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The population ecology of *Rattus exulans* on Tiritiri Matangi Island, and a model of comparative population dynamics in New Zealand

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Abstract On Tiritiri, a small predator-free island in northern New Zealand, kiore (*Rattus exulans*) were live and snap trapped in grassland and forest. In both habitats, kiore abundance peaked in late summer/autumn. The increase followed a 3 month breeding season during which females produced two to three litters, each averaging 7 young. During the population decline in autumn and winter, animals lost weight. Few bred in the breeding season of their birth and none lived to breed in a second breeding season, so the population consisted of distinct age cohorts. These patterns may relate to a highly seasonal food supply.

Kiore elsewhere in New Zealand show seasonal breeding, but the length of breeding, sexual maturation, and litter size vary. Other studies of kiore in the Pacific show less marked seasonal fluctuations, longer breeding seasons, and smaller litters. We propose a model to explain the variation in rodent demography in New Zealand. The model is based on the seasonal availability of food, along with the modifying influences of predation and dispersal.

Keywords *Rattus exulans;* kiore; population ecology; density; reproduction; maturation; survival; predation; competition; islands; demographic model

INTRODUCTION

The Polynesian rat or kiore, *Rattus exulans* (Peale), is widespread throughout the central and western Pacific including the Asiatic mainland. New Zealand is its southern limit and it is believed to have been distributed by the Polynesians (Williams 1973).

Kiore were once widespread in New Zealand, but since the introduction of *R. rattus, R. norvegicus,* and *Mus musculus* last century, they have become largely restricted to offshore islands (Watson 1956; Atkinson 1973; Taylor 1978). Many of these islands are important fauna and flora reserves, and kiore are believed to have an adverse effect on other biota (Atkinson 1972; Crook 1973; Whitaker 1973; Ramsay 1978; Campbell 1978). Information on kiore is urgently required to help manage these reserves.

Studies in tropical areas (e.g., by Tamarin & Malecha 1972; Wirtz 1972; Dwyer 1978) show annual cycles in kiore numbers despite an 8–12 month breeding season. These cycles tend not to be extreme with lows and highs differing by a factor of only 1–3. With such long breeding seasons differentiation of age classes is minimal. Although there are such common features of tropical populations, the details vary with differences in habitat, land area, and the presence and absence of predators and competitors. When this study began there were only limited data for kiore populations in New Zealand. The preliminary study of Watson (1956) indicated annual cycles of abundance but provided no data on other aspects of demography such as breeding season.

The first aim of this study was to document the demographic changes in kiore populations in a temperate area. Secondly, we wished to accumulate similar demographic data from other detailed studies in more tropical areas and from more short-term studies in other areas of New Zealand. Finally, using these data from a range of habitats, latitudes, land areas, and from populations with and without the influence of competitors and predators, we wished to postulate a model which may explain some of the observed differences.

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STUDY AREA

Tiritiri Matangi Island

Tiritiri Island (174°54′E, 36°36′S) is one of the inner islands of the Hauraki Gulf. The island's 220 ha is administered by the Hauraki Gulf Maritime Park Board as a Scientific Reserve.

The presence of middens, kumara pits, and terraces testifies to early Maori habitation, and this probably explains the presence of kiore. European farming started before 1865, when the lighthouse was erected. Farming led to the removal of all woody forest species from the island except along a coastal fringe and in four small gullies. The grazing lease for most of the island was terminated in June 1971, and the last sheep, cattle, horses, and goats were removed by December 1972. With the exception of a small (10 ha) farm around the lighthouse, the island has been left to revert to native forest. In 1983, a planting programme (Mitchell 1985) was begun to speed the return of forest cover.

The present flora of Tiritiri has been described by Esler (1978). The grassland communities on the ridges are dominated by prairie grass (*Bromus unioloides*) and cocksfoot (*Dactylis glomerata*) although perennial ryegrass (*Lolium perenne*), sweet vernal (*Anthoxanthum odoratum*), Yorkshire fog (*Holcus lanatus*), and paspalum (*Paspalum dilatatum*) are locally important.

All four forested gullies have similar but extremely patchy canopies. Approximately 40% of the forest live trapping area was dominated by kanuka (*Kunzea ericoides*), 20% was dominated by pohutukawa (*Metrosideros excelsa*), 20% was dominated by a mixture of kohekohe (*Dysoxylum spectabile*), mahoe (*Melicytus ramiflorus*), taraire (*Beilschmiedia tarairi*), and tree ferns (*Cyathea* spp., *Dicksonia* spp.), and the remaining 20% was dominated by a mixture of mapou (*Myrsine australis*) and kanuka. A dense understorey of *Coprosma rhamnoides* is present in places. Bracken fern (*Pteridium aquilinum* var. *esculentum*) is common around all forest areas and is rapidly invading the grassland.

Kiore are the only mammals found on the island now that domestic stock and feral cats (*Felis catus*) have been removed. The only important predator is the Australasian harrier (*Circus approximans*).

METHODS

Two live-trapping grids were established (Fig. 1), one in forest and one in grassland. From February 1975 to June 1976, the traps were set over 2–6 nights at about monthly intervals, the shorter periods being dictated by bad weather. Less intensive trapping was carried out from June 1976 to May 1977. Kiore were trapped in dome-shaped wire cage traps ('Taika' brand) which had a spring-loaded door triggered by a bait hook. The funnel entrance in the top of the cage was closed and a shelter of PVC pipe was wired inside each trap. All traps were left permanently in position.

The forest grid had 7 rows of 10 traps spaced at 15 m intervals and the grassland grid had 8 rows of 9 traps spaced at 15 m intervals. In an experiment to measure the effect of trap spacing on density estimates, the grassland grid was altered in March 1976. Eleven traps were removed from one corner and, along with 28 new traps, these were used on part of the grid to form a sub-grid of traps spaced at 7.5 m. Three rows of the forest and grassland grids at 15 m intervals were adjacent.

Traps were baited late each afternoon with a disc of carrot covered with jam or peanut butter and were cleared each morning. From December 1976, cheese was used as bait and was replaced in the morning after the trap was cleared. Where the bait was not touched, the cheese was replaced every second or third day. To prevent kiore dying of exposure, traps were cleared at least once at night from May to September and during all nights of heavy rain. Traps from which rats were released in the middle of the night were not reset until the next afternoon.

After capture, each rat was transferred to a clear polythene bag and manoeuvred into one corner for examination. A numbered fish fingerling tag was put in one ear of previously unmarked rats. At all captures the following data were recorded: grid location, tag number, weight, and sex (for males, testes scrotal or abdominal; for females, vagina perforate or not, and nipples not, medium, or greatly enlarged).

Kiore were snap-trapped for autopsy using standard breakback traps baited similarly to live traps. Traps were set at about 15 m intervals in grassland along transects which followed mown tracks and in the forested gullies not used for live trapping from December 1974 onwards (Fig. 1). Additional animals were snap-trapped for autopsy on removal grids (7.5 m interval) in grassland and by trapping out the forest grid in May 1977. At autopsy, in addition to the information recorded on live animals, the following data were collected: total length; body and head length using the British Museum method of Jewell & Fullagar (1966); for females — uterus size (undeveloped, moderately developed, and enlarged); number and size of embryos; numbers of uterine scars; for males — testis length; and the presence or absence of visibly enlarged tubules of the cauda epididymis.

During the initial period of this study, the eyes of all kiore autopsied were preserved in 10% formalin, dissected, dried, and weighed to the nearest

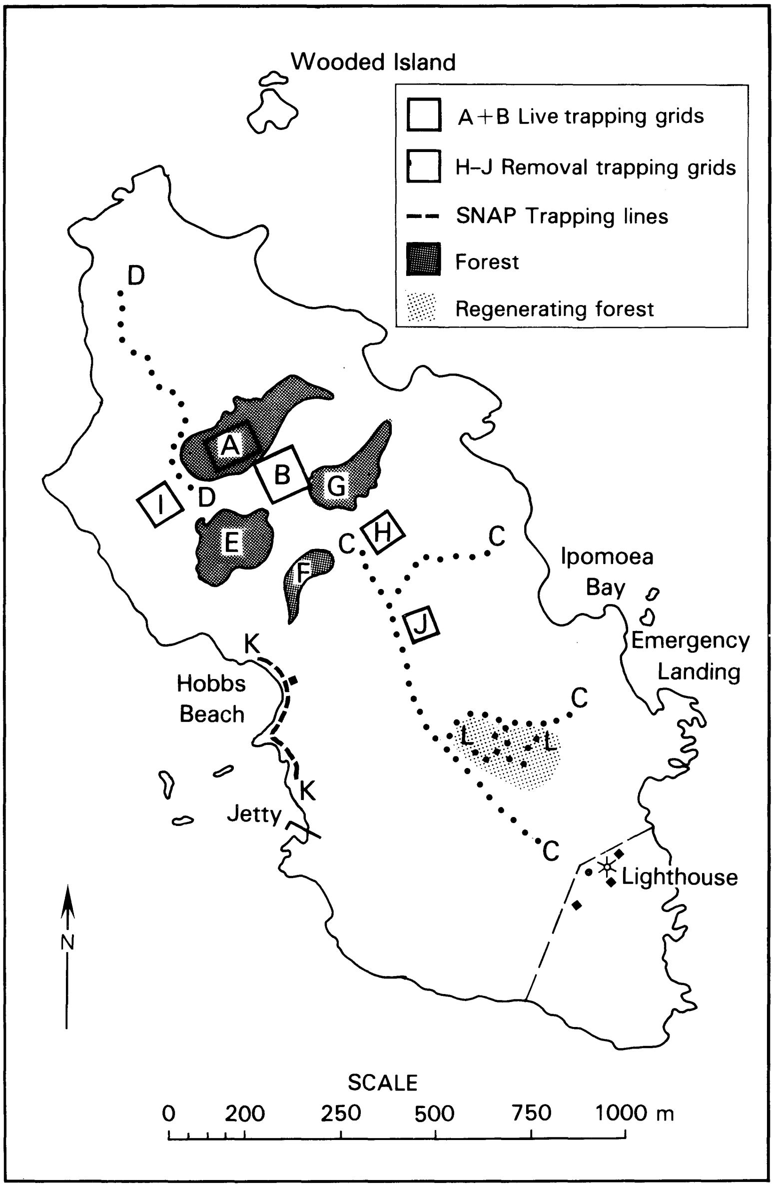

Fig. 1 Tiritiri Matangi Island showing position of live trapping grids (**A, B**), removal grids in grassland (**H, I, J**), and lines of snap traps in forest (**E, F, G**), grassland (**C, D**), manuka (**L**), and along the shoreline (**K**).

0.01 mg as an index of age (Williams 1976). From November 1975 the carcasses were left intact and preserved in 70% alcohol. To gauge the effect of the change in preservative, one eye of each of 35 kiore was fixed in 10% formalin and the other in 70% alcohol. On average, the lens preserved in alcohol weighed 0.27 ± 0.10 mg less than that of its partner preserved in formalin, a difference which was significantly different ($t=2.74$, d.f.$=34$, $P<0.01$) from zero. A pair of eye lenses therefore averaged 0.54 mg less when preserved in 70% alcohol than when preserved in 10% formalin.

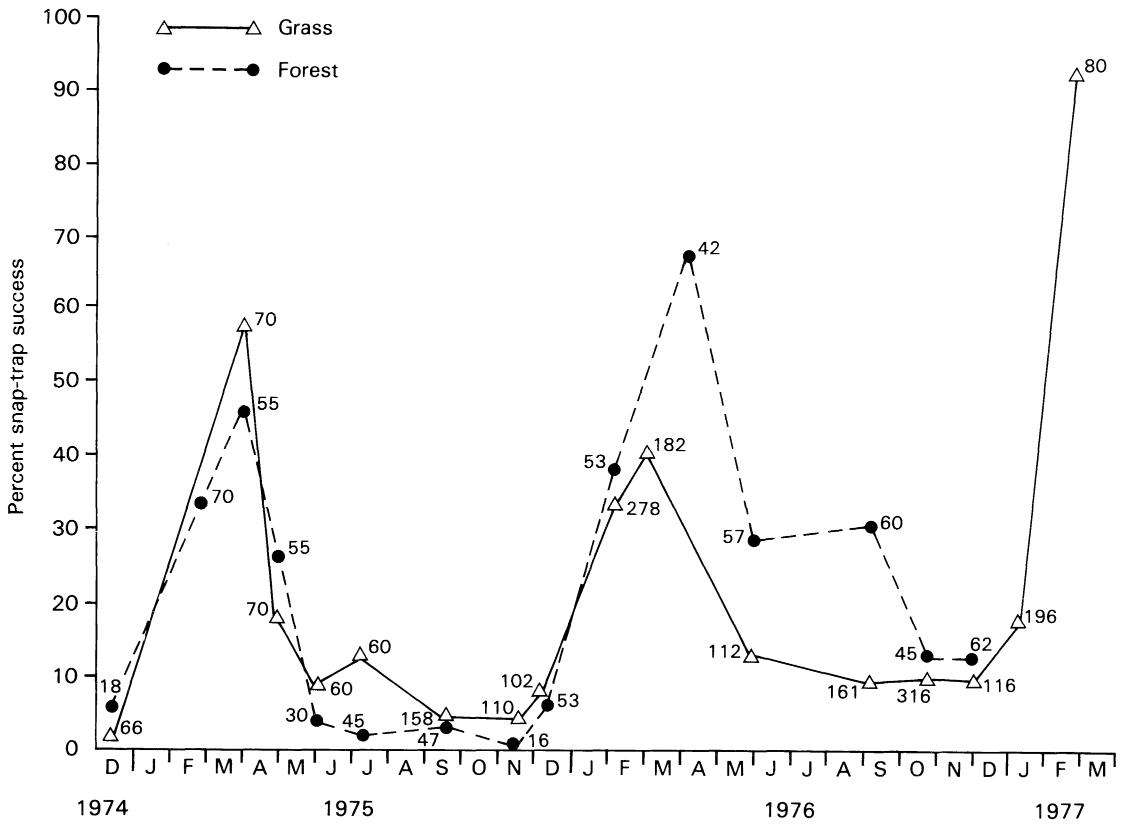

Fig. 2 Corrected percentage snap trap success for forest and grassland. The number of trap nights set is given beside each point.

Calculation of absolute density

The number of rats living on the two live trapping grids was estimated by the "Enumeration" or "Minimum Number Alive" (MNA) calculation (Krebs 1966) and the "Jolly-Seber" method (Seber 1973). Each night's catch was treated as a separate sample when calculating Jolly-Seber estimates, but all captures in each trap session were used when calculating the MNA. As recommended by Seber (1973), the Jolly-Seber estimates include only those samples where the random input variables m_i and r_i were both greater than 10.

In the first three sample periods MNA increased but this is an artifact due to an increasing proportion of the population being tagged. Therefore, only corrected MNA estimates are plotted on Fig. 3 for the first two sessions. These more reliable estimates of MNA were obtained by adding to each of these the untagged rats caught in Period 3 which would have been of trappable age in these previous periods. This assumes that the untagged rats caught in sample 3 had been present during the earlier trapping. As breeding had ceased before the first sampling (see below) this assumption is justified although it also assumes zero net migration.

The absolute density of rats was calculated by dividing these population estimates by the Effective Trapping Area (ETA) for each grid. The ETA was calculated by adding to the trap grid area a boundary strip (Dice 1938) half as wide as the average distance moved between successive captures of males and females combined (19.7 m in forest; 15.2 m in grassland). For the forest grid the ETA was 1.69 ha, and for the grassland grid 1.68 ha until 2 March 1976 and 1.43 ha thereafter.

To check population estimates, rats were removed from the forest grid over 4 days at the end of the study in May 1977.

RESULTS

Relative population index

Corrected snap trap success (Nelson & Clark 1973) suggested annual cycles of kiore abundance (Fig. 2).

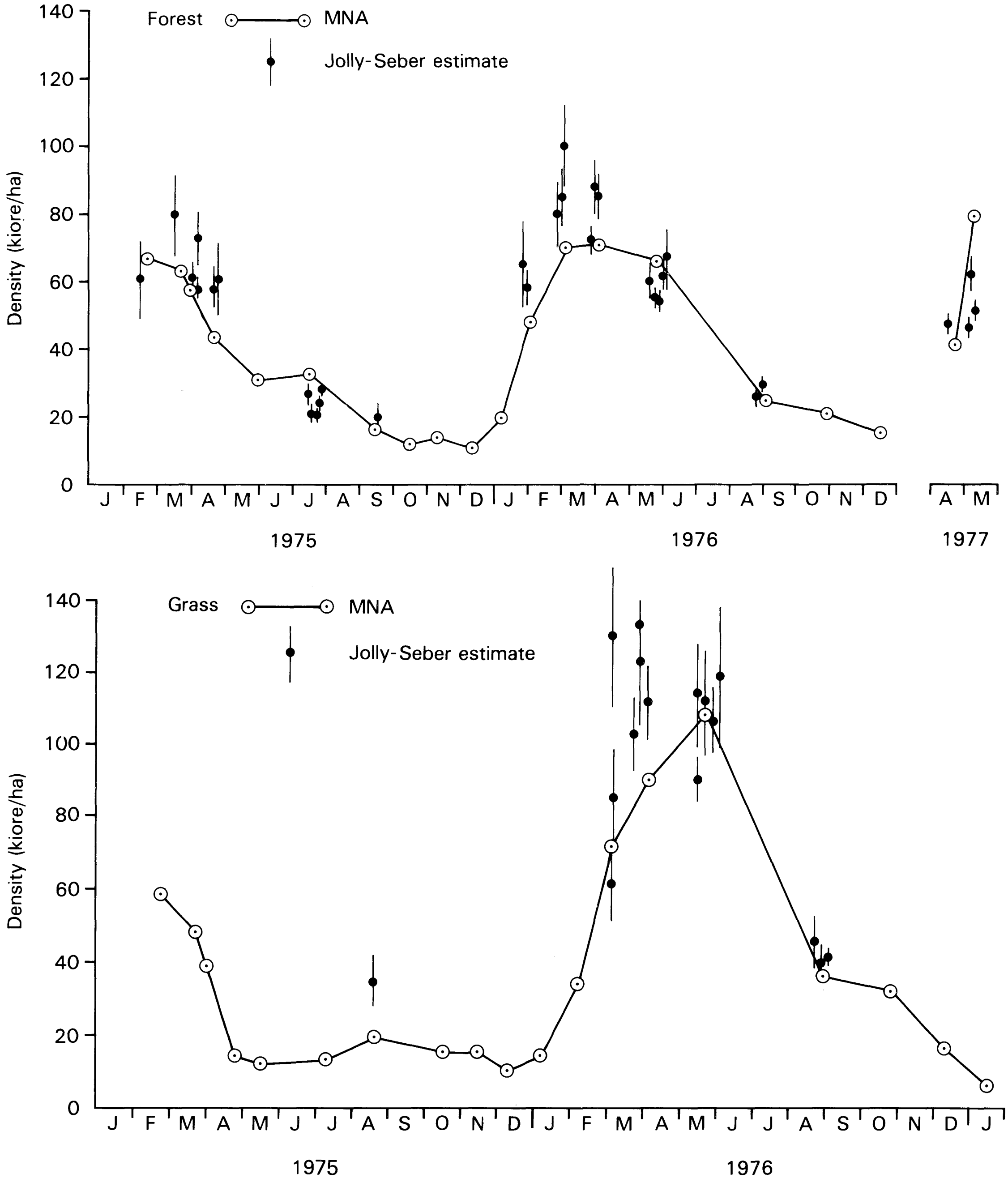

Fig. 3 Minimum number alive and Jolly-Seber estimates of absolute density for forest **(Top)** and grassland **(Bottom)**. The minimum number alive was corrected for the first two sample periods as described in the text.

Trap success was highest in late summer and early autumn each year and lowest during winter and spring. The rate of decline in the two autumns varied whereas the pattern and rate of rapid increase between December and March was similar in the 2 years.

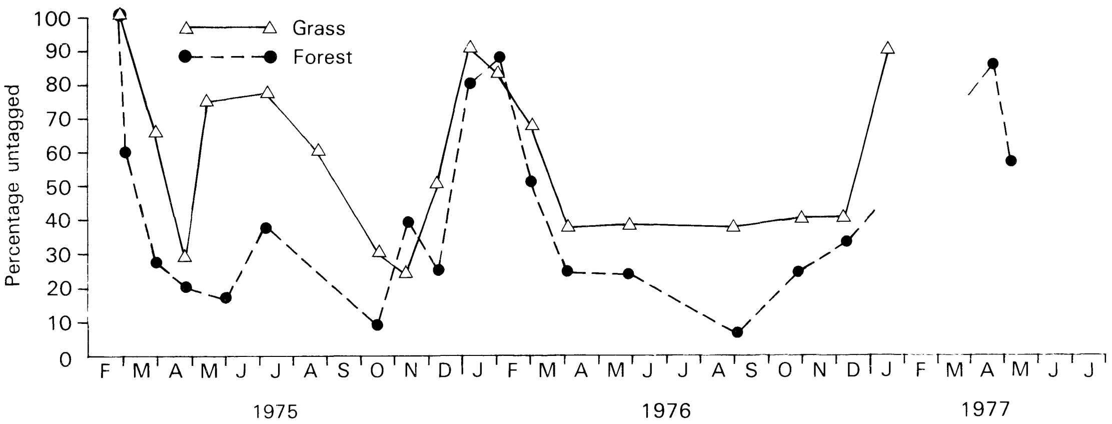

Fig. 4 Percentage of untagged kiore in forest and grassland grid samples.

Minimum number alive

MNA shows the same pattern of fluctuation as the snap trap index (Fig. 3). Trapping in grassland provided a reliable estimate of peak density of 108 ha^{-1} in May 1976. In forest, peak densities in both years were about 70–80 ha^{-1}. Minimum densities of 6–15 ha^{-1} were recorded on both grids in December or January. The density declined early in 1975 (March) and low numbers persisted throughout autumn, winter and spring whereas in 1976, the population did not begin to decline until June.

MNA underestimated rat density because, at all times, some untagged kiore were caught in the samples (Fig. 4). The proportion marked was higher on the forest grid than on the grassland grid except during rapid population rises, suggesting a greater underestimation of numbers in the grassland. This came about partly because males on the grassland grid were less trappable ($t=3.14$, d.f.$=32$, $P<0.01$) than those in forest; i.e., 75±5% ($n=16$) of males known to be alive on the forest grid were captured in each sample period, compared to only 52±8% ($n=17$) on the grassland grid.

Trappability of rats was affected by the availability of traps. In grassland, the higher proportion of marked animals in a sample after March 1976 coincided with the addition of the sub-grid (Fig. 4) suggesting that MNA would have markedly underestimated rat numbers before March 1976.

Jolly-Seber estimates

Jolly-Seber density estimates were usually higher than MNA (Fig. 3), particularly in mid summer when a large proportion of the rats living on the grids were untagged (Fig. 4). Peak densities of 130±20 ha^{-1} and 101±12 ha^{-1} were obtained on the grassland and forest grids respectively (Fig. 3).

There were several indications that the probability of capture was not constant within the populations. Marked males were retrapped more often than marked females on the forest grid: 75±5% of males known to be alive were recaptured in any sample period ($n=16$) compared with 52±8% ($n=17$) of females. In addition, the pattern of first captures, between nights within a sample period, differed for untagged and tagged kiore (Fig. 5). That this led to an underestimation of kiore numbers was confirmed by the removal trapping which allowed estimates of MNA that were consistently higher than Jolly-Seber estimates for the same time period (Table 1).

Length of breeding season

Vaginal perforation, enlarged uteri, pregnancy, and the presence of uterine scars can all be used as estimates of sexual maturity. Vaginal perforation was a poor indicator of sexual maturity, as several young perforate females (one weighed only 35 g) showed no enlargement of the reproductive tract, no corpora lutea, and no uterine scars. The number of perforate females autopsied (Appendix 1) is therefore an overestimate of the number of mature (potentially pregnant) females trapped. Conversely, the number of females carrying uterine scars (Appendix 1) is a minimal estimate of the number of mature females, particularly near the beginning of the breeding season when females ovulate for the first time (see later).

All pregnant females were trapped in the 4 months November–February inclusive (Appendix 1). In 1975, so few females were caught in September and October that the onset of breeding could not be recorded. However, the first juveniles were caught on 11 December 1975, and weighed 15 g and 17 g; they would have been born at the end of

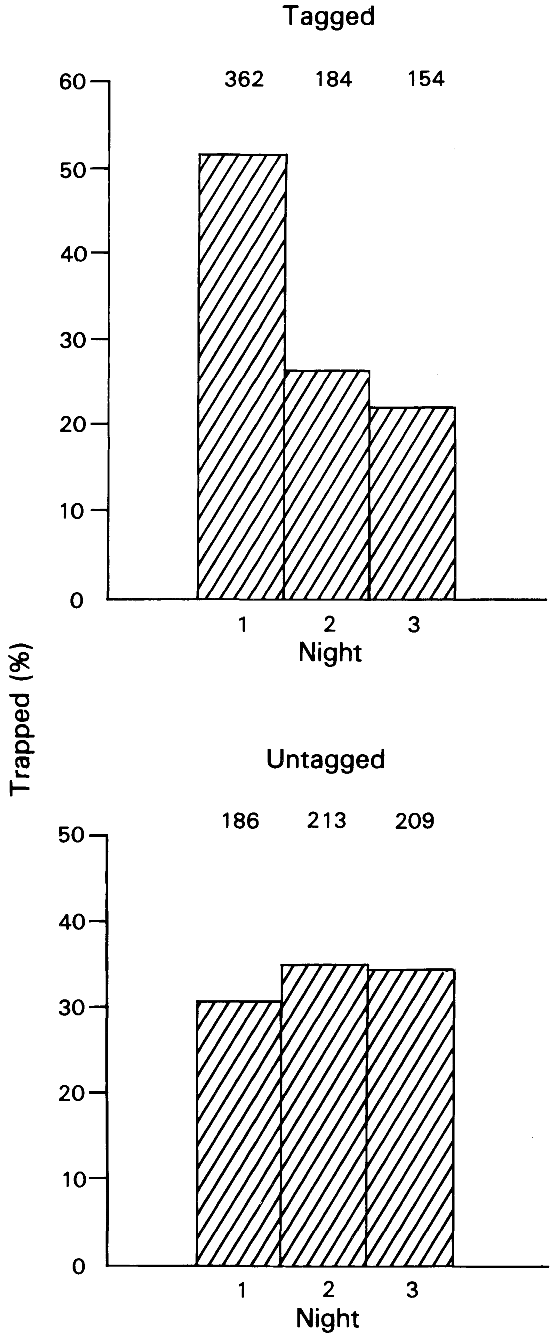

Fig. 5 Percentage of tagged and untagged kiore first caught on successive nights of trapping. Sample sizes are indicated above each bar of histogram. (Test of independence of night of first capture for tagged versus untagged rats gave $\chi^2=60$, d.f.$=2$, $P<0.001$).

Table 1 Population estimates and number of kiore removed on forest grid in May 1977.

Date	MNA*	Jolly-Seber	Kiore removed	
			Tagged	Untagged
6 May	123	78 ± 4	3	2
7 May	118	105 ± 8	6	3
8 May	109	87 ± 5	3	2
9 May	—	—	53	15
10 May	—	—	10	10
11 May	—	—	6	2
12 May	—	—	2	6

*Calculated by subtracting trap deaths from total of different rats trapped 6–12 May.

the third week in November (Moller 1977). The heaviest juveniles live trapped in January 1976 weighed 44 g and would have been born between mid and late November.

Seven of 8 females trapped in late October 1976 had greatly enlarged uteri but were not visibly pregnant. The first juveniles of the season were live trapped on 16–17 January 1977; 42 kiore caught in December 1976 were all adults. The heaviest of these juveniles were a male and female of 42 g each, which puts their birth at about the last week in November.

The lack of juveniles in the 19 December 1974 sample, along with the marked increase in population (Fig. 2), suggests that the first young were probably born in late November 1974 as well.

Breeding stopped in late January or early February each year as there were no pregnant females in the large snap-trap samples of late February and early March. Furthermore, in all years, the weights of the youngest juveniles caught in late summer or autumn indicate that they were born in late January or early February. Thus in all years births were restricted to a 10–12 week period from late November to late January or early February.

Age structure

The frequency distributions of total eye-lens weight were bimodal in both 1975 and 1976 (Fig. 6), as expected for a restricted breeding season. Young first entered the trappable population in January. Some juveniles trapped in March 1976 had considerably lighter eye-lenses than in March 1975, which suggests that breeding was prolonged in the second year (Fig. 6) as also inferred from pregnancies.

Litter size and annual production

The mean number of live embryos per pregnant female on Tiritiri was 6.7 ± 0.38 (Fig. 7a). The sam-

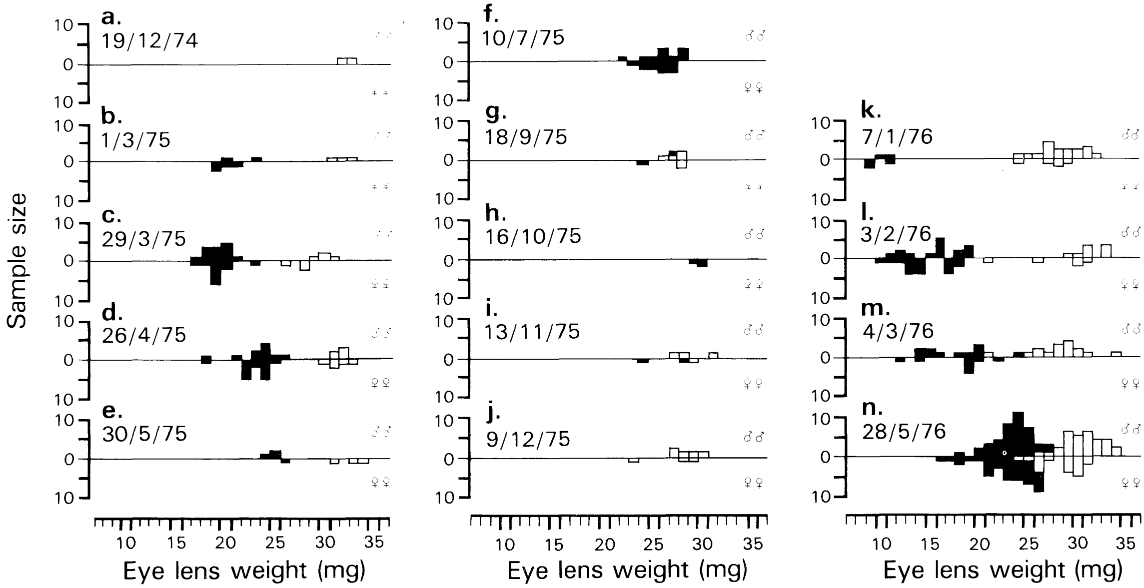

Fig. 6 The existence of age cohorts as demonstrated by seasonal patterns of eye-lens weight. Open bars represent males with tubules in cauda epididymis or parous females; blackened bars represent all non-reproductive males and females.

ple ($n=15$) is too small to compare months, habitats or years. One female was resorbing one embryo and another was resorbing two embryos.

The number of litters per year (L) can be estimated by modifying the method of Emlen & Davis (1948) such that $L=t \times p/18$ (where t=number of days in breeding season; p=proportion observed pregnant during season; 18=number of days of visible pregnancy). Considering all females with perforate vaginas in the 1975/76 breeding season gives $p=0.46$ and $L=2.7$ litters/year. Using only adult females (few juvenile females bred), $p=0.52$ and $L=3$ litters year^{-1}. These values represent maximum and minimum values and, with the 1975/76 mean litter size of 7.0, give production values of 19 and 21 young female^{-1} respectively for this breeding season. The combined data for 1975/76 and 1976/77 breeding seasons give an estimate of 2.3–2.6 litters female^{-1} year^{-1} or 15.5–17.5 embryos female^{-1} year^{-1}.

Annual production can also be measured by counting the uterine scars of females trapped after the completion of each breeding season. This is particularly accurate in the present study because very few kiore bred in the breeding season of their birth (see below) and none of the marked females survived to breed in a second breeding season.

It was possible to count scars in 49 kiore, and in a further 18 the scars were too indistinct to be counted reliably. The scar counts were distributed modally (Fig. 7b). The peaks at 14 and 20 scars per female correspond almost exactly with 2 and 3 times mean litter size, which gives confidence in the reliability of our measures of production (cf. Emlen & Davis 1948). The mean number of scars for these females trapped after the 1975/76 breeding season was 16.9$\pm$0.68 which closely approximates annual production estimates for this season (see above). The lack of females with fewer than 9 scars after the 1974/75 and 1975/76 breeding seasons further suggests that few adult females had a single litter in these seasons and that the young did not breed near the end of the season they were born in. However, 5 of the 15 females trapped in February and March 1977 had fewer than 9 scars (Fig. 7b) and therefore probably bore only one litter in the 1976/77 breeding season. The mean numbers of uterine scars in separate breeding seasons (Table 2) were significantly different (t-tests not assuming variances equal, $P<0.05$).

Table 2 Mean number of uterine scars carried by parous females after living through a complete breeding season.

	Breeding season when scars produced			
	1974/75	1975/76	1976/77	All seasons
Mean no. of scars	13.5	16.9	9.8	14.3
SE	1.18	0.68	1.02	0.69
n	6	28	15	49

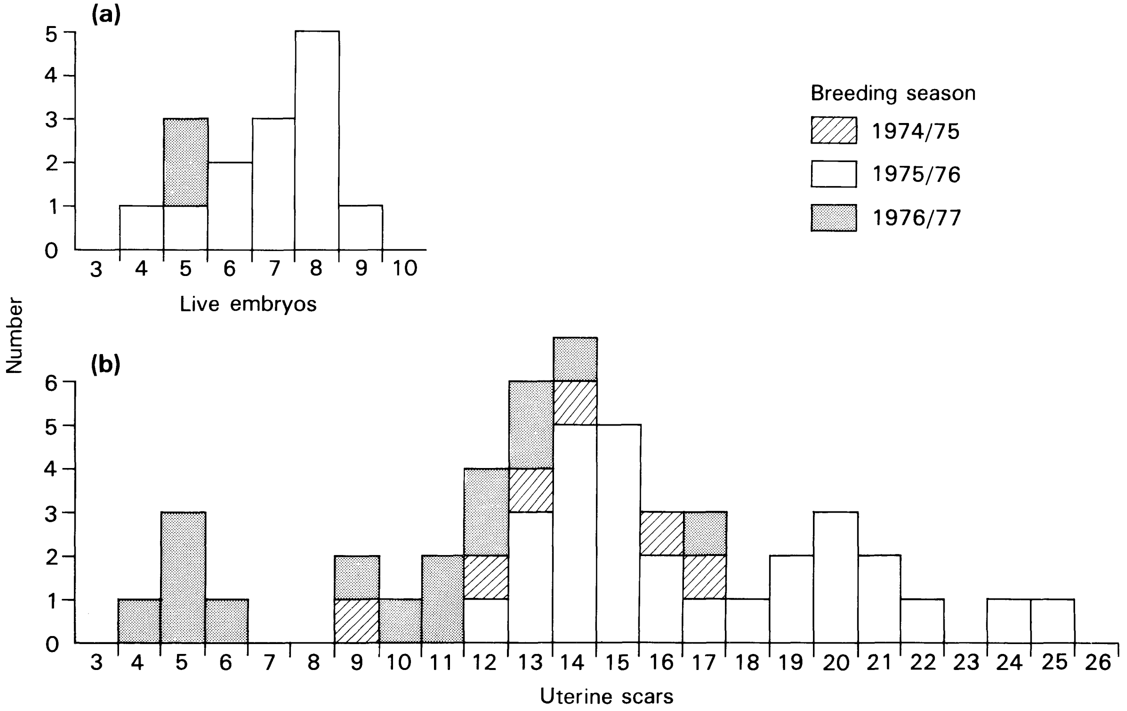

Fig. 7 Reproductive parameters of female kiore: **(a)** number of live embryos per pregnancy; **(b)** number of uterine scars per parous female captured outside breeding season.

Sexual development

Males from each older cohort (as indicated by eye-lens weight; Fig. 6) all had tubules visible within their cauda epididymis and thus were sexually mature (Jameson 1950). Therefore, males were reproductive long after females ceased breeding. The absence of visible tubules in all males from the young cohort trapped in 1975 indicates that no young males attained sexual maturity in the 1974/75 breeding season. Similarly, all but one of the males born in the 1975/76 breeding season did not attain sexual maturity until after their parents ceased breeding for the year. The exception was one male trapped on 4 March 1976 that had an eye-lens weight of 21 mg and visible tubules. In 1975, nearly all males matured between July and September when they were 6–10 months old.

Attainment of sexual maturity in males varied with habitat in 1976 as a higher proportion of live trapped males had scrotal testes in April and June 1976 (151 caught) than in March (38 caught) for the grassland but not in the forest (Fig. 8). Testes descended into the scrotal position as they enlarged (Moller 1977).

Parous females (i.e., with embryos or uterine scars) caught in 1975 all belonged to the old cohort as indicated by eye-lens weight (Fig. 6). One young female weighing only 47 g was pregnant in our January 1976 sample. A pregnant female trapped on 5 February 1976 also had uterine scars and was therefore probably an old (1974/75 cohort) female, even though her lenses weighed only 21 mg. Six females trapped in May 1976 had uterine scars and lens weights of 24–27 mg, and some of them may have been young of the year. The remaining 61 young females trapped between February and June 1976 were non-parous. Therefore the vast majority of females on Tiritiri did not reproduce until the breeding season after their birth, when they were 8–12 months old.

Causes of death

A pair of harriers lived on Tiritiri but more were present in late summer and autumn (Fig. 9) and we saw harriers flying from the adjacent mainland. M. Dawe (pers. comm.) disturbed a harrier eating a live rat, so these hawks were killing rats as well as perhaps scavenging.

Social interference and stress might have increased mortality rates. Several kiore had scars on their rumps, tails and ears, probably from bites from other rats as Davis (1979) found for captive

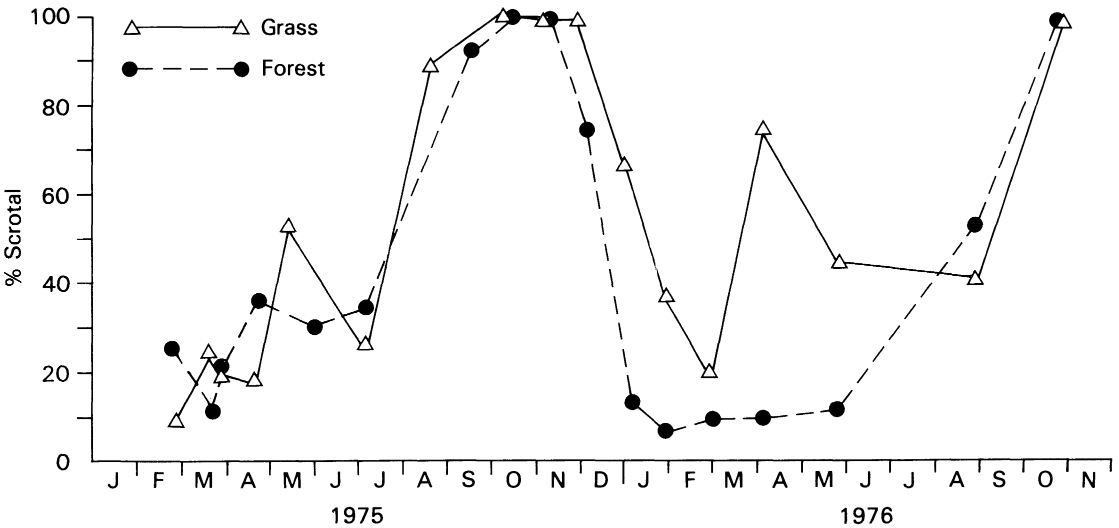

Fig. 8 Proportion of male kiore with scrotal testes in forest and grassland.

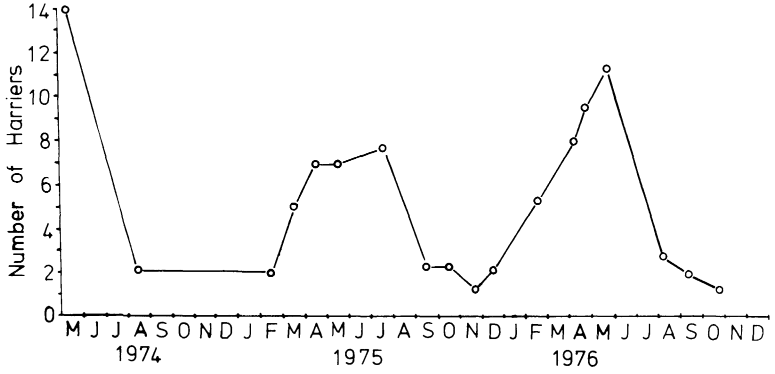

Fig. 9 Maximum number of harriers sighted on the wing at the same time during each visit to Tiritiri Island.

kiore. Calls were heard and frantic chasing was often observed at night.

Some kiore had large bare patches around the rump and up the spine, possibly caused by ectoparasites. G. Ramsay (pers. comm.) identified four species of mites collected from kiore: *Radfordia ensifera* (Poppe); *Hypoaspis nidicorva* (Evans & Till); *Hypoaspis claviger* (Berlese); and *Mesolaelaps australiensis* (Womersley). Only one species of flea, *Pygiopsylla phiola,* was present (Smit 1979). Lice were identified as *Hoplopleura pacifica* Ewing (R. L. C. Pilgrim pers. comm.).

Recovery rates of tagged rats

An index of survival rates was gained from the proportion of rats captured and then released in sample i which reappeared in sample $i + 1$ or subsequently. This proportion was adjusted for variable intervals between trapping sessions to give the monthly (30 day) probability of reappearance (Fig. 10). Probabilities of reappearance were particularly low in the grassland grid after the February and March 1975 samples and highest throughout the winter on both grids, decreasing in the breeding months (November to January).

The average probability of reappearance in grassland was lower in 1975 than in 1976 (Mann-Whitney U=72.0, P=0.05). None of the other differences between years in the same habitat, or between habitats in the same year (Table 3a) was statistically significant. Differences in probability of appearance of the sexes (Table 3b) in grassland (U=331.5, P=0.975) or forest (U=435.0, P=0.06) were not significant, but males were more trappa-

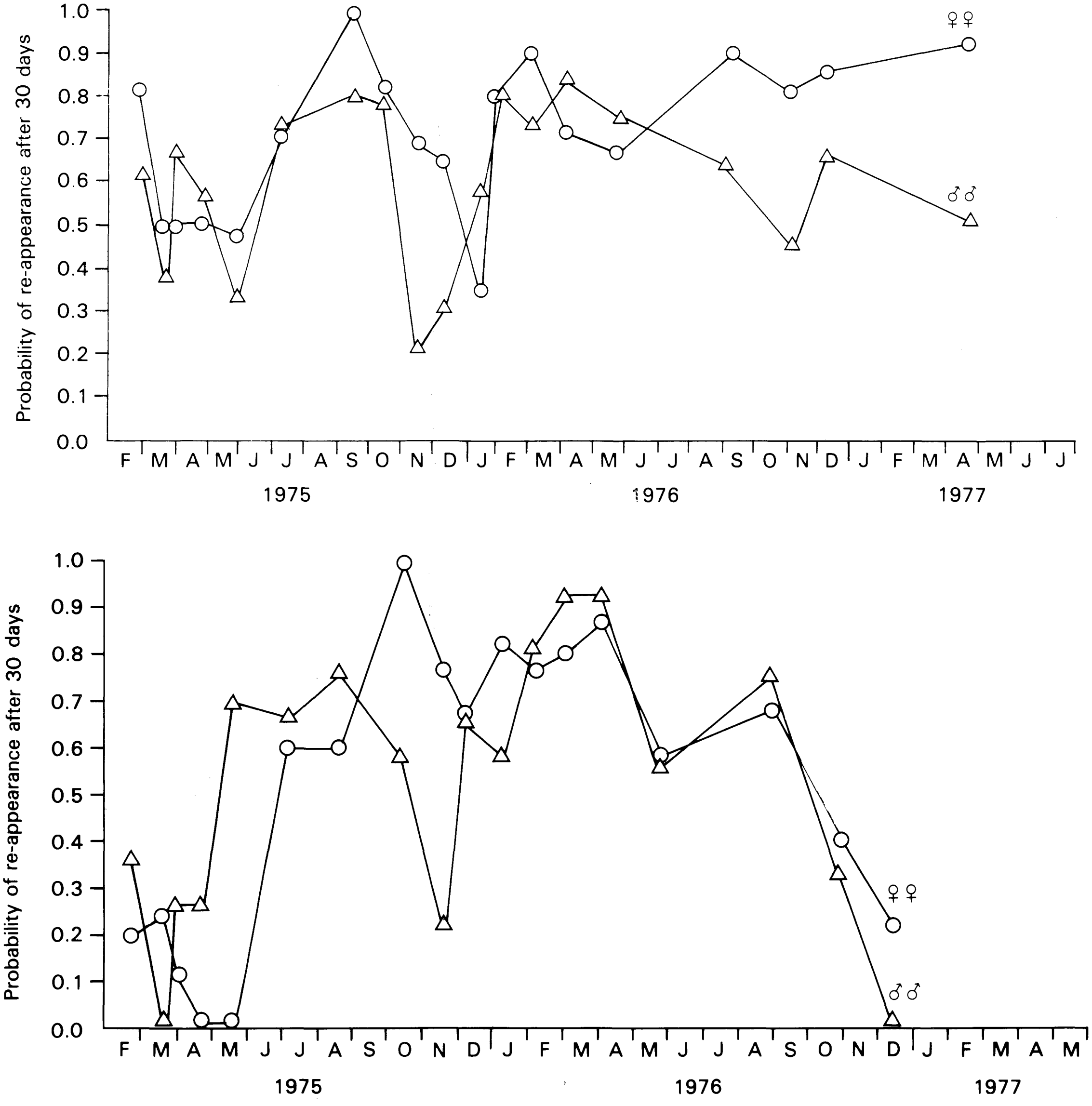

Fig. 10 Monthly probability of reappearance for male and female kiore on the forest grid **(Top)** and on the grassland grid **(Bottom)**.

ble than females in forest (see above), so real differences in survival between the sexes may still have occurred in this habitat.

Few tagged rats lived longer than 12 months and none longer than 15. No adult rats were present on the live-trapping grids for two breeding seasons.

Survival with respect to age and sex

Seasonal changes in survival for the whole population might be biased if survival was age or sex dependent. We could estimate survival for separate cohorts because newly live-trapped kiore could be readily assigned to the young or old generation at the beginning of each year from their weight, testis position, size of mammae, and degree of scarring on their ears and tail. Comparisons of the number of young and old rats of each sex known to be alive at the end of March 1975 (when enumeration of the population was most complete) with those in July 1975 (the last month when newly tagged kiore could be reliably aged) will index relative survival,

Table 3 Mean monthly probability of reappearance for years, habitats, and sexes.

	Forest				Grassland			
	Median	X̄	SE	*n*	Median	X̄	SE	*n*
(a) Combined sexes								
1975	0.59	0.63	0.051	10	0.43	0.42	0.080	10
1976	0.76	0.72	0.042	8	0.72	0.61	0.092	8
All periods	0.70	0.67	0.033	19	0.60	0.50	0.063	18
(b) Combined years								
Males	0.64	0.60	0.043	19	0.58	0.52	0.068	18
Females	0.71	0.72	0.042	19	0.60	0.52	0.074	18

Table 4 Minimum number of male and female kiore of young and old cohorts known to be alive in autumn and winter 1975 and 1976.

	Born before 1975/76 season		Born in 1975/76 season		Born in 1976/77 season	
Habitat and date	Males	Females	Males	Females	Males	Females
(a) Forest						
29 March 1975	12	13	33	36	—	—
9 July 1975	4	3	15	29	—	—
2 March 1976			4	9	52	49
29 May 1976			2	4	46	46
(b) Grassland						
29 March 1975	3	12	30	19	—	—
10 July 1975	2	2	12	5	—	—

provided that the net migration rates are independent of age. There was a trend of a higher proportion of young rats remaining in winter in both 1975 and 1976 in forest (Table 4) but the differences were not significant ($\chi^2=3.18$ and 1.80 respectively, d.f. = 1, $P>0.05$). In grassland, a similar proportion of old and young rats were alive in early July as in March 1975 ($\chi^2=0.18$, d.f. = 1, $P=0.6$). No comparison could be made in 1976 as the testes of juvenile males developed earlier in that year compared with 1975 (Fig. 8) and so age was difficult to assign after April.

If there was zero net migration and the population was equally well enumerated, the ratios of initial and final rat numbers in Table 4 will estimate the absolute probability of survival over the intervening periods. The 30 day survival probabilities calculated from these ratios were considerably higher than the monthly reappearance probabilities of tagged rats over the equivalent months (Table 5). This discrepancy could have been caused by emigration from the trapping grid.

Movements

Seven marked kiore were snap trapped 140–540 m away from the live-trap grids. This shows that some kiore moved long distances, but little snap trapping was done elsewhere on the island so the prevalence of such long-range movements is difficult to judge from these data. Most animals live-trapped were caught within part of one grid, and only three rats from each grid moved onto the other grid. This indicates that very few rats moved between the forest and grassland and therefore each can be considered as a discrete population.

Males moved greater distances between successive sample periods during October, November, and December in both grids (Moller 1977). This happened at the beginning of the breeding season, and may explain the low reappearance rates for males at this time (see Fig. 10). Distances moved by females were more similar in all seasons and no consistent patterns appeared.

Weight changes

Seasonal changes in reproduction and mortality suggest that fluctuations in ecological conditions were influencing the rats. One index of nutrition is their weight.

Rats were, on average, heaviest in spring and lightest in summer after the influx of young rats (Fig. 11). These weight changes were not just caused by a changing population age structure because tagged kiore fluctuated markedly in weight between successive captures (Fig. 12). Kiore lost weight in late summer, autumn, and early winter in 1975 but

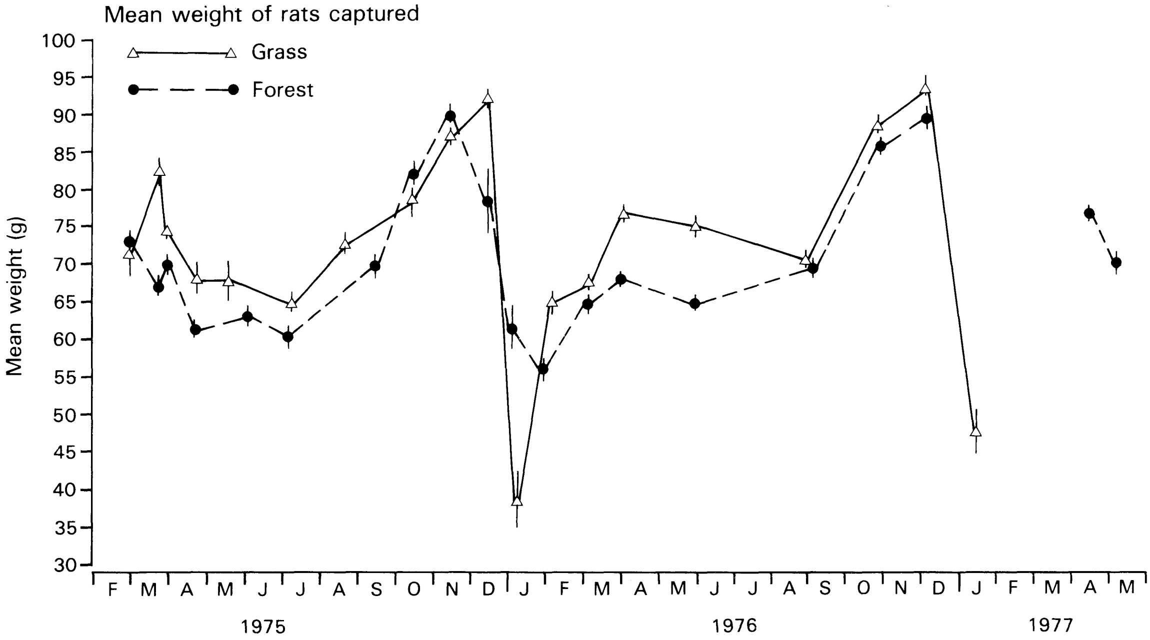

Fig. 11 Mean weight (±95% confidence interval) of kiore captured in each sample on forest and grassland live-trapping grids.

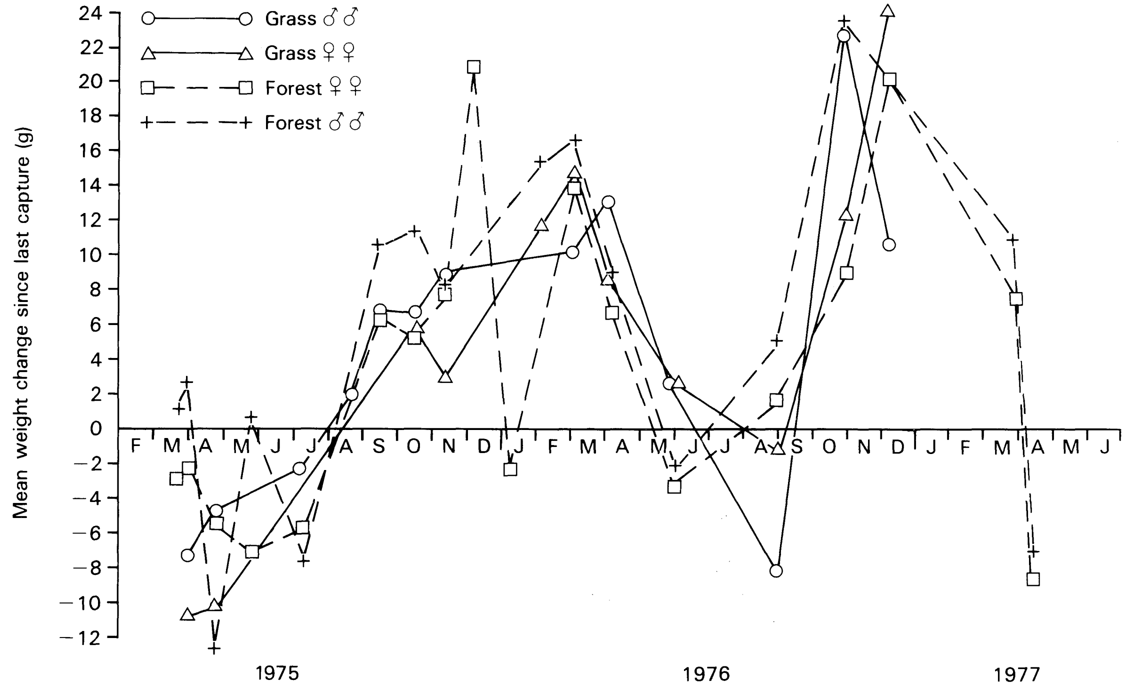

Fig. 12 Mean weight change since previous capture for male and female kiore in forest and grassland.

Table 5 Monthly (30-day) probability of reappearance of tagged rats and monthly probability of survival over the same periods: probability of survival was calculated from decrease in MNA of each age cohort (data given in Table 4).

Habitat and period	Monthly probability of reappearance	Monthly probability of survival
Forest, 29 March–9 July 1975	0.57	0.83
Forest, 2 March–29 May 1976	0.79	0.97
Grassland, 29 March–10 July 1975	0.26	0.72

those rats remaining after July increased steadily in weight to peak in summer and early autumn 1976. The rats then increased in weight more slowly and by late autumn and early winter 1976 began losing weight. After August 1976 the rats increased in weight again. In autumn 1977 the few rats recaptured lost weight. Individual weight loss of 20–30 g was common in March and April 1975. One scrotal male declined in weight from 125 g on 31 March 1975 to 80 g on 25 April 1975, a loss of 36% in 25 days.

Weight loss varied between habitats. Forest males showed more pronounced loss in April–May 1976 than did males in grassland (Fig. 12). This coincided with a faster testis growth of males in grassland (see above).

DISCUSSION

Rat density

Absolute densities of small mammals are difficult to assess because the methods assume equal probabilities of capture and survival, and the effective trapping area is difficult to measure. Kiore were not equally trappable on Tiritiri. This underestimates population density (Eberhardt 1969; Carothers 1973a, b). The Jolly-Seber estimates were lower than MNA in May–June 1976 and May 1977 even though MNA is known to underestimate density. The Jolly-Seber method responds instantaneously to input of young during the breeding season whereas adequate enumeration of the population is delayed, by which time the real peak in density is likely to have passed. Therefore Jolly-Seber and MNA are best used together as biased underestimates of rat density.

We have recalculated some published estimates of density of kiore in the Pacific and Asia (Table 6) by including a boundary strip when estimating ETA (Jackson & Strecker 1962; Wodzicki 1969; Wirtz 1972). Comparisons of corrected estimates suggest that the peak densities on Tiritiri were high and approach the extremes elsewhere in the Pacific. The densities of kiore measured on Tiritiri are much higher than those reported for other rodents in New Zealand (Bettesworth 1972b; Daniel 1972, 1978; Fitzgerald et al. 1980; Hickson et al. 1986).

Snap trap success suggests that the density of kiore on Tiritiri is similar to that on northern offshore islands of New Zealand which do not have predators (stoats and cats) or other rodent competitors (Appendix 2, Fig. 13). Zero trap success on two islands (3 and 4 in Fig. 13) in the Mokohinau Group (which are known to have kiore present) is probably because the only trapping done was in spring when the population would have been at a minimum (Fig. 2, 3). Otherwise the only small northern offshore island with low kiore trap success, even in autumn, is Moturua (number 2 in Fig. 13). Low density there may result from the presence of Norway rats, stoats and a small population of feral cats (Moller & Tilley 1986). The islands with other rodents present tend to have lower kiore density, but these same islands also tend to have predators present, are larger, and are situated further south in New Zealand. A latitudinal trend of lowered kiore density, or a decrease in density consequent from increased dispersal on larger islands, the presence of predators, or the presence of rodent competitors each might wholly, or in part, explain the trends seen in Fig. 13. Comparisons of density on the same island before and after the removal or introduction of competitors or predators are necessary to unravel the influence of each. Atkinson (1973, 1978) and Taylor (1975, 1978) have emphasised competition in limiting kiore. Daniel (1972, 1978) and Fitzgerald (1978) suggest predators lower the numbers of the other rodents in New Zealand.

Kiore have been blamed for the demise of many of our smaller vertebrates and larger invertebrates (reviewed by Dingwall et al. 1978; Campbell et al. 1984; Craig 1986). The very high densities recorded in our study make this impact more likely, since even a comparatively minor constituent of the diet might suffer severe depredation. The crashes observed in the kiore population on Tiritiri with the concomitant weight losses suggest that the rat density sometimes exceeded the level sustainable. Pressure on minor or non-preferred food species may be strong during these periods of over-population. However, the wide differences in the density

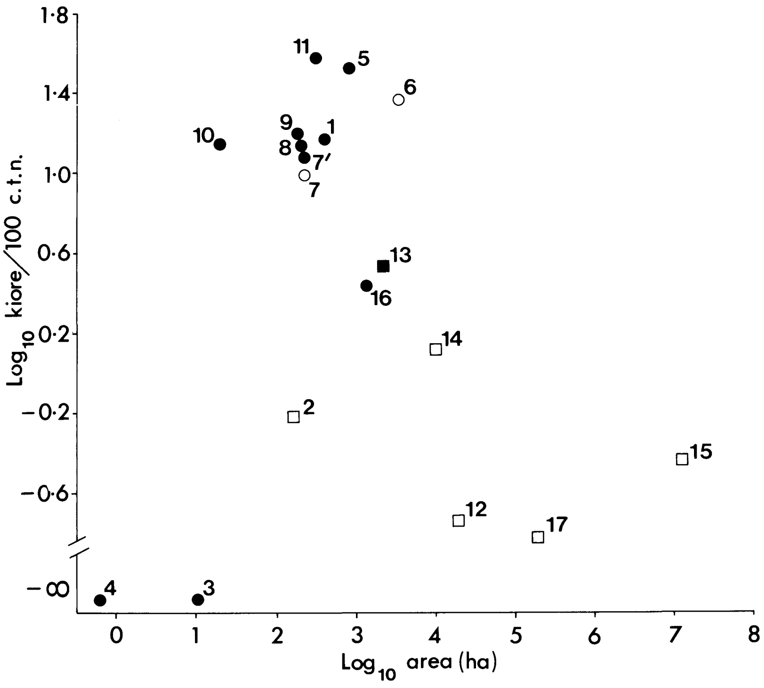

Fig. 13 Snap trap success for *Rattus exulans* plotted against island area for 17 offshore islands of New Zealand. Trap success is corrected by the method of Nelson & Clark (1973). A single average is given for islands which have been repeatedly sampled. Habitat, seasonal coverage, trap type and bait vary considerably. Squares indicate that rodents other than kiore are also present on the island, circles indicate that kiore alone is present. Solid symbols indicate that cats and mustelids are not present, open symbols that cats or stoats are present. The number beside each symbol indicates the island's name. Islands are listed in rank order of latitude, i.e.,: 1 = Motukawanui; 2 = Motuorua; 3 = Hokoromea; 4 = "Stack G", Mokohinau Group; 5 = Hen; 6 = Litter Barrier; 7 = Cuvier, with cats; 7′ = Cuvier, after cats removed; 8 = Tiritiri; 9 = Red Mercury; 10 = Korapuki; 11 = White; 12 = D'Urville; 13 = Kapiti; 14 = Arapawa; 15 = South; 16 = Codfish; 17 = Stewart.

of kiore in different parts of New Zealand (Fig. 13) suggest that it may be unwarranted to extrapolate from our knowledge of the northern island populations. Before we can generalise about kiore populations in pre-European times and their possible effect on other fauna we must attempt to isolate the effects of latitude, habitat, predators, and competitors.

Seasonality of population dynamics

Kiore showed marked seasonal fluctuations in numbers over the 3 years of our study. Information on reproduction and age structure from autopsied rats and survival of marked rats were all consistent with the density fluctuations observed. An intense breeding season of 3–4 months produced many young rats between December and January February, and the population increased rapidly from its low in spring to a peak in late summer and autumn. The population then declined in autumn and winter after breeding stopped and as rats died.

The same seasonal pattern occurred in the year preceding our study. The density of kiore in May 1974 was so high that A. Harrison (pers. comm.) was able to kill 38 rats by clubbing them with a stick. None of the 18 females autopsied were pregnant and the lightest weighed 52 g.

Watson (1956) gave tentative evidence of a rapid increase in kiore population density from January to February on Little Barrier Island, which suggests that breeding started at about the same time there as on Tiritiri. Similarly, the sharp decline in the number of rats caught in June suggests that breeding stopped in winter in that population. However, he found kiore breeding in March 1954 whereas on Tiritiri most breeding ceased in January. Dick (1985) caught pregnant kiore on Kapiti Island in November, January, and April. Sample sizes were small, so the breeding season was probably longer than the 6 months of November–April. Compared with Tiritiri, both Little Barrier and Kapiti Islands are large and predominantly forested.

On Cavalli and Cuvier Islands, kiore were inconspicuous in summer but numerous around the houses in autumn and winter (Watson 1956). Oliver (1910) saw few kiore on the Kermadecs in January, but they then increased to become plentiful in March–April, and were very numerous in June. Thereafter, their numbers decreased so that by September–October very few were seen. On Red Mercury Island, Bettesworth (1972a) trapped 10 perforate female kiore in August 1971; none were lactating or pregnant. D. J. Campbell (pers. comm.) caught 22 females on Taranga (Hen Island) between 23 August and 2 September 1963 and none of these were pregnant or lactating. Three of 11 females trapped on Korapuki Island, Mercury Islands, in late November–early December 1974 were pregnant (Hicks et al. 1975). Mean weights and lengths

Table 6 Maximum and minimum densities recorded for *R. exulans*.

Source and country	Locality	Habitat	Boundary strip	Method of estimation	Maximum density (kiore/ha)	Minimum density (kiore/ha)
Present study, New Zealand	Tiritiri Island	Forest	+	MNA Jolly-Seber	79 101±12	10 —
		Grassland	+	MNA Jolly-Seber	108 130±20	6 —
Wirtz (1972) Hawaii	Kure Atoll	Scaevola scrub	+[1]	Hayne (1949)	140	40
Tamarin & Malecha (1971) Hawaii	Oahu Island	Kiawe forest	—	MNA	30	2
Tomich (1970) Hawaii	Hawaii Island	Trees and grass (Gulch)	?	Hayne (1949)	32	1
		Grassland (Spencer field)	?	Hayne (1949)	6	—
		Sugarcane (field 001)	?	Hayne (1949)	15	—
		Sugarcane (field 101b)	?	Hayne (1949)	35	—
		Sugarcane (field 33b)	?	Hayne (1949)	12	—
Twibell (1973) Tonga	Niuatoputapu Island	Coconut plantation	?	?	99	—
Williams (1974) Fiji Islands[2]	Vanua Levu	Coconut plantation (Salt lake)	+	Jolly-Seber	58±6	24±1
	Viti Levu	Cocoa plantation (Namara Rd)	+	Jolly-Seber	145±9	50±6
	Viti Levu	Coconut plantation (Wainigata)	+	Zippen (1958)	137±28	25±7
Baker (1946) Mariana Islands	Guam	Grassland, modified forest, and coconuts	—	Number of different rats caught	21	3
Wodzicki (1969) Tokelau Islands	Motuakea Motu	Coconut plantation	NA[3]	Smit (1968)	36±7	—
	Tepuka N. Motu	Coconut plantation	NA[3]	Smit (1968)	23±4	—
	Motu-Fogalaki -Matagi	Coconut plantation	NA[3]	Smit (1968)	5±.3	—
	Awalau	Coconut plantation	+[4]	Smit (1968)	42±2	—
	Nukunonu West (1967)	Coconut plantation	+[4]	Smit (1968)	77±8	—
	Nukononu West (1968)	Coconut Plantation	+[4]	Smit (1968)	119±7	—
Strecker (1962)	Ponape	Grassland	+[5]	Hayne (1949)	29	17
		Coconut grid A	+	Hayne (1949)	113	49
		grid B	+	Hayne (1949)	68	35
Dwyer (1978) New Guinea	Eastern highlands	Grass	+	MNA	22.8	18.9

"Boundary Strip" refers to the additional area outside that of the trapping grid sometimes added to estimate the effective trapping area. In many cases estimates of this table have been recalculated from the data of the original authors (listed at 'source') according to the criteria outlined in the footnotes. Localities are arranged in order of decreasing latitude.

[1] Boundary strip calculated using mean average distance moved by sub-adults, non-breeding adults, and adults as given in fig. 12 of Wirtz (1972).

[2] Predominantly *R. exulans* but includes some *R. rattus*.

[3] Not applicable since complete islet trapped.

[4] Boundary strip calculated using mean distance moved between captures at Awalau and Nukunonu West 1967 grids from fig. 6 of Wodzicki (1968).

[5] Boundary strip calculated from table 32 of Jackson & Strecker (1962) (using median distance in each frequency class 1–60, 61–120, etc.).

Table 7 Reproductive parameters of *R. exulans* populations.

Source	Locality	Latitude	Length of breeding season (months)	Mean	Foetuses per pregnancy range	Sample size	Annual number of litters	Annual production (embryos/ year)	Comments
Dick (1985)	Kapiti Island, New Zealand	40.8°S	—	4.7	—	6	—	—	
Present study	Tiritiri Island, New Zealand	36.6°S	3–4	6.7	4–9	15	2.7–3.0	19–21	
Watson (1956)	Little Barrier Island, New Zealand	36.3°S	—	4.7	2–6	12	—	—	Jackson's (1962) estimates for production make false assumptions of continuous breeding
Hitchmough (1980)	Motukawanui Island, New Zealand	35°S	—	6.7	4–8	7	—	—	
Wirtz (1972)	Kure Atoll	28°N	8	3.81	1–8	125	?	?	Figures for incidence of pregnancy and production are in doubt
Nicholson & Warner (1953)	New Caledonia	22°N	—	3.0	1–5	9	—	—	Bimodal breeding pattern suggested but sample size too small to gauge length of breeding season
Tamarin & Malecha (1972)	Oahu, Hawaiian Islands	21°N	12	4.0	—	7	4.3	17.2	
Williams (1974)	Fiji	17°S	10	3.1	—	—	4.0	12.4	
Harrison & Woodville (1949)	Rangoon, Burma	17°N	—	4.0	2–6	62	—	—	
Mosby (1971)	Tokelaus	8°–10°S	—	3.2	—	—	3.2	10.2	
Jackson (1962)	Ponape	7	12	2.5	—	203	3.9	9.8	
Jackson (1962)	Majuro Atoll	7	—	3.0	—	68			
Dwyer (1978)	New Guinea	6	12	3.4	—	68	7.7–11.4	25.9–38.1	Grassland and gardens only
Harrison (1951)	Malaya	3	12	4.5	1–7	38	5.7	25.6	

for 11 juveniles trapped were markedly less than those for 19 adults. This strongly bimodal distribution of age indicates that the rats had not bred in the preceding winter. The presence of juveniles in the trappable population in late November suggests that breeding began earlier on Korapuki than on Tiritiri. Hitchmough (1980) also detected a strongly bimodal size and age distribution amongst kiore trapped on Motukawanui Island in January.

Evidence from Tiritiri and these other eight islands suggests that seasonal breeding may be a general pattern for kiore in New Zealand. However, the exact timing of the onset and termination of breeding varies between populations, or between years.

Geographic patterns of demography

The strongly seasonal pattern of reproduction in kiore on northern offshore islands of New Zealand contrasts with the pattern for *R. exulans* in the tropics. There *R. exulans* reproduce for all or most of the year (Table 7) and the resulting population fluctuations are less pronounced than in New Zealand. The pattern on Tiritiri is most similar to that on Kure Atoll (Wirtz 1972) where the population fluctuated from 40 to 140 kiore per hectare (Table 6) over an 8 month breeding season (Table 7).

Mean litter size increases significantly with latitude (Table 7: $r=0.69$, d.f.$=12$, $P<0.01$). Lord (1960) and Jackson (1965) suggested that an increase in litter size (for *R. exulans* and for small mammals in general) with latitude indicates that animals at higher latitudes have evolved higher reproductive rates. Higher reproductive rates were supposed to balance the higher mortality that results from increased predation. However, there is no correlation between latitude and the annual productivity of mature females (Table 7: $r=-0.26$, d.f.$=5$, $P>0.05$), maximum density (Table 6: $r=0.33$, d.f.$=8$, $P>0.05$), or survival rates (Moller 1977) in *R. exulans*. Lord's (1960) and Jackson's (1965) explanation for latitudinal increases in litter size subscribes to group selection arguments since it implies that females in tropical areas have lower reproductive rates than they could otherwise attain. Spencer and Steinhoff (1968) state:

> "We believe the shorter seasons of more northern latitudes or higher altitudes limit the number of times an animal resident in those areas is able to reproduce in its life-time compared to its relatives in lower or more southern regions. It therefore becomes more advantageous for an animal to invest its energies in a few, large, early litters even though doing so reduces its life expectancy and total reproductive contribution below the maximum achievable by many small litters. This is so because short seasons make it impossible for an animal to realise the returns from the conservative approach within its life-time."

The data for *R. exulans* are consistent with Spencer & Steinhoff's (1968) hypothesis in that the extremely large litters, compared to other populations, are coupled with a very short breeding season and females rarely survive to a second breeding season. The length of the breeding season declines significantly with increasing latitude (Table 7: $r=-0.89$, d.f.$=5$, $P<0.01$). The breeding season of kiore on Tiritiri is so short that at most three litters could be produced and few if any females survive to reproduce in two successive breeding seasons. Even if the production of such large litters seriously impairs the expectation of further life of females on Tiritiri, this is of little consequence since they will only breed once or twice more anyway. In terms of reproductive contribution to the next generation, it is of no consequence whether parous females die just after the breeding season or just before the next one, 8 months later.

An explanatory model of kiore demographic patterns

The results of our study along with those of other areas within New Zealand and the Pacific allow the development of a model (Fig. 14) that may explain some of the observed differences. Clearly numerous factors are involved and only experimental tests will confirm the relative importance of each.

In our study the basic features of seasonal reproduction and population fluctuation were repeated each year, but they also varied somewhat from year to year and between habitats. In summer 1975 reproduction ceased early, old females carried fewer uterine scars, animals lost weight in March and April, and severe mortality brought about a population crash. Animals lost most weight, and mortality was most severe in grassland. In summer 1976 breeding extended into February, old females carried more uterine scars, rats maintained weight and survived better, and the population declined more slowly especially in forest. Young males in grassland matured earlier than in the previous year. Animals lost more weight in the forest in 1976 and males did not mature earlier in this habitat. These observations suggest that rates of reproduction, growth, sexual development, and mortality respond together to some factor or factors varying with habitat, season, and year.

One such factor may be variation in food supply. The onset of breeding in November corresponds with a spring flush of growth and seeding by the dominant grasses, prairie grass and cocksfoot. Kiore foods in forest on Tiritiri and other northern offshore islands include a wider variety of plants and animals (Campbell et al. 1984), but quantitative information on diet and food availability is needed. The massive weight loss and high mortality of rats in autumn and winter suggests that the rats may have been starving. Inadequate nutrition in summer might have prevented adults from breeding and young from maturing.

The key factor underlying the pattern is the length of the hypothesised seasonal pulse in food. Habitats and localities which differ in absolute food abundance or its seasonal distribution are predicted to vary in length of breeding season, sexual maturation, litter size, and population dynamics. For example, in habitats of low diversity or at higher latitudes, food abundance is likely to be more seasonal, and breeding will be concentrated in a short time and may be by the production of large litters. After the food pulse, however, rats will mature slowly. Therefore, there will be sharp peaks in population density. In diverse habitats and at lower latitudes, the lack of such a marked food pulse may spread breeding effort in time and reproduction may be by several small litters. Furthermore, with a longer supply of food suitable for breeding, young will have the opportunity to mature in the season of their birth. In these habitats and regions, damped population peaks will be the rule. This will tend to hold true even if dispersal is limited or if there is little predation.

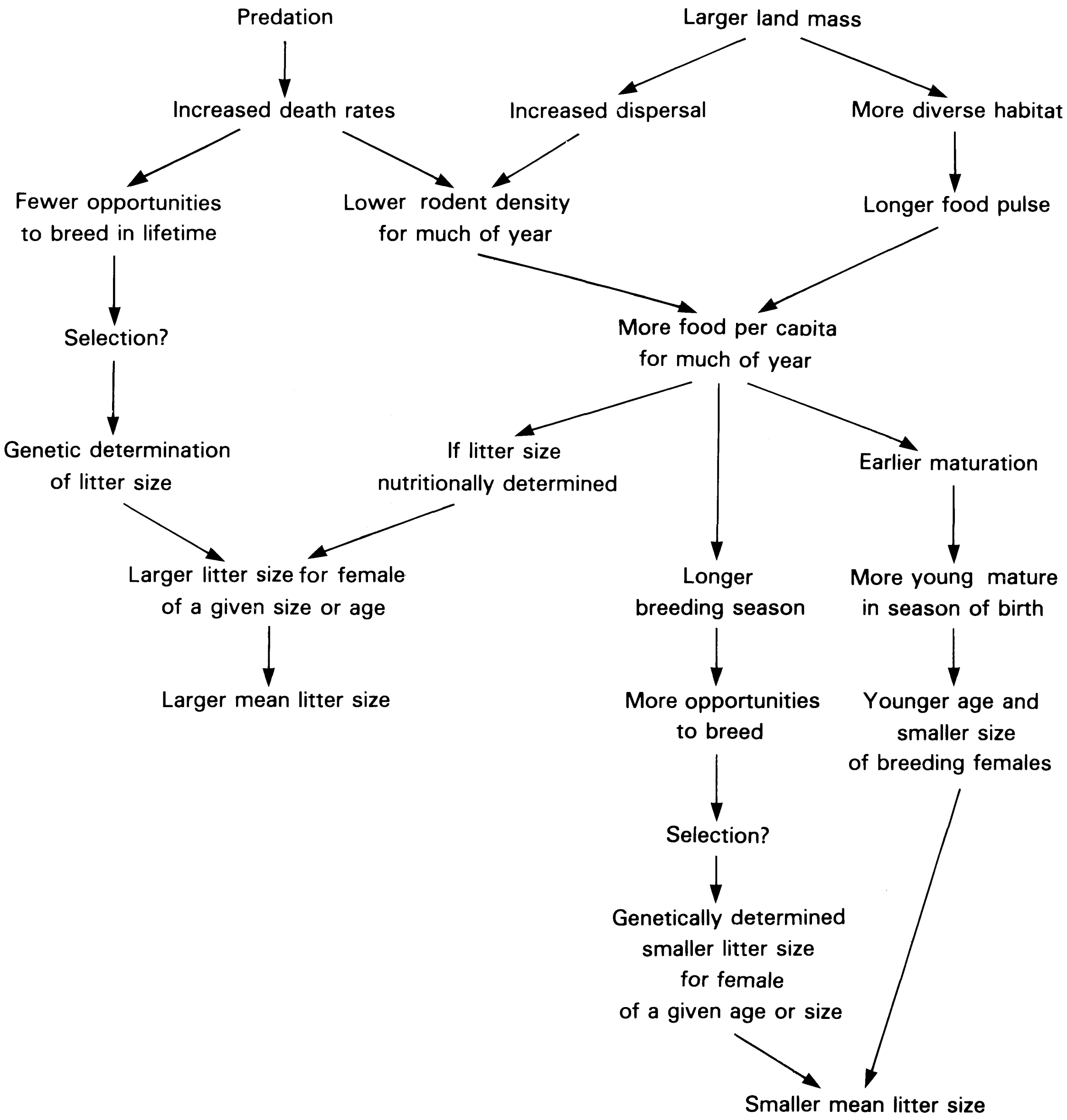

Fig. 14 A hypothesis for the modifying influence of predators and dispersal on rodent population dynamics.

On larger land masses, where predation and dispersal are greater, the strongly seasonal pattern of population dynamics imposed by seasonal variation in the food resources will be ameliorated (Fig. 14). If predation or dispersal lowers the local rodent density there will be more per capita food and less competition. Reproduction could then proceed for longer, sexual maturation may be faster, occur earlier, and more young will have time to mature in their season of birth. Younger and smaller females would then breed, and they usually have smaller litters (Sadleir 1969).

If ovulation rates are partly genetically controlled, as has been shown for other small mammals (Sadleir 1969), a hypothesis (Fig. 14) involving selection can be advanced. If the breeding season is usually more prolonged where predators are present or there is opportunity for dispersal, females will have more opportunities to breed and selection may then favour production of more but smaller litters in the female's reproductive life-span, as discussed above (Spencer & Steinhoff 1968). This would mean that short, intense breeding seasons with delayed maturation and large litter size will occur more often on predator-free islands. On the other hand, predation may increase death rates of adult females to such a degree that they have fewer opportunities to breed, and so selection would favour the production of fewer but larger litters. If litter size is in part nutritionally determined, predation and increased dispersal will also tend to increase litter size by increasing the amount of food available per rat. Until the relative strength of these conflicting forces are known we can not predict whether litter size will be smaller or larger on predator-free smaller islands (Fig. 14).

The model we advance predicts short intense breeding seasons with delayed maturation will occur more often on small predator-free islands with monotypic vegetation. Annual fluctuations in density will be marked, their timing predictable, and peak densities will be higher but maintained briefly. On larger more diverse (typically forested) islands food pulses will be longer and breeding and population cycles will be less pronounced. The presence of predators will further depress population cycles.

These ideas might explain the differences in kiore population ecology already evident from within the New Zealand region. Watson (1956) recorded breeding in March of 1954 on Little Barrier, 2 months after breeding ceased on Tiritiri. Mean litter size was significantly higher on Tiritiri (this study) than on Little Barrier in 1954 (Watson 1956: $t=4.04$, d.f. $=25$, $P<0.001$) and 1958 (unpublished data on Ecology Division File 4/12/1: $t=2.21$, d.f. $=23$, $P<0.05$). The median weights and lengths at maturity were much lower on Little Barrier than on Tiritiri (Moller 1977) and very small females (one weighing only 44 g) were pregnant in Watson's samples. Thus, females on Little Barrier often breed in the season in which they are born. Litter size increased significantly ($r=0.44$, d.f. $=20$, $P<0.05$) with increase in body size in Watson's (unpublished data). Smaller size alone does not explain lower litter size on Little Barrier since exclusion of females less than 280 mm (the minimum length of females trapped on Tiritiri in October, November, or December) from his samples gives a litter size of 5.47 ± 0.34 live embryos, which is still significantly ($t=2.48$, d.f. $=28$, $P<0.05$) lower than on Tiritiri. Feral cats which ate kiore were present on Little Barrier during Watson's study (Marshall 1961). Animals may disperse more on Little Barrier because it is larger and has a greater variety of habitats than Tiritiri. These factors, along with the less pronounced seasonal fluctuations in food supply in Little Barrier's predominantly forest habitat than on Tiritiri where grassland predominates, may have altered the seasonal pattern in the ways predicted (Fig. 14). Kiore on Kapiti Island, which is also predominantly forested, probably also had a longer breeding season than on Tiritiri (Dick 1985). Litter size did not differ significantly between Kapiti and Tiritiri ($t=0.49$, d.f. $=19$, $P>0.10$). There were indications that kiore matured earlier and bred later or for a more prolonged period on Moturua than on Tiritiri (Moller & Tilley 1986). This may have been because predators kept density low on Moturua (Fig. 13) so that sufficient food remained for kiore to breed and mature in the autumn (Fig. 14).

More studies are now required to establish whether the length of the breeding season, rate of sexual maturation, litter size, and population density vary together in response to habitat variables such as food availability, island size, and presence of predators. The additional effects of light cycles should not be ignored (Gander 1980). Measurement and manipulation of food supplies is the most important test of the hypothesis before the additional effects of island size and predation are investigated. Bunn (1979) subsequently supported our food pulse model by stimulating a longer breeding season and a less pronounced annual cycle by supplementary feeding of kiore in grassland on Tiritiri. The hypothesis might also predict the variation in demography of the other rodents living in New Zealand ecosystems.

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APPENDIX 1: REPRODUCTIVE CONDITION OF AUTOPSIED FEMALES.

Date	Number autopsied	Number perforate	Number carrying uterine scars	Number pregnant
1974				
12 May*	18	9	7	0
1975				
28 Feb	12	7	2	0
29 Mar	18	9	5	0
25 Apr	24	16	6	0
30 May	7	6	3	0
10 Jul	11	11	0	0
18 Sep	5	5	0	0
16 Oct	3	3	0	0
13 Nov	2	2	0	1
9 Dec	7	7	1	5
1976				
7 Jan	10	8	5	6
3 Feb	30	11	6	1
4 Mar	8	5	0	0
5 Apr	22	16	7	0
28 May	67	42	19	0
4 Sep	17	11	0	0
29 Oct	8	8	0	0
8 Dec	7	7	0	2
1977				
17 Jan	5	3	2	0
27 Feb	31	26	15	0
10 May	53	26	3	0

*A. Harrison (pers. comm.)

APPENDIX 2: CORRECTED TRAP SUCCESS FOR *RATTUS EXULANS* ON 17 NEW ZEALAND ISLANDS.

Trap sessions with less than 40 effective trap nights are excluded. Trap success is corrected by the method of Nelson & Clark (1973).

Island (in rank order of latitude)	Presence of mammals	Year	Month(s)	Habitat	Effective trap nights	Trap success (kiore/100 corrected trap nights)	Source and comments
1 Motukawanui		1979/80	Dec/Jan	Grassland & garden	170	21.2	Hitchmough (1980)
2 Moturua	1†, 2†, 5†	1984	Mar	Forest	548	0.5	Moller & Tilley (1986)
				Grassland	415	2.2	
				Shoreline	43	0	
3 Hokoromea		1973	Nov	Forest?	60	0	A. H. Whitaker (pers. comm.)
4 "Stack G", Mokohinau		1973	Nov	Forest?	56	0	A. H. Whitaker (pers. comm.)
5 Hen		1963	Sep	Forest	65	52.3	D. J. Campbell (pers. comm.)
6 Little Barrier	1†	1954	Mar	Forest	79	26.4	Watson (1956). Grassland equated with "Homestead" area; all other equated with forest.
				Grassland	62	56.0	
		1956	Aug	Forest	93	3.2	J. S. Watson unpubl. data on file at Ecology Division, DSIR
				Grassland	125	14.4	
7 Cuvier	1†	1960	Jun	Forest	22	4.2	R. Edgar (pers. comm.) cats still present
7 Cuvier		1977	Jan	Forest	109	17.4	C. R. Veitch (pers. comm.) cats eradicated
8 Tiritiri		1974–77	All	Forest	42–58	21.5	(average) Range = 2–38
				Grassland	55–282	20.8	(average) Range = 1–91 Present study

APPENDIX 2 (*continued*): CORRECTED TRAP SUCCESS FOR *RATTUS EXULANS* ON 17 NEW ZEALAND ISLANDS.

Trap sessions with less than 40 effective trap nights are excluded. Trap success is corrected by the method of Nelson & Clark (1973).

Island (in rank order of latitude)	Presence of mammals	Year	Month(s)	Habitat	Effective trap nights	Trap success (kiore/100 corrected trap nights)	Source and comments
9 Red Mercury		1971	Aug	Forest, shoreline	120	23.2	Bettesworth (1972a)
10 Korapuki		1974	Nov	Forest, shoreline	158	21.0	Hicks et al. (1975)
11 White		1964	Nov	Gannetry, factory	45	57.8	F. H. Robertson unpubl. notes on Ecology Division, DSIR files
12 D'Urville	1†, 2†, 3†	1978/79	Dec/Jan	Forest	917	0.01	R. Buckingham & G. Elliott (pers. comm.). Trap lines through mixed habitats excluded. Maximum estimate of catch success since calculation assumes all kiore caught in rat traps (and not in mouse or Fenn traps which were also set).
				Grassland	276	1.1	
				Scrub	57	0	
				"Settlement"	42	0	
13 Kapiti	5†	1959	Feb	Forest, swamp, "settlement"	60	1.6	Unpubl. data of J. S. Watson on Ecology Division, DSIR files
		1965	Dec	Forest, coastal vegetation	49	2.0	D. J. Campbell (pers. comm.)
		1966/67	May, Sep, Mar, & Aug	Forest	70–110	0–7.2	Daniel (1969)
			Mar & Aug	Grassland	53–56	12.4–18.7	Daniel (1969)
		1976	May	Forest	259	0.8	J. Innes (pers. comm.)
		1977	Feb	Forest	355	0	Baird (1977)
				Grassland	115	0	
		1983/84	All	Forest	42–134	9.2	(averages given) Range 0–28.4
				Grassland	49–91	0	Excludes grid
14 Arapawa	1†, 2†, 3†, 4†	1975	Nov	"Settlement"	115	5.2	A. H. Whitaker (pers. comm.)
		1978	Apr	Forest	70	1.4	H. Moller (unpubl.)
				Scrub	71	0	
				"Settlement"	42	0	
15 South	1†, 2†, 3†, 4†, 5†						
Esperance Valley		1974	Mar	Scrub	69	2.9	D. V. Merton (pers. comm.)
		1974	Dec	Scrub	44	2.3	
		1975	Feb	Scrub	69	1.4	
Sinbad Gully		1974	Nov	Forest	40	0	D. V. Merton (pers. comm.)
Sinbad Ridge		1974	Nov	Scrub, tussock	45	0	D. V. Merton (pers. comm.)
Jacksons Bay		1964	May	Forest	430	0.2	Choate (1965)
Holyford		1974–80	Feb, May Aug, Nov	Forest	216	0.3	(estimated average) King (1983); assumes 9% of rats caught were kiore, over-estimate because assumes none of kiore were caught in Fenn traps.
Haast/Arawata		1979	Mar/Apr	Forest	372	1.9	H. A. Robertson (pers. comm.)
16 Codfish		1963	Sep	Forest	659	1.4	A. H. Whitaker (pers. comm.)
		1966	?	Sand-dunes, scrub, forest	704	1.3	R. Nilsson, unpubl. report 13.10.76, Wildlife, Internal Affairs file WIL 30/3/23.
		1975	?		215	7.2	R. Nilsson, unpubl. report 13.10.76, Wildlife, Internal Affairs file WIL 30/3/23.
		1976	?		245	13.0	R. Nilsson, unpubl. report 13.10.76, Wildlife, Internal Affairs file WIL 30/3/23.
17 Stewart	1†, 4†, 5†	1950	Dec	Forest & scrub	107	0.9	Taylor (1975)
		1964	May	Forest	127	0	Choate & Gibbs (1964)
		1980	Mar	Forest	166	0	Gales (1980)
		1984	Aug/Sep	Forest	210	0	Hickson et al. (in press)

1† = cats, 2† = stoats, 3† = mice, 4† = ship rats, 5† = Norway rats.