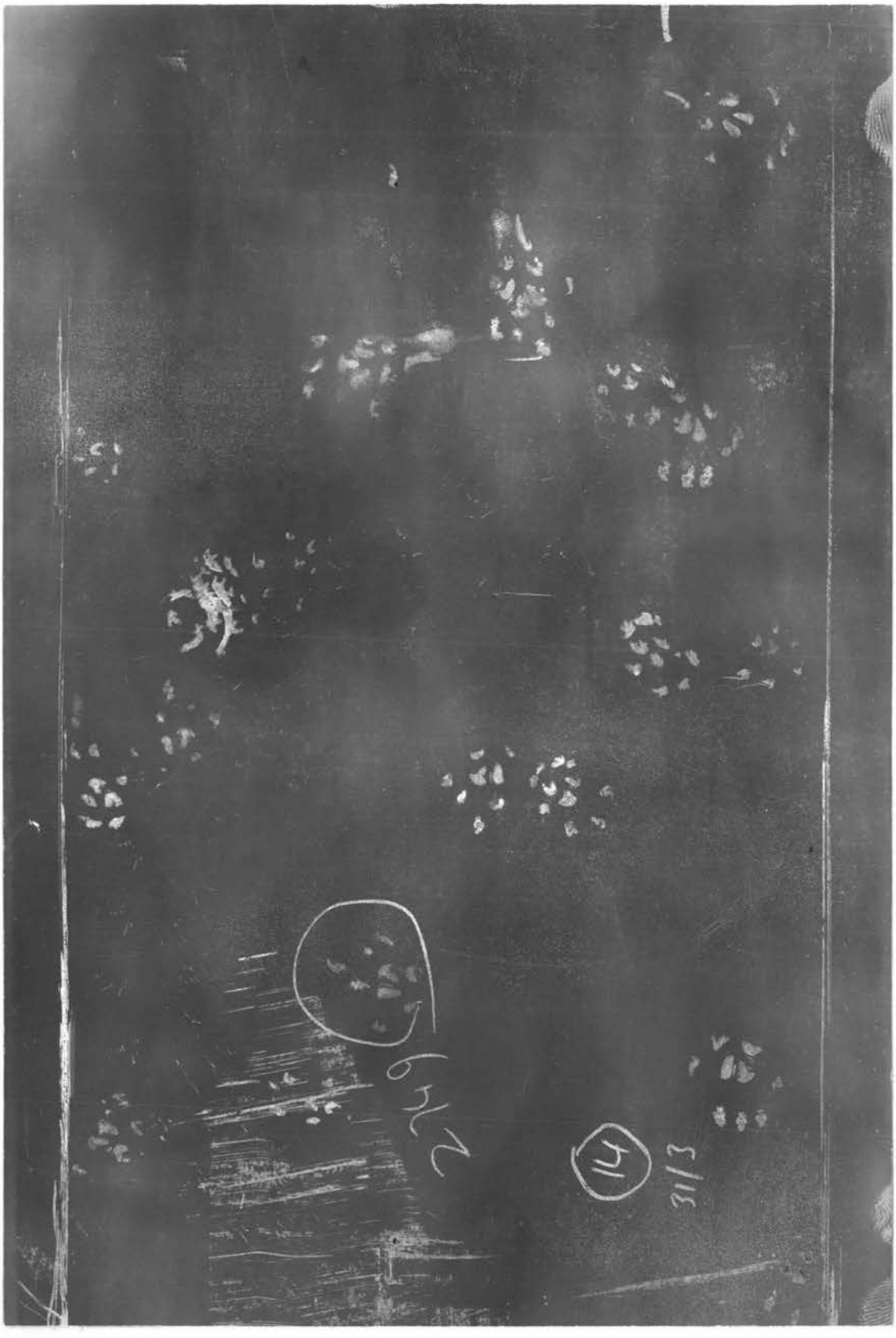
Line	Consecutive Nights	First three nights in
1	0 4 2 2 1 2 0 1 2 0 0 1	March
2	3 1 1 4 1 0 2	April I
3	2 2 4 3 5 2 2 1 3 5 4	April II
4	1 4 4 1 1 1 2 1 0 0 2 2 0	May
5	3 5 4 5 1 3 0 0 0 2 0	June
6	2 3 0 0 1 2 1 1 0 0	July
7	7 5 4 4 3 2 5 4 2 1 0 0 1	August
8	7 4 5 0 0 1 1 2 2 1 2 1 4	September
9	6 0 0 0 1 0 0 0 0 3	October
10	2 1 5 2 3 0 1 0 4 0 1 0	November
11	0 3 2 2 6 2 1 2 0 2 2 0 1 1 0	December
12	0 1 1 3 1 1 3 2 1 0 0 1 3 1 1 1 2 0 1 0	January
13	3 3 1 4 1	February

Appendix 1: Snap trapline histories at Tiritea. Tabulated figures show number of rats caught for each night of each trapline.



appendix 2 Ship rats known alive at time t ($\log_e N_t$) versus time



Appendix 3: Tracked smoked paper