

NORWAY RATS (*RATTUS NORVEGICUS*) ON THE NOISES AND MOTUKAWAO ISLANDS, HAURAKI GULF, NEW ZEALAND

Summary: The Noises and Motukawao Islands in Hauraki Gulf are small (maximum size 26 ha) and bush-clad, and none is permanently inhabited. Norway rats reached the Noises about 1956, but their history on the Motukawao group is unknown. Live and kill-trapping was carried out between August 1977 and December 1981, mainly on the Noises Islands. Trapping success was high initially but declined rapidly and remained very low after mid-1978. Rats travelled widely between consecutive captures in live-traps and three home ranges of males averaged 1.2 ha. Density on one of the Noises Islands was estimated to be 2.6-4.2 rats/ha. The age distributions of kill-trapped rats and skulls found on the Noises were both weighted towards older individuals. Adult males and females were generally similar in body size and condition, but Motukawao rats were in better condition than Noises rats. Males remained fertile throughout the year, whereas females were in breeding condition only between August and April. Histological examination of females showed that, compared with urban and rural Norway rats, maturity was delayed, litters were small and some females ovulated but failed to breed. The most common foods on the Noises were insects, seeds and fruits, and other plant material. Potential factors limiting rat numbers on the Noises are discussed, especially shortages of protein-rich foods and fresh water.

Keywords: Rodentia; *Rattus norvegicus*; Noises Islands; Motukawao Islands; New Zealand; trapping; morphology; breeding; food habits; home range; island populations.

Introduction

All three species of rat in New Zealand were introduced. The Maori brought *Rattus exulans* about 1000 years ago, and Europeans introduced *R. norvegicus* between 1770 and 1820 and *R. rattus* between 1858 and 1865 (Atkinson, 1985). *R. exulans* is now mainly restricted to offshore islands, but the other two species are widespread on the mainland and many islands. The spread of rats to islands has had two important consequences: they have severely reduced or eliminated populations of some birds, reptiles and invertebrates (Dingwall, Atkinson and Hay, 1978), and the presence of *R. rattus* and *R. norvegicus* renders those islands unsuitable for the re-establishment of endangered native fauna. Few rat-free islands are available for endangered species conservation but more can be made available by eradicating rats from infested islands.

Research on the Noises Islands was designed to provide information on the ecology of Norway rats (*Rattus norvegicus*) on small islands (< 25 ha), and to test the practicability of exterminating them. This paper includes data on the trapping, size, reproduction, age structure, diet and movements of the rats, together with comparative information from two samples of Norway rats trapped on the Motukawao Islands, 38 km east of the Noises group.

The methods and results of the campaigns to eradicate Norway rats from the Noises Islands are described by Moors (1985). Other scientists from the New Zealand Wildlife Service and Botany and Entomology Divisions, Department of Scientific and Industrial Research, have also studied the birds, insects, vegetation and soils of the Noises Islands.

Most New Zealand studies of Norway rats have been carried out on islands. Beveridge and Daniel (1965) observed a dense population on Mokoia Island in Lake Rotorua, and other investigations have taken place on Whale Island, Bay of Plenty (Bettesworth, 1972), Kapiti Island near Wellington (Daniel, 1969; Baird, 1977), and five islands in the Bay of Islands, Northland (Moller and Tilley, 1984). Daniel (1978) reviewed the ecology of Norway rats in New Zealand, both on the mainland and islands.

The Noises Islands

The Noises Islands (36° 42'S, 174° 58'E; Fig. 1) lie in Hauraki Gulf about 24 km northeast of Auckland. The main islands are Otata (21.8 ha), Motuhoropapa (9.5 ha), Maria (2.0 ha) and the David Rocks (2.0 ha). There are also five islets, the largest of which is Scott Island (0.6 ha). The islands are mainly composed of complexly folded argillite and greywacke rocks (Mayer, 1968). The shorelines are heavily indented and wave-cut platforms up to

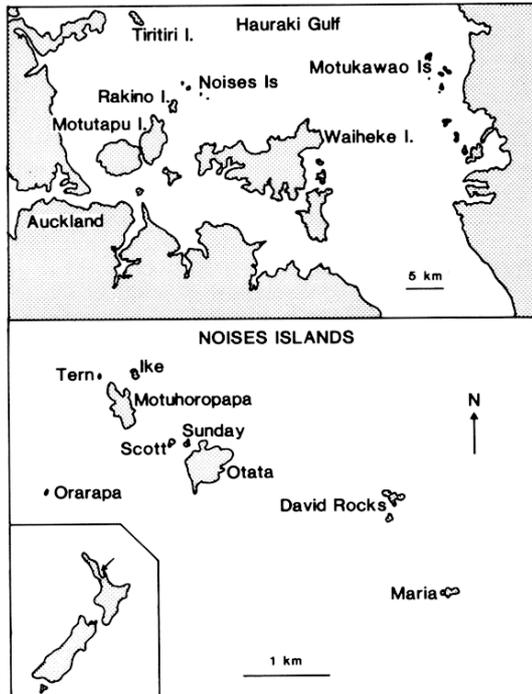


Figure 1: Location of the Noises and Motukawao Islands in Hauraki Gulf, and map of the Noises group.

25 m wide are exposed at low tide. All islands lack permanent fresh water, although seepages and rock pools provide temporary supplies after rain. Rainfall is greatest in winter (average 343 mm) and least in summer (average 181 mm). A small house on Otata was permanently occupied from about 1947 until 1957, but since then has been used only for holidays. In summer the island is often visited during the day by boating parties. The other islands are uninhabited and rarely visited.

Vegetation

Otata is mostly covered with native forest and scrub regenerating after a fire sometime between 1925 and 1930. The canopy is now generally closed and 4-8 m high, its main components being *Myrsine australis*, *Metrosideros excelsa*, *Coprosma macrocarpa*, *Pittosporum crassifolium*, *Pseudopanax lessonii* and *Meliccytus ramiflorus*. *Leptospermum scoparium* is of local importance. Tall *Metrosideros excelsa* and *P.*

crassifolium are common on the coastal slopes, in some places forming closed forest up to 15 m high. The understorey is fairly open, with local thickets of *M. australis*, *Pteridium esculentum*, *Gahnia lacera* or *Astelia banksii*. The main ground cover is leaf litter. Open grassy areas with clumps of *Phormium tenax* and *Scirpus nodosus* persist on the western slopes.

Motuoropapa is clothed in both mature and developing forest with a closed canopy generally 6-10 m high, and up to 20 m high in a basin on the southwest side of the island. The canopy is largely *Metrosideros excelsa*, *Pittosporum crassifolium*, *Pseudopanax lessonii*, *Melicope ternata*, *Coprosma macrocarpa* and *Meliccytus ramiflorus*. The understorey consists mainly of seedlings of the canopy species and also of *Dysoxylum spectabile*, with scattered dense stands of *Astelia banksii*. Leaf litter is the main ground cover.

Apart from Tern Rock, which lacks vegetation almost completely, the other islands in the group are capped by forest or dense low scrub consisting of *P. crassifolium*, *Coprosma repens*, *P. lessonii* and *Myoporum laetum*.

Atkinson (1984) has recently prepared a species list for the whole Noises group.

Fauna

Seven species of seabird and at least 11 species of landbird breed on the Noises Islands, and a further 14 species of landbird have been recorded there (Cunningham and Moors, in press). The skinks *Cyclodina aenea* and *Leiopisma smithi* and the gecko *Hoplodactylus maculatus* are present on Otata. The gecko also inhabits Maria Island, but no reptiles have been found on the remaining islands (D. R. Towns, pers. comm.). The list of identified terrestrial invertebrates for the whole group currently exceeds 500 species (J. C. Watt, pers. comm.). Otata used to be inhabited by rabbits (*Oryctolagus cuniculus*) and stoats (*Mustela erminea*). The rabbits died out about 1944-45, approximately three years before the first stoats were encountered; no stoats have been seen since the mid-1950s (B. P. Neureuter, pers. comm.).

Rats were found first on Gtata. They are thought to have arrived about 1956 (Gard, pers. comm.) and were certainly present by the end of 1957 (B. P. Neureuter, pers. comm.). Rats identified as *R. norvegicus* were found on Maria Island late in 1959, when they appeared responsible for the recent deaths of hundreds of white-faced storm petrels (*Pelagodroma marina*) (in Merton, 1960). Rat sign was first reported from the David Rocks in

November 1960 (Merton, 1960) and from Motuhoropapa in November 1962 (Skegg, 1963). During the present study Norway rats have been trapped on Ike, Scott and Sunday Islands, and fresh droppings and runways found on Orarapa Island, the most isolated member of the Group (Fig. 1). Rats disappeared from both Maria Island and the David Rocks after sporadic laying of warfarin rodenticide between 1960 and 1964 by the Royal Forest and Bird Protection Society and the New Zealand Wildlife Service. The remaining islands were not treated until the recent eradication campaigns described by Moors (1985).

There are three routes by which Norway rats could have colonised the Noises Islands. From the late 1920s until 1972 garbage from ships used to be held on the Auckland waterfront before being dumped at sea several kilometres southwest of the Noises. Norway rats commonly live in waterfront areas, and any dumped with the garbage could have floated to the Noises on the rafts of refuse which often washed ashore there (B. P. Neureuter, pers. comm.). Being strong swimmers, Norway rats are well adapted to survive a water-borne journey like this. Alternatively, rats could have reached Otata while the island was permanently inhabited, and Maria Island during construction of a navigation light in 1953 and its subsequent servicing every three months. The least likely possibility is that rats could have been carried from the eastern shores of Motutapu and Rakino Islands (Fig. 1) by the strong ebb-tide current. The Noises Islands lie directly across the northeasterly flow of this current. However this would require the rats to stay afloat for several kilometres, much further than the limit of about 600 m which seems to apply elsewhere in northern New Zealand for Norway rats crossing water barriers (Atkinson, in press). No shipwrecks, except of small pleasure boats, are known at the Noises group.

Nothing is known about the rats' spread within the Noises group. Motuhoropapa and Otata are sufficiently close together for rats to have colonised one by swimming from the other, using Scott and Sunday Islands as "stepping stones". The widest water gap to be crossed at low tide on this route is about 400 m. Ike Island, about 150 m from Motuhoropapa, could have been colonised in the same way, and rats made this crossing in 1981 (Moors, 1985). Orarapa and Maria Islands and the David Rocks are much more isolated, with water

gaps of 1.1-4.5 km separating them from their neighbours. The David Rocks and Maria were, therefore, probably colonised independently, especially since rats have not recolonised either of them from infested neighbours during the past 20 years.

The Motokawao Islands

The Motokawao Islands (36° 41'S, 175° 23'E; Fig. 1) lie on the eastern margin of Hauraki Gulf several kilometres off the coast of the Coromandel Peninsula. Norway rats were trapped on two islands in the group, Motuwi (26 ha) and Motukaramarama (18 ha). The following vegetation descriptions are summarised from Esler (1978). Nearly the whole of Motuwi is forested with young *Metrosideros excelsa*, with a light understorey of *Myrsine australis* on the gentler slopes. A scrubland of *Leptospermum scoparium* occupies sections of the summit ridge and the south and east of the island. Motukaramarama has a closed-canopy forest of *Dysoxylum spectabile*, *Melicactus ramiflorus*, *Corynocarpus laevigatus* and *Planchonella costata*. A shrubland of *Pseudopanax lessonii* covers the summit and gentle slopes with much *D. spectabile* in the understorey. On the north and west of the island gannets (*Sula serrator*) have two large and several smaller breeding colonies, which in November 1980 contained 3290 pairs (Waghorn, 1983).

The history of the Norway rats on Motuwi and Motukaramarama is not known.

Methods

This paper contains information collected between August 1977 and the end of 1981. Regular fieldwork commenced in February 1978, the islands being visited for 1-2 weeks every two months or so.

Rats were live-trapped only on Motuhoropapa. Thirty wire-mesh box traps (43x15x12 cm) were set briefly in December 1977 and January 1978. In February 1978 92 traps were placed permanently at sites every 25 m along tracks around the island. The traps were usually set for nine nights during each of the six trapping sessions in 1978, and were baited with a mixture of peanut butter and rolled oats. Between sessions they were left baited but not set. Captured rats were anaesthetised with ether and then sexed, weighed, ear-tagged and toe-clipped, and their breeding condition noted. In an attempt to determine if any rats remained on Motuhoropapa all the live traps were set continuously from February 1979 until February 1980.

At one time or another kill-traps were set on all islands in the Noises group, but the most intensive trapping was on Motuoropapa and Otata. Most trapping was done with standard break-back traps, although Fenn traps and small gin traps were also used. Fourteen sessions of kill-trapping were held on Motuoropapa between August 1977 and December 1981, and 15 on Otata between August 1977 and October 1980. No kill-trapping was carried out on Motuoropapa while live-trapping was under way between December 1977 and February 1979.

In the Motukawao Islands kill-traps were set for two nights on Motukaramarama in August 1977, and for three nights on both Motukaramarama and Motuwi in March 1979.

Kill-trapping procedures followed those described by Cunningham and Moors (1983) for index trapping. Traps were spaced 15-20 m apart in pairs and baited with rolled oats and peanut butter. They were set for three successive nights and inspected daily. The number of trap-nights was corrected for sprung traps (Nelson and Clark, 1973), and trapping success was expressed as the number of rats caught per 100 trap-nights. Captured rats were sexed, weighed, measured, their breeding condition noted, and their upper molars, stomachs and reproductive systems preserved in 70% ethanol. An index of body condition, previously used for Norway rats by Davis and Hall (1951), was calculated with the formula

$$C = \frac{W}{HBL^3} \times 10^5$$

where W is weight (g) and HBL is head-body length (mm). Dead rats and skulls picked up on the islands were assigned to seven age classes according to the stage of eruption and degree of wear of the upper molars (Karnoukhova, 1971). The age classes extend over progressively longer time spans as the rats become older and tooth wear increases.

All ovaries were serially sectioned at a thickness of 8 microns, every fifteenth section being mounted and stained with haematoxylin and eosin. Selected uteri were sectioned and stained in the same way to check for early stages of pregnancy. Each pair of testes was weighed, and five serial sections were taken from the central portion of one testis. These were stained with haematoxylin and eosin and checked for mature sperm. Females were considered sexually mature if corpora lutea were present, and males if mature sperm were present in the seminiferous tubules.

Diet was investigated only on the Noises Islands. Food remains were identified in the stomachs of kill trapped rats and in 13 samples of droppings collected mainly on Motuoropapa between April and October 1978. The percentage volumes of foods in stomachs were estimated visually as trace (< 10%), medium (10-50%) or large (> 50%) amounts. Plant foods other than seeds were not specifically identified, but animal foods and seeds were identified as completely as possible. This information was supplemented with observations on food caches and other feeding sign.

Results

Capture success was high when trapping started in August 1977, but early in 1978 it declined rapidly and thereafter remained very low on both Motuoropapa and Otata (Tables 1, 2). No rats were caught on Motuoropapa even when all 92 live-traps were set continuously from February 1979 until February 1980.

Fourteen rats were kill-trapped on Motuoropapa and 23 on Otata (Table 1). Two carcasses were cannibalised on Motuoropapa (14.3%) and three on Otata (13.0%). Three of these were almost entirely devoured, only the skin, skull and extremities being left. Six rats (5 males, 1 female) were live-trapped on Otata in February 1978 while investigating possible lead poisoning from the traps (see below). Apart from analysis of their livers, these rats were treated in the same way as kill-trapped rats and are, henceforth, included in the kill-trap sample from Otata. Also included in this sample are a female caught on Scott Island and another on Sunday Island in August 1977.

Seven male and six female rats were live-trapped on Motuoropapa 65 times between December 1977 and October 1978 (Table 2). Three were captured only once, and the largest number of captures was 10. Males were caught 46 times (70.7% of total captures) and females 19 times, the sex ratio of captures being biased significantly towards males ($\chi^2 = 5.61$, $P < 0.02$). Except in February 1978, females were rarely caught, and none were trapped after April 1978.

No rats were trapped in more than three trapping sessions and only two were known to have been present for more than three months (Table 2). These short periods of residence were partly due to four rats dying in the traps. Lead poisoning was a

Table 1: Summary of kill-trapping of Norway rats on Motuoropapa and Otata Islands between August 1977 and December 1981.

	No. trap	No. rats trapped		No. trap-nights	No. caught per 100 trap-nights
	sessions	Males	Females		
Motuoropapa Island					
1977 August	1	0	3	41.5	9.6 ¹
November	1	3	4	79.5	8.8
1979 February - September	4	0	0	1060	0
1980 February - October	3	0	0	386	0
1981 January - December	5	0	3	874	0.3
Total	14	3	10	2441	0.6 ¹
Otata Island					
1977 August	1	2	4	30.5	19.7
1978 February	1	3	4	40	17.5
April	1	2	2	256	1.6
June	1	1	1	270	0.7
August	1	1	0	180	0.6
October	1	1	0	261	0.4
December	1	0	0	170.5	0
1979 February - October	5	0	2	823	0.2
1980 February - October	3	0	0	440	0
Total	15	10	13	2471	0.9

¹ includes an unsexed cannibalised rat.

Table 2: Summary of live-trapping of Norway rats on Motuoropapa Island between December 1977 and December 1978 (* died in trap).

Rat	Sex	Age at first capture	No. captures								Total	No. sites at which caught
			Dec	Jan	Feb	Apr	Jun	Aug	Oct	Dec		
6000	M	Ad	1*								1	1
6001	F	Ad	2								2	2
6002	M	Ad	1								1	1
6003	F	Ad		1	4"						5	4
6004	M	Ad		1	4	2					7	7
6005	F	Ad		2*							2	2
6006	M	Ad		2	5	2					9	9
6007	M	Ad		1	9*						10	8
6008	F	Ad			1	2					3	3
6009	M	Ad			2	0	0	3	4		9	9
6010	F	Ad			6						6	4
6011	F	Juv			1						1	1
6012	M	Ad			2	6	1				9	9
Total captures			4	7	34	12	1	3	4	0	65	
No. trap-nights			-	90	960	710	820	820	1000	820	5220	
Trap success/100 t-n			-	7.8	3.6	1.5	0.1	0.4	0.4	0	1.2	

possible additional mortality factor. In their efforts to escape, rats often chewed the traps and swallowed fragments of lead-based paint. The lead concentrations in the livers of four Otata rats confined in live-traps for 9-36 hours varied from 1.00-4.17 mg lead/kg fresh liver tissue, and a female which had been caught five times on Motuhoropapa contained 1.09 mg lead/kg liver. These concentrations were much higher than those of 0.03 and 0.16 mg lead/kg liver in two Otata rats which had never been in live-traps. Comparisons with data summarised by Roush and Kehoe (1964) suggest that levels of 1-5 mg lead/kg liver may not cause death directly, but may reduce overall fitness.

Live-trapping commenced on Motuhoropapa shortly after the population had been substantially depleted by the kill-trapping of 11 rats (Table 1), although the extent of this reduction was not evident at the time. The minimum number of rats on Motuhoropapa in December 1977 can be estimated from those known or assumed to be present. All 12 adults live-trapped would have been alive then, and the 11 rats kill-trapped in August and November

1977 are likely to have survived. Another two adults are known to have died naturally between December 1977 and February 1978. Thus at least 25 rats would have been present in December, giving a minimum population density of 2.6 rats/ha. Using live-trapping data for December 1977-April 1978 (Table 2), the method of weighted means (Begon, 1979) gives a population of 13 rats, with 95% confidence limits of 0.8-26.8 rats. Substituting this upper limit for the number of live-trapped rats in the previous calculations gives a density of 4.2 rats/ha.

Movements and home range on Motuhoropapa Island

Rats were rarely caught twice at the same trap-site (Table 2). They travelled widely between successive captures, the average distance in the same trapping session being 113 m for males and 49 m for females ($t = 2.58, P < 0.01$). Figure 2 shows that males tended to travel much further than females, 46% of their successive captures being more than 100 m apart, compared with only 10% for females. The longest movement recorded was 330 m in 48 hours. Motuhoropapa itself is only about 600 m long, so the rats were well able to cover it from end to end in a few days.

In January and February 1978, when at least nine rats were present (Table 2), there was considerable overlap in trap-revealed home ranges both within and between sexes. The ranges together covered much of the island, with the largest overlaps and most rats apparently being in the central and northern sections of the island (Fig. 3). The home ranges of three rats trapped in three consecutive sessions varied in size from 0.8-1.8 ha (average 1.2 ha), equivalent to 8.4-18.9% of the total area of Motuhoropapa. Distance travelled and home range size both increase for Norway rats as food becomes more dispersed (Hardy and Taylor, 1979). Presumably the travelling necessary to exploit the terrestrial and littoral foods eaten by the rats (see below) explains the large area of these ranges.

Kill-trapping on the Motukawao Islands

On Motukaramarama three females were caught in 42 trap-nights (7.1 rats/100 trap-nights) during August 1977, and 10 males and two females in 101.5 trap nights (11.8 rats/100 trap-nights) during March 1979. Also during March 1979, three rats of each sex were caught on Motuwi in 49.5 trap-nights (12.1 rats/100 trap-nights). A female from Motuwi was cannibalised on the neck and thorax.

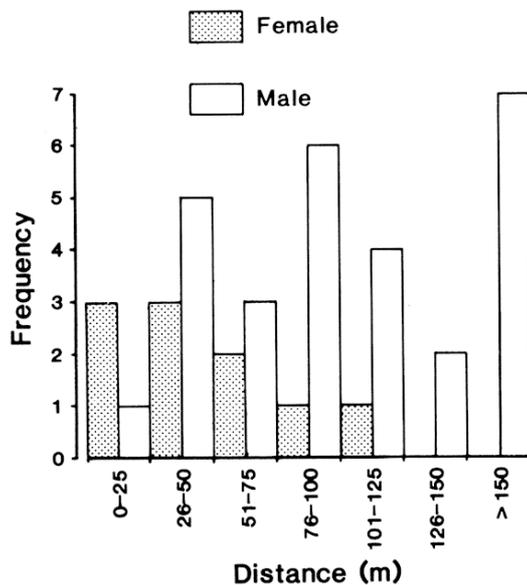


Figure 2: Frequency distribution of distances between consecutive captures of male and female Norway rats on Motuhoropapa Island.

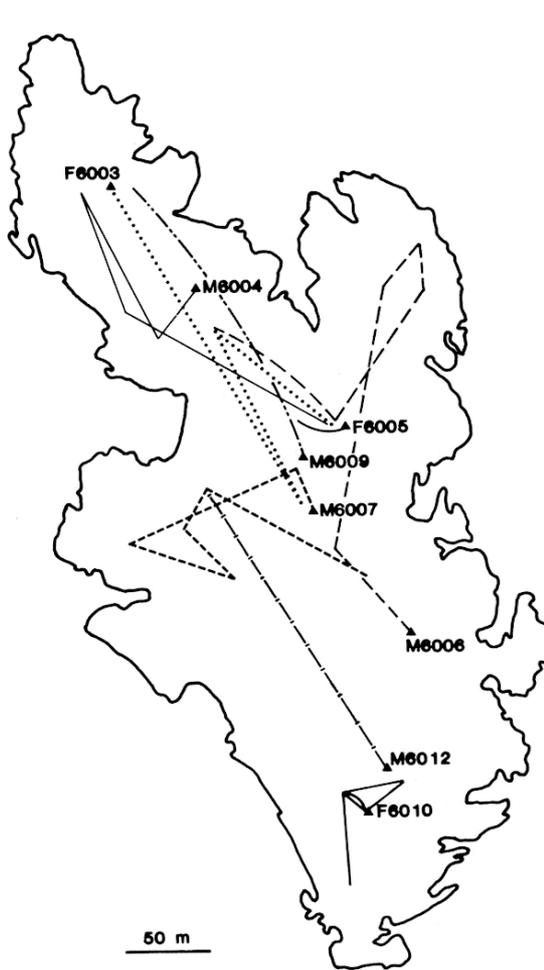


Figure 3: Successive capture sites of Norway rats live-trapped at least twice on Motuhoropapa Island in January and February 1978. Multiple captures at the same site are not shown Δ = site of first capture.

Age structure

The age structures of kill-trapped rats from Motuhoropapa and Otata are shown in Figure 4a. The MotUhoropapa sample includes two males and two females found dead in live-traps. There were no significant differences in age distributions between the sexes on each island, but the combined sample for Motuhoropapa differed from that for Otata (G-

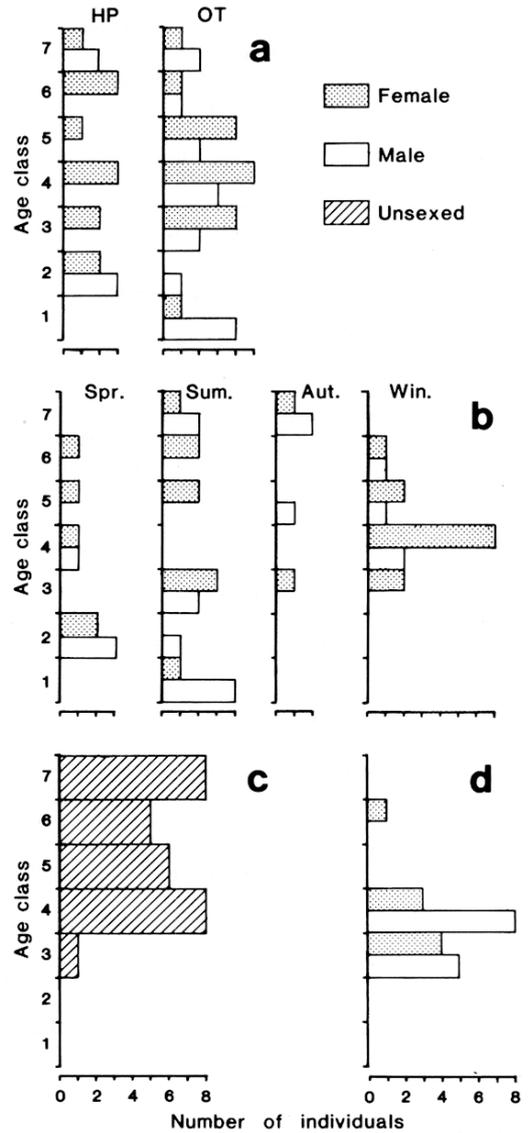


Figure 4: Age distribution of Norway rats as determined by molar wear: (a) males and females from Motuhoropapa (HP) and Otata (OT) Islands; (b) seasonal distribution on the Noises Islands (each season lasts three months; spring begins in September); (c) unsexed skulls found on the Noises Islands; (d) males and females from the Motukawao Islands.

tests (Sokal and Rohlf, 1969); $G = 14.31$, $p < 0.05$). I attribute this difference to sampling bias, because only two age classes were present in the few males from Motuhoropapa, and the Motuhoropapa sample was also seasonally clumped (76.5% of rats were caught between August and December, compared with only 32.3% from Otata). The age distributions were weighted towards the older age classes on both islands. Taking the Noises sample as a whole, 10 males (50.0%) and 19 females (67.9%) belonged to class 4 or above.

Grouping the Noises sample into seasons reveals that young and old rats tended to be caught in summer, compared with mainly intermediate-aged rats in winter (Fig. 4b). The autumn sample was too small for analysis, but among the other seasons the only significant difference was between summer and winter ($G = 27.84$, $P < 0.01$). These contrasting age distributions would result from each year's cohort of juveniles appearing in summer and then passing through the population.

All except one of the 28 skulls picked up on the Noises Islands belonged to rats in age class 4 or older (Fig. 4c), an age distribution which was significantly older than that of the Noises kill-trapped sample with both sexes combined ($G = 17.17$, $P < 0.01$). It is unlikely that the skull sample was biased towards older rats through juvenile skulls not being found. Much of the skull collection consists of small and inconspicuous fragments such as might be formed when juvenile skulls break up. The skulls provide a sample of ages at natural death, whereas the trapped material gives a sample of ages from living populations. Both samples contain many middle-aged and old-aged individuals.

In normal circumstances Norway rats apparently survive well on the Noises Islands, and once an animal has entered the population its expectation of further life is high.

Only one rat kill-trapped on the Motukawao Islands was not in age class 3 or 4 (Fig. 4d). The age distributions of males and females did not differ, but the absence of older individuals did produce a significant difference between the age distributions of Motukawao rats and Noises rats at the same time of year ($G = 13.21$, $P < 0.05$).

Body size and condition

There were no significant differences in average adult weights either between the sexes or the Noises and Motukawao Islands (Table 3). The heaviest rat caught during the study weighed 426 g when live-trapped on Motuhoropapa in August 1978. The mean head-body lengths (HBL) of adult males and females were similar on the Noises, but on average females were shorter than males on the Motukawao Islands ($t = 2.55$, $p < 0.02$). There were no significant differences between the island groups in the mean HBL for each sex, nor between the sexes or island groups in the mean length of the tail.

The average condition indices of rats from the Noises and the Motukawao Islands did not differ significantly between the sexes (Table 3). However, indices from the Motukawao Islands were significantly higher than those from the Noises Islands, even when the more restricted time of collection of the Motukawao rats was taken into account (t-tests, all $p < 0.05$). The better condition of Motukawao rats may have been related to more plentiful food supplies, for example from the gannet colonies on Motukaramarama Island.

Table 3: *Body measurements of Norway rats trapped on the Noises and Motukawao Islands. Sizes are from reproductively mature rats only; condition indices are from all age classes.*

	Males			Females		
	No.	Mean	Range	No.	Mean	Range
Noises Islands						
Weight (g)	6	267	196-390	18	255	155-360
Head-body length (mm)	7	215	195-234	20	203	170-240
Tail (mm)	7	175	155-204	18	172	152-192
Condition index	9	2.89	2.31-3.61	25	2.98	2.34-3.65
Motukawao Islands						
Weight (g)	11	285	208-324	6	246	156-355
Head-body length (mm)	11	206	185-222	8	190	160-205
Tail (mm)	11	186	160-204	8	171	152-185
Condition index	13	3.25	2.64-3.63	6	3.44	2.64-4.18

The Noises index altered little with age: the average was 2.82 for rats in classes 1 and 2, 3.03 for those in classes 3 and 4, and 2.92 for those in classes 5-7. There was, however, significantly greater variation in condition among older rats, the coefficient of variation being 14.7% for classes 5-7 but only 6.7% for classes 1 and 2 ($F = 5.12, p < 0.05$). No seasonal variation in condition was apparent.

Eighteen rats from the Noises were infected with the intestinal nematode *Mastophorus muris*, and one also harboured a large cestode, probably *Hymenolepis diminuta*. The number of nematodes per gut ranged from 1 to 36 (average 7.4). There was no correlation between the body condition of the rats and the number of nematodes which they carried.

Breeding

i) Males

Eight males from the Noises (47.1 %) and 11 males from the Motukawao Islands (84.6%) were reproductively mature (Table 4). Mature males were trapped on the Noises Islands in all seasons, and they apparently remained fertile throughout the year once they had become sexually mature. Scrotal testes or the presence of enlarged epididymal tubules are commonly used as indicators of sexual maturity, but these methods would have diagnosed three rats (10.0%) incorrectly, two mature males being misclassified as immature (one by each indicator) and one immature male being misclassified as mature (by both indicators).

Judging from Figure 5, sexual maturity is reached

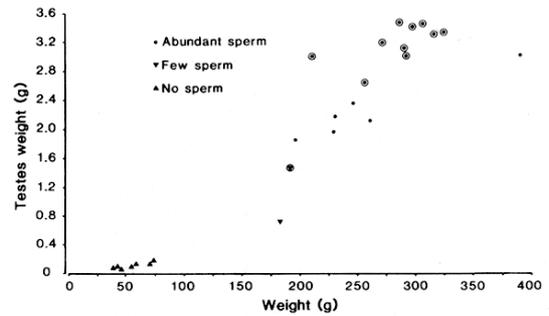


Figure 5: Total testes weight and abundance of sperm in relation to the body weight of male Norway rats from the Noises and Motukawao Islands. Motukawao data points are circled.

at body weights between 175-200 g; the smallest mature male weighed 196 g. There was a positive correlation among mature males between testes weight and body weight (all mature males pooled; $r = 0.67, P < 0.01$). The average weight of paired testes from mature males in the Noises sample was 2.26 g (range 1.85-3.03 g), compared with 0.19 g (range 0.06-0.74 g) for immature males. The mean for mature males in the Motukawao sample was 3.05 g (range 1.49-3.48 g), significantly heavier than for Noises males ($t = 3.44, P < 0.01$).

ii) Females

Nineteen females from the Noises Islands (73.1 %) and all eight from the Motukawao Islands were reproductively mature (Table 4). All females older

Table 4: Reproductive status of male and female Norway rats trapped on the Noises (NS) and Motukawao (MK) Islands. Males with plentiful sperm and females with corpora lutea (CL) were classed as being sexually mature.

Age class	Males						Females								
	No. rats		Scrotal testes		Sperm plentiful		No. rats		Vagina perforate		CL present		Uterine scars		
	NS	MK	NS	MK	NS	MK	NS	MK	NS	MK	NS	MK	NS	MK	
1	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	4	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	1	5	1	5	0	4	6	4	4	4	2	4	0	0	0
4	2	8	2	8	2	7	7	3	7	3	7	3	1	0	0
5	2	0	1	0	2	0	5	0	5	0	5	0	4	1	1
6	1	0	1	0	1	0	3	1	3	1	3	1	3	0	0
7	3	0	2	0	3	0	2	0	2	0	2	0	2	0	0
Total	17	13	7	13	8	11	26	8	21	8	19	8	10	1	1

than class 3 were mature. The smallest mature female from the Noises weighed 155 g and from Motukawao 156 g. Body condition was not correlated with reproductive condition; the mean condition index for all immature females was 2.89:±0.15 and for all mature females 3.12:±0.45.

Fresh corpora lutea from a recent ovulation (distinguished by large luteal cells; Hall and Davis, 1950) were present in 26 females from the Noises Islands, the mean number being 5.1 per ovary (range 1-11). The average number in females from the Motukawao Islands was 5.6 per ovary (range 2-9). Females on the Noises Islands stopped undergoing oestrous cycles in late autumn. Ovarian activity began again in August and was apparent in all adult females caught from then until April.

Three pregnant females were trapped. One (age class 5) caught in November 1977 on Motuhoropapa had seven embryos, two of which were being resorbed; she also had nine corpora lutea of pregnancy, so four ova (44.4%) had failed to produce viable embryos. Two Motukawao females (both age class 3) trapped in March 1979 each had six viable embryos and six corpora of pregnancy. A lactating female (age class 5) was trapped on Otata in February 1978. Placental scars from past pregnancies were present only in females older than age class 3 (Table 4). The average number of scars per female was 16.4 (range 6-31), with a mean of 7.7 (range 0-20) on each uterine horn. Assuming an average litter size of about seven (see also Bettsworth, 1972; Moller and Tilley, 1984), five females would have borne two or three litters and two females would have borne four. There was no consistent relationship between numbers of litters or

scars and the age of the female: for example, a class 5 female had probably produced four litters whereas a class 7 female had bred only once.

Although the likelihood of pregnancy certainly increased with age, 13 of the 27 mature females in these samples had never been pregnant. Judging from the distinct generations of corpora lutea in their ovaries, eight females from the Noises and five from the Motukawao Islands had undergone between them at least 20 oestrous cycles without conceiving. Six of them had fresh corpora lutea, but when one uterus from each was serially sectioned no blastocysts or implanting embryos were found.

Food habits on the Noises Islands

i) Analysis of stomach contents

Insects, seeds, fruit and other plant material comprised most of the stomach contents of the rats (Table 5). Invertebrate or vertebrate prey were present in the stomachs of 20 females (87.0%) and 11 males (84.6%). Annelids, molluscs, other invertebrates and birds tended to be present less often in males than in females. This was most obvious for molluscs, which were recovered from eight females (34.8%) but only from one male (7.7%). Similarly, with marine foods, polychaetes, marine molluscs and crustacea were identified in nine females (39.1%) but only two males (15.4%). The main foods volumetrically were seeds, molluscs and insects (Table 5). The first two in particular were sometimes eaten avidly: for example two Otata females trapped in August 1978 and January 1979 contained 7.4 g and 9.6 g of mollusc flesh, which represented 3.3% and 3.2% of their respective body

Table 5: Occurrence and volumes of foods found in the stomachs of 13 male (M) and 23 female (F) Norway rats trapped on the Noises Islands. (Trace, < 10% by volume; medium, 10-50%; large, > 50%).

Food	Occurrence in stomachs		Volume present					
			Trace		Medium		Large	
	M	F	M	F	M	F	M	F
Seed and fruit	7	13	2	4	2	6	3	3
Other plant material	8	13	7	12	1	1	0	0
Insect	10	14	6	11	2	1	2	2
Annelid	1	6	0	2	1	4	0	0
Mollusc	1	8	0	2	1	2	0	4
Other invertebrate	1	6	1	6	0	0	0	0
Bird	1	5	1	5	0	0	0	0
Unidentified animal	2	4	1	3	1	1	0	0

weights. The sample of stomachs was too small and clumped in its monthly distribution for seasonal changes in diet to be investigated.

Foods positively identified are listed in Table 6, together with the number of stomachs in which they were found. The seeds eaten most often were *Pitosporum crassifolium* and *Solanum* spp. *Pitosporum* was present in medium or large amounts in six of the seven stomachs in which it occurred. Three species of *Solanum* grow on the Noises (*S. aviculare*, *S. nigrum*, *S. nodiflorum*) but they could not be separated in the stomach contents.

Six of the seven rats which had eaten *Solanum* were adults and four had consumed medium or large amounts.

Wetas (family Orthoptera) were the commonest insect prey, being present in 13 stomachs (Table 6). They were not preyed on equally by male and female rats: cave wetas (*Pleioplectron* sp. and *Neonetus* sp.) were found in the stomachs of seven females but no males ($\chi^2 = 4.91$, $P < 0.05$), whereas the large *Hemiandrus furcifer* and *Hemideina thoracica* were recovered from five males but only one female. This difference may reflect different foraging sites or

Table 6: Foods identified in the stomachs of 13 male (M) and 23 female (F) Norway rats and in 13 samples of rat droppings collected on the Noises Islands. (* eaten as larvae; ¹ including one adult *O. xanthosticta*).

Food	Occurrence in stomachs		Occurrence in droppings
	M	F	
Seeds and fruits			
<i>Pitosporum crassifolium</i>	3	4	7
<i>Solanum</i> spp.	2	5	3
<i>Disphyma australe</i>	0	1	5
<i>Marcopiper excelsum</i>	0	1	2
<i>Melicope ternate</i>	0	0	2
<i>Carex flagellifera</i>	0	0	2
<i>Metrosideros excelsa</i>	1	0	0
<i>Silene gallica</i>	0	0	1
Insects			
Orthoptera			
Cave wetas (<i>Pleioplectron</i> sp., <i>Neonetus</i> sp.)	0	7	2
<i>Hemiandrus furcifer</i>	3	1	3
<i>Hemideina thoracica</i>	2	0	1
Coleoptera			
<i>Odontria xanthosticta</i> *	1	2	3 ¹
<i>Ocnodeus piceus</i> *	0	2	1
<i>Chrysopeplus expolitus</i>	0	1	0
<i>Minopeus elongates</i>	0	0	1
Lepidoptera			
<i>Graphania ustistriga</i> *	2	1	0
<i>Aletia moderata</i> *	0	1	0
Molluscs			
<i>Lepsiella scobina</i>	0	2	4
<i>Onchidella</i> cf. <i>nigricans</i>	0	5	0
<i>Cellana</i> spp.	0	3	1
Mussels	0	4	0
<i>Eatoniella</i> spp.	0	3	0
<i>Arion hortensis</i>	1	1	0
<i>Diloma</i> sp.	0	1	0
<i>Nerita atramentosa</i>	0	1	0
Crustacea			
<i>Pinnotheres novaezelandiae</i>	0	1	0
<i>Chamaesipho columna</i>	0	1	0
Bird (feathers)			
<i>Eudyptula minor</i>	0	1	0
<i>Pterodroma macroptera</i>	0	1	0

methods by males and females. The amphibious marine slug *Onchidella* cf. *nigricans* was the most important molluscan food both in volume and frequency of occurrence (Table 6). This slug lacks an external shell and is often active on rocks in the upper tidal zone (Powell, 1979), making it vulnerable to rats. The intertidal limpet *Cellana* sp. was always present with *Onchidella* remains. Mussels, mainly the small *Xenostrobus pulex* when identification was possible, were also a favoured prey. *Xenostrobus* has a thin shell and forms dense littoral mats readily accessible to rats. The only terrestrial mollusc identified was the introduced slug *Arion hortensis*, found in two rats from Otata.

Other invertebrates recovered included polychaetes (7 stomachs), amphipod fragments (1), barnacles *Chamaesipho columna* (1) and a pea crab *Pinnotheres novaezelandiae*. The crab is symbiotic in mussels and was found in a stomach with many mussel remains. The barnacle and also the gastropod *Eatoniella* sp. are very small and both grow on the shells of larger molluscs; they were probably eaten accidentally.

Feathers were found in six rats, two from Motuhoropapa and four from Otata. Feathers in four stomachs could not be identified; the others came from a grey-faced petrel *Pterodroma macroptera* chick and an adult little blue penguin *Eudyptula minor*, both on Otata. None of the feathers were present with flesh, and it was impossible to tell if the rats had fed from carrion or from birds which they had killed.

ii) Foods in rat droppings

The droppings were composed mostly of unrecognisable material (probably vegetation) and grains of soil, but remains from seeds, insects and molluscs were also found (Table 6). Seeds occurred most frequently, being present in 12 samples; insects were present in 10 and molluscs in six. The commonest seeds were from *Pittosporum crassifolium*; those of *Melicope ternata*, *Carex flagellifera* and *Silene gallica* were recovered from droppings but not from stomachs. Wetas were the most common insects. Four collections contained opercula from the marine mollusc *Lepsiella scobina*.

iii) Feeding sign and additional foods

In February 1978 a cache of 45 fresh *Pittosporum crassifolium* fruit capsules were found on Ike Island.

Rats had harvested the capsules by biting cleanly through stalks at the tips of branches up to 2 m high on nearby *Pittosporum* shrubs. The capsules can have been reached only by agile climbing, which is unusual for Norway rats (cf. Hutterer, 1974; Hill, Robertson and Sutherland, 1983). The cache also contained a partly-eaten crab *Leptograpsus variegatus* with a carapace 45 mm wide. In April 1981 an occupied burrow on Ike contained a hoard of several hundred *Pittosporum* capsules, and elsewhere on the island there were browsed fronds of *Asplenium*, gnawed *Pittosporum* capsules and three partly-eaten crabs. Also in April 1981, freshly chewed *Pittosporum* capsules and *Planchonella costata* drupes were found at several places on Motuhoropapa.

Rat-chewed eggs of grey-faced petrels were found on Motuhoropapa twice in October 1978, as well as on Otata in September 1979 and June 1980. A dead grey-faced petrel chick with the right side of its skull eaten away was also discovered on Motuhoropapa in October 1978.

Empty shells of the common littoral gastropods *Turbo smaragdus* and *Thais orbita* were often encountered in and around rat burrows on Ike and Otata Islands. Another mollusc eaten by the rats was the large terrestrial flax snail *Placostylus hongii*. On 3 March 1934 Dr W. R. B. Powell (in litt.) liberated 100 adult snails from Aorangi Island, Poor Knights group, on the northern part of Motuhoropapa. The snails built up a dense population in the 20 years or so before rats arrived, but declined thereafter. We have found many rat-damaged juvenile shells, usually with the lower spirals chewed open or the apex of the spiral removed. Adult shells are too massive to be opened. The population declined probably because of the heavy predation on juvenile snails.

Discussion

Most of the few published studies of free-living Norway rats have been concerned with commensal populations in cities or on farms. The Noises study is one of only a handful carried out on wild rats living totally without human support: these others include three studies in New Zealand (Beveridge and Daniel, 1965; Bettesworth, 1972; Moller and Tilley, 1984), Pye and Bonner's (1980) research on South Georgia, and Lattanzio and Chapman's (1980) on St. Clements Island, Maryland. Urban environments, and agricultural ones to a lesser degree, are characterised by ample food and cover and

Table 7: Average adult body sizes of wild male (M) and female (F) Norway rats in the New Zealand region and elsewhere. (1 = this study; 2 = Beveridge and Daniel, 1965; 3 = Moors, unpubl.; 4 = Lattanzio and Chapman, 1980; 5 = Pye and Bonner, 1980; HBL = head-body length.)

Island	Weight (g)		HBL (mm)		Tail (mm)		Reference
	M	F	M	F	M	F	
Noises	267	255	215	203	175	172	1
Mokoia	233	245	187	192	156	162	2
Stewart	218	189	181	175	164	158	3
Campbell	223	245	187	192	156	162	3
St. Clements	287	273	215	213	188	187	4
South Georgia	-	215	-	-	-	-	5

opportunities for buffering climatic extremes. These advantages are reduced or absent in the habitats occupied by wild rats. Consequently, as was apparent with the Noises rats, their populations tend to be sparser and they differ in various aspects of their biology.

Body size and condition

The average dimensions of mature Norway rats from the Noises are similar to those from other islands in the New Zealand region and elsewhere (Table 7). Variations between the samples are partly due to differences in the authors' criteria for adulthood and in the sizes at which rats mature. Most rats in the samples in Table 7 weighed 175-300 g and individuals exceeding 400 g were rare. Only one such rat was encountered on the Noises Islands, and none were present in the samples from Stewart and Campbell Islands and South Georgia. The heaviest rat among the 141 adults from Mokoia Island weighed 422 g, and the heaviest caught on Waewaetorea Island weighed less than 350 g (Moller and Tilley, 1984). By contrast, individuals weighing more than 400 g were common in the urban and rural samples analysed by Perry (1945), Davis and Hall (1948, 1951), Leslie, Venables and Venables (1952), and Bishop and Hartley (1976).

Seasonal body condition indices reported by Davis and Hall (1951) for female rats from Baltimore varied from 3.11 to 3.87 (mean 3.67). There were no significant differences between seasons. These indices generally exceed those for Noises and Motukawao rats of both sexes, indicating that the Baltimore females were relatively heavier for their body length. Norway rats on St. Clements Island exhibited no significant differences in body condition between sexes or seasons, but juveniles had lower indices than adults (Lattanzio and Chapman, 1980). The greater weight and better condition of urban

and rural rats may result from their food being more reliably available or of higher quality. Davis (1949) found that Norway rats in Baltimore city were larger than on a nearby farm, and by manipulating the diet of captives from each population he was able to show that farm rats were smaller because their diet was deficient. The apparent differences between wild and commensal Norway rats should therefore be tested with samples from populations whose diets are known in detail.

Breeding

The general pattern of reproduction encountered in this study, with males being continuously fertile and females in breeding condition between spring and early autumn, corresponds with the results from many other investigations of Norway rats (e.g. Perry, 1945; Davis and Hall, 1948; Bettesworth, 1972; Andrews et al., 1972; Lattanzio and Chapman, 1980). However, compared with commensal rats there were several important differences in the details of female breeding which greatly reduced their reproductive output.

Histological examination showed that eight mature females (42.1%) from the Noises and five (62.5%) from the Motukawao Islands had ovulated but failed to conceive. These missed opportunities to breed may have resulted from the females avoiding copulation or, less likely given the size of the islands and the mobility of the rats, their failing to meet a male during oestrus. Two alternative explanations, that males were infertile or that conception occurred but implantation failed, are not supported by the available information. Perry (1945) also found females in this condition, but they represented only 14.1 % of 660 adult females. This percentage is significantly less than the figure of 48.1 % for my combined sample ($\chi^2 = 23.06, p < 0.001$).

Given that body weight broadly reflects age of

Norway rats (Bishop and Hartley, 1976), males and females in this study matured later than the urban and rural rats investigated so far. My smallest mature male weighed 196 g, whereas the weights at which 50% of males were mature varied from 93 to 190 g in seven populations reviewed by Davis (1953), with five populations having the 50% point below 150 g. Similarly, Davis gives a range of 113-153 g for the 50% maturity point in five samples of females, compared with a weight of 155 g for my smallest mature female. Norway rats on Waewaetorea Island also displayed delayed maturity, the 50% maturity point being 189 g for males and 180 g for females (Moller and Tilley, 1984).

Perry (1945) and Leslie et al. (1952) found that pregnancies are more frequent and litter sizes larger among heavier, older females. On the Noises Islands female rats were relatively light, the number of litters borne was unrelated to age, and pregnant females carried small litters (counts of healthy embryos were 5,6,6). Although very small, this sample agrees with information available on litter sizes from other New Zealand islands: mean litter size was 6.7 on Waewaetorea Island (Moller and Tilley, 1984), 6.5 on Whale Island (Bettesworth, 1972) and 8.0 on Mokoia Island (Beveridge and Daniel, 1965). These are lower than all but two of the 27 average embryo counts listed by Davis (1953). Among the rural females examined by Leslie et al. (1952) the average embryo count was 8.3 for rats weighing 195-294 g and 9.4 for those weighing 295-394 g. These weights encompass virtually all females in the three New Zealand samples, but their average counts were markedly lower. The small litters on the Noises and Motukawao Islands were not due to reduced fertility: females there shed an average of 10.8 ova at each oestrus, compared with 10.0 ova shed by urban and rural females (Perry, 1945). Apparently at these islands fewer ova were fertilised, or fewer blastocysts implanted, or more embryos were resorbed.

The reproductive output of island populations of rodents is generally less than that of their mainland counterparts (Gliwicz, 1980). Gliwicz highlighted four mechanisms responsible for this reduction: an abbreviated breeding season, some mature females failing to breed, delayed maturation and small litters. Norway rats on the Noises and Motukawao Islands displayed three of these traits, the only exception being a breeding season of normal length.

Food habits

Rats on the Noises Islands ate a diverse selection of animal and plant foods. Similar diets have been

recorded elsewhere in New Zealand by Beveridge and Daniel (1965), Bettesworth (1972) and Bettesworth and Anderson (1972), and overseas by Drummond (1960), Fellows and Sugihara (1977) and Pye and Bonner (1980). Age-dependent consumption of *Solanum* berries has also been reported by Clark (1980), who observed that only adult *Rattus rattus* ate *S. nodiflorum* fruits on the Galapagos Islands. *Solanum* stems, leaves and fruits contain alkaloid toxins which can cause respiratory difficulties, diarrhoea, vomiting and even death in a variety of mammals (see Weller and Phipps, 1979). Adult rats must be able to avoid or greatly reduce the harmful effects of these toxins, perhaps by metabolising them.

There is circumstantial evidence implicating rats in the decline or disappearance of several animal species on the Noises Islands. The near-loss of *Placostylus* snails from Motuhoropapa has already been described. White-faced storm petrels once bred on the David Rocks, but did not survive the brief colonisation of Norway rats in the early 1960s (Cunningham and Moors, in press). The beetle *Mimopeus elongatus* thrives in the absence of rats on the David Rocks and Maria Island, and the large centipede *Cormocephalus rubriceps* is also present, but the two species are rare and absent, respectively, from Otata and Motuhoropapa (J. C. Watt, pers. comm.). *Mimopeus* remains have been found in a rat dropping (Table 6); and Ramsay (1978) has noted the same distribution pattern for *Cormocephalus* on islands with and without *Rattus exulans*. Elsewhere in New Zealand, Norway rats are thought to be devastating many groups of invertebrates on Breaksea Island, Fiordland (Bremner, Butcher and Patterson, 1984), and in some years to be responsible for breeding failures of grey-faced petrels on Whale Island (Imber, 1978, 1984).

Factors limiting the abundance of Norway rats on the Noises Islands

Apart from my estimate of 2.6-4.2 rats/ha on Motuhoropapa, the only other information on the density of Norway rats in New Zealand is 5-10 rats/ha on Whale Island (Bettesworth, 1972). Lattanzio and Chapman (1980) calculated a maximum density of 3.3 rats/ha on St. Clements Island. These population levels are well below those described for commensal Norway rats in urban or agricultural environments (e.g. Venables and Leslie, 1942; Davis, 1953), or in Calhoun's (1962) outdoor enclosure.

Table 8: Kill-trapping success (rats caught per 100 trap-nights) for wild Norway rats on islands in the New Zealand region. Bracketed figures show the ranges in success between trapping sessions or habitats (1 = this study; 2 = Moller and Tilley, 1984; 3 = Bettesworth, 1972; 4 = Beveridge and Daniel, 1965; 5 = Daniel, 1969; 6 = Baird, 1977; 7 = Moors, unpubl.)

Island	No. rats caught	Trapping success	Reference
Motuhoropapa	11	9.1	1
Otata	13	18.4	1
Motukaramarama	15	10.5	1
Motuwi	6	12.1	1
Four islands in Bay of Islands	7	0.1-0.7	2
Waewaetorea	122	27.5 (25.6-55.6)	2
Whale	158	15.0 (6.9-23.6)	3
Mokoia	197	37.3 (8-64)	4
Kapiti	109	15.7	5
Kapiti	28	11.0 (2.4-19.6)	6
Stewart	38	0.6	7
Campbell	27	14.7	7

The initial abundance of rats on the Noises can also be gauged by comparing kill-trapping results from the first two trapping sessions (Table 1) with those from the other studies listed in Table 8. The capture rates for Motuhoropapa and Otata are in the mid to upper range of these values, but are substantially less than the highest rates on Mokoia and Waewaetorea Islands. However, subsequent trapping success for the Noises (Table 1) is among the lowest reported. These comparisons suggest that at first the density of rats on Otata exceeded that on Motuhoropapa, but on neither island were the rats as abundant as they can be in the most favourable habitats. Both populations were apparently unable to maintain these numbers once trapping began.

What factors were likely to be limiting Noises rats to densities below those reached on some other islands? There is no evidence that either disease or parasitism was responsible. The only predators were a few harriers (*Circus approximans*) which preyed mainly on birds (Cunningham and Moors, in press). The quantity of food available (as distinct from its quality) may have been responsible, although I have no measurements of the abundance or availability of foods. The factors leading to the low reproductive output already discussed are another possible cause. Judging from the results of other *Rattus* studies, two factors could have restricted breeding: a shortage of nutritionally adequate food for breeding females and growing juveniles, and/ or a shortage of fresh water.

Pregnancy, lactation and growth require a diet rich in protein (Lloyd, McDonald and Crampton, 1978). Norway rats obtain much of their protein from animal foods, mainly invertebrates, which are an important component of the diet (see previous references on food habits). These prey generally contain a better balance of essential amino acids than plant foods (Lloyd et al., 1978). During the Noises breeding season three types of animal prey (cave wetas, molluscs and polychaetes) were present only in the stomachs of females, often in substantial amounts. On Whale Island breeding commenced and was highest when the rats were feeding on the eggs and young chicks of grey-faced petrels (Bettesworth, 1972). In the Galapagos Islands Clark (1980, 1981) found that *Rattus rattus* ate more animal prey when breeding than at other times. She suggested that rat numbers were limited by the availability of protein-rich foods immediately after breeding, when young rats were growing (Clark, 1980). Shortages of protein in Norway rats can prolong gestation, induce resorption of embryos, reduce birth weight and restrict the growth of young (Widdowson and Cowen, 1972; Chow and Rider, 1973; Woodside et al., 1981).

The protein-rich diet needed for breeding increases the water requirements of Norway rats (Fitzsimons and Le Magnen, 1969). Water intake is also proportional to dietary salt concentration (Richter and Mosier, 1954), so that marine foods like molluscs and polychaetes would require additional water. These extra demands for water would coincide at the Noises with the period of minimum rainfall between November and February. At nearby Tiritiri Island the average rainfall in these months is 252 mm (24% of the annual mean), the driest months usually being December (61 mm) and January (51 mm). However, summer rainfall varies, and in 1978 only 47 mm fell between January and the end of March. Norway rats cannot survive on seawater alone (Barker and Adolph, 1953) and in dry summers at the Noises they would therefore have to rely mainly on moisture in food. Under similarly dry conditions Norway rats on an island in Japan lost weight, ceased breeding and some died from thirst (Yabe, 1982).

Norway rats have now colonised at least 36 islands and island groups in the New Zealand region (Atkinson, 1978, in press). Despite having such a wide distribution and what is thought to be a serious impact on some prey species, the factors limiting

these rat populations have scarcely been studied. This information is needed to help understand how the rats have fitted into island ecosystems, and to assist in planning the management of islands for wildlife conservation.

Acknowledgements

I am most grateful to Mr B. P. Neureuter for allowing the New Zealand Wildlife Service to have free access to the Noises Islands, to stay in the house on Otata, and to construct tracks and other facilities. He and his family provided valuable information about the history of the islands and enthusiastically supported the research. I thank John Carruthers, Duncan Cunningham, Ian McFadden, Dr Christoph Imboden, Dr Ian Atkinson and many past and present staff of the Wildlife Service for their assistance with fieldwork and logistics. Ross Pickard advised on methods of population estimation, and sorted and identified rat foods with specialist help from Entomology Division, D.S.I.R. (insects), Mrs M. Bulfin (seeds and fruits), Dr F. M. Climo (molluscs), Dr G. Hicks (crustacea) and Mr J. A. Bartle (birds). Mr S. Bisset identified the intestinal parasites, and Dr S. R. B. Solly analysed the livers for lead. Travel to the islands would have been less reliable without the boating skills of the late Arthur Calvert, Joe Gaunt and Marten Meenken. John Gard supplied information about Otata, and Dr J. C. Watt, Dr D. R. Towns and Prof. P. D. G. Skegg allowed me to quote unpublished data. The manuscript benefited from critical comments by Dr B. M. Fitzgerald, Dr M. C. Crawley and a referee.

References

- Andrews, R. V.; Belknap, R. W.; Southard, J.; Lorincz, M.; Hess, S. 1972. Physiological, demographic and pathological changes in wild Norway rat populations over an annual cycle. *Comparative Biochemistry and Physiology* 41A: 149-65.
- Atkinson, I. A. E. 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. (Editors). *The ecology and control of rodents in New Zealand Nature Reserves*. pp. 7-30. Department of Lands and Survey Information Series No.4.
- Atkinson, I. A. E. 1984. (unpublished). *Vascular flora of the Noises Islands, Hauraki Gulf*. D.S.I.R. Botany Division Internal Report No. 502.
- Atkinson, I. A. E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *International Council for Bird Preservation Technical Publication* 3: 35-81.
- Atkinson, I. A. E. In press. Rodents on New Zealand's offshore islands: distribution, effects and precautions against further spread. In: Wright, A. E.; Beever, R. E. (Editors). *The offshore islands of northern New Zealand*. Department of Lands and Survey Information Series No. 14.
- Baird, G. G. 1977. (unpublished). A snap-trap survey of rats on Kapiti Island. B.Sc (Hons.) thesis, Victoria University.
- Barker, J. P.; Adolph, E. F. 1953. Survival of rats without water and given sea water. *American Journal of Physiology* 173: 495-502.
- Begon, M. 1979. *Investigating animal abundance*. Edward Arnold, London.
- Bettesworth, D. J. 1972. (unpublished). Aspects of the ecology of *Rattus norvegicus* on Whale Island, Bay of Plenty, New Zealand. M.Sc. thesis, University of Auckland.
- Bettesworth, D. J.; Anderson, G. R. V. 1972. Diet of *Rattus norvegicus* on Whale Island, Bay of Plenty, New Zealand. *Tane* 18: 189-95.
- Beveridge, A. E.; Daniel, M. J. 1965. Observations of a high population of brown rats (*Rattus norvegicus* Berkenhout 1767) on Mokoia Island, Lake Rotorua. *New Zealand Journal of Science* 8: 174-89.
- Bishop, J. A.; Hartley, D. J. 1976. The size and age structure of rural populations of *Rattus norvegicus* containing individuals resistant to the anticoagulant poison warfarin. *Journal of Animal Ecology* 45: 623-46.
- Bremner, A. G.; Butcher, C. F.; Patterson, G. B. 1984. The density of indigenous invertebrates on three islands in Breaksea Sound, Fiordland, in relation to the distribution of introduced mammals. *Journal of the Royal Society of New Zealand* 14: 379-86.
- Calhoun, J. B. 1962. *The ecology and sociology of the Norway rat*. US Department of Health, Education and Welfare. Public Health Service Publication Number 1008.

- Chow, B. F.; Rider, A. A. 1973. Implications of the effects of maternal diets in various species. *Journal of Animal Science* 36: 167-73.
- Clark, D. A. 1980. Age- and sex-dependent foraging strategies of a small mammalian carnivore. *Journal of Animal Ecology* 49: 549-63.
- Clark, D. A. 1981. Foraging patterns of black rats across a desert-montane forest gradient in the Galapagos Islands. *Biotropica* 13: 182-94.
- Cunningham, D. M.; Moors, P. J. 1983. *A guide to the identification and collection of New Zealand rodents*. New Zealand Wildlife Service Occasional Publication No.4, pp. 1-20.
- Cunningham, D. M.; Moors, P. J. In press. The birds of the Noises Islands, Hauraki Gulf, New Zealand. *Notornis*.
- Daniel, M. J. 1969. A survey of rats on Kapiti Island, New Zealand. *New Zealand Journal of Science* 12: 363-72.
- Daniel, M. J. 1978. Population ecology of ship and Norway rats in New Zealand. In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. (Editors). *The ecology and control of rodents in New Zealand Nature Reserves*. pp. 145-52. Department of Lands and Survey Information Series No.4.
- Davis, D. E. 1949. A phenotypical difference in growth of wild rats. *Growth* 13: 1-6.
- Davis, D. E. 1953. The characteristics of rat populations. *Quarterly Review of Biology* 28: 373-401.
- Davis, D. E.; Hall, O. 1948. The seasonal reproductive condition of male brown rats in Baltimore, Maryland. *Physiological Zoology* 21: 272-82.
- Davis, D. E.; Hall, O. 1951. The seasonal reproductive condition of female Norway (brown) rats in Baltimore, Maryland. *Physiological Zoology* 24: 9-20.
- Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. (Editors). 1978. *The ecology and control of rodents in New Zealand Nature Reserves*. Department of Lands and Survey Information Series No.4.
- Drummond, D. C. 1960. The food of *Rattus norvegicus* Berk. in an area of sea wall, saltmarsh and mudflat. *Journal of Animal Ecology* 29: 341-7.
- Esler, A. E. 1978. Botanical features of islands near the west coast of the Coromandel Peninsula, New Zealand. *New Zealand Journal of Botany* 16: 25-44.
- Fellows, D. P.; Sugihara, R. T. 1977. Food habits of Norway and Polynesian rats in Hawaiian sugarcane fields. *Hawaiian Planters' Record* 59: 67-86.
- Fitzsimons, T. J.; Le Magnen, J. 1969. Eating as a regulatory control of drinking in the rat. *Journal of Comparative Physiology and Psychology* 64: 59-67.
- Gliwicz, J. 1980. Island populations of rodents: their organisation and functioning. *Biological Reviews* 55: 109-38.
- Hall, O.; Davis, D. E. 1950. Corpora lutea counts and their relation to the numbers of embryos in the wild Norway rat. *Texas Reports in Biology and Medicine* 8: 564-82.
- Hardy, A. R.; Taylor, K. D. 1979. Radio tracking of *Rattus norvegicus* on farms. In: Amlaner, C. J.; Macdonald, D. W. (Editors). *A handbook on biotelemetry and radiotracking*. pp. 657-65. Pergamon Press, Oxford.
- Hill, D. A.; Robertson, H. A.; Sutherland, W. J. 1983. Brown rats (*Rattus norvegicus*) climbing to obtain sloes and blackberries. *Journal of Zoology, London* 200: 302.
- Hutterer, R. 1974. [Norway rats, *Rattus norvegicus*, climb sunflowers and remove the centre of the flower caps]. *Zoologische Garten N. F. Jena* 44: 243-6. (Translation by Dept. Internal Affairs).
- Imber, M. J. 1978. The effects of rats on breeding success of petrels. In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. (Editors). *The ecology and control of rodents in New Zealand Nature Reserves*. pp. 67-74. Department of Lands and Survey Information Series No.4.
- Imber, M. J. 1984. Exploitation by rats *Rattus* of eggs neglected by gadfly petrels *Pterodroma*. *Cormorant* 12: 82-93.
- Karnoukhova, N. G. 1971. Age determination of brown and black rats. *Soviet Journal of Ecology* 2: 144-7.
- Lattanzio, R. M.; Chapman, J. A. 1980. Reproductive and physiological cycles in an island population of Norway rats. *Bulletin of the Chicago Academy of Science* 12: 1-68.
- Leslie, P. H.; VENABLES, U. M.; VENABLES, L. S. V. 1952. The fertility and population structure of the brown rat (*Rattus norvegicus*) in corn-ricks

- and some other habitats. *Proceedings of the Zoological Society, London*. 122: 187-238.
- Lloyd, L. E.; McDonald, B. E.; Crampton, E. W. 1978. *Fundamentals of nutrition*. (Second edition). W. H. Freeman, San Francisco.
- Mayer, W. 1968. The stratigraphy and structure of the Waipapa group of islands of Motutapu, Rakino and the Noises group near Auckland, New Zealand. *Transactions of the Royal Society of New Zealand, Geology Series* 5: 215-33.
- Merton, D. V. 1960. (unpublished). Rats on the Noises Islands. Wildlife Service Report, file WIL 30/3/35.
- Moller, H.; Tilley, J. A. V. 1984. (unpublished). *Rodents and mustelids in the eastern Bay of Islands*. D.S.I.R. Ecology Division Report, file 6/20/1.
- Moors, P. J. 1985. Eradication campaigns against *Rattus norvegicus* on the Noises Islands, New Zealand, using brodifacoum and 1080. *International Council for Bird Preservation Technical Publication* 3: 143-155.
- Nelson, L.; Clark, F. W. 1973. Correction for sprung traps in catch / effort calculations of trapping results. *Journal of Mammalogy* 54: 295-8.
- Perry, J. S. 1945. The reproduction of the wild brown rat (*Rattus norvegicus* Erxleben). *Proceedings of the Zoological Society, London* 115: 19-46.
- Powell, A. W. B. 1979. *New Zealand mollusca*. Collins, Auckland.
- Pye, T.; Bonner, W. N. 1980. Feral brown rats, *Rattus norvegicus*, in South Georgia (South Atlantic Ocean). *Journal of Zoology, London* 192: 237-55.
- Ramsay, G. W. 1978. A review of the effect of rodents on the New Zealand invertebrate fauna. *In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. (Editors). The ecology and control of rodents in New Zealand Nature Reserves*. pp. 89-95. Department of Lands and Survey Information Series No.4.
- Richter, C. P.; Mosier, H. D. 1954. Maximum sodium chloride intake and thirst in domesticated and wild Norway rats. *American Journal of Physiology* 176: 213-22.
- Roush, G.; Kehoe, R. A. 1964. Toxicology: inorganic. *Annual Review of Pharmacology* 4: 427-64.
- Skegg, P. D. G. 1963. (unpublished). Note concerning rats and petrels on Noises Islands. Wildlife Service Report, file WIL 30/3/35.
- Sokal, R. P.; Rohlf, F. J. 1969. *Biometry*. W. H. Freeman, San Francisco.
- Venables, L. S. V.; Leslie, P. H. 1942. The rat and mouse populations of corn ricks. *Journal of Animal Ecology* 11: 44-68.
- Waghorn, E. G. 1983. Population changes of the Australasian gannet *Morus serrator* (Gray) at the Motu Karamarama gannetry, Hauraki Gulf, New Zealand. *Emu* 82: 286-295.
- Weller, R. F.; Phipps, R. H. 1979. A review of black nightshade (*Solanum nigrum* L.). *Protection Ecology* 1: 121-39.
- Widdowson, E. M.; Cowen, J. 1972. The effect of protein deficiency and calorie deficiency on the reproduction of rats. *British Journal of Nutrition* 27: 85-95.
- Woodside, B.; Wilson, R.; Chee, P.; Leon, M. 1981. Resource partitioning during reproduction in the Norway rat. *Science* 211: 76-7.
- Yabe, T. 1982. Influence of dehydration on breeding, body size and kidney structure in Norway rats (*Rattus norvegicus*) on an islet. *Physiology and Ecology Japan* 19: 7-13.