Ecology of brown kiwi and causes of population decline in Lake Waikaremoana catchment

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1. Introduction

This report was commissioned by the Department of Conservation, East Coast Conservancy, Gisborne. The brief was to:

1. *"Summarise the current state of knowledge of kiwi in the Waikaremoana basin, with emphasis on habitat use, population ecology and trends, and relations to introduced animals."*

2. *"Review all available evidence bearing on the hypothesis that modification of Lake Waikaremoana's margins by hydroelectric development has accelerated the decline of kiwi (and perhaps other threatened species) in the Waikaremoana basin."*

The information presented here was collected between November 1992 and January 1996 during a detailed study of the impacts of introduced predators (mustelids and cats) on brown kiwi, *Apteryx mantelli*, in the catchment of Lake Waikaremoana. The study involves a large-scale field experiment, in which chick survival and population growth in kiwi is being compared in areas with and without predator control. The study is still in progress, with an expected finish date of about 2000. All the data are unpublished except for those relating to kiwi survival; these results were included in a recent nationwide review of predator impacts on kiwi in mainland forests (McLennan *et al* in press).

2. Study area

Te Urewera National Park (212 072 hectares) is the fourth largest of New Zealand's 12 national parks and contains the largest remaining area of virgin forest in the North Island. Lake Waikaremoana (5170 ha) lies in the southeast corner of the park, at an altitude of about 582 m a.s.l. Its catchment is steep and almost entirely forested, with mixed beech, podocarp and tawa on the lower slopes and pure beech at higher altitudes (Nicholls 1966). The lake shore is fringed by grasslands and regenerating vegetation, growing on what was old lake bed, exposed in the late 1940s when the lake level was lowered permanently for hydroelectric development. The catchment contains a variety of endangered native fauna and flora, including brown kiwi, the short-tailed bat, kaka, and the parasitic plant *Dactylanthus taylori*. It is also home to a diverse range of introduced mammals including red deer, feral pig, feral cat, possum, mouse, rabbit, European hare, ship rat, Norway rat, stoat, weasel, and ferret.

The kiwi study and predator removal experiment is centred mainly on Puketukutuku, a large (750 ha) peninsula jutting in from the northern shore of Lake Waikaremoana. Some kiwi and introduced mammals in other parts of the catchment are also being monitored for comparative purposes.

3. General methods

3.1 ESTIMATES OF KIWI DENSITY WITHIN THE WAIKAREMOANA CATCHMENT

We (JAMcL. and field assistants) determined the whereabouts and numbers of kiwi within the catchment by listening for their calls at night and by searching for their sign (droppings and probe holes) during the day. Most of the surveys were undertaken in winter to coincide with the annual peak in vocal activity. So far, more than 500 hours have been spent surveying in the catchment, sufficient to locate most of the birds living within 1 kilometre of the shoreline.

3.2 RANGE SIZE AND HABITAT USE

We determined the ranges, movements, and habitat use of adult and juvenile kiwi by locating and mapping the positions of radio-tagged individuals, both by day and by night. The range size of each individual was calculated by the convex polygon method, as used by McLennan et al. (1987). Habitat preference was evaluated by determining whether kiwis used particular vegetation types in direct proportion to their abundance in the landscape.

3.3 BREEDING SUCCESS AND PRODUCTIVITY

We located nests by radio-tagging and tracking breeding males. We determined clutch size and breeding success by examining nests at night after incubating males had emerged to feed. On a few occasions the contents of a nest were not visible, even with the use of an optic fibre probe. We could, however, still measure productivity by estimating hatching date (from the onset of incubation) and observing whether chicks emerged from the nest at about this time. Kiwi chicks became juveniles when they left their nest for good, usually 15-30 days after hatching. Juveniles became adults at 12 months (males) to 18 months (females).

3.4 JUVENILE AND ADULT SURVIVAL

The analysis of adult and juvenile survival was based only on records for kiwi carrying active radio transmitters. The ages of adults were not known, but all were sexually mature. Young kiwi were radio-tagged 3-15 days after hatching then monitored at least once a week thereafter.

Predators were blamed for the death of a kiwi when one or more of the following conditions were met: 1) there were puncture injuries on the neck, skull, or body; 2) the carcass had been buried or hidden; 3) there was evidence of a struggle; 4) there were mammal hairs under the victim's claws; and 5) the victim had been eaten soon after death. Even so, some birds may have been scavenged rather than killed, and not all the culprits may have been correctly identified.

3.5 POPULATION TRENDS

The estimates of productivity and survival were used to model population trends of kiwi in the catchment of Waikaremoana and the significance of predation by introduced mammals. The model is outlined in McLennan *et al.* (in press), and a copy is held by G.Wake, Dept. of Mathematics, Auckland University.

3.6 ABUNDANCE AND DISTRIBUTION OF INTRODUCED MAMMALS

Transects were established on Puketukutuku and Whareama peninsulas to measure changes in the abundance and distribution of rats, mice, stoats, ferrets and cats, and the effectiveness of the predator control programme (Appendix 1). Footprint tracking tunnels were placed at 200 m intervals along each transect, and cage traps baited with rabbit meat at 300 m intervals. In all, there were about 100 tunnels and 50 cage traps on each peninsula, spread along approximately 20 km of index lines. The traps and tunnels were activated and monitored for 8 days on three separate occasions before May 1995, when predator control started, and twice thereafter.

We also recorded sightings of predators in the catchment to obtain a second, independent index of abundance and are obtaining a third measure, on Puketukutuku peninsula only, by monitoring changes in kill rates in the lethal traps (see below).

3.7 PREDATOR CONTROL

In 1994 Fenn traps were positioned at 150 m intervals along each of the transects on Puketukutuku peninsula, and on several ridges between the transects. Traps were spaced at 25 m intervals over the neck of Puketukutuku peninsula to try and intercept animals moving in from neighbouring forest. Two Fenn traps were positioned side by side at each of 47 stations along the Puketukutuku shoreline so that different baits could be compared under similar conditions. Conibear traps are currently being added to some of the transects to compare their catch rates with those of Fenn traps.

Both types of kill trap are set under a wooden tunnel or box, partially closed at either end, to prevent non-target animals from entering them. The traps have operated continuously since May 1995. Most have been baited with either a whole hen's egg or a piece of rabbit, but a few have been left unbaited as controls.

4. Results

4.1 DENSITY AND DISTRIBUTION OF KIWI

Since November 1992 we have located 58 kiwi within the catchment of Lake Waikaremoana - 23 pairs, 9 solitary males, and 3 subadults 10-20 months old (Appendix 2). Four of these birds are now known to be dead, and another 9 have disappeared and are presumed to be dead.The present known adult population is 45, comprising 18 pairs and 9 males. Twenty of these birds live entirely on Puketukutuku peninsula. Three live on the neck of the peninsula, and enter the treatment (predator control) area from time to time. Five of the nine 'solitary' males may have a mate, and four definitely do not. We have not yet searched intensively for kiwi at the south-western end of the Wairau Arm, nor in the head of Whanganui Inlet; these areas probably contain an additional 3 or 4 pairs, giving a total of 50-55 birds in the 'catchment' (i.e. in the forests within 1.0-1.5 km of the shore; Appendix 2). We have caught and banded 34 kiwi, and currently have a functioning radio transmitter on 2 juveniles, 2 unpaired males, and at least 1 member of 14 different pairs.

Adult density varies within the catchment from 0 to 2.8 per km^2. Some large tracts of forest within the catchment no longer contain kiwi; and in several areas, pairs or individuals are separated from other kiwi by a kilometre or more of unoccupied forest. Adult densities are significantly higher on the northern side of the lake (approx. 2.5 per km^2) than on the southern side (approx. 0.2 per km^2) with an overall average of about 1 adult per km^2 in the forests bordering the shoreline (approx. 5100 ha).

4.2 RANGE SIZE AND USE OF DIFFERENT HABITATS BY KIWI

4.2.1 Adult kiwi

The social system of brown kiwi in the Waikaremoana catchment is similar to that elsewhere in the North Island, i.e. pairs form long-lasting bonds and occupy territories which they defend against other kiwi. The birds at Waikaremoana are monogamous, even though there is a surplus of males and some paired females have up to two solitary males as neighbours. Bonded pairs at Waikaremoana have territories of about 45 ha (Appendix 3) similar to that in all other areas of the North Island except Northland. Solitary males usually have larger ranges (up to 140 ha) which often overlap the territories of neighbouring pairs. Some unpaired males live entirely within the ranges of bonded pairs, but avoid the resident male. These satellite males appear to be waiting for the resident female to become available, a strategy which is uncommon but probably appropriate when unpaired females are extremely rare.

Eleven vegetation types are represented in the catchment of Lake Waikaremoana (Nicholls, 1966). Three of these (I_5, I_2, and K_6) each cover between 22% and 25% of the catchment and are the dominant associations (Appendix 4). None of the remaining associations cover more than 10% of the catchment, and four of them cover less than 3%.

Most of the kiwi territories in the catchment span two or more vegetation types. Two of the main forest types (I_2 and K_6) are represented in kiwi territories in direct proportion to their abundance in the landscape. The other main vegetation type (I_5) is significantly under-represented, suggesting that the birds avoid this vegetation, or have failed in it more quickly than in other forest types. Broad-leaved shrub associations (R_1-R_2) and rimu-rata-tawa-kamahi associations (D_1) feature in kiwi territories more often than expected by chance, suggesting that the birds actively seek them out.

However, these results have to be interpreted with caution. The area occupied by kiwi in the catchment is now small, and habitat preferences may have little or no influence on their current distribution. Apparent habitat preferences could change significantly with the addition or loss of just one or two pairs. It is possible that adult and/or chick survival varies between forest types, but this remains to be tested.

4.2.2 Young kiwi

Kiwi chicks stay near their nests for their first 20-30 days of life, then disperse as fully independent juveniles. Most chicks initially feed in forest habitats because most of the nests at Waikaremoana are sited in forests (74% of 31). After moving up to 2 km, juveniles settle and stay for the next 4-6 months within a relatively small home range (< 3 ha), sometimes within the territory of their parents. At Waikaremoana, 7 (58%) of 12 juveniles that survived their first 15 days of independence settled in dense stands of regenerating scrub and/or toetoe, selecting these associations significantly more often than expected by chance (X^2 = 39.4, P = <0.0001). At Waikaremoana, such habitats are relatively rare and restricted mainly to the edge of the lake. The remaining five juveniles remained within forest.These birds showed no strong preference for particular types of vegetation, terrain or aspect, but had slightly larger ranges than those which settled in scrub. We do not yet have sufficient information to compare the survival and growth rates of juveniles in shrubland and forest habitats.

4.3 BREEDING SUCCESS AND PRODUCTIVITY OF KIWI AT WAIKAREMOANA

At Waikaremoana kiwi lay from late June to the end of January. With one possible exception, all pairs attempt to breed at least once each season, and most (75%) make 2 or 3 attempts. Clutches contain either 1 (21%) or 2 eggs (79%, n = 29) and females usually lay 3-5 eggs each season. Some males move immediately from one successful clutch to another, and so incubate continuously for up to 200 days each year.

About half (52%) of the eggs laid each season hatch, and 76% of chicks survive to become independent juveniles. Decay and putrefaction, presumably caused by bacteria, is the single biggest cause of egg loss (42%). About 10% of eggs disappear without trace and 8% are smashed. Introduced mammals seldom eat eggs but may sometimes cause males to desert nests. One nest on Puketukutuku peninsula was probably dug out and destroyed by a pig, presumably when the male was absent (it survived). Recent video footage shows that ship rats and mice often enter nests at night when the incubating male is absent, but neither species appears to harm eggs or chicks.

Over the past two years production at Urewera has averaged 1.2 juveniles per pair per season, more than double the national average (0.51). Some pairs have bred consistently well, fledging up to three chicks a year, while others have failed consistently, usually for the same reasons (eg, desertion late in incubation). This imbalance in productivity between pairs is characteristic of many birds, and often related to territory quality. However, at Waikaremoana egg production (perhaps the most sensitive index of territory quality in kiwi) does not vary significantly between females. Furthermore, all breeding males are fertile, and we have only twice recorded eggs that failed to develop during incubation. In both instances, they were part of a two-egg clutch, and the other egg hatched successfully.

4.4 SURVIVAL OF CHICK, JUVENILE AND ADULT KIWI

4.4.1 Chick and juvenile survival

In the 93/94 and 94/95 breeding seasons, 8 monitored pairs at Waikaremoana hatched 13 chicks (Appendix 5). One died in its nest within two days of hatching, apparently of natural (but unknown) causes. Another chick died near its nest after it became infested with maggots. Two more chicks disappeared while foraging outside their nests, either because they suffered an accident or were killed by predators. Both were radio-tagged, but neither the transmitters nor the carcasses were recovered. Nine chicks survived their first three weeks of life and dispersed as independent juveniles. We lost contact with two of these juveniles after they shed their transmitters, 2-37 days after fledging. Two juveniles disappeared suddenly within a week of fledging. We suspect that mustelids killed them and cached the bodies in deep holes which blocked the signals from the transmitters. Mustelids definitely killed three juveniles, and a fourth was killed by a cat. Another juvenile reached an age of 117 days and then died after falling into a 3m-deep hole.

Overall, mammalian predators killed a minimum of 31% of the young kiwi produced by the monitored pairs at Waikaremoana in the 93/94 and 94/95 breeding seasons. Predators may have killed as many as 60% if (as we suspect) they were the main cause of chick disappearance. No radio-tagged juvenile survived for more than 118 days. Indirect evidence (faeces and probe holes) indicates that one juvenile who shed its transmitter reached 9 months of age, then dispersed as a subadult. Its calls, heard just before it dispersed, revealed that it was a male.

The 1995/96 breeding season is still in progress. Thus far (up until late January 1996) nine chicks have hatched and five males are still on nests. Four of the chicks were produced on Puketukutuku peninsula (the predator control area), and five elsewhere in the catchment (no predator control). All four chicks on Puketukutuku peninsula survived till fledging. One shed its transmitter 10 days after fledging, and has not been seen since. One is still alive at age 22 days, and another at age 120 days. The fourth was killed by a ferret or stoat when it was 71 days old and 650 g in weight - about one-third the size of an adult male kiwi.

One of the five chicks elsewhere in the catchment disappeared before fledging, and two have not yet reached fledging age (approx. 21 days after hatching). Both of the remaining chicks fledged but shed their transmitters after 45-61 days.

Survival analyses based on 761 tracking days and 9 confirmed deaths show that young kiwi at Waikaremoana have an average life expectancy of just 84 days. If disappearances are classed as deaths, life expectancy falls to 58 days. The maximum probability of a young kiwi surviving from one month to the next is 0.643, and the probability of surviving one year is just under 1%. These mortality rates, although exceptionally high, are similar to those recorded for young kiwi elsewhere in New Zealand (McLennan *et al.*, in press).

So far the samples are too small to show whether predator control is increasing the survival of young kiwi on Puketukutuku Peninsula. Clearly, however, our control methods, initiated 5 months before chicks began hatching, have not entirely eliminated losses to predators. On the other hand, one juvenile on the peninsula is now beginning its fifth month of life, and has lived longer than any other juvenile monitored over the preceding two years.

Updated figures (as at 25 April 1996) for the 95/96 breeding season are as follows: Four of six chicks monitored in unmanaged parts of the catchment were killed by predators, and two shed their transmitters. Mean life expectancy of these young was 76 days. On Puketukutuku peninsula, one chick was killed, three had transmitter failures, and three are still alive and radio-tagged. Mean life expectancy for these young is now 375 days and still increasing.

4.4.2 Adult survival

We have now tracked 31 adult and three subadult kiwi for periods ranging from 33 to 919 days (mean = 392 days). Four of these birds died and one disappeared (presumed dead) in 36.55 tracking years, giving an annual mortality estimate of 13.7% and an average adult lifespan of 6.8 years.

One subadult male was eaten (and probably killed) by a pig. Its remains were found on the forest floor, indicating it had been captured while active at night. An adult male was killed by a possum, apparently in a dispute over a den site. There were clumps of feathers in the den chamber, in the tunnel leading to the den, and on the forest floor near the entrance. The kiwi had possum fur lodged under its claws, revealing the attacker's identity, and showing that the bird had attempted to defend itself by kicking. The kiwi died outside the den from a bite to its skull; its body was left uneaten. Two adult males were killed and eaten by ferrets. Another adult male disappeared along with its transmitter, and was probably also killed by a ferret (see below).

All adult deaths were recorded in winter, from mid May to mid July. One death was recorded in 1993, four in 1994, and none in 1995. Predator control on Puketukutuku peninsula has not yet produced any *measurable* benefits for adult kiwi; none of the 14 monitored birds on the peninsula has died since control began in May 1995, but neither has any of the 10 monitored adults in other, unmanaged, parts of the catchment. On the other hand, predator control may have saved some adults that would have otherwise been killed, so the estimate of adult mortality (13.7%) in the catchment could be conservative.

Five untagged adults and one radio-tagged adult disappeared from the Whareama peninsula in May/June 1994, in the same 5-week period that ferret kills were recorded elsewhere in the catchment (at Waitio and Maraunui bays). Only one adult, a radio-tagged female, survived on Whareama peninsula after May 1994. She stayed there until mid August, then moved 3 kilometres to a 'new' territory beneath the Panekiri Range.

We attribute all these losses to ferrets because: 1) they occurred when ferrets were known to be killing kiwi elsewhere in the catchment; 2) given that deaths of adult kiwi are infrequent events, it seems highly unlikely that two different agents of adult death were operating independently at exactly the same time; 3) there was no evidence that dogs, the only other mammalian predator capable of causing such rapid losses, were present on Whareama peninsula during this period; and 4) a disease epidemic, which has never been recorded in wild kiwi, would probably spread beyond the Whareama peninsula.

The predation episode in May/June 1994 coincided with a rise in lake level after a prolonged period (6 months) of low lake levels. This indicates that it may have been partly triggered by a reduction in access to aquatic foods, although the first kiwi was killed before the lake rose significantly. Alternatively, the correlation could be completely spurious if the heavy rains directly reduced the availability of terrestrial food, and just happened to increase lake levels at the same time. Although the triggers remain unclear, it is apparent that such predatory episodes are rare. Ferrets appear to tackle adult kiwi only when alternative prey is scarce.

Adult mortality in the catchment of Waikaremoana (based on radio-tagged birds only) is significantly higher than the national average for northern brown kiwi (8% per annum), and 4-5 times higher than mortality rates near Whangarei in Northland (where ferrets are present but recent immigrants; H. Robertson, pers. comm.). The mortality estimate for the Waikaremoana population would be even higher if untagged adults were included in the sample, but this would bias the mortality estimates upwards and prevent comparisons with other populations.

4.5 POPULATION TRENDS

Even the most unsophisticated analysis shows that the population at Waikaremoana is declining. Ten adults have died or disappeared over the last 3 years and none has been replaced. Two dispersing subadults passed through the study area, and may still be alive.

Calculations based on the survival and productivity of radio-tagged birds show that the average rate of population decline is 13.3% per annum. If this rate continues unchecked, the present population of about 50 kiwi will decline to about 28 by the end of 2000, and to about 7 birds by 2010. They will by then be effectively extinct within the catchment, with the population containing just a few widely scattered individuals, probably with a significant bias towards one sex.

To halt this decline both adult and juvenile survival have to increase significantly (Appendix 6). At present levels of productivity (1.2 juveniles/pair/year) and adult mortality (13.7%), 28% of juveniles have to reach adulthood for the population to remain stable. At 95% adult survival, stability is achieved with 10% juvenile survival. Juvenile survival rates above those shown in Appendix 6 would promote population recovery. For example, if annual survival rates were 90% for adults and 40% for juveniles, the population would increase by 60% over 5 years.

4.6 ABUNDANCE AND DISTRIBUTION OF SMALL INTRODUCED MAMMALS

4.6.1 Species present

Kill trapping and monitoring (live-trapping and tracking tunnels) has revealed that mice, ship rats, Norway rats, ferrets, cats and stoats are present on both the northern and southern sides of the catchment. Weasels are present on Puketukutuku peninsula, and undoubtedly occur elsewhere in the catchment (their presence can be detected only by kill-trapping, currently restricted to Puketukutuku peninsula). Rabbits, hares and possums are also present, but are not included in the monitoring programme. Hedgehogs appear to be absent in the catchment, but are present in the upper Waikare Taheke valley.

4.6.2 Distribution and relative abundance

So far, 7 ferrets, 7 cats and 2 stoats have been caught in the live cage traps on the Whareama and Puketukutuku peninsulas. The kill traps on Puketukutuku Peninsula have caught 2 ferrets, 2 cats, 7 weasels, 46 stoats, and about 350 rats in 40 060 trap nights.

By 25 April 1996 the total catch of predators on Puketukutuku was 70 stoats, 11 weasels, 2 ferrets, and 2 cats in about 66 000 trap nights (Fenn and Conibear traps combined).

On Puketukutuku peninsula 50% of the cage traps (n=50) and 46% of the kill traps (n= 212) are positioned along or within 50 m of the shoreline, with the remainder in forest up to 1.3 km from the lake (Appendix 7). The distribution is similar on Whareama, with 45% of 40 cage traps in forest, and 55% along the shoreline.

For all species the proportion of captures in forest and shoreline habitats has departed significantly from the random expectation determined by trap distribution. Ferrets, cats, weasels, and Norway rats have been caught almost exclusively along the shoreline, whereas stoats and ship rats have been caught more often than expected by chance in forest (Appendix 8).

All the cats were caught near shelters, huts, or campsites, suggesting they are partly dependent on food brought in by visitors. Ferrets and weasels, on the other hand, appear to be distributed widely along the shoreline. Both species enter forest occasionally, and have been caught up to 300 m from the lake edge. Norway rats are probably restricted to habitats near water, the only place where they appear to be able to compete with ship rats (Moors, 1990).

Stoats and ship rats have been caught in all forest types on Puketukutuku peninsula. They appear to show no significant preferences for particular associations, with actual capture rates being similar to expected values in all the main forest types. The monthly catch rates of rats on Puketukutuku peninsula have declined from winter (45) to summer (20), perhaps indicating a real decrease in abundance. Stoats have shown the opposite trend, with catches increasing from less than 1 per month in winter and spring to an average of 16 in December and January. Young of the year have comprised about half of the summer catch (52% of 33 captures) the remainder being adult males and females (each 50% of 16 captures). These adults were probably present on the peninsula throughout the preceding winter and spring but, for whatever reason, were largely uncatchable during this period.

The total catch of 46 stoats in 750 ha of forest over a 9-month period is high by North Island standards (Murphy and Bradfield, 1992; Murphy and Dowding, 1995a), and may partly be a consequence of high rodent abundance following the seeding of beeches (*Nothofagus* spp.) in the catchment in 1994. Clearly, however, there was a significant number of adult stoats present before the beeches seeded, suggesting that their biomass in the forests of Waikaremoana may be relatively high in all years.

Tracking tunnel indices show mice and rats to be widespread throughout the catchment (Appendix 9). The pooled sample (December 1994 to October 1995 inclusive) shows that: 1) mice were significantly more abundant in shoreline habitats than in forest (X^2 = 84.5, $P < 0.0001$) on both Puketukutuku and Whareama peninsulas; 2) rats were more abundant in forest than shoreline habitats on both peninsulas (X^2 = 10.9, $P < 0.001$); 3) mice were more abundant on Puketukutuku peninsula than on Whareama peninsula (X^2 = 84.5, $P < 0.001$); 4) rat abundance was similar on both peninsulas (X^2 = 0.60, not significant); and 5) rats were much less plentiful than mice on both peninsulas.

Rats and mice increased in abundance on both peninsulas from December 1994 to October 1995 (Appendix 10). This increase was evident in both shoreline and forest habitats, though at no time did mice become as plentiful in forest as they were along the shoreline. Mice near the shoreline often had access to grass seed as well as beech seed, which may partly explain why densities there were always higher than in forest. On both peninsulas, tracking tunnels in or near grassy areas were visited by mice significantly more often than those in non-grassy areas elsewhere along the shoreline (Appendix 11).

Too few mustelids passed through the tunnels for measures of their relative abundance to be derivable.

In summary, the catchment of Waikaremoana, with its grassland, forest, and freshwater habitats, supports an exceptionally diverse community of small mammals. The presence of both rabbits and Norway rats in a predominantly forested landscape is unusual, and sympatric populations of all three species of mustelid are considered to be uncommon (King, 1990). The catchment contains all the mammalian predators currently extant in New Zealand, with the possible exception of kiore and hedgehog.

The mammals form a community in their own right, and interact with each other as well as with native wildlife. For example, competition from ship rats probably restricts Norway rats to shoreline habitats; predation by stoats may partly limit the abundance of weasels; ship rats may sometimes regulate the abundance of mice; and rodent abundance undoubtedly influences the diet, movements, reproductive success, and abundance of stoats.

These relationships need to be considered when exotic mammals are controlled to benefit indigenous wildlife, because removal of one species from the mammal community may have unwelcome repercussions elsewhere in the ecosystem. On the other hand, there is considerable potential to exploit these relationships in control programmes, both to enhance the efficacy of existing techniques and to develop new methods. At Waikaremoana, for example, mice could be used to dispense anticoagulant poison to stoats.

4.7 SUMMARY OF RELEVANT POINTS

So far the research at Waikaremoana has shown:

- mortality rates of juvenile kiwi are extremely high, as they are elsewhere in the North Island;
- mortality rates of adult kiwi vary between months and years, but overall are high by North island standards;
- the kiwi population in the catchment is declining at about 13% per annum and, in the absence of remedial action, will be extinct by about 2010;
- the catchment supports an unusually diverse array of introduced mammals, and relatively high numbers of stoats;
- small mammals are generally more abundant in shoreline habitats than in forest, and at least two species appear to be entirely restricted to shoreline habitats.

5. Effect of power generation on predator impacts

In this section I examine whether power generation at Lake Waikaremoana influences the abundance and diversity of small mammals in the catchment and their impacts on native fauna.

5.1 THE POWER SCHEME AT LAKE WAIKAREMOANA AND ITS IMPACT ON THE TERRESTRIAL ENVIRONMENT

Lake Waikaremoana formed about 2200 years ago when a large slip impounded the headwaters of the Waikare Taheke River. A power scheme was established below the natural outlet of the lake in the late 1920s. It was expanded and modernised over the following decades, and today comprises three generating stations with a combined production capability of about 137 MW

Development of the third power station, Kaitawa, involved sealing much of the natural leakage of the lake and lowering of the lake levels in 1946, to allow controlled discharge by tunnels. In recent years the lake level has been managed at an average of 5.3 m below its natural level.

5.2 EFFECT OF LOWERED LAKE LEVEL

Lowering the lake permanently exposed about 300 ha of lakebed and beaches. Large expanses of soft sediments (about 100 ha in total) were uncovered near the outflows of most of the rivers and streams. These were colonised mainly by toetoe, introduced grasses (chiefly tall fescue and Yorkshire fog) and weeds. In most places today these flats resemble paddocks of rank pasture, with dense stands of fescue and/or toetoe 0.5 - 2.0 m high. The exposure of these sediments also created the only significant areas of flat land in the catchment. Rock substrates, rather than sediments, were exposed along the steeper shorelines. These were colonised by native hardwood shrubs and ferns, which in some places are now being overtopped by emergent canopy species.

The colonisation of exposed sediments by introduced and native grasses created a new type of habitat that would have otherwise been rare in the catchment if the lake had remained at its natural level (see section 5.3.1). The grasslands differ fundamentally from forest, and introduce a pastoral element into an otherwise native ecosystem. The area covered by grasses is small, but the habitat is distributed widely around the lake shore, forming a network of pockets and ribbons. In other parts of the shoreline the grasslands merge gradually into hardwood associations. Clumps of toetoe grow amongst manuka, and introduced grasses develop in a thin strand along the edge of beaches.

The grasslands allow some species of introduced mammals and birds to live in the catchment that would otherwise be absent or rare if the area were covered entirely in native forest. Rabbits and various finches depend entirely on the grasslands for their existence, while magpies, weasels, ferrets, cats and European hares depend on it to a large extent. The trapping data shows clearly that weasels, ferrets, and cats live mainly near the shoreline, in the habitats that developed on exposed lakebed.

The grasslands and shoreline habitats support higher densities of mice than do the surrounding forests (even in mast years) presumably because the seeding grasses and weeds provide mice with additional food. The mice in turn probably increase the numbers of predators in the catchment, since studies elsewhere in New Zealand show clearly that predator abundance is linked closely to prey abundance (King and McMillan, 1982; King, 1990; Murphy and Dowding, 1995b; Pierce and Maloney, 1989). Limited comparative information indicates that stoat densities at Waikaremoana are high by North Island standards (Murphy and Dowding, 1995a; Murphy and Bradfield, 1992) but slightly lower than those in South Island beech forests following mast years (King, 1990). For example, in a 1400 ha remnant forest at Mapara in the King Country, 23 stoats were caught in the summer of 89/90 and 38 in 90/91. On Puketukutuku peninsula (half the size of Mapara) 61 stoats were caught during the summer of 95/96. On the other hand, the population of ferrets at Waikaremoana is sparse relative to those in rabbit-infested areas of Central Otago (Pierce, 1987). It also appears to be lower than those in Manuwatu dunelands (Roser and Lavers, 1976) and in bush remnants in agricultural landscapes in Northland (Hugh Robertson, pers. comm.).

Although lowering the lake level appears to have increased the abundance and diversity of predators in the catchment, it has had no *measurable* impact on the overall rate of loss of young kiwi. Mortality rates elsewhere are so close to 100% that the high density and diversity of predators at Waikaremoana cannot make a significant difference. It has merely raised the question of which species of predator will be the first to find and kill them.

On the other hand, modification of the Waikaremoana catchment for power generation has undoubtedly increased mortality rates of *adult* kiwi. The average rate of loss of adults in the catchment is high by national standards because of predation by ferrets. This is the main difference between the Waikaremoana population and those in other parts of the country; and the main reason why the overall rate of population decline in the catchment exceeds the national average. If the three radio-tagged adults known (2) or presumed (1) to be killed by ferrets are removed from the sample, adult mortality rates at Waikaremoana decline from 13.7% to 5.5% per annum, and approximate those in other mainland forests.

If the current rate of population decline at Waikaremoana (13.3% per annum) is extrapolated backwards, the catchment would have contained c. 530 kiwi 20 years ago (1 per 10.6 ha). Nearly 40% of this population (205 individuals) would still be present today if adult mortality rates from 1976 onwards were 5.5% per annum rather than 13.7% per annum. The difference of 155 adults (205 minus present population of approx. 50) is attributable to losses to ferrets. Clearly, such calculations make no allowances for emigration and immigration, and assume constant mortality rates over long periods of time. Even so, they suggest strongly that ferrets have accelerated the demise of kiwi in the catchment of Waikaremoana.

The relationship between kiwi and ferrets at Waikaremoana is complex. Predation by ferrets on adult kiwi is both rare and episodic, implying that it is triggered by a combination of circumstances which arises infrequently. These triggers probably include changes in the availability of staple foods (rodents, rabbits, and aquatic animals) and periodic increases in ferret numbers. For most of the time, however, ferrets do not prey on adult kiwi, even though the two species must encounter each other rather often.

In summary, the creation of pockets of grassland around the edge of lake Waikaremoana has probably increased both the diversity and abundance of predators in the catchment, and predation impacts on adult kiwi. There is no information to test whether there has also been an increase in predation impacts on other native species. It nevertheless seems likely that both ferrets and weasels kill significant numbers of young waterfowl; that stoats prey heavily on nesting kaka and kakariki; and that the populations of mice in the grasslands maintain predator numbers at higher average levels than would otherwise exist in an entirely forested catchment.

5.3 SOME COUNTER-ARGUMENTS AND QUESTIONS

1) That kiwi living near grasslands should be exposed to greater predation pressure and decline more rapidly than those in other parts of the catchment.

It is not realistic to test this, because pockets of grassland are found around the entire lake. Predators undoubtedly commute between them, especially when the lake is low and the exposed beaches make for easy travel. All the kiwi near the lake edge probably have similar predation risks, irrespective of whether they live near grassland or forested shorelines.

Adult survival may be better in entirely forested catchments elsewhere in Te Urewera NP, where ferrets are likely to be rare or absent. We have no comparative measurements to test this view. So far none of 4 tagged adults that live well back from the lake edge (> 1 km) has been killed by ferrets, perhaps suggesting that predation risks decline sharply with increasing distance from the shoreline.

2) That the catchment would contain some grasslands even if the lake had not been lowered; therefore the additional ones created by lowering the lake are of little consequence.

The catchment contains natural herbfields and boglands, especially at the eastern end near Lake Waikareiti. These herbfields are associated with poorly-draining, infertile, acidic sites, and they differ greatly from the largely introduced communities which have colonised fertile lake sediments.

Toetoe communities similar to those along the shoreline do develop on slips near the lake. Slips and light gaps in fully forested areas away from the shoreline are generally colonised by dicots rather than monocots.

Some grasslands would have existed around the shoreline of Waikaremoana before the lake was lowered in 1946. Aerial photographs taken on 19 April 1945 show numerous small grasslands at the mouths of most streams. Collectively, these are about one-fifth the size of the ones that exist today. The lake level was 613.2 m on 19 April 1945, having fallen markedly over the preceding 8 months. The grassy areas in the 1945 photographs were submerged through most of the summer of 1943/44 (as shown by lake level curves).

The photographs show clearly that grasslands were part of the natural lake regime, occupying the zone that was alternately submerged and exposed. However, these grasslands were both small and ephemeral, so could not have sustained permanent populations of small mammals and their predators, as do the ones present in the catchment today. Similarly, the natural toetoe associations on slips near the lake are too small and too few to sustain populations of predators.

3) The ferret population at Waikaremoana owes its existence to farming and land clearance in the lake catcbment before 1946, rather than to the grasslands created by lower lake levels.

The aerial photographs show that there were few areas of open grassland and pasture in the catchment in 1945. These were limited to small patches at Te Maraateatua, Takanga Point, and behind Te Puna and Paraharaha Bays. There were slightly larger areas on the ridge crest above Rosie Bay, and on the Lake House dairy farm at Okereru Stream. Most of the clearings on Maori land were by then already covered in secondary forest and scrub.

It is not known when ferrets first arrived in the catchment of Waikaremoana. Ferrets were, however, absent or rare in the East Coast and Poverty Bay districts in the late 1940s (Wodzicki, 1950) but were present near Wairoa in 1961 (Marshall, 1963). Ferrets probably did not reach Waikaremoana till the early 1950s, when there were few patches of farmland left in the catchment.

4) That most of the ferrets and weasels in the catcbment come in from neighbouring farmland, and that they would have done so even if the lake catcbment bad not been modified.

Unlikely. Several people have reported seeing family groups of ferrets in the catchment. We also find dens (mainly under toetoe) which appear to have been used for breeding over the summer months. The population there is probably self-sustaining. Nevertheless, some animals probably do immigrate into the catchment from time to time, especially near Onepoto, where the farmland comes to within a couple of hundred metres of the lake. The virtual absence of kiwi on the true eastern side of the lake may be partly due to the ongoing immigration of cats and ferrets along the road.

5) The kiwi population in the catcbment is doomed because of stoat predation on juveniles, so what does it matter ifferrets accelerate the decline by killing a few adults?

The kiwi population on Puketukutuku peninsula is perhaps the most defensible of all populations in Te Urewera NP Predator densities can probably be reduced to low levels on the peninsula because the lake restricts mammal access and re-invasion rates. Whareama peninsula also has the same potential to become a managed 'mainland island' though it no longer supports any kiwi. Juvenile recruitment must be increased if kiwi are to be saved in the catchment. Fewer juveniles are needed to promote population recovery if adult losses are small (see Appendix 6). Minimising adult losses is therefore an essential part of the recovery process.

6) Why have kiwi declined more slowly on Puketukutuku peninsula than elsewhere in the catchment?

Probably because the extensive shrublands on Puketukutuku have provided cover for juveniles, thereby reducing losses to predators. This protection may have been particularly significant a few decades ago when bracken was abundant on the peninsula. The bracken has now disappeared, and the shrublands may no longer be any safer for juveniles than the surrounding forests.

5.4 EFFECT OF FLUCTUATING WATER LEVELS ON THE TERRESTRIAL ENVIRONMENT

Lake levels at Waikaremoana fluctuate over a range of about 3 m. Sometimes the lake is below 'full' for several months, creating a strip of beach along much of the shoreline. Browsing animals (especially possums) feed on the aquatic plants exposed by the receding waters, and on the weeds and grasses that establish in their place. Carnivores probably also benefit from low lake levels, with increased access to aquatic foods (tadpoles, frogs, and koura) and easy travel from one part of the catchment to another.

Although predation by ferrets on adult kiwi may be partly triggered by rises in water level, there is no evidence to suggest that power generation increases either the frequency or intensity of such episodes. The combination of circumstances that appear to trigger events would still occur under a natural regime. If anything, the managed regime might suppress rather than increase predation episodes, by increasing average water levels over the summer months.

In summary, the aquatic and terrestrial environments of the Waikaremoana catchment clearly do not function as separate entities. Predation by ferrets on kiwi may be influenced by fluctuations in lake level and changes in the availability of aquatic foods. This process needs to be understood so that: 1) pre-emptive action can be taken when an episode appears imminent, and 2) it can be established whether fluctuations induced by power generation exacerbate or alleviate the problem.

5.5 SUMMARY AND CONCLUSIONS

- Lowering Lake Waikaremoana in 1946 to enhance its electricity generating capability created a new ecosystem around the lake margins.

- This ecosystem includes a high density and diverse mixture of predators, including ferrets, not normally found in deep forest.

- In the absence of ferrets, mortality rates of adult kiwi would be significantly lower than they are now, and would approximate the average rate for the species.

- It appears highly likely that the lowering of Lake Waikaremoana accelerated the decline of kiwi in the catchment.

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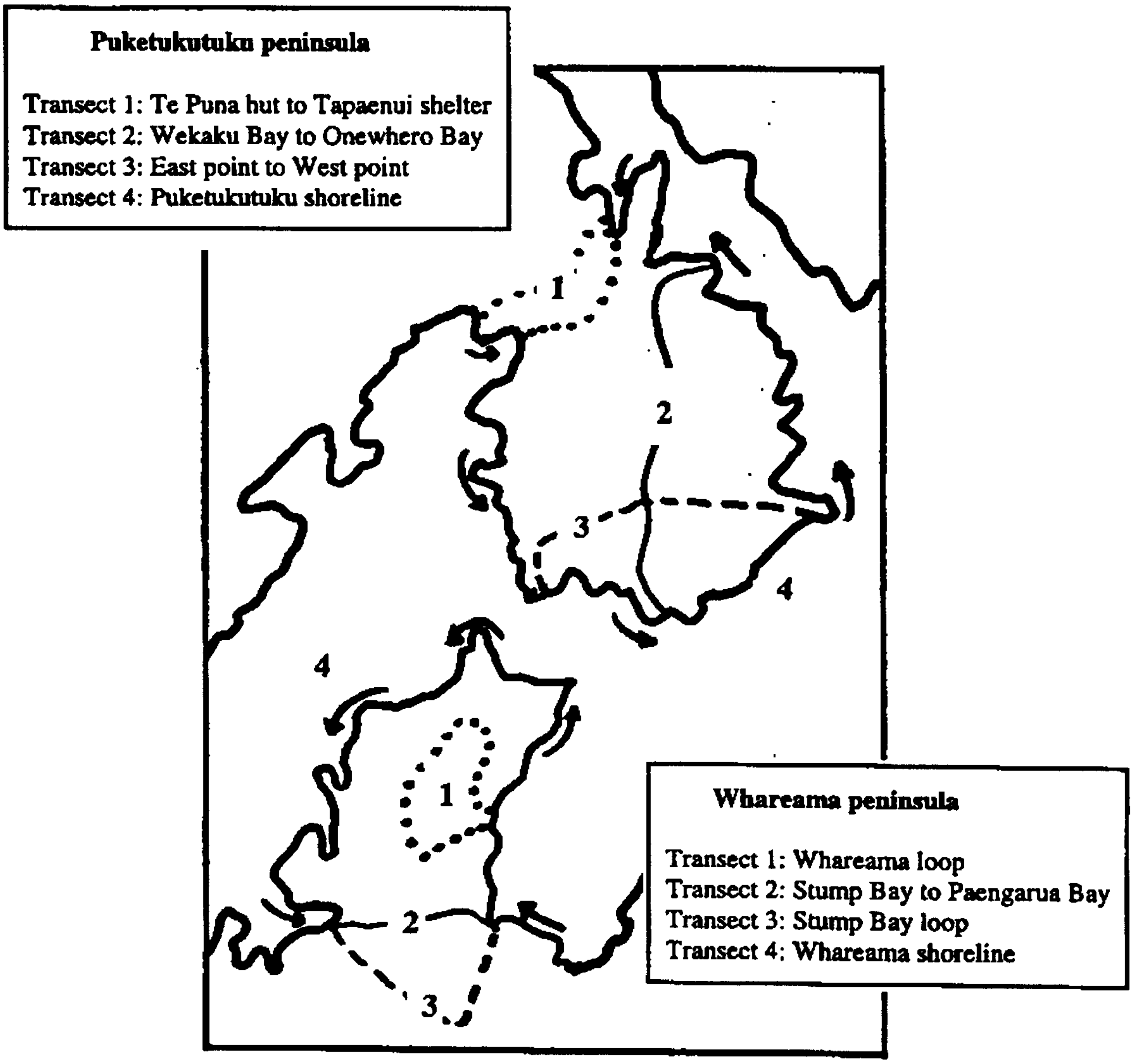
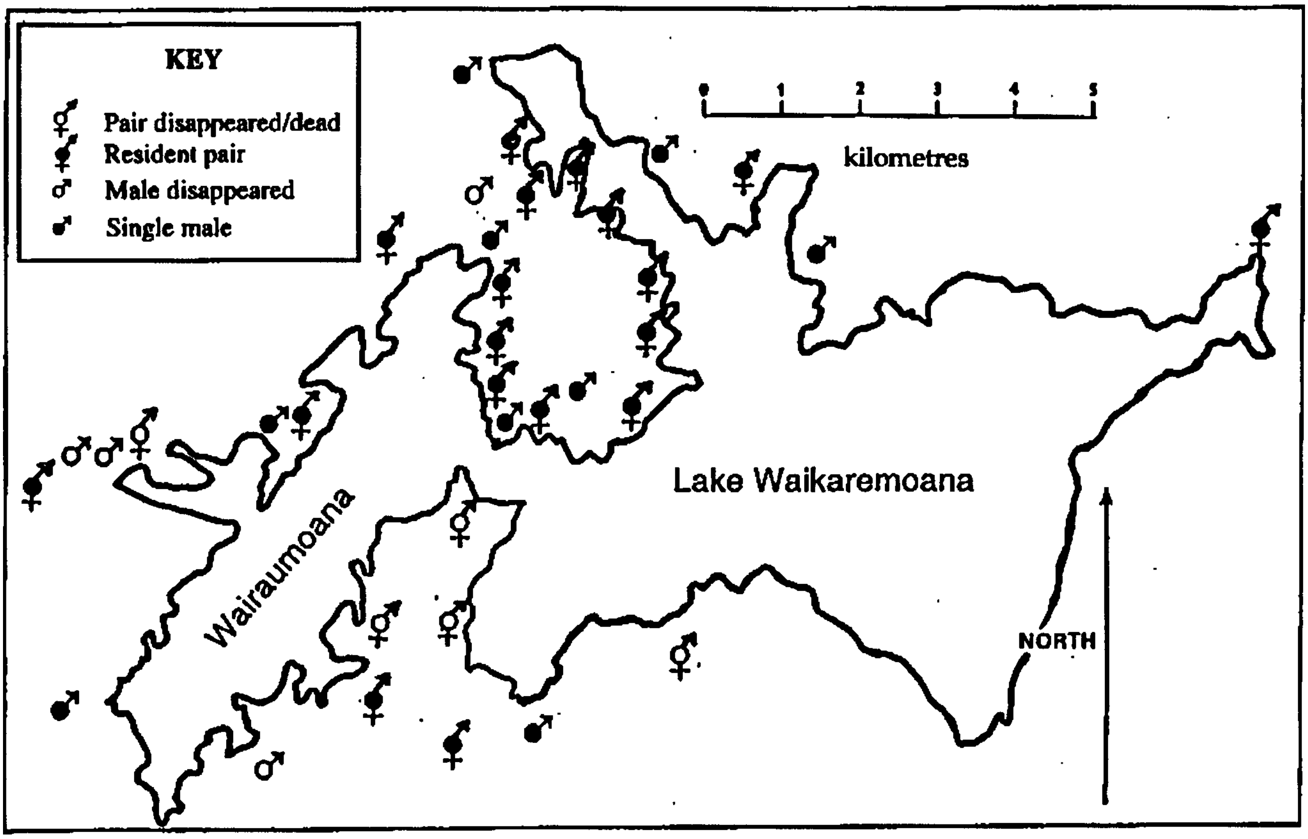
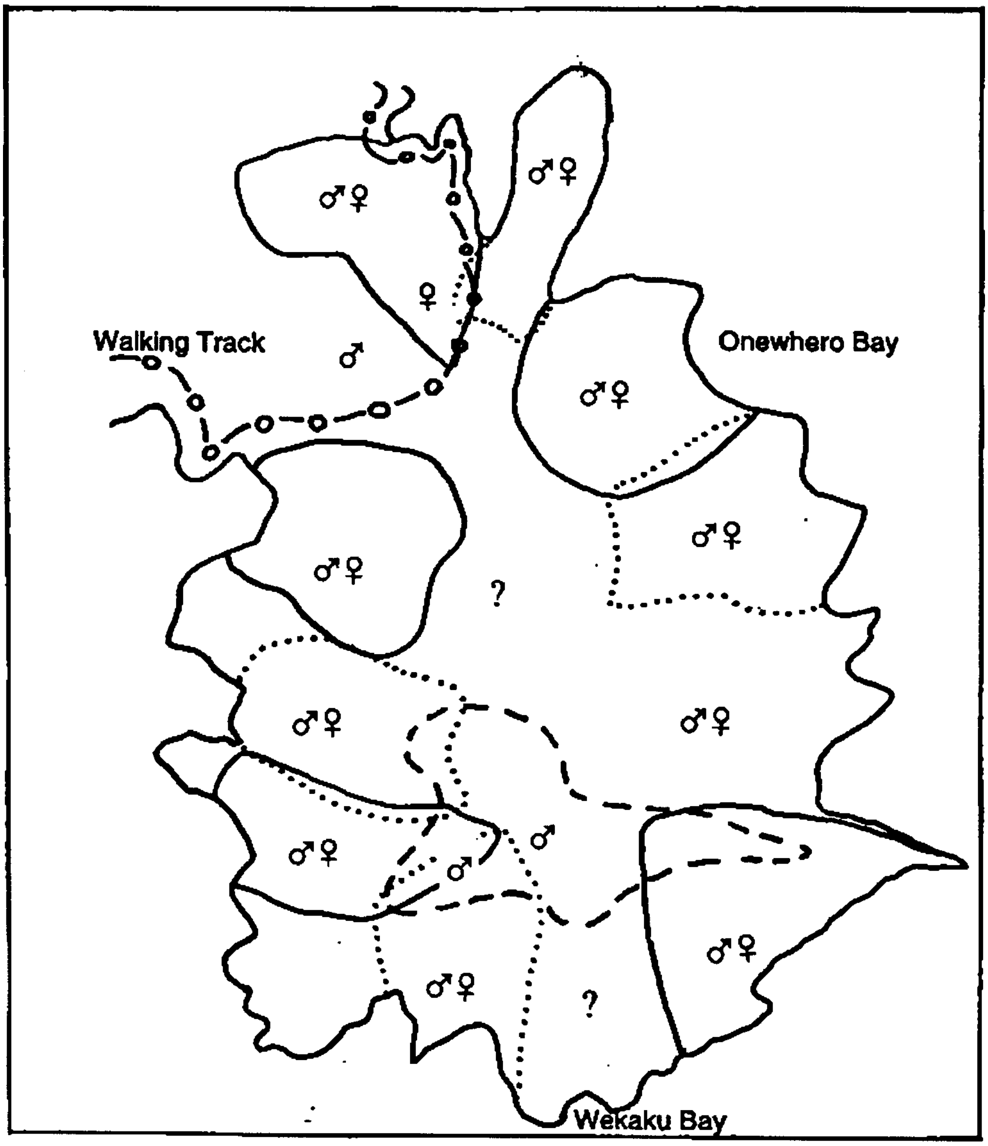
Appendix 1: Location of transects on the Puketukutuku and Whareama peninsulas.



Appendix 2: Location of adult kiwi in the catchment of Lake Waikaremoana.



Appendix 3: Layout of territories on Puketukutuku peninsula, Lake Waikaremoana.



Appendix 4: Distribution of kiwi in the main vegetation types within 1 km of the shore of Lake Waikaremoana. Vegetation codes after Nicholls (1966).

Vegetation code	Description	% of catchment	% in kiwi territories
N_1	Tawa-kamahi	0.2	0
N_2	Rata/tawa-kamahi	6.6	<1
R_1-R_2	Manuka, broad-leaved shrubs, tree ferns	9.7	16
K_1	Silver beech	2.4	0
H_3	Rimu-red beech/tawa-kamahi-hard beech-silver beech	1.7	0
I_5	Rimu-miro-red beech/kamahi-tawari -hard beech-silver beech	24	7
D_1	Rimu-rata/tawa-kamahi	9.5	23
I_2	Rimu-miro-red beech-silver beech/ kamahi-tawari	22	27
K_6	Red beech-silver beech	24	27

Appendix 5: Survival of kiwi chicks at Waikaremoana, 1993/94 and 1994/95.

Age	No. observed	Died	Killed	Disappeared	Dropped Tx	Survived
Chicks	13	2	0	2	0	9
Juveniles	9	1	4	2	2	1?

Appendix 6: Survival rates of adult and young kiwi needed to maintain population stability. Numbers in italics are current estimates for the population at Waikaremoana.

Adult survival (% per annum)	Mean lifespan (years)	Recruitment rate required for population stability (%)
86.3	*6.8*	28
90	9.5	20
95	19.5	10

Appendix 7: Distribution of cage and kill traps on the Puketukutuku and Whareama peninsulas.

Peninsula	Trap type	No. of traps	% in forest	% along shoreline
Puketukutuku	kill	212	54	46
Puketukutuku	cage	50	50	50
Whareama	cage	40	44	56

Appendix 8: Captures of small mammals in the Waikaremoana catchment in relation to habitat type (shoreline vs forest). Significance values relate to differences in the expected and actual numbers of captures in each habitat type. An asterisk denotes significantly more captures than expected. Some rats (approx. 120) were excluded from this analysis because their exact capture sites had not been recorded.

Species	No. Caught	% in forest	% along shoreline	Significance
Ferret	9	11	89*	$P < 0.01$
Weasel	7	14	86*	$P < 0.05$
Cat	9	0	100*	$P < 0.01$
Stoat	46	63*	37	$P < 0.01$
Norway rat	2	0	100	n.s.
Ship rat	235	63*	37	$P < 0.01$

Appendix 9: Distribution and abundance of mice and rats on Puketukutuku and Whareama peninsulas, December 1994 to October 1995 inclusive.

Peninsula	Sample size (tunnel nights)	Habitat	Tunnels tracked per 100 nights: Mice	Rats
Puketukutuku	1438	shoreline	40.7	8.0
		forest	17.3	11.1
Whareama	1388	shoreline	28.0	6.7
		forest	5.1	10.3

Appendix 10 : Seasonal changes in abundance of rodents on Puketukutuku and Whareama peninsulas. N, number of tracking nights; Mean, number of visits per 100 tracking nights; -, no measurement.

		Rats		Mice			
		Overall		Shoreline		Forest	
Peninsula	Month	N	Mean	N	Mean	N	Mean
Puketukutuku	Dec. 94	99	0	60	18.3	-	-
	Jan. 95	631	7.7	374	30.2	257	13.6
	Apr. 95	368	7.3	235	69.0	133	18.0
	May 95	294	18.3	68	64.7	225	23.5
	Oct. 95	46	19.5	-	-	46	32.6
Whareama	Dec. 94	8	0	-	-	-	-
	Jan. 95	515	3.1	281	12.4	234	15.4
	Apr. 95	443	10.8	116	45.1	186	2.6
	May 95	164	20.1	-	-	164	28.0
	Oct. 95	258	22.8	119	69.7	93	24.7

Appendix 11: Abundance of mice in grassy and non-grassy areas along the Whareama and Puketukutuku shorelines. Asterisk denotes significantly more tracks than expected on the basis of tunnel distribution.

		Tunnels in grass		Tunnels not in grass	
Peninsula	**Month**	**Tracked**	**Expected**	**Tracked**	**Expected**
Puketukutuku	Dec. 94	1	2	10	9
	Jan. 95	36*	22	77	91
	Apr. 95	40*	31	122	131
	May 95	13*	8.4	31	35.6
Whareama	Jan. 95	18*	5	17	30
	Apr. 95	19	17	97	99
	Oct. 95	18*	12	65	71