Interactions between petrels, rats and rabbits on Whale Island, and effects of rat and rabbit eradication

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Abstract: Norway rats (*Rattus norvegicus*) were present on Whale Island (Moutohora), Bay of Plenty, New Zealand between about 1920 and 1987. During 1969-1971 they reduced by less than 10-35 % the breeding success of grey-faced petrels (*Pterodroma macroptera gouldi*), by eating unattended eggs and killing young or weak chicks. Rabbits (*Oryctolagus cuniculus*), introduced to Moutohora (240 ha surface area) in about 1968, multiplied rapidly to reach a density of up to 375 individuals/ha by early 1973. Their young and corpses were also eaten by rats, and this additional food, available when petrels were absent or less vulnerable (February-June), apparently increased the rat population. During 1972 to 1977, production of fledged young by the petrels was negligible. Applications of anticoagulant baits to kill rats in 1978, 1980 and 1982 resulted in large numbers of young petrels fledging only in those years; there was no carry-over effect in following years. Island-wide laying by hand of brodifacoum baits (Talon 50WB) in 1985 decimated the rat population. Further poisoning, associated with a tandem operation to kill rabbits, led to the eradication of both mammals by late 1987. Breeding success of the petrels from 1985 to 1988 (no data for 1989), and from 1990 to 1994, was consistent and increasing. This study shows that the effect of rats as predators of petrels may be modified by external factors governing the abundance and annual cycle of the predator.

Keywords: breeding success; grey-faced petrel; interactions; *Oryctolagus cuniculus*; pest eradication; predation; *Pterodroma macroptera gouldi*; rabbits; rats; *Rattus norvegicus*.

Introduction

Whale Island or Moutohora (37°52'S, 176°58'E), New Zealand (Fig. 1) is largely a dormant volcanic cone rising to an elevation of 348 m, with a surface area estimated by planimetry of 240 ha. The vegetation has undergone major changes during this study (Ogle, 1990); the present major features are shown in Fig. 1. When Parris *et al*. (1971) reported on the vegetation, much of it was reflective of effects of burning by humans, followed by heavy grazing by sheep (*Ovis aries* L.) and feral goats (*Capra hircus* L.) (Ogle, 1990). Both herbivores have since been removed. Extensive areas were occupied by grassland, with Gramineae dominant in some parts but with the sedge *Isolepis nodosa* (Rottb.) being prevalent over large areas. Subsequently, rabbits [*Oryctolagus cuniculus* (L.)] denuded the grasslands, thus allowing kanuka [*Kunzea ericoides* (A. Rich.)] to regenerate extensively, but rabbits hindered regrowth of other native plants. Grasslands have been almost totally replaced by kanuka scrub up to 6 m high, in turn being gradually replaced by emerging coastal broadleaf forest, which represents the climax vegetation type.

The ecology and breeding success of grey-faced petrels [*Pterodroma macroptera gouldi* (Hutton)] on Moutohora have been studied since 1968 (Imber, 1976, 1984; Harrison, 1992). With an estimated 30,000 to 40,000 breeding pairs present on the island in 1971 (Imber, 1976), this is probably the largest population of this New Zealand endemic subspecies. Grey-faced petrels (505-560 g average mass) are highly pelagic seabirds with a potential foraging range of over 500 km, which return to land only to breed (Imber, 1973, 1976). They nest in burrows during winter, the breeding season being prolonged with birds returning to land in March-April to prepare burrows and mate. They then spend two months at sea before laying in late June through July. Both sexes incubate. Hatching occurs from mid-August to late September, and fledglings depart from early December to the end of January (Imber, 1976). Occasionally during incubation the single egg that is laid is left unattended (embryos can survive chilling of up to at least five days), and it is at this time that eggs are vulnerable to rats (*Rattus* spp.) (Imber, 1984). After

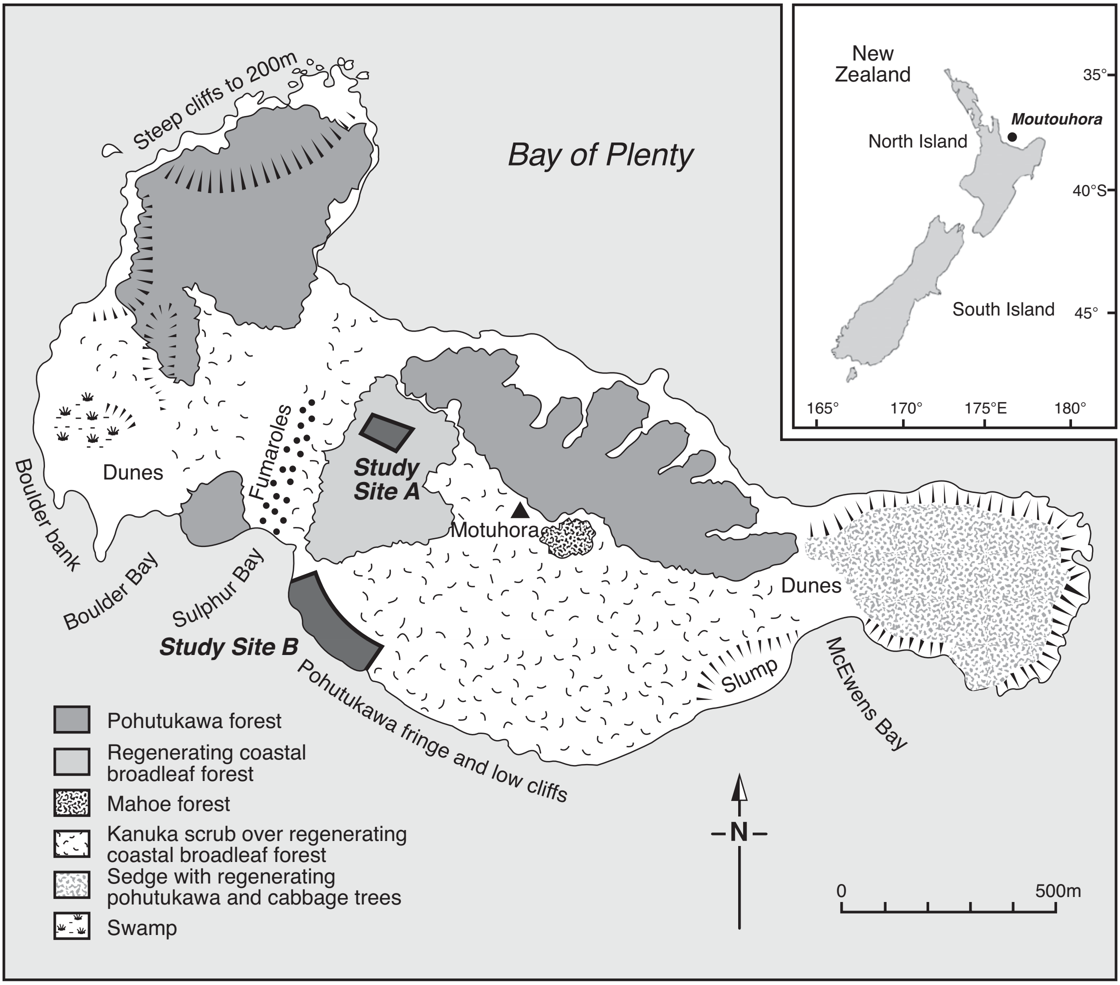

Figure 1. Map of Whale Island (Moutohora) showing its geographical location, vegetation (as in 1999) and features mentioned in the text, and locations of the grey-faced petrel study sites.

hatching the chick is regularly attended by a parent for only 0.5-3 days, following which it is extremely vulnerable to rats (Imber, 1976). At this stage the chick is still very small, weak, sleepy and with poor vision. This vulnerability lessens during the next three weeks but chicks are constantly at risk of being killed by rats.

Rats are known predators of eggs and chicks of petrels, and are capable of exterminating entire colonies (Imber, 1975, 1976, 1984; Norman, 1975; Grant *et al.*, 1981; Atkinson, 1985). Norway rats [*R. norvegicus* (Berkenhout)] are the most menacing of the three commensal rat species to petrels [ship rats (*R. rattus* (L.)) and Polynesian rats (*R. exulans* (Peale)) are the others], because they are the largest, are more terrestrial in habit, and are probably more carnivorous (Bettesworth, 1972; Cunningham and Moors, 1983). Norway rats were present at the beginning of this study on Moutohora, having invaded the island probably in around 1920 when rock was barged from the island to the nearby mainland and workers lived on the island (Moore, 1987).

The first indication that the petrel population was under stress was in 1962, when muttonbirders (local people of Maori descent with hereditary rights to kill for food the young petrels before they fledge), concerned at the scarcity of petrel chicks for exploitation, requested a ban on the harvest (rahui) in 1963 and 1964 (Imber, 1976). Wildlife Refuge status imposed on Moutohora in 1964 has legally protected the petrels since then. During a study on Moutohora of the breeding biology and ecology of grey-faced petrels, Imber (1976) found that, although rats ate some eggs and killed chicks, less than 10-35% of chicks were killed by rats in 1969, 1970 and 1971. The petrels' breeding success was considered good during the four years 1968-71 (Imber, 1976). Rat poison was laid in 1970 and 1971 in a restricted area with a low density of petrel burrows (where all chicks had been killed by rats in 1969), to test its local effect on the petrels' breeding success. In both years no losses could be attributed to rats in this area, and breeding success was high.

The first evidence of rabbits on Moutohora (presence of fur, browsed clover) was found in August 1968, but no rabbits were seen until December 1968 when numbers were still low. It has been suggested (Pedersen and Roche, 1973) that rabbits were introduced by fishermen to provide bait for crayfish (*Jasus* spp.) pots. Previously, Moutohora's 1000+ feral goats apparently provided such bait, but they were almost exterminated in 1964 (Imber, 1976). The last goats were killed in 1977. Ironically, crayfishing is now virtually defunct locally. The rabbits multiplied rapidly to reach up to an estimated density of 375 individuals/ha in early 1973 (Pedersen and Roche, 1973).

Breeding success (measured by the proportion of occupied burrows from which fledglings departed each year) of Moutohora's grey-faced petrel colony has been assessed annually from 1968 until 1994 (except in 1979 and 1989). In this paper we examine this breeding success during the periods when rat and rabbit populations were high, and subsequently up to 1994. We focus especially on the deterioration in the breeding success of the petrel population during 1972 to 1977, following which widespread, intermittent rat poisoning began.

Methods

Petrel breeding success

In 1968 the only assessment of the petrels' breeding success was an exploratory visit to find out whether banding large numbers of fledglings outside burrows at night in December was feasible. During 1969, 135 study burrows (study site A in Fig. 1) were set up to study the petrels' breeding biology (Imber, 1976), and results from these formed the basis for estimates of annual breeding success until 1982. The study burrows all had an artificial access hole (sealed with a rock) which was dug to the nest chamber so that the nest could be reached or its contents observed by researchers. About 85% of these burrows were occupied annually by breeding pairs during 1969-71 (Imber, 1976). The proportion of the study burrows that produced fledglings (breeding success) was found by inspection in early December each year, as fledglings had begun to leave by 7 December (Imber, 1976).

As the years passed, the number of study burrows where the study hole enabled the nest to be reached declined because some petrels altered their burrows. This was particularly so during the years of negligible breeding success, as petrels often extended their burrows after a breeding failure. Also, some study burrows were taken over by rats or rabbits, while others became disused, probably as a result of declining recruitment of young birds. The last year that study site A burrows were used to determine the breeding success rate was 1982. However, study site B was initiated in 1982 (Fig. 1) (Harrison, 1992) and this enabled continuous monitoring of breeding success, with the overlap in that year for a comparison of results from study site A and study site B.

Study site B (1.4 ha) was in a different area of Moutohora. However, banding of fledglings during 1969 to 1982 had shown that breeding success there was similar to that in study site A. In site B, the number of burrows in plots of 2 m radius (12.57 m^2) counted in 1982, 1985 and 1991, and of 3 m radius (28.29 m^2) counted in 1986, gave estimates from 820 to 3000 (Harrison, 1992). However, the number of burrows is likely to have remained relatively constant, as past experience has shown that new burrows were rarely completed, whereas existing burrows were maintained year after year. The only exception was grassland areas at the western end of the island (now kanuka scrub in Fig. 1), where rabbits usurped most burrows. Study site B was in kanuka scrub with relatively few rabbits.

Therefore, we assessed the number of burrows in study site B as follows. In 1993, about 850 chicks were reared in study site B from mark-recapture estimates (nightly estimated number = total captures on that night x cumulative total banded on previous nights / recaptures of banded birds on that night) on 14 nights up to 26 December (M. Harrison, *unpubl.*). A fledgling had been reared to departure in about 38% of burrows, as measured by knock-downs of sticks erected in burrow mouths from 7 December to 26 December 1993. This indicates that there were about 2250 burrows in the 1.4 ha study area, and we have used this figure in subsequent calculations of breeding success rate.

Harrison (1992) estimated the numbers of fledglings in study area B annually by mark-recapture analysis of numbers of fledglings banded and recaptured outside burrows over successive nights in December. He showed that the estimates increased through the month as more fledglings began temporarily leaving their burrows at night. The highest estimates were obtained around 25 December, when the peak of departures of fledglings was reported (Imber, 1976).

An alternative mark-recapture estimate, which we use, takes account of the range of departure dates and the time spent leaving burrows before departure by fledglings. Laying dates ranged from 23 June to 29 July, incubation periods ranged from 53 to 57 days, and chick-rearing periods ranged from 108 to c.128 days (Imber, 1976). Thus fledgling departure dates would extend from about 1 December to 31 January. Utilising the distribution of laying dates (Table 5 in Imber, 1976), and the ranges of incubation and chick-rearing periods, we calculated the distribution of fledgling departure dates in three-day intervals.

Fledglings leave burrows almost nightly to exercise their wings and search for take-off sites over about 15 days before departure, as shown by recapture patterns of fledglings during banding. This figure was applied to the distribution of departure dates to give the proportions of the total number of fledglings likely to be encountered outside burrows (and therefore available to be captured) in similar three-day periods. The highest proportions occurred between 16 and 24 December: 51% during 16-18 December, 54% during 19-21 December, and 52% during 22-24 December. Thus, calculation of the total number of fledglings in study area B using mark/recapture data was preferably made within these periods.

In using the recapture data, allowance was made for departures of banded fledglings, and we assumed for practical purposes that this occurred at a constant rate over a 15-day period (as fledglings come out for about 15 nights before leaving); that is, one fifteenth of all fledglings banded on any night would leave on each successive night, and all of this cohort would have left 15 nights later. In fact, departures are erratic and are dependent on wind in particular. An additional indication of the number of fledglings in the study area was provided by the maximum number of fledglings handled per person per night there each year.

Rat control

In 1969 only a few rats were trapped (using break-back traps) around the study burrows and camp, with the intention of identifying the species present and to protect camp food. However, during that year, 100% predation of young chicks by rats was observed in study burrows at the western end of the island (Imber, 1976). Petrel burrow density was low in that area. Thus, from 1970 to 1972, the part of this area containing study burrows was treated each year with rat poison about May to July. The poison used was Warfarin®, a first-generation anticoagulant, marketed as Prodide® in 25 g packets of ground grain. The packets were slit open and placed in dry situations, under rocks if possible.

In addition, during 1971, 348 rats were killed with break-back traps in five areas of Moutohora during a one-year study of these rats (Bettesworth, 1972). These areas were beach, kanuka scrub, pohutukawa (*Metrosideros excelsa* Sol. ex Gaertn.) forest, grassland and mature kanuka scrub. The last was near petrel study site A. In that study, the density of rats was determined at around 10.9/ha, but it was considered that this figure possibly overestimated the population by as much as 100%, mainly because it was calculated for grassland which supported the highest rat density. Thus, at that time Moutohora held only about 1500 rats, and killing of 348 during Bettesworth's (1972) study may have appreciably reduced their impact on the petrel population that year.

No rat control took place from 1973 to 1976 inclusive (Table 1). In 1977 bait containing a male chemosterilant (Epibloc®) was spread by hand all over Moutohora in an operation supported by the Royal New Zealand Air Force and the New Zealand Army. These baits were in small plastic packets which may have been poorly accepted by the rats. During August 1978, about 60 kg of a Warfarin-based bait, Racumen® (0.3% poison in wheat grain bound in wax blocks) was laid by hand in the main areas of burrows and near camp.

In 1980 the New Zealand Ministry of Agriculture and Fisheries (MAF) used Moutohora's rabbit population for trials of a new second-generation anticoagulant, brodifacoum. During July 1980 large quantities of jam-based baits containing brodifacoum or 1080® (sodium monofluoroacetate) were experimentally laid out in several areas of Moutohora. These areas were in the western part of the island and on the lower southern half of the main peak; the latter being in or close to the higher-density areas of petrel burrows. Although intended for rabbits, the baits may have also been attractive to rats. At the same time, ICI New Zealand supplied for trial a quantity of their new Talon® 50WB baits for rats; each 17 g bait contained more than enough brodifacoum to kill a fully-grown Norway rat. These egg-shaped briquettes of wheat grain bound with wax, coloured green to reduce their attractiveness to birds, were placed in recesses in denser areas of petrel burrows away from the MAF trial areas.

In 1982, 1470 Talon 50WB baits were laid in the denser areas of burrows, i.e. the western to southern slopes of the main peak. The reason for poisoning the rats in alternate years was that studies during 1969 to 1972 had shown that many pairs of grey-faced petrels bred successfully in alternate years only (M. Imber, *unpubl.*) and poisoning every year might therefore not be as effective as poisoning every second year. We also wanted to assess if there was a beneficial effect of poisoning in the year after poison was laid. Further, we were aware of the possibility of poison resistance developing in rats, so did not want to expose them

Table 1. Breeding success of grey-faced petrels (*Pterodroma macroptera gouldi*) from 1968 to 1978 and from 1980 to 1985 on Moutohora, New Zealand, and details of rat and rabbit control.

Year	Rat control	Rabbit control	Petrel breeding success % of burrows with fledgling[1]	 Number of fledglings banded[2]
1968	none	none	NA[5]	77[3]
1969	c. 20 trapped	none	37	131
1970	Warfarin baits over 3 ha	none	25	110
1971	Same as 1970, 348 trapped	none	40	170
1972	Same as 1970	none	4	NA[5]
1973	none	1080-carrots	0	2
1974	none	none	7	16
1975	none	none	0	0
1976	none	none	0	3
1977	Epibloc widely	none	0	9
1978	Racumen widely	none	NA[5]	81
1980	Talon 50WB widely	1080 & brodifacoum	45	98
1981	none	none	0	0
1982	Talon 50WB widely	none	32 (40)[4]	97
1983	none	none	(0.6)[4]	4
1984	none	none	(0)[4]	0
1985	Talon 50WB widely	1080-carrots	(35)[4]	102

[1]% of 135 study burrows with fledglings present.
[2]Maximum number of fledglings banded per person per night.
[3]Exploratory banding; petrel numbers likely to be comparable to those in next three years.
[4]Based on study site B containing an estimated 2250 burrows.
[5]NA = no information is available.

excessively to poison before an attempt at total eradication.

In 1984 poison baits for rats were not lain, to see whether alternate-year breeding success would enable the petrels to be more successful that year without rat-poisoning in the previous two years. When this did not happen, a major reduction of rats was attempted in 1985. The strategy was based on the moderate rat density believed present at that time, the obvious effectiveness and acceptability to rats of Talon baits, and the ability to kill a rat with one 50WB bait. In mid July 1985 about 2100 of these baits were lain throughout the island.

In July 1986, island-wide searches were made for evidence of rats and evidence (faeces, footprints in sand, eaten eggs) was found at only five sites. There was no sign in study site B. About 850 Talon 50WB baits were laid during this search, particularly where sign was found. Jansen (1993) detailed the various methods used from August 1985 to September 1987 to rid Moutohora of rabbits and the last of the rats. These included island-wide distribution on six occasions by fixed-wing aircraft, by helicopter or by hand, of 1080-infused carrots, 1080 in pollard, Talon 20p or bromodialone baits, and localised applications of Talon 20p baits and bromodialone in jam.

Rabbit control

The first attempt to control rabbits on Moutohora was in April 1973 (Pedersen and Roche, 1973), when the Bay of Plenty Pest Destruction Board carried out a standard aerial poisoning operation with 1080 in carrots. Another reduction of the rabbits took place in July 1980, as a result of the MAF trials of brodifacoum mentioned above. A second 1080-carrot aerial poisoning operation, also by the Bay of Plenty Pest Destruction Board, took place in August 1985 (Jansen, 1993). This was the overture of the 2-year campaign summarised in the preceding paragraph, which completed the eradication of both mammals. Gin traps were used in July 1987 to remove some of, and perhaps the last of, the rabbits (Jansen, 1993).

Results

Breeding success of petrels in presence of rats

From 1968 to 1971, the breeding success of grey-faced petrels on Moutohora was considered good (Imber, 1976), with between 25% and 40% of study burrows producing a departing fledgling annually (Table 1). As about 85% of burrows were occupied by breeding pairs each year (Imber, 1976), this equates to 29% to 47% of breeding pairs successfully rearing a fledgling. The degree of rat control during this period was minimal: none in 1968 and only in a low-density burrow area at the western end of the island in 1969 and 1970. However, the trapping of 348 rats in 1971 (Bettesworth, 1972) probably caused a considerable reduction of the rat population. During this period the rabbit population was exploding. In 1968 only sparse evidence of rabbits' presence was seen. In 1971 rabbits were abundant throughout grassland, and had grazed the formerly rank grasses (up to 40 cm high) to a low sward in favoured places.

From 1972 to 1977, the output of departing fledglings by the petrels was minimal (Table 1): none in 1975; perhaps a few hundred in 1973, 1976 and 1977; and an estimated 1500 in 1972 and 2400 in 1974. These estimates are based on the percentage of burrows which were successful in producing fledglings (see Table 1), combined with there being about 35,000 burrows which were used by petrels over that time (Imber, 1976). The total number of fledglings reared during the six years from 1972 to 1977 inclusive was estimated to be less than 6000, yet this population was then capable of producing at least 15,000 fledglings annually, as was observed in 1971 (M. Imber, *unpubl.*). There was almost no rat control during this period (Table 1), the trial with the chemosterilant in 1977 having been a failure.

The poisoning of rabbits by 1080 in 1973 had no noticeable effect on the rat population. In fact the petrels had their worst breeding season on record that year, presumably because of predation by rats. The rabbits recovered to great abundance by 1977, when they were causing much disruption to petrel burrows in grassland, with most petrels abandoning their burrows. This adverse effect of rabbits resulted from rabbits extending petrels' burrows and filling petrel nest chambers with soil, making the burrows narrower with depth exceeding width (in most petrel burrows width exceeds depth), diminishing the burrows' insulation by digging extra entrances, and simply by disturbance including possible injury to chicks.

From 1978 the biennial, extensive poisoning of rats was associated with good breeding success by the petrels (Table 1). The total, or near total, failures in years when no poisoning was carried out strongly suggested that rats were responsible for the majority of petrel breeding failures. We calculated that a population of about 1500 rats could eliminate the breeding effort of about 40,000 breeding pairs of petrels. Data from Imber's (1976) study showed that 74% of 139 eggs hatched (rats then ate 7.75% of eggs laid). Thus about 29,600 chicks might have hatched annually. Rats obtained relatively little food from chicks as they usually ate only the muscle, fat and skull contents and left the stomach. Thus, they probably could each have killed one chick per day, and chicks were vulnerable for up to at least three weeks of age (Imber, 1976). In other words, 1500 rats, each taking 20 chicks, could have killed 30,000. There was evidence in 1977 (a year of near-total annihilation) that killing continued virtually throughout the chick-rearing period.

Table 2. Estimated numbers of grey-faced petrel fledglings reared in a 1.4 ha study area of about 2250 burrows on Moutohora, New Zealand, from 1985 to 1988 and from 1990 to 1994 (with 95% confidence intervals). Estimates were based on mark-recapture data of banded fledglings caught outside burrows at night. Breeding success was calculated assuming 90% of the estimated 2250 burrows were occupied by breeding pairs (see text for description and estimation of % occupancy).

Year	Estimated number of fledglings in 1.4 ha	Breeding success (%)	Maximum of fledglings caught/night
1985	700 ± 105	35	102
1986	550 ± 110	27	59
1987	500 ± 65	25	65
1988	550 ± 90	27	70
1990	700 ± 105	35	106
1991	900 ± 150	44	113
1992	850 ± 150	42	124
1993	850 ± 135	42	122
1994	1050 ± 130	52	170

Breeding success from 1985 to 1994

Our breeding success estimates covered the period during which rats ceased to be a factor affecting the breeding success of the petrels (1985 to 1986), and subsequent to their extermination (1987). Petrels bred moderately to very successfully every year (Table 2). Initially in 1985 there was high success, which came after two years of negligible output of fledglings (Table 1). This was followed by several years of modest output of fledglings, gradually increasing to the highest level in 1994, the last year of study. Although the occupancy rate of burrows by breeding pairs was assumed for practical purposes to be 90% (Table 2), it is likely to have reached that level only latterly. The occupancy rate in 1985 was likely to have been considerably less, because of attrition of the petrel population caused by poor recruitment after more than a decade of intense rat predation. Further, some burrows had been taken over by rabbits and rats, and these would have become vacant during 1985-87.

Burrows were regained by petrels since 1985, and occupancy rates by breeding pairs should have increased, although there has been little evidence of the digging of new burrows. Population expansion has occurred by recolonisation of abandoned habitats, especially present and former grasslands, and vacant burrows around the periphery of the main areas of burrows on the central cone (Fig. 1). This increase has been particularly apparent west of Sulphur Gully (Fig. 1).

Discussion

Grey-faced petrels on Moutohora were affected by Norway rat predation of eggs and chicks in 1969-1971 (Imber, 1976) but the colony still bred successfully, with an estimated 15,000 fledglings reared in 1971. These petrels evidently became much more vulnerable to rats after 1971, with the level of predation of eggs and chicks during 10 breeding seasons (from 1972 to 1977, probably in 1979, and in 1981, 1983 and 1984) likely to have endangered this major population of this endemic petrel if it had been allowed to continue.

Rabbits seem to be implicated in this altered ecology, yet Bettesworth's (1972) study did not indicate how this occurred. The most likely effect of the exploding rabbit population would have been to provide Norway rats with additional food when petrels as a source of food were scarce or absent (February to June). This period coincided with peak numbers of rats on Moutohora (Bettesworth, 1972), so a supplementary food source at that time of the year could have increased the rat population.

Norway rats are known to attack and kill young rabbits (Bettesworth, 1972; B. Zonfrillo, University of Glasgow, Scotland, *pers. comm.*; M. Imber, *pers. obs.*). They were also strongly attracted to dead rabbits when used as bait in cage traps on Moutohora in May 1980 (A. Munn, Department of Conservation, Gisborne, N.Z., *pers. comm.*). Rabbits on Moutohora apparently bred virtually throughout the year, so young rabbits would have been available to rats during February to June. Increasing mortality of rabbits at various ages as the island population grew would also have provided a new food source for rats during February to June.

Surprisingly, Bettesworth (1972) did not find rabbit flesh to be important in rats' diet, though it did attain its highest percent by volume of rat stomach contents in March and May (the only months from January to June when he obtained samples). There may have been several reasons for rabbit flesh not being an important component of rat diet in his study. Firstly, inkweed (*Phytolacca octandra* L.) fruits were most important during March and May in the diet of rats in grassland and scrub (Bettesworth, 1972). Most petrel burrows occurred in these habitats. This plant itself proliferated during the early 1970s, possibly after over-grazing of grasses by rabbits, but declined within the decade as successional vegetation smothered it. Secondly, Bettesworth's (1972) trapping of 348 rats more than likely reduced the rat population significantly, so that rats may have been able to feed mainly on easily-obtained foods (fruits, seeds, invertebrates) during March and May, rather than needing to attack rabbits. Thirdly, the rabbit population was still increasing during 1971 when Bettesworth (1972) studied it, and yet to become limited by its food resources. It may have been that rabbit flesh would become much more accessible to rats when the rabbit population increased further and peaked, resulting in increased mortality of various age-classes, and young rabbits possibly becoming more vulnerable due to poorer parental attention and/or starvation.

Rabbits were an important food of Australasian harriers (*Circus approximans* Peale) on Moutohora. The number of harriers frequenting the island increased from about four to six in 1969-1971 before rabbits were abundant (Croxall and Millener, 1971; Bettesworth, 1972), to about 18 in May 1980 (M. Imber, *unpubl.*) when rabbit numbers were at or near their maximum. In June 1999 only two harriers were seen.

The results presented in this paper strongly suggest that the increased impact of Norway rats on the grey-faced petrel population on Moutohora from 1972 to 1984 inclusive (except in years of extensive poisoning of rats) was caused by an increase of the rat population. This apparently resulted from the plentiful availability of rabbits as food for rats during February to June, when petrel eggs and chicks were unavailable, and dead adult petrels were rarely available, as food.

Jansen (1993) considered that the application of 1080-poisoned carrots to combat rabbits in August 1985 was responsible for the very large reduction of the rat population. However, he seemed unaware that the extensive laying of Talon 50WB baits had occurred a month earlier. A similar 1080 operation in 1973 (Pedersen and Roche, 1973) was followed by greatly decreased breeding success of the petrels, arguably because of increased rat predation. Norway rats on Moutohora were not attracted to carrots. They may also have been able to detect and avoid 1080-poisoned baits, as I. McFadden (Department of Conservation, Wellington, N.Z., *pers. comm.*) found with Polynesian rats, though ship rats are known to take bait containing 1080 (I. Flux, Department of Conservation, Wellington, N.Z., *pers. comm.*). We believe that the 1985 1080-carrot operation would have had little or no effect on the rat population of Moutohora, which was likely to have been already decimated by Talon a month earlier.

The breeding success of the petrel population from 1985 to 1988 and from 1990 to 1994 was consistently high. There were no years of massive failure, suggesting that such failures before 1985 were indeed caused by predation of eggs and chicks by rats. The high breeding success in 1985 was likely to be the result of two previous years of failures, so that virtually all intact breeding pairs of petrels would have been in good condition for breeding. They would have had maximum time to moult and recover condition after breeding failure 9 to 11 months earlier. In the breeding seasons of 1986 onwards, many pairs had only five months to recover after rearing a chick, and this would have adversely affected the ability of some pairs to breed successfully in the following season (M. Imber, *unpubl.*). Thus, fewer fledglings were reared in the study area in 1986, and thereafter the numbers reared slowly increased. The increasing breeding success of petrels in the study area suggests that the proportion of burrows occupied by breeding pairs was increasing. There was no obvious evidence of new burrows being dug by the petrels in the latter years of this study, despite the availability of vacant ground for this to occur.

The continuation of the long-term study of grey-faced petrels on Moutohora, in the absence of rats and rabbits, would increase our knowledge of their breeding success, population dynamics and ecology.

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