Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with brodifacoum

SASCHA HOOKER

Department of Zoology
Pembroke College, Oxford University
Oxford, England*

*Present address: Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1.

JOHN INNES‡

Manaaki Whenua - Landcare Research
Private Bag 3052
Rotorua, New Zealand‡

‡Present address: Manaaki Whenua - Landcare Research, Private Bag 3127, Hamilton, New Zealand.

Abstract   We radio-tracked five male and four female rats for 6 nights in primary forest at Rotoehu, North Island, New Zealand. From trapping we estimated rat density at the study site to be 6.2 rats/ha. Radio-tracking revealed mean (± SE) restricted polygon home ranges to be three times greater in males (1.1 ± 0.29 ha) than females (0.3 ± 0.04 ha). Male ranges overlapped considerably, whereas those of females were largely exclusive. The ranges of males encompassed several female ranges. Four radio-collared rats were retrapped and administered a lethal dose of the anticoagulant poison brodifacoum. During the 3–5 nights after poisoning but before death, we detected no significant change in home range area or utilisation, arboreality, or movements. Further research is required to determine if rats prey on other fauna while fatally intoxicated or cause secondary poisoning after being eaten by other predator species.

Keywords   ship rat; *Rattus rattus*; radio-tracking; poisoning; brodifacoum; home range

INTRODUCTION

Two of the most important factors in the loss of island fauna are habitat destruction (loss or fragmentation) and the artificial introduction of exotic or alien species (Moors 1985). One of the most destructive alien species is the ship rat or black rat, *Rattus rattus*, the world-wide success of which stems from its ability to disperse, its competitive superiority over similar species in disturbed or secondary habitats, and its ability to reproduce successfully in a wide variety of habitats (Clark 1980). Endemic in the Indian subcontinent, the ship rat spread to Britain with the Romans around 20 B.C. (Reumer 1986). Since then, with humankind as its dispersal agent, it has colonised six continents and thousands of islands, including New Zealand (Atkinson 1985).

Today, ship rats are widespread and important pests in New Zealand indigenous forests (Atkinson 1973, 1978; Innes 1990). Control operations have covered areas ranging from <1 ha to reduce the risk of rats boarding ships (Hickson et al. 1986) to 1400 ha to protect nesting kokako (Innes et al. in press). Behavioural data obtainable by radio-tracking (the amount of time the rats spend in trees, the distances they move, their home range areas, and social organisation) are essential prerequisites of any effective management strategy and may facilitate the design of more efficient control operations.

In buildings and laboratory colonies, ship rats occupy a group territory with a dominance-based social hierarchy (Barnett 1967; Ewer 1971). However, little is known of the social organisation of forest-dwelling ship rats, in New Zealand or elsewhere. Nocturnal, arboreal, and alert, ship rats are difficult to observe directly. Trapping, footprint-tracking studies, and nest observations have indicated that they are not colonial, but that individuals or family groups are dispersed rather evenly through available habitat (Daniel 1972; Innes & Skipworth 1983). The first part of this study was an investigation of the home range size, social organisation, and movement patterns of several male and female ship rats, using radio-tracking.

Our second aim was to investigate the effect of the anti-coagulant brodifacoum on rat movements. Rats that are fatally intoxicated with poison may still prey on other fauna, or they may be eaten by predators which might themselves be poisoned as secondary kills. Many of the problems of commensal rat population control are the result of neophobia (Cowan 1977) and the social learning of diet preference and aversion (Galef 1988). Control strategies can minimise opportunities for social learning. Poisons used for long-term control of rat populations are therefore usually of the chronic type like brodifacoum, so that social transmission of bait aversion is avoided. Brodifacoum is slow-acting, taking 3–7 days to cause death with a single dose.

By recapturing four of the radio-collared rats and feeding them poison bait, we were able to track them during the period after ingestion and before death and to determine experimentally whether poisoning altered the rats' movements.

Fig. 1 Map of ship rat study site, Rotoehu Forest, showing central trapping grid and altitude contours (m a.s.l.). Crosses in the central 68 × 80 m grid show cage-trap positions.

METHODS

Study site

The 9 ha study site was located in tall (to 30 m) forest of tawa, *Beilschmiedia tawa*, and kohekohe, *Dysoxylum spectabile*, within the current North Island kokako research study area (37°58′S, 176°32′E) in the Pongakawa Ecological Area of Rotoehu Forest, North Island, New Zealand. (Plant nomenclature follows Allan 1961 and Connor & Edgar 1987.) The nearest weather station was formerly located at Rotoehu Forest Headquarters, 5 km to the north. Over the period 1941–70, mean annual rainfall was 1680 mm and mean temperatures ranged from 7.7°C (July) to 17.8°C (February) (Leathwick et al. 1983).

To record the locations of rats, numbered pegs marked with reflective tape were laid out in a 10 × 16.7 m grid system over the 300 × 300 m (9 ha) study area.

Trapping and poisoning

Four trapping sessions were undertaken between 1 December 1991 and 21 January 1992. During the periods 7–12 and 20–22 December, 24 rats were live-trapped in 45 cage-traps set at the grid markers in a rectangle of 9 × 5 stations covering 68 × 80 m (0.54 ha) in the centre of the 9 ha study area, in order to estimate population density and to attach radio-transmitters to particular rats (Fig. 1). The first four adult males and four adult female rats to be captured were radio-collared. Subsequently, a further
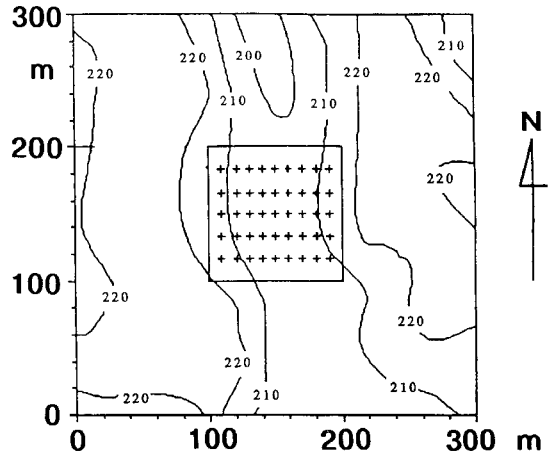
adult male rat was captured and collared when one of the original males (M5) could not initially be relocated.

Each live-trapping session was preceded by 2 days of prebaiting to accustom the rats to using the traps. A carrot disk smeared with peanut butter was used as bait. Traps were set during the afternoon and cleared between 2400 and 0300 h NZST to reduce the time rats spent in traps. Traps were also covered with metal tunnels to further reduce stress on the trapped rats. No trapped rats died during the study. Captured rats were anaesthetised in a plastic bag using cotton wool soaked in ether, then sexed, weighed, and individually marked by toe-clipping. Four adult female and five adult male rats were radio-collared.

Subsequently, between 3 and 8 January, two female and two male collared rats were retrapped and fed brodifacoum poison ("Talon WB50", ICI Tasman Ltd) in their cages between 2400 and 0100 h. They were then released and radio-tracked (nights only) until they died.

At the end of the study (16–21 January), a kill-trapping programme was carried out in order to estimate population density, using 45 Fenn Mk IV traps and 52 wooden rat snap traps ("Ezeset Supremes") laid out through the central 0.54 ha of the study site. The traps were set during the afternoon and cleared the following morning. This provided a minimum count of rats exposed to the trapping site, from which an estimation of rat density was calculated. To check that all rats had been

caught, baited tracking tunnels (King & Edgar 1977) were placed throughout the grid and monitored during the kill-trapping programme.

All traps and tracking tunnels were set on the ground, since previous studies found that no rats were entirely arboreal (Daniel 1972; Innes & Skipworth 1983).

Radio-tracking techniques

While each rat was under light anaesthesia, an AVM SS-1 transmitter (Biotrack U.K. Ltd, Wareham, Dorset) was fitted around its neck with a non-release nylon cable tie collar. Rats were released at the same site after recovering full locomotor function. The transmitter was generally detectable over 25–30 m, but the range varied according to the rat's (and therefore the antenna's) orientation and to intervening obstructions.

AVM receivers were used, together with a three-element hand-held Yagi aerial. A radio-fix recording the location of each rat to an accuracy of ±2 m was taken every 10 min. The radio-fixes were taken 5–10 m away from the rat, at which distance no evidence of disturbance was detected.

Four rats were radio-tracked each night from dusk until dawn, for a minimum of 5 nights, except during the poisoning study when each rat was tracked until death (between 3 and 5 nights). Rats M2, M4, F1, and F2 were tracked between 15 and 21 December; M1, M3, F3, and F4 were tracked on 22 and 26–30 December and 3 January; M5 was tracked on 4 and 10–12 and 14 January; M1, M2, F1, and F2 were poisoned and tracked between 4 and 11 January; and the neighbouring non-poisoned females, F3 and F4, were tracked on 9 and 12 January.

Data were analysed using the "Wildtrak" computer program on Macintosh computers (Todd 1992).

Arboreality and nests

To obtain an estimation of arboreality, the approximate height of the rat above ground was recorded at each fix. Heights were banded as 0–2, 2–8, and >8 m. Nest-sites were located to within 5 m^3 by radio-fixing the position of the rat once it became stationary at the end of the night.

Error estimation

We determined the accuracy of fixes in the field by placing test transmitters in various unknown (to observers) positions and habitats throughout the study area and taking fixes on these. The horizontal component error averaged 2.5 m over 60 trials (standard deviation 3.7 m; range 0–24.9 m).

The error check showed the vertical fix to be the least accurate of the position data, with 10 of 60 fixes placed in the wrong height band. Most inaccuracies arose when the test transmitter was placed near the 2 m boundary between lower and middle bands.

Response of neighbours to poisoning

The removal of rats by poisoning was more likely to effect changes in the ranges of adjacent females rather than males, since previous work (Daniel 1972; Innes & Skipworth 1983; Hickson et al. 1986) indicated that female ranges were probably discrete, whereas those of males were probably overlapping. Therefore we radio-tracked two non-poisoned female rats for 2 nights during and immediately after the poisoning study, to check for home range changes following the poisoning of their neighbours.

Home range analysis

The home range is defined after Burt (1943) as the area normally traversed by an individual during its activities of food-gathering, mating, and caring for young. Three non-statistical techniques (min. convex polygons, restricted polygons, and grid cells) were used to analyse various aspects of the home range for each rat. These methods permit the use of temporally autocorrelated fixes (fixes which are not independent) when the number of fixes and the time period over which they are taken are constant between ranges, or when the ranges are exhaustively documented (Harris et al. 1990).

The time interval required for independence of fixes was found for each rat by plotting values of Schoener's Index for increasing time intervals (Swihart & Slade 1985). This indicated that more than an hour between successive fixes would be required for independence, and non-statistical methods of data analysis should be used.

These analyses allow for use of autocorrelated data, but require that the data have been collected over a sufficiently long time to obtain a representative sample. This can be checked visually by plotting the percentage home range area against the number of fixes (Voigt & Tinline 1980). Such analyses (Fig. 2) showed that 80% of each range had been described by about the 200th fix. All rats were therefore tracked for long enough to describe their home range accurately.

Minimum convex polygons

The minimum convex polygon (MCP) method (Mohr 1947) is still the most frequently used technique. The range boundary is constructed by drawing
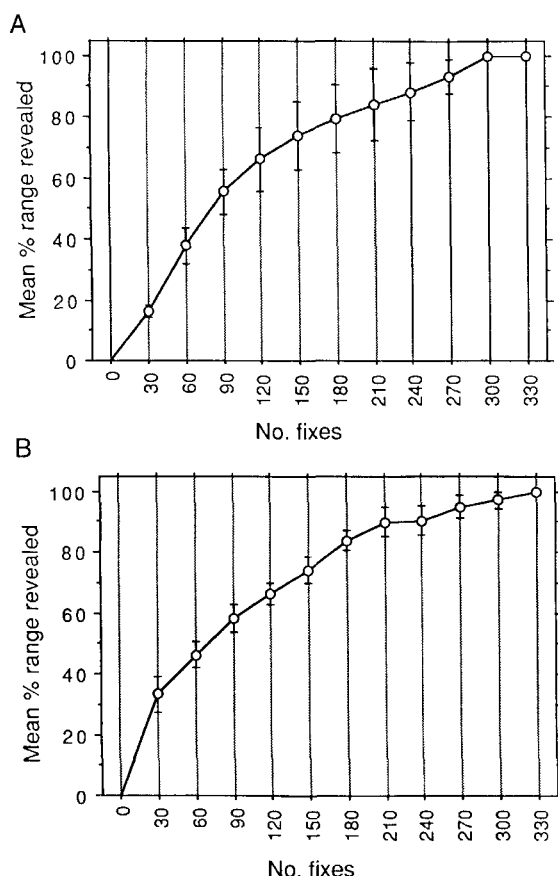
A

B

Fig. 2 Mean % revealed home range area (restricted polygon method) against number of radio-telemetry fixes for male (**A**) and female (**B**) ship rats. Bars show standard errors.

a line around the outermost locations recorded for an animal. This limits its utility, since range size is strongly influenced by peripheral fixes, and the nominal range area may include large areas which are never visited. The standard modification to overcome this problem (White & Garrott 1990) is to eliminate the "outliers" by calculating 95% polygons based on ordering criteria for the locations.

Restricted polygons

The restricted polygon (RP) method (Wolton 1985) determines home range by joining up the outermost of the set of fixes gathered for the animal, but with the proviso that the maximum length of a line between two peripheral points is limited to the mean distance between fixes and the arithmetic mean centre of activity. Some outlying fixes may not be

included into the polygon, but these fixes are treated as temporary excursions.

Grid cells

The overlaying of grid cells (Siniff & Tester 1965) is useful as a representation of spatial utilisation and static interaction between individuals, but is less useful for calculating home range area. The area over which an animal has moved is dissected using a grid of cells, or blocks. The number of animal fixes is tabulated for each of these cells, and the sum of the areas of cells containing locations is taken as the estimate of home range area. The main problem with this method is the disjointedness that arises with low sampling intensity—an animal may pass through many grid cells but never actually be recorded there. A technique to overcome this is to add influence cells around the cells containing fixes and then to remove (trim) those that do not border a certain proportion of cells containing fixes. This fills in holes but does not add to the outer boundaries of the range. A grid cell resolution of 5 m, at least twice the accuracy of the data, was used for this study.

In this study, the RP method was preferred for quantitative home range estimation, but the MCP method was also included for comparison with other studies (as recommended by Harris et al. 1990). Grid cells were used in analysis of home range utilisation.

Impact of poisoning on range

To investigate the impact of poisoning, we compared the ranging behaviour of the four poisoned rats over 3 nights before poisoning with their behaviour for 3 nights afterwards. In this way the numbers of fixes taken in the two periods were similar. The same comparison was also made for four non-poisoned rats, which acted as a non-treatment group for comparison with poisoned rats. For this comparison, tracking dates "before" (Time 1) versus "after" (Time 2) were 15–17 December versus 18–21 December for M4; 22, 27–28 December versus 29, 30 December, and 3 January for M3; 26–28 December versus 30 December and 3, 9 January for F3; and 22, 26, 27 December versus 28, 30 December and 3 January for F4.

Change in home range overlap

The spatial overlap of two home ranges is termed "static interaction" (Dunn & Gipson 1977). We investigated the home range overlap of the same rats before and after poisoning. The grid cell method was used to calculate the percentage of shared cells between the two ranges, and this provided an indication

as to whether home range was significantly different after poisoning. The home range sizes (RP method) were compared using paired *t*-tests for rats before and after poisoning, and, for rats not poisoned, at Time 1 and Time 2.

Rat movement

The distance travelled per night was calculated as the total distance between successive fixes. The mean distance travelled per night was compared before and after poisoning and, for rats not poisoned, at Time 1 and Time 2 using paired *t*-tests.

Home range utilisation

Grid cell plots (5 m, trimmed influences) of fixes for the four poisoned rats were compared before and after poisoning for changes in patterns of home range use.

RESULTS

Population density

Initial cage-trapping

Twelve adult male and 12 adult female rats were caught. All were of the frugivorus (agouti; white-bellied) morph. Means (±SD) of rat weights were 155.9 ± 20.9 g for males (range 121–190 g), and 141.4 ± 22.9 g for females (range 108–187 g). Criteria of maturity were perforate vagina for females and scrotal testes for males.

Final kill-trapping

Twenty rats—eight adult females, 10 adult males, and two juveniles—were kill-trapped after the two

adult males and two adult females died from poisoning. The assumption that all rats resident on the grid were caught is likely to have been true, since all radio-collared rats except one male (which could not be located) were caught in the kill traps, and no rat tracks were detected in 45 baited tracking tunnels on the grid at the end of trapping, although tracks were recorded regularly beforehand.

To calculate ship rat population density it is necessary to know or estimate the area covered by the counts. The area of exposure to trapping will differ for males and females because males have bigger home ranges and so are more likely to encounter traps. These areas can be calculated by adding a border of one-half of the mean home range "diameter" to the trapping grid, representing the average distance outside the grid included within the ranges of the trapped animals (Dice 1938). Home range "diameter" assumes circularity of ranges, so is inapplicable for many of the ranges observed. We estimated it by a parameter Av.D., the average of range length and width. Range length is the longest possible straight line inside the range, and range width is the length of the line at right angles to this and measured at its midpoint. Using MCP range dimensions,

Table 1 Home range length, width, and average diameter (Av. D.) (m) (defined in text) for ship rats, Rotoehu Forest, calculated from minimum convex polygon home ranges based on radio-tracking data taken between 15 December 1991 and 3 January 1992 for all rats except M5 (4–14 January).

Males	Length	Width	Av. D.	Females	Length	Width	Av. D.
M1	197	73	135	F1	109	91	100
M2	179	129	154	F2	111	70	90
M3	143	104	123	F3	109	54	81
M4	150	104	127	F4	82	64	73
M5	300	95	197				
Mean	194	101	147		103	70	86
SE	28	9	13		7	7	6

Table 2 Home range areas (ha) for ship rats in Rotoehu Forest before and after poisoning (RP = restricted polygon, MCP = minimum convex polygon; M = male, F = female). Pre-poison ranges were derived from radio-tracking data taken from 15 December 1991 to 3 January 1992 for all rats except M5 (4–14 January), and post-poison ranges from data taken during 4–10 January.

	Rat	RP	MCP (100%)	MCP (95%)	No. fixes
Pre-poison	M1	0.665	1.155	1.007	243
	M2	0.766	1.186	0.597	302
	M3	0.562	1.066	0.636	342
	M4	1.319	1.654	1.36	287
	M5	2.133	2.564	2.178	233
	Mean (SE)	1.08	1.52	1.15	281
		(0.29)	(0.28)	(0.29)	(20)
	F1	0.283	0.685	0.292	338
	F2	0.411	0.547	0.366	291
	F3	0.289	0.397	0.259	216
	F4	0.218	0.352	0.197	281
	Mean (SE)	0.30	0.49	0.28	281
		(0.04)	(0.07)	(0.03)	(25)
Post-poison	M1	0.905	1.137	1.01	273
	M2	0.626	0.894	0.62	171
	F1	0.109	0.187	0.126	162
	F2	0.368	0.496	0.396	173

Av.D. for males was calculated as 147 m and for females as 86 m (Table 1). The trap-exposed area (trapping grid area + Av.D./2) was thus calculated to be 2.6 ha for adult females and 4.9 ha for adult males.

Rat density was therefore calculated as 10/2.6 = 3.8 adult females/ha and 12/4.9 = 2.4 adult males/ha, giving a total rat density of 6.2 adults/ha. This density estimate is roughly confirmed by the home range data obtained. Mean female home range size was 0.3 ha (RP method, Table 2). If female ranges were contiguous and non-overlapping (the pattern found for the radio-tracked females), this would be equivalent to a density of 3.3 females/ha.

Rats released from cage traps before 0200 h showed no or little damage to their noses from rubbing on cage bars, although some released after this time did. No rats died in cages, although death of trapped rats was problematic for Daniel (1972), Innes (1977), and Hickson et al. (1986). We suggest that clearing traps during the night on which they are set rather than during the following day greatly reduces stress to the rats, both by detaining them for less time and by releasing them into darkness rather than daylight.

Home ranges

RP home ranges for male and female rats are shown in Fig. 3A, B. The female ranges were discrete, whereas the male ranges overlapped each other and partially overlapped the ranges of several females. The trapping data corroborated this: no other females were trapped >10 m within the range of a radio-collared female.

All tracked rats spent the entire night moving around their ranges. They left the nest at or just before dusk (1930–2000 h) and returned to the same nest or a different one at daybreak (0500–0600 h). Occasional observations of rats showed them to be very active, running along supplejack vines (*Ripogonum scandens*) or up and down trees as well as moving laterally around their home range. The rats covered most of their range each night, although apparently not in any systematic way.

Arboreality and nests

Overall, 26% of all fixes were recorded in the 0–2 m height band, 56% in the 2–8 m band, and 18% in the +8 m height band (but see *Error estimation* in Methods). There were no significant differences between the foraging heights of males and females nor between poisoned and non-poisoned rats. Repeated measures ANOVA (split-plot analysis) with
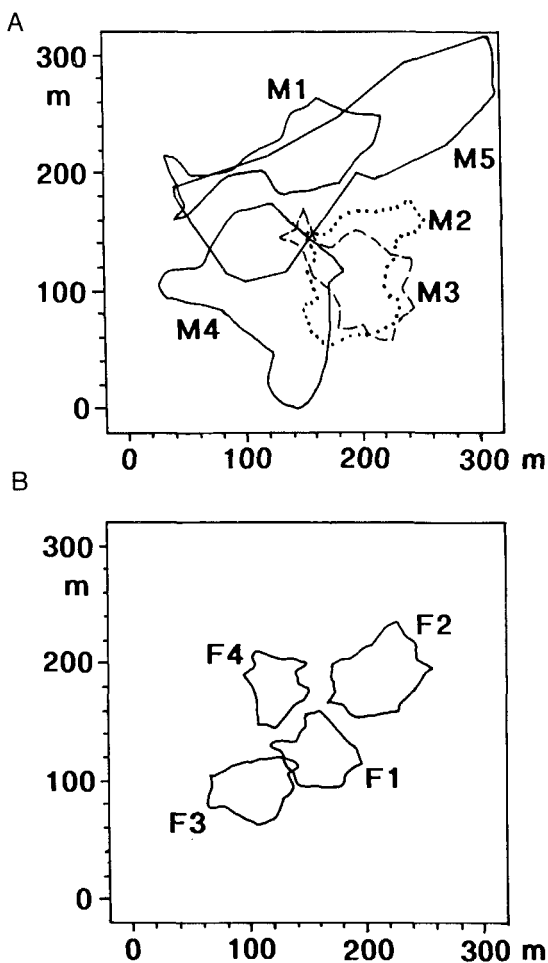

Fig. 3 Home ranges (restricted polygon method) of (A) male and (B) female ship rats at Rotoehu Forest, shown on 300 × 300 m grid.

sex/poison as the whole-plot factor and position as the sub-plot factor gave $F_{1,6} = 0.03$, $P = 0.873$ and $F_{1,6} = 0.73$, $P = 0.425$, alternately.

Unusually high numbers of ground fixes were observed for M5 and F4, both of which had >40% of fixes between 0–2 m ($\chi^2 = 123.01$ for M5, against expected values based on average of other males, $P < 0.001$ (2 d.f.); and $\chi^2 = 66.7$ for F4, against expected based on average of other females, $P < 0.001$ (2 d.f.)). M5 utilised two centres of activity 230 m apart and travelled on the ground between the two. F4, on the other hand, had young unweaned rats in the nest, but we do not know why this required her to spend more time on the ground.

Day nests were always up trees, but from the

ground we could not locate exact nest sites. Only one nest (for M5) was recovered; this was a loosely woven structure in a small rimu tree.

Two females (F2 and F4) each used the same nest tree during the pre-poisoning phase of the study (15–21 December and 22 December – 4 January, respectively), but were later recorded using a different tree. F4 had young in the nest at this time, and F2 probably also did, since she later appeared to come into oestrus. The other rats each used 3–5 different nest trees during the study. We detected no regular pattern of use during the period studied; some rats used one tree for 3–4 consecutive days then moved to a new one, whereas others changed after only 1 day. Rats were never observed to share the same nest tree.

Rat activity and behaviour

Rats were active from dawn until dusk, regardless of moon phase or weather, although they sometimes stopped moving during heavy rain. Mean speed of movement over the ground (all fixes) showed that males were significantly less active after midnight than before (mean speed of males = 1.59 ($\pm$SD 0.17) m/min before midnight and 1.3 ($\pm$0.29) m/min after midnight: two-sample t-test—before > after, $T =$ 1.94, $P = 0.05$, $n = 5$). A similar though non-significant trend was found for females.

We often saw and heard rats moving, though usually between fixes. They were actually in view during only 3% of fixes. Rats were often noisy, rustling the vegetation or making squeaking vocalisations. Several untagged rats were known to be present in the study area (15 of the initial 24 cage-trapped rats were not collared), and were sometimes seen near tagged rats.

Although they had individual home ranges, rats were occasionally located together. Up to two collared males were located in the vicinity of a collared female, but there was no evidence of long-term associations between individuals. On one occasion a male and a female were tracked (and observed) together for 10–20 min. In another incident, a male near a female was observed apparently chasing another male away. The commonest observation was of one rat following another.

One female (F4) had three juveniles present in her home range, which was the smallest of all the female ranges. The three juveniles were seen travelling with their mother several times before their cage-capture over 3–5 January, when they weighed 22, 24, and 27 g. The latter was 10 cm in body length and 11 cm in tail length. On 4 January, two of the juveniles were cage-trapped together, and the third juvenile kept

running up to the cage and the observer. Two rats, each weighing 42 g, were kill-trapped on 16 and 19 January and were probably these juveniles. Before this, the adult female, who had apparently just rejected the juveniles, had at least two adult males around her, possibly indicating oestrus. No females were pregnant or lactating when necropsied at the end of the study.

Poisoning

Poison baits were weighed before and after consumption by rats. The rats each consumed on average 10.7 g of bait (range 7.3–13.9 g), which would contain 0.54 mg of brodifacoum, a lethal dose.

Each rat was regarded as dead at the last detected movement. F1 died on the fourth night after poisoning, F2 and M2 died on the fifth night, and M1 died on the sixth night. Three of the rats died in trees: two (M1 and M2) in nest trees already known, one (F1) in an epiphyte clump likely to have been a nest (this later fell to the ground). The other (F2) died in a hole in the ground below her nest tree.

Home ranges before and after poisoning

There was no significant difference between the home range areas before and after poisoning (paired t-test, $t_3 = 0.60$, $P = 0.59$), nor was there a significant difference between the home range areas of non-poisoned rats at Time 1 and Time 2 (paired t-test, $t_3 = -0.71$, $P = 0.53$). There was also no significant difference in the percentage of shared cells for the poisoned rats compared with the non-poisoned rats (two-sample unpaired t-test, $t = 1.26$, $P = 0.25$).

There was also no significant difference between mean distances travelled per night before and after poisoning (paired t-test, Ho: no difference before and after poisoning, $t_3 = -1.26$, $P = 0.30$), nor was there a significant difference between mean distances travelled at Time 1 and Time 2 for the non-poisoned rats (paired t-test, $t_3 = 0.57$, $P = 0.61$) (Fig. 4). Thus, rat movement did not appear to be restricted during the nights before death.

These statistical tests are not very powerful because of the small sample sizes, but they would detect large differences.

Home range utilisation

Visual inspection (Fig. 5) shows that there were few differences in range utilisation for rats before and after poisoning, nor were there significant differences in the foraging heights of poisoned and non-poisoned rats (repeated measures ANOVA, $P = 0.425$). The differences in location of darker shaded
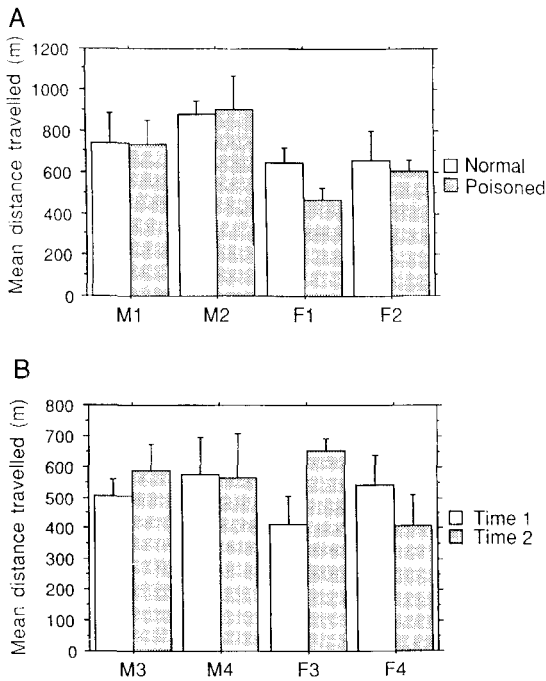
A

B

Fig. 4   Mean distances moved per night by (**A**) poisoned ship rats during 3 nights before and after poisoning, and (**B**) non-poisoned rats in two 3-night periods to enable comparison to those in (A). Bars are standard errors; $n = 4$ in all instances.

areas represented change in nest sites used. These changes from before to after poisoning followed no set pattern.

Inspection of grid cell plots (Fig. 6) for the two neighbouring non-poisoned females for the 5 days of tracking before other rats were poisoned, and the 2 days of tracking after, reveals little difference in home range use. There are several fixes which appear to represent excursions from the home range, although only one of these is towards the newly vacated ranges.

DISCUSSION

Population density

The estimated density of 6.2 ship rats/ha measured at Rotoehu in January 1992 is high compared with densities measured in other New Zealand forests. Previous estimates obtained by trapping and tracking were 2.0–2.5 rats/ha on Stewart Island in early spring (Hickson et al. 1986) and 0.7–9.4 rats/ha over

8 years in the Orongorongo Valley (Daniel 1978). The Rotoehu estimate was taken late in the breeding season at a time of year when density is expected to be high, although rats do not produce major population peaks regularly each year (Daniel 1978; Innes 1990).

These densities are much lower than some measured in subtropical zones, such as the 12–15 rats/ha in Cyprus macchie scrub (Watson 1951), 2–22 rats/ha in uncultivated Hawaiian scrubland (Tomich 1970), and up to 64 rats/ha in Hawaiian kiawe forest (Tamarin & Malecha 1971). Clark (1980) found 0.4–19 rats/ha in a range of scrub and forest habitats on the Galapagos Islands, where the density and biomass of rats was correlated with an index of vegetation biomass.

Home ranges

The observation of overlapping home ranges of some male but not female ship rats at Rotoehu is consistent with other studies in New Zealand forests and elsewhere (Granjon & Cheylan 1989). Daniel (1972) first showed (but did not state) this, although his data were from a small number of cage-trapping records taken over many months, and may not have given a precise picture of the relationships between adjacent ranges. Innes & Skipworth (1983) and Hickson et al. (1986) combined cage-trapping and tracking to generate many more location records in a shorter time; both found largely exclusive female ranges, but obtained too few data on males to comment on them in detail. At Rotoehu, the ranges of some radio-tracked males overlapped considerably, and the picture may be even more complicated by the presence of other males that were not radio-tracked. It may be misleading, however, to infer the combined use of common ground from overlapping MCP ranges. For example, the range of M1 is mostly contained inside that of M5 (Fig. 3A), but in fact M5 mostly used two separated parts of his range which avoided M1.

Although females' MCP ranges at Rotoehu were about the same size ($0.5 \pm$ SE 0.07 ha, $n = 4$) as the monthly ranges measured by Hickson et al. (1986; 0.56 ± 0.07 ha, $n = 8$), their typical range shapes differed. On Stewart Island, ranges were long and thin (132 ± 16 m $\times 43 \pm 4$ m), perhaps because they were aligned to rivers and the coastline (Hickson et al. 1986, fig. 5). At Rotoehu, ranges in the more homogeneous forest were more nearly circular (103 ± 7 m $\times 70 \pm 8$ m).

Radio-tracking quickly generates copious amounts of location data, but is also very laborious,

which restricts the possible sample size if adjacent animals are followed simultaneously. Hence, this study reports on rather few individuals. Cage-trapping alone generates few location data, but trapping and baited tracking together are much more effective (Innes & Skipworth 1983; Hickson et al. 1986). However, only radio-tracking permits monitoring of the simultaneous movements of neighbours, detailed study of range use and overlap between ranges which is not dependent on trap or tunnel spacing, analysis of temporal movement patterns in three dimensions within a home range, and the location of nests and verification of mortality and its possible causes.

The arboreal location of nest sites found in this study supports previous observations that epiphytes and tree-hollows are preferred sites, but that sparrow-like nests (such as that recovered for M5) are built if other sites are not available (Innes 1990). Rotoehu ship rats were mostly arboreal, with 73% of fixes above 2 m, but were nevertheless recorded on the ground fairly regularly. The frequent (but not prolonged) use of the forest floor by rats to move from tree to tree provides intermittent opportunities for feral cats (for which ship rats are important prey—Fitzgerald & Karl 1979; Karl & Best 1982) and other predators to hunt them without climbing.

Social organisation

Observations of wild ship rats with young are rare and therefore worth reporting. Three juvenile rats (<30 g) were seen and eventually cage-trapped with an adult female, presumably their mother. Rats of such light weight are rarely trapped in New Zealand, despite extensive kill-trapping, suggesting that these young rats were undertaking some of their first trips around their mother's range. In one sample of 307 ship rats snap-trapped at Tiritea in the northern Tararua Range, the lightest rat trapped was 35.5 g (J. Innes unpubl. data). This is not because the rats are too light to set the traps off, because rat traps regularly catch mice (*Mus musculus*) which weigh 20 g or less. Ship rats in captivity wean young at 21–28 days old (Cowan 1981). In one of the young rats, the tail was longer than the body, supporting the observation by Ewer (1971) that tail length outstrips body length by the time that the young leave the nest.

No adult male was seen accompanying the female with young. Other anecdotes of wild ship rats with young in a nest (van Riper 1974; Innes 1977) also mention one adult only. In captivity, female ship rats drive the male away shortly before giving birth, and raise the litter alone (Cowan 1981). Ewer (1971) studied a commensal wild colony and observed that

females abandoned their young quickly after weaning; sometimes the young's first foray away from the nest was without the parent female.

Rats were often seen together, usually one following another. Some interaction between males and females was observed. M2 and F1 moved together for 10–20 min in the branches and fed together on the ground. A female, perhaps in oestrus, was followed by two collared males. One male left upon the approach of the other, but returned later.

The quality of data provided by radio-tracking allows inferences to be made about the study animal's social organisation. Home range configurations over a 4-week period in the breeding season were different for males and females. Females' ranges were small and non-overlapping, whereas males' ranges were larger and some overlapped considerably. Each male's range touched the ranges of several females.

Compared with commensal ship rats, feral ship rats at Rotoehu had very different home ranges and, by implication, a different social system. Rats at Rotoehu did not live in colonies but were dispersed rather evenly through the study area. Data suggested that there were no long-term associations between males and females, and that females alone raised young. Ewer (1971) recorded behavioural observations of ship rats in a commensal environment (the laboratory roof and an adjacent courtyard). Ewer's study groups each had a single dominant male and linear male hierarchy, with one or more high-ranking females depending on the group size. Females were responsible for most of the routine defence of the group's territory, and top-ranking females rarely attacked each other. Territories were marked by rubbing cheeks and ventral surface on branches, and the boundaries were defended less often the further they were from the nest.

Ship rats can apparently form either group or exclusive territories, depending on the clumped or scattered supply of food and shelter and the costs of defending these, as can *Mus musculus*, another cosmopolitan commensal rodent pest (Fitzgerald et al. 1981).

Ship rat social organisation can be explained as food-determined female dispersion, which in turn determines male dispersion. This type of social system implying male promiscuity and female territoriality is not uncommon in small mammals (Gipps 1985; Ostfeld 1985). However, few data have been collected for free-living rat species, most studies having been carried out on commensal rats. Multi-male polygyny has been documented in "clans"
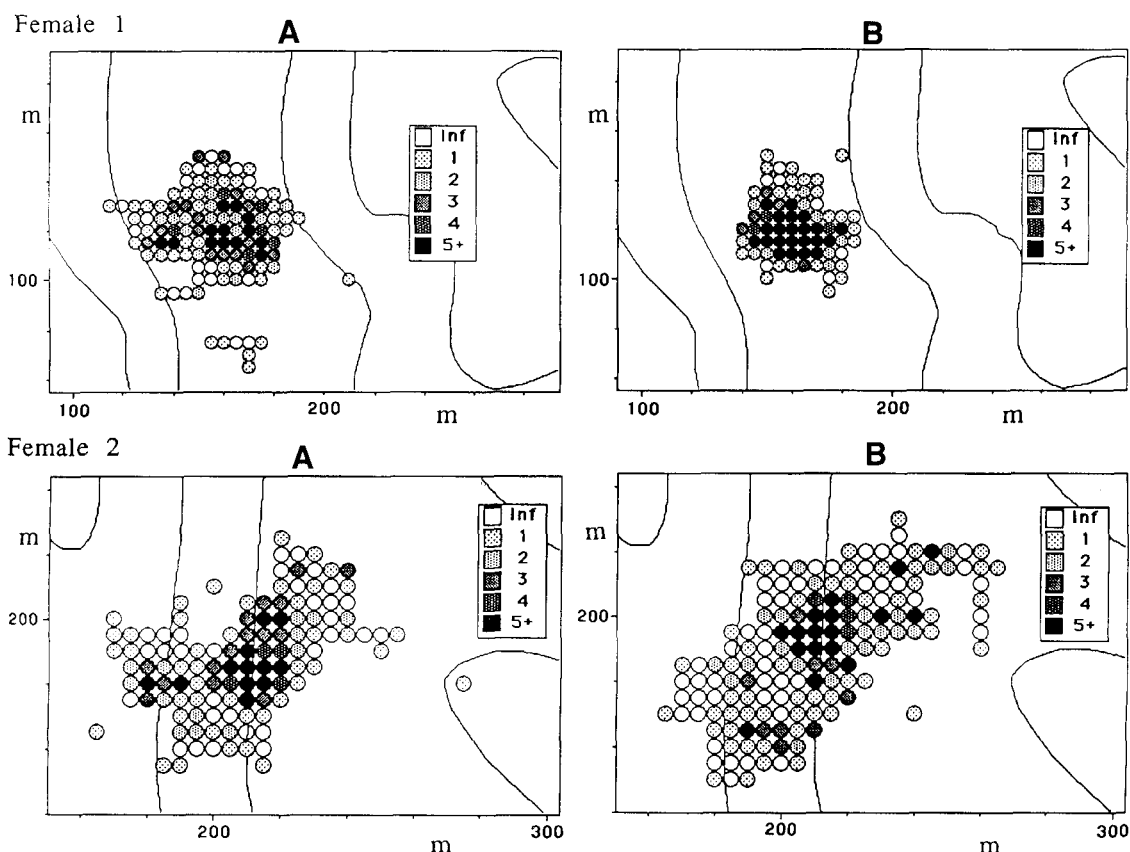
Female 1

Female 2

Fig. 5   Grid cell plots (5 m, trimmed influences) of home ranges of the four poisoned ship rats before (**A**) and after (**B**) poisoning. Areas of progressively darker shading represent more intensive use.

(subgroups within a colony) of brown rats, *R. norvegicus*, on agricultural land (Fenn 1989).

Poisoning

The mean lethal dose (LD_{50}, the amount of poison needed to kill 50% of the population) of brodifacoum for wild ship rats is 0.69 mg/kg (Dubock & Kaukeinen 1978). The mean weight of rats poisoned at Rotoehu was 170 g; the average rat therefore needed to ingest 0.117 mg brodifacoum to receive a mean lethal dose. Average consumption for the poisoned rats was 4.6 times the LD_{50} dose, and even the rat which ate only 7.3 g of bait consumed over three times the LD_{50} dose.

The rats poisoned with "Talon" died 3–6 days after ingestion. Hickson et al. (1986) estimated 2–3 days to death, although their measurement was based on the time to which footprints were no longer observed in tracking tunnels.

Further research is needed to determine if fatally intoxicated ship rats are still a predation threat to

other fauna during the few days before their deaths. Cox & Smith (1992) showed that intake of food and water declined rapidly in anticoagulant-treated, caged *Rattus norvegicus*. They also observed a pre-lethal reversal of light-dark activity pattern, but no evidence of this was found for ship rats at Rotoehu, which maintained normal nocturnal movement and showed no nest change between dawn and dusk.

Implications for control of ship rats in New Zealand

Direct observations of ship rats at Rotoehu confirmed that they were superbly agile in trees, that they ranged widely throughout their home ranges each night, and that they were not colonial but evenly dispersed through the forest study area. These facts indicate the potential threat of this species to avifauna, since every bird nest is likely to be in the range of at least two rats, and the rats are likely to pass by each nest sooner or later. Clearly, to target all individuals, the control effort must be spread
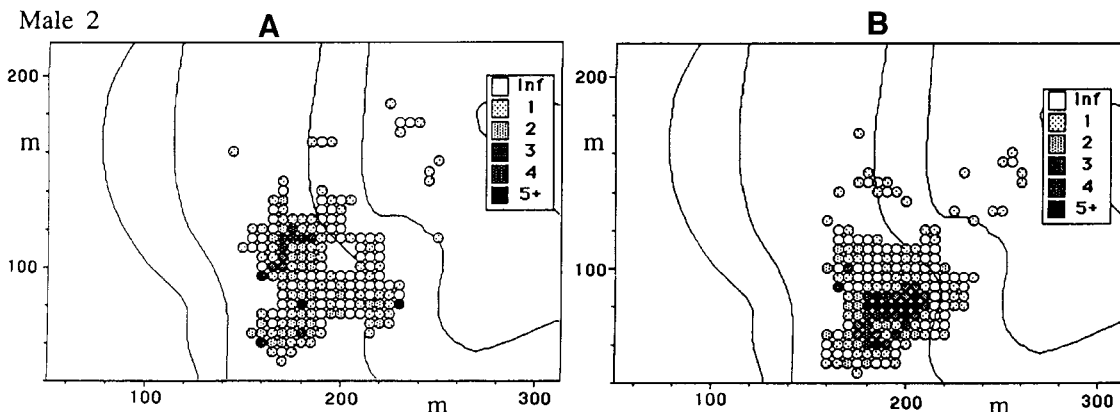
Fig. 5 (contd)

throughout the entire area for which protection is sought.

Traps, poison baits or stations, and population monitoring devices such as tracking tunnels can all be set effectively on the ground, since the rats often travelled there despite spending most time up trees. They moved extensively (400–900 m) inside their home ranges each night; range lengths averaged c. 100 m for females and twice that for males, and rats were active in all weathers. Rats are highly likely to find traps or bait stations anywhere inside their ranges, especially if they are lured. Bait stations on a grid at 100 m intervals would expose most rats to poison, and at 50 m intervals would expose all rats, wherever rat density is similar to that at Rotoehu.

Ship rats have been eradicated by ground-poisoning from five New Zealand islands, the biggest of them being Somes I. at 32 ha (Veitch & Bell 1990), and were significantly reduced during a 5 ha ground-poisoning operation on Stewart I. (Hickson et al. 1986). Since 1990 several large-scale aerial

poisoning programmes (mostly using "1080"—sodium monofluoroacetate) have been targeted at ship rats in forest on the mainland to protect North Island kokako for the duration of the nesting season (Innes et al. in press). Most future large-scale operations are likely to be aerial, for reasons of cost, and it is important to estimate an appropriate sowing rate. Current aerial operations with 1080 are targeted primarily at brushtail possums, Trichosurus vulpecula, another widespread introduced forest pest, usually at a minimum sowing rate of 8 kg of baits/ha (1 bait/ 7.5 m²). Such a sowing rate delivers 1470 and 400 baits to average Rotoehu male and female rat ranges, respectively. Since each bait contains many times the required lethal dose for a ship rat, bait density for operations concerned with rats rather than possums could be hugely reduced and still be adequate to kill all rats.

Most rats died in their nests after poisoning, suggesting that few dead rats will be found in the open after a Talon poisoning operation. However there is
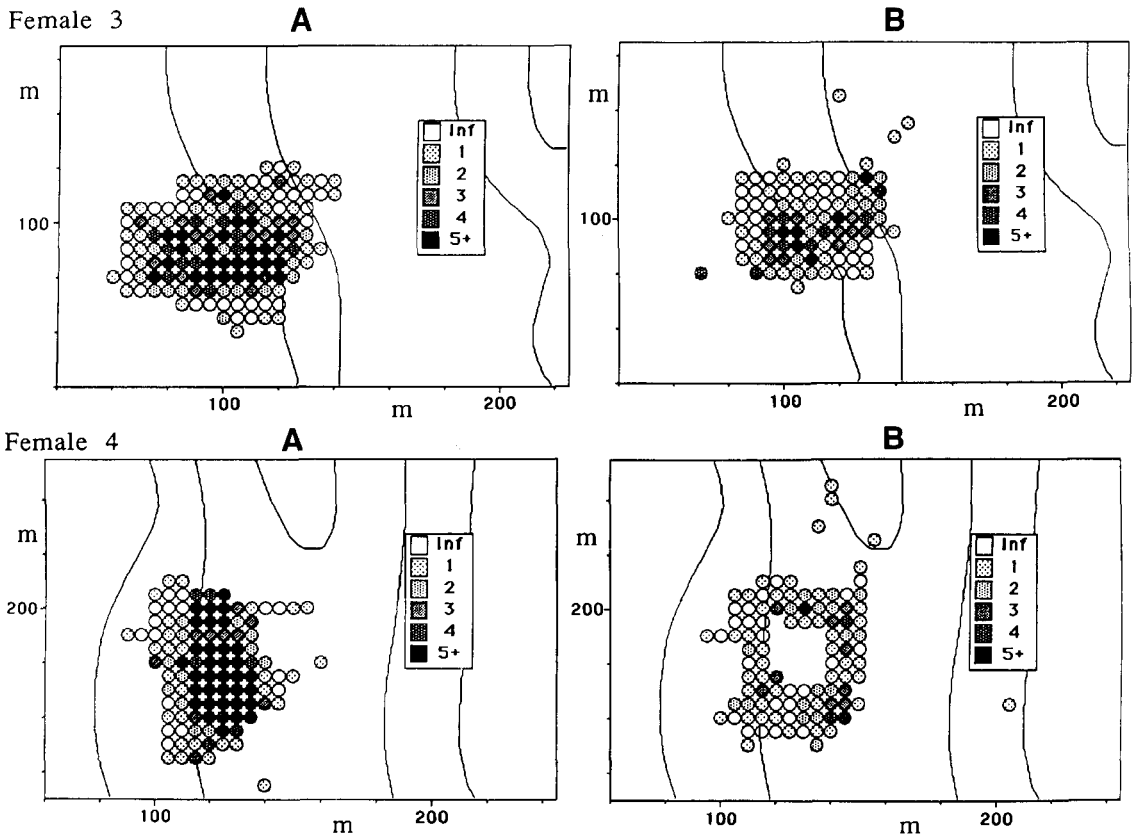
Fig. 6 Grid cell plots (5 m, trimmed influences) of home ranges of Female 3 and Female 4 (neighbours of poisoned rats) for six tracking-days before the other rats were poisoned (**A**) and two tracking-days after (**B**). Areas of darker shading represent more intensive use.

still a risk of non-target poisoning of native avian predators such as the ruru (Strigidae, *Ninox novae-seelandiae*), or introduced mammal predators such as cats and stoats, from the normally ranging intoxicated rats. This is especially so if the rats leave blood trails or react sluggishly to touch as observed by Cox & Smith (1992) with Norway rats.

Ship rats fed brodifacoum poison and radio-tracked at Rotoehu died after 4–6 days, suggesting that the interval between pulses of brodifacoum should be 7 days. This time to death is less than the average of 10 days (range 5–14) reported for ship rats in a laboratory (Redfern & Gill 1976). The lack of a colony-based hierarchical social system among forest-dwelling ship rats may reduce the time needed to poison them relative to commensal rats, because dominant individuals in colonies keep subordinates away from feeding stations until the dominant rats die (Timm & Salmon 1988). In the Philippines, West

et al. (1975) found significantly greater bait consumption by *R. rattus* from several small bait containers compared with one large one, and hypothesised that this was due to reduced interaction between rats.

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