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## ROLE OF PREDATION IN THE DECLINE OF KIWI, *APTERYX* SPP., IN NEW ZEALAND

**Summary:** Kiwi have declined markedly in abundance and range since human settlement of New Zealand. Three of the four species are still extant in mainland forests, despite decades of co-existence with various introduced mammals. Little spotted kiwi is now probably confined to offshore islands. The role of introduced mammals in these population declines was evaluated by measuring the survival rates of adults, eggs and chicks of brown kiwi (*A. mantelli*) and great spotted kiwi (*A. haastii*) in mainland forests. Mortality rates of adults ranged from 5%-16% and did not differ significantly between species or sexes. Overall, 14 out of 209 adult kiwi died during 159.6 radio-tracking years. Predators definitely caused five of these deaths. Sixty-nine (68%) of 102 eggs from 77 nesting attempts by 48 pairs failed to hatch. Predators probably caused about 10% of egg failures. Only three of 49 chicks probably survived to adulthood, indicating a juvenile mortality rate of about 94%. Predators killed at least 8% of chicks, 45% of juveniles, and possibly as many as 60% of all young kiwi. Ferrets and dogs were the main predators of adult kiwi, possums and mustelids were the main egg predators, while stoats and cats were largely responsible for the deaths of young kiwi. Population models show that northern brown kiwi are currently declining at 5.8% per annum. This decline could be halted by cutting the current predation rates on young kiwi by about 34% to 33%.

**Keywords:** kiwi; ratite; *Apteryx* spp.; population declines; mammalian predators; mustelids; mainland reserves; predator control.

### Introduction

All four species of kiwi (Apterygiformes) have declined significantly in range and/or abundance since human settlement. Little spotted kiwi (*A. owenii* Gould) are now probably extinct on the mainland; great spotted kiwi (*A. haastii* Potts) are now mainly confined to high rainfall regions in the northwestern corner of the South Island (McLennan *et al.*, *unpubl. data*); and northern brown kiwi (*A. mantelli* Bartlett) have disappeared from the lower third of the North Island (McLennan and Potter, 1992). The conservation status of southern brown kiwi (*A. australis* Shaw and Nodder) is unclear, though the species is still locally numerous in parts of Fiordland and Stewart Island (R. Colbourne, *unpubl. data*).

Over the last century, kiwi abundance has probably declined by at least 90% in most North Island forests. Accounts by Buller (1877, 1888) suggest former densities of 40-100 adults km<sup>-2</sup> whereas present densities seldom exceed 4 adults km<sup>-2</sup> (McLennan and Potter, 1992; Miles, 1995). Some parts of Northland and some offshore islands (e.g., Kapiti) still support 50-100 adults km<sup>-2</sup> (H. Robertson, *unpubl. data*). The sex ratio of adults varies from place to place in North Island forests

(McLennan, Rudge and Potter, 1987; Potter, 1989; Taborsky and Taborsky, 1991) but there is no consistent bias, implying both sexes have similar average survival rates. Mainland populations, however, contain significantly fewer juveniles (McLennan and Potter, 1993) than do similar populations on predator-free offshore islands (Colbourne, 1992).

The former densities of kiwi in South Island forests are not known, though historical accounts also point towards a decline over the last century. Densities of adult great spotted kiwi are still relatively high (8-10 km<sup>-2</sup>) in wet (>4800 mm rainfall per year) areas of northwest Nelson and the Paparoa Range (McLennan and McCann, 1991a). The populations of brown kiwi at Okarito (northern species) and Haast (southern species) are small and endangered (Molloy and Davis, 1994) with the former containing a high proportion of partially blind (23%) and possibly very old kiwi (Reid, Joyce and Lyall, 1994).

Kiwi evolved in the absence of mammalian predators, but co-exist today with as many as seven obligate or facultative carnivores (Appendix) introduced by Polynesians and Europeans (Wodzicki, 1950). Recent studies show that some of these animals eat kiwi eggs (McLennan, 1988),

juveniles (Reid *et al.*, 1994) and adults (Taborsky, 1988); and several authors now consider predators the prime suspects in the decline of kiwi in mainland forests (e.g., McLennan and Potter, 1993). Indeed, some suggest that the connection is beyond dispute, and merely question why such vulnerable birds (with their flightlessness, strong smell, ground nests, prolonged incubation, and defenceless young) have managed to co-exist with mammalian predators for so long.

There is, however, no unequivocal published evidence linking predation with the decline of kiwi, except in one instance, where a single dog killed about 500 kiwi (c. 50% of the total population) in Waitangi State Forest over a few months (Taborsky, 1988). Here we analyse and review all available information on the impact of predators on kiwi adults, eggs, and chicks, then assess the role of predators in population declines.

## Methods

Published and unpublished data were used to determine the survival rates of adults, eggs, and chicks in mainland forests, and the mean annual productivity of bonded pairs.

### Adult survival

Analysis of adult survival was based only on records for kiwi carrying active radio-transmitters. The ages of these birds were not known, but all were believed to be sexually mature. Individuals which carried a transmitter on several separate occasions were treated as separate birds in the survival analysis. The

periods between captures, when they were not carrying a functioning transmitter, were ignored to avoid artificially increasing the survival estimates.

The records for adult northern brown kiwi came from Hawke's Bay, Okarito, and Northland (Table 1). These sites span the full geographical range of the species, and its extremes in population density. The records for great spotted kiwi came from Saxon River and Kahurangi Point, Northwest Nelson, and from the coastal ranges near Karamea (Table 1). Saxon River is a subalpine habitat with 8-10 adults km<sup>-2</sup> (McLennan and McCann, 1991a), one of the highest densities recorded for this species (McLennan and McCann, 1994). The other two sites, in lowland or coastal forest, were on the fringes of the species' range and supported fewer adults (4-6 km<sup>-2</sup>).

### Breeding attempts, egg survival, and annual productivity

The information used to calculate the breeding success of northern brown kiwi came from McLennan (1988), Potter (1989), and a study currently in progress in Te Urewera National Park (J. McLennan *et al.*, *unpubl. data*). A breeding attempt was defined as the laying of at least one egg in a nest. Annual productivity was defined as the number of independent young produced per pair per breeding season (June to February). Young kiwi passed from "chicks" to "juveniles" when they became independent and left their nest permanently, usually 17-27 days after hatching in the North Island, but some months after hatching in the South Island (J. Reid *et al.*, *unpubl. data*). Juveniles became "adults" at sexual maturity, about 18 (males) to 24 (females) months after hatching (Reid and Williams, 1975).

Table 1: Sources of information used in the analysis of adult survival.

Locality	Number of tracking periods		Source
	Males	Females	
<i>Northern brown kiwi</i>			
Waitere, Hawke's Bay	1	5	McLennan <i>et al.</i> , 1987
Haliburtons, Hawke's Bay	4	6	Ibid
Urewera, Hawke's Bay	16	8	J. McLennan and L. Dew, <i>unpubl. data</i>
Okarito, West Coast	11	6	J. Reid and J. Lyall, <i>unpubl. data</i>
Purua, Northland	15	7	H. Robertson, <i>unpubl. data</i>
Riponui, Northland	11	3	Ibid
Rarewarewa, Northland	25	26	Ibid
Hodges, Northland	6	1	Ibid
Tangiteroria, Northland	18	23	Potter, 1989
<i>Great spotted kiwi</i>			
Saxon, Northwest Nelson	14	16	McLennan and McCann, 1991b
Kahurangi, Northwest Nelson	6	3	Ibid
Karamea, West Coast	3	4	J. Lyall, <i>unpubl. data</i>

The estimates of annual productivity of great spotted kiwi were taken from McLennan and McCann (1991a). Female great spotted kiwi help incubate, so nests are seldom unattended and therefore difficult to examine (McLennan and McCann, 1989, 1991b). Consequently, productivity estimates for this species are not as precise as those for brown kiwi, and there are no measures of chick mortality between hatching and independence.

### Chick and juvenile survival

Estimates of chick and/or juvenile survival were obtained from McLennan (1988), Potter (1989), and from current field studies in Northland (H. Robertson *et al.*, *unpubl. data*), Te Urewera National Park (J. McLennan, *et al.*, *unpubl. data*) and Okarito (J. Reid *et al.*, *unpubl. data*). Some chicks were monitored until independence, but not thereafter; while others were radio-tagged 4-15 days after hatching, then tracked every 1-7 days for up to 17 weeks.

### Identifying causes of death and nest failure

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 in a cavity, (3) there was evidence of a struggle (e.g., trails of feathers and/or blood spots, (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 of the culprits may have been correctly identified, especially if the victim was killed by one animal then subsequently scavenged by another.

On two occasions we considered predators had killed chicks even though none of the above conditions was met. On one occasion, a stoat with the remains of a kiwi chick in its digestive tract was caught near a nest from which a chick had disappeared 13 days beforehand; while on the second occasion, a chick transmitter (but no skeletal remains) was found in a stoat's nest. The tunnel

leading to this nest was too small (4.6 cm diam.) for an intact chick to pass through.

Egg failures were attributed to mammalian predators only when there was positive evidence (e.g., a hole chewed in an egg). Some desertions and losses of intact eggs may have been caused by predators but, in the absence of any supporting information (e.g., hair in a nest burrow), were classed as "unknown".

### Population model

The estimates of productivity and survival were used to model population trends of northern brown kiwi and the significance of predation by introduced mammals. The model will be described in detail elsewhere (Wake *et al.*, *unpubl.*; copy held at Mathematics Department, Auckland University). This model is based on an age structure in three classes: chicks, juveniles and adults differentiated by sex. Using linear dependence of predation and death rates on the population size, it is possible to calculate the threshold predation rate - especially on chicks and juveniles - below which survival is assured and above which the cohort is doomed to extinction. The model is a considerable mathematical novelty and leads to a linear delay-differential equation. Transform techniques reveal that the transient behaviour will vary like  $\exp(\lambda t)$ , where  $\lambda$  is related to a balance between birth rates and predation rates in various age-classes. The sign of  $\lambda$  governs the behaviour, and  $\lambda = 0$  determines the threshold between survival and extinction.

## Results

### Adult survival

For northern brown kiwi, we recorded a total of 192 tracking periods from 171 birds (Table 2). Males were tracked more often than females (56% and 44% of tracking records respectively) and for longer periods; but sufficient females were sampled to obtain a reliable estimate of their annual mortality.

Table 2: *Survival estimates for adult kiwi in mainland forests.*

	Brown Kiwi		Great Spotted Kiwi	
	Males	Females	Males	Females
No. Tracking periods (individuals)	108 (99)	84 (72)	23 (20)	23 (18)
Tracking period (years $\bar{x} \pm SE$ )	$0.72 \pm 0.05$	$0.52 \pm 0.05$	$0.84 \pm 0.14$	$0.80 \pm 0.09$
Sum (years)	78.1	44.0	19.2	18.3
No. Deaths	8	2	3	1
Mortality (%/year)	10.2	4.5	15.6	5.5
Av. Mortality (%/year)		8.2		10.7

Eight deaths were recorded during 0.72 radio-tracking years in population of 108 male northern brown kiwi, giving a mortality of 10.2% per year (95% CI = 5% - 18%). The estimate for females was 4.5% (95% CI = 0% - 14%) based on two deaths in 0.52 tracking years amongst 84 individuals. The difference between sexes was not significant ( $\chi^2 = 1.1$ ,  $P < 0.25$ ; expected values based on total tracking years for each sex). The average mortality rate for both sexes combined was 8.2% per year (95% CI = 4% - 14%).

Brown kiwi in Te Urewera National Park had significantly higher mortality rates (21.5% per year) than those in Northland (5.3% per year;  $\chi^2 = 5.2$ ,  $P < 0.025$ ). The samples were too small to test for yearly variations within sites.

Four great spotted kiwi died during 37.5 radio-tracking years, giving an annual mortality rate of 10.7% (95% CI = 3% - 25%; Table 2). This does not differ significantly from the estimate obtained for brown kiwi ( $\chi^2 = 0.19$ ,  $P < 0.70$ ). The samples for great spotted kiwi were too small to test for differences between sexes, seasons and sites.

### Adult mortality and significance of predation

A total of 14 adult kiwi died during 159.6 years of radio-tracking in mainland forests. Five deaths (36%) were attributed to predators, six (43%) to natural causes, and three (21%) to unknown causes. The predators responsible for adult deaths were dog (1), feral pig (1), ferret (2) and possum (1). Three of the natural deaths were accidents (e.g. hit by a falling tree), two birds died while incubating, and one was a casualty of a fight between kiwi. The "unknown" category includes two carcasses which were too decomposed to determine the cause of death, and a kiwi which disappeared suddenly along with its transmitter.

On average, introduced mammals killed one adult every 32 radio-tracking years. This low incidence of predation indicates that adults can defend themselves against all of the common mammalian predators in mainland forests. If losses to predators are ignored, annual adult survival increases by only 3% in both northern brown kiwi and great spotted kiwi. However, this seemingly small increase in survival increases the average longevity of adults from 11.7 to 18.7 years, and average lifetime productivity by as much as 60%. Predators of adult kiwi may therefore be significant agents of decline even though they kill relatively few birds.

### Egg survival

The data for northern brown kiwi comprised 58 nesting attempts of 33 pairs. These birds produced

83 eggs between them, of which 26 (31%) hatched (Table 3). Predators ate just two eggs (2%) with the probable culprits being possum (1) and mustelid (1). The single largest cause of egg failure was desertion (29%). Six eggs were apparently deserted because they were infertile, and nine because we disturbed the incubating males. Introduced mammals may have contributed to the desertion of a further nine eggs (11%) though there was no evidence that they had visited the nest burrows, and all of the eggs were intact.

Six eggs (7%) disappeared without trace. On two occasions, one egg disappeared from a two-egg clutch. These eggs were apparently rolled out of nests, sometimes up steeply sloping burrows. We suspect they were ejected by kiwi, but cannot discount the possibility that predators, especially stoats, removed some of them.

The other substantial cause of egg loss was embryo death and decay (16% of failures). Typically this occurred late in incubation, and usually resulted in the partial loss of a two-egg clutch. Sometimes the rotten egg split, leaking its contents into the nest; nevertheless some males continued to incubate the remaining egg, despite the smell. We do not know whether bacteria killed these embryos, or merely fed on them afterwards. If the former is true, bacteria rather than introduced mammals are the main predators of kiwi eggs.

Northern brown kiwi hatched, on average, 0.85 chicks per pair per breeding season, and fledged 0.51 juveniles (Table 3).

The sample for great spotted kiwi was much smaller, comprising just 19 breeding attempts from 15 pairs (Table 3). Their hatching success (37%) and

Table 3: *Survival of kiwi eggs in mainland forests.*

	Brown Kiwi (33 pairs)	Great Spotted Kiwi (15 pairs)
Nesting attempts	58	19
No. eggs	83	19
No. hatched	26 (31%)	7 (37%)
No. eaten	2 (2%)	0
No. smashed	8	3
No. disappeared	6	2
No. rotten	13 (16%)	3 (16%)
No. deserted	24	4
No. buried	2	0
No. other	2	0
No. chick hatched per pair/year (x ± SD)	0.85 ± 0.87	0.39 ± 0.5
No. chicks fledged per pair/year (x ± SD)	0.51 ± 0.72	0.39 ± 0.5

causes of egg failure were very similar to those of northern brown kiwi. None of their eggs was eaten by mammals. Great spotted kiwi laid fewer eggs each season than did northern brown kiwi, and were only about half as productive (0.4 chicks per pair per year). We do not know the age at which great spotted kiwi chicks become independent, so the estimate of fledging rate in Table 3 is given as a probable maximum.

In summary, mammalian predators were definitely responsible for the loss of at least 2% of eggs laid by kiwi in mainland forests. Their maximum impact was 20%, assuming that they were responsible for all of the unexplained desertions and disappearances. We estimate that predators probably caused about 10% of egg losses.

### Chick and juvenile survival

A total of 49 northern brown kiwi chicks were monitored for up to 14 weeks. Of these 22 (45%) died in their first three weeks of life (Table 4). Nine of the fatalities were classed as natural, nine chicks disappeared without trace, and four were killed by predators. Most of the natural deaths resulted from accidents. Some chicks tumbled out of nests; others fell down steep slopes into streams, and some became entangled in vegetation or cleft sticks. Two chicks died within 24 h of hatching, and one died after becoming infested with fly maggots (Diptera, Calliphoridae).

The nine chicks which disappeared were 5-20 days old. They had started to feed outside their nests at night, but still returned to them each day. Accidents and predators probably accounted for most of these losses. In four cases, the chicks were radio-tagged, but neither their bodies nor the radio transmitters were recovered.

Twenty-seven (55%) of the 49 chicks reached fledging age and left their nest for good (Table 4). Seven were not radio-tagged and their fates are unknown. The radio transmitters fell off five of the remaining 20 juveniles 3-38 days after fledging. One juvenile reached the age of 99 days, then died after falling into a deep hole. Five juveniles disappeared along with their transmitters, and nine were killed by predators.

Mustelids were responsible for 10 (77%) of the 13 confirmed predations on young kiwi (chicks and

juveniles combined). Stoats were the main predators in all localities (Okarito, Te Urewera National Park and Northland). Weasels may have killed two chicks in Northland (the remains of the chicks were cached in very small cavities, probably too small for stoats to enter). Other predators of young kiwi were harrier (1) and feral cat (2).

Overall, predators killed at least 8% of the chicks and 45% of the juveniles monitored. They may have killed over 60% of young kiwi, if predation was the main cause of chick disappearance. No radio-tagged juvenile survived for more than 100 days. Indirect evidence (feeding sign, faeces and footprints) indicates that two of the five individuals who shed their transmitters survived. One male reached 10 months of age, then dispersed as a sub-adult; the other was re-caught at an age of 7 months.

From these figures we estimate that 82% to 95% of young northern brown kiwi fail to reach adulthood. The lower estimate assumes that all seven juveniles in the "unknown" category in Table 4 survived to adulthood. The upper estimate is derived from the 42 young whose fates were "determined". Our best estimate is 94% mortality (95% CI = 89 - 98%). This assumes that one of the seven unmonitored juveniles reached adulthood - a probable outcome given the survival rates of monitored juveniles.

Finally, the mortality estimates, although high, may be conservative. They were derived almost entirely from young kiwi in their first 100 days of life. Juveniles probably take at least another 300 days to reach full adult size, and undoubtedly suffer further losses during this time. We have no measures of this mortality because so few of our cohort reached this age. Older juveniles undoubtedly survive better than younger ones, but we do not know at what size and age their predation risks become similar to those of adults.

### Population trends of northern brown kiwi and significant of predation

Our estimates of adult survival, productivity, and recruitment show that populations of northern brown kiwi are declining (Fig. 1). This, of course, merely confirms what is already common knowledge. The pooled data show that the overall rate of decline is

Table 4: *The fate of kiwi chicks and juveniles in mainland forests. Alive refers to fledging for chicks. In juveniles, alive refers to individuals which shed their transmitters.*

Age	No. observed	Died	Natural	Disappeared	Killed	Alive	Unknown
Chick	49	22 (45%)	9	9	4	27 (55%)	0
Juvenile	27	15 (55%)	1	5	9	5 (19%)	7

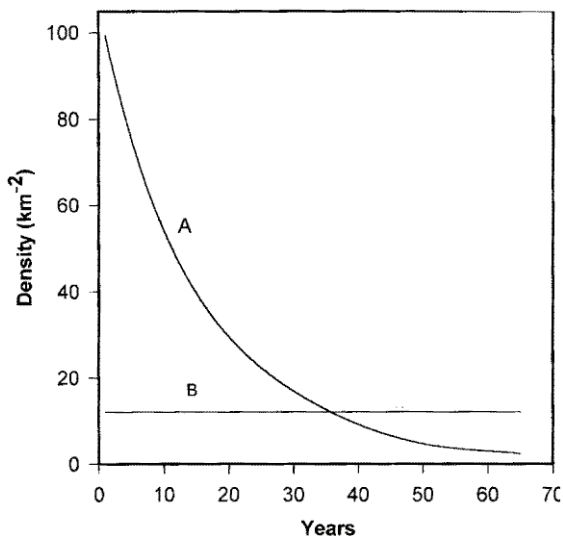


Figure 1: Density of northern brown kiwi in mainland forests given adult mortality of 8.2% per annum, a productivity rate of 0.85 chicks hatched per pair per year, and juvenile mortality of 94% per annum (A). Density assuming a recruitment rate of 19% per annum (B).

5.8% per annum. There is, however, considerable variation between areas, depending on the various values of the input parameters. The Urewera population, for example, with its high rates of adult mortality, is declining about six times faster (at 18% per annum) than populations near Whangarei in Northland (3.2% per annum).

It would take about 65 years for the density of a kiwi population to decline from  $100 \text{ km}^{-2}$  to  $2 \text{ km}^{-2}$  if the average loss rate is 5.8% per annum (Fig. 1). The process would take 95 years at a loss rate of 4% per annum. We do not know the actual rate over the last 100 years, but it probably falls between these two values, given Buller's rough indications of kiwi density in mainland forests at the turn of the century.

Population decline ceases if the proportion of young kiwi surviving till adulthood increases from 6% (present levels) to 19% (Fig. 1); and recruitment rates above this promote recovery. To achieve population stability, predation rates on young kiwi have to fall by about 34% from present levels (c. 50%) to 33%. Lower levels of predation are required than those predicted by the model (33%) to sustain current population levels because some juveniles spared from predators would die for other reasons before they reached adulthood. Clearly, some losses to predators are tolerable; indeed, halving the present predation rate on young kiwi would be sufficient to

facilitate population recovery. Eliminating predation on adults **and** eggs would not in itself promote population recovery, though it would slow the rate of decline to about 2.7% per annum.

## Discussion

This paper presents the first quantitative data on the impact of introduced mammalian predators on kiwi in mainland forests, and quantitative predictions on the declines in predation rates required to reverse population declines. The results confirm the suggestions of McLennan and Potter (1992, 1993) and others that predators are the primary culprits in the widespread decline of kiwi on mainland New Zealand.

### Adult survival

The vulnerability of a kiwi to predators changes throughout its life, and different predators are important at different stages. Adult brown and great spotted kiwi suffer few losses (3% per annum) apparently because they exceed the threshold prey size of cats and stoats, the largest of the common forest-dwelling predators. This threshold is surpassed by both sexes, even though male kiwi (2200 g) are generally about 20%-30% lighter than females (2900 g; Reid and Williams, 1975). The persistence of brown and great spotted kiwi in mainland forests is thus largely attributable to their evolutionary history, which happened to favour a relatively large adult body size. Little spotted kiwi, at 1100-1400 g, remain vulnerable to predators throughout adulthood, and are now found only on offshore islands where these animals are absent.

The impact of ferrets and dogs on adult kiwi in mainland forests is both unpredictable and episodic, but both species can cause massive and rapid reductions in local populations. These reductions involve the sudden loss of adults and are much more drastic than those resulting from poor recruitment. Taborsky (1988) documented an episode in Waitangi State Forest where a single dog killed about 50 kiwi in a few months. The population in Paerata Wildlife Management Reserve in Northland dropped from approximately 90 to 30 kiwi between 1988 and 1994, probably because of one or more predatory episodes by ferrets or dogs (H. Robertson and M. Potter, *unpubl. data*). Other populations in Northland have also collapsed since the 1970s, particularly in areas recently colonised by ferrets and possums (Miller and Pierce, 1995). Adult kiwi seldom persist for more than a few years in forest remnants in agricultural landscapes (McLennan and

Potter, 1992) presumably because of predation by dogs and ferrets.

In this study, one of eight radio-tagged populations suffered episodic predation from ferrets. The event itself lasted just a few weeks, but resulted in the disappearance of at least 17% of 40 known adults (tagged and untagged). We do not know, however, whether the frequency of episodic predation events in the samples used to construct our model approximates the average rate for all mainland populations - and thus whether our estimate of adult survival is high or low.

One periodic cause of adult mortality - accidental trapping and poisoning by possum hunters - is under-represented in our sample, mainly because our data were collected in years when low fur prices discouraged hunting. Extensive surveys show that some 10% of the current crop of adult kiwi in mainland forests have damaged or missing toes, indicating that "predation" by leghold traps has been significant over the previous two or three decades (McLennan and McCann, 1994; Potter, 1989; J. McLennan, *unpubl. data*). Some birds are injured fatally by traps, so actual capture rates are probably 30%-50% higher than those indicated by the number of maimed birds. Furthermore, some 8% of kiwi "marked" by leghold traps probably die each year, thereby further reducing the apparent incidence of capture. This natural attrition would halve the proportion of birds with marks (from 20% to 10%) in 9-10 years if no new birds were injured during this period.

We have no measures of annual mortality rates attributable to traps and cyanide baits. However, in years of high fur prices, such losses may exceed 5%, and significantly reduce the average longevity and lifetime productivity of kiwi in mainland forests.

### **Egg survival**

Kiwi lose few eggs (*c.* 10%) to mammalian predators compared with most forest birds (average 39%; Moors, 1983). This is remarkable given that kiwi eggs are potentially at risk for up to 85 days, two to five times longer than those of all other forest birds (Oliver, 1955). The high survival of eggs is probably attributable to four factors: nest site selection and camouflage; the attentiveness of incubating adults; the ability of adults to repel would-be egg predators; and the large size and weight of the eggs.

The relative contribution of the first two factors varies between northern and southern populations. Cryptic nests are a feature of kiwi in the North Island, where males alone incubate, and eggs are left unattended for up to 10 hours each night.

Conversely, in the South and Stewart Islands, kiwi often nest in large and obvious burrows, but share incubation and seldom leave eggs unattended. Unlike the northern species, they rarely camouflage the entrance of their breeding burrow with leaves and twigs, presumably because the near continual presence of an adult in the nest is an adequate defence in its own right.

In part, then, defensive behaviours which may have evolved to protect eggs against avian predators also appear to be partially effective against introduced mammals. However, the historical legacy of greatest benefit is probably egg size; by chance, the eggs of kiwi are too large to be punctured or removed by rats, the most numerous egg predator in mainland forests.

### **Chick and juvenile survival**

Young kiwi suffer exceptionally high mortality, especially in their first 100 days of life. Our figures suggest at least 94% of young kiwi fail to reach adulthood, an estimate which is remarkably close to an earlier one (92%) derived from the age structure of kiwi populations in the presence and absence of predators (McLennan and Potter, 1993).

Predators, chiefly stoats, cause about half of these losses. Young kiwi have no behaviours or defences that protect them against introduced mammals. They forage independently from their parents at an early age, and often emerge from daytime shelters in the early evening, up to an hour before adults. They frequently respond to an approaching predator by "freezing" rather than by fleeing. This response may be appropriate for predators which detect prey by sight and/or sound (birds of prey), but is entirely ineffective against mammals hunting prey by scent. Young kiwi selectively inhabit dense, regenerating vegetation (J. McLennan, P. Miller, *unpubl. data*), possibly because such habitats afford protection from birds of prey. The same habitats provide little if any protection against introduced mammals. Predation by introduced mammals on young kiwi is the single most important factor contributing to the demise of mainland populations.

### **Management of mainland populations**

Northern brown kiwi will be saved in mainland forests only by creating relatively predator-free habitats, or by releasing sufficient captive-raised chicks (at least 7 months old) to compensate for adult mortality. The birds have already disappeared from some districts and suffered large declines elsewhere. Declines can be halted if predation rates on young

kiwi fall by a third from present levels (*c.* 50%) to 33% and overall survival of young kiwi increases from 6% to 19%. The extent to which stoat and cat populations have to be reduced to achieve this target is not known, but three studies are currently evaluating whether intensive trapping removes sufficient predators to increase juvenile survival.

Adult survival must also be maintained at high levels. In many places, the inevitable loss of the current crop of adults as they die of old age will result in local extinction, with no prospect of immigration from surrounding areas. Options for future management diminish with each localised extinction. Currently, it is not possible to save all of the remaining populations, because present methods of predator control are too expensive and inefficient to apply on a large scale. However, this could change in the next few decades if priority is given to producing cheaper and more effective methods. Until then, at least two populations in each region should be intensively managed to preserve genetic diversity and lessen the risk of extinction of mainland populations.

Procedures are already being applied to enhance juvenile survival and boost the productivity of adult brown kiwi at Okarito. Elsewhere in the South Island, great spotted kiwi appear to be holding their own in high rainfall refugia, generally at high altitudes (McLennan and McCann, 1994). Such habitats may have fewer stoats than drier areas, possibly because they contain fewer staple prey items. It is too early to tell whether these remnant populations will also require intermittent management in the future; however, for the moment, their conservation status is less serious than that of their counterparts in the North Island.

The combinations of adult, egg and young survival rates which promote population recovery differ between species, and will be described fully elsewhere (McLennan *et al.*, *unpubl. data*).

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Appendix: *Common and scientific names of mammalian predators referred to in the text.*

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Cat	<i>Felis catus</i> L.
Dog	<i>Canis familiaris</i> L.
Ferret	<i>Mustela furo</i> L.
Pig	<i>Sus scrofa</i> L.
Possum	<i>Trichosurus vulpecula</i> Kerr
Stoat	<i>Mustela erminea</i> L.
Weasel	<i>Mustela nivalis vulgaris</i> Erxleben

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