Size matters: predation risk and juvenile growth in North Island brown kiwi (*Apteryx mantelli*)

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Abstract: This study investigated how predation risk in North Island brown kiwi changes as the birds grow and develop. Over a 10-year period, 53 adult and 126 young kiwi were radio-tagged at Lake Waikaremoana and studied to determine survival rates, causes of death, and rates of growth. Predation loss amongst adults was low (2.49% year^{-1}) and caused mainly by ferrets. Young kiwi suffered intense predation from stoats during their first four months of life, but thereafter became too large (> 800 g) for stoats to kill. Juveniles took at least 880 days to attain adult size, about four times longer than expected for a 2–3 kg bird. Growth rates peaked at about the point of hatch, rather than later on in development as in other birds. We suggest that a long evolutionary history dominated by resource limitation rather than predation may account for slow rates of development in kiwi, and that differences among kiwi species in their ability to persist in the presence of stoats are explained by differences in the time that they take to reach safe-size.

Keywords: *Apteryx mantelli*; juvenile growth; Lake Waikaremoana; North Island brown kiwi; safe-size; stoat predation.

Introduction

Over the last 1000 years, flightless birds on the three main islands of New Zealand have experienced significantly more extinctions (80% of 30 species) than have volant species (33% of 58 land and freshwater species; Holdaway, 1999). Today, North Island brown kiwi (*Apteryx mantelli*) and weka (*Gallirallus australis*) are the last extant remnants of 20 species of flightless birds that inhabited the North Island at the time of human colonisation. They share the prize for persistence, but not for permanence. Their declines have merely been slower than those of other flightless species, but inexorably towards the same endpoint (McLennan and Potter, 1992; Beauchamp *et al.*, 1998).

North Island brown kiwi have survived more than 100 years of coexistence with introduced mammalian predators because of their size, longevity and fecundity. The adults at 2–3 kg are too large to be tackled by rats (*Rattus* spp.) and stoats (*Mustela erminea*), the most abundant predators in deep forest tracts. The adults are both long-lived (20+ years) and highly productive (about one chick per adult female per year) so populations can withstand long periods of inadequate or intermittent recruitment. Finally, the eggs are too large and heavy to be opened or removed by rats.

Predation is limited largely to young kiwi, and it is the losses at this stage of life that are causing populations to decline (McLennan *et al.*, 1996).

At some point between hatching and maturity, young kiwi reach a size (or age) at which they cease to be vulnerable to stoats. It is important for conservation managers to know when this happens, so they can release captive-raised juveniles at a safe size, and design stoat control programmes to protect wild chicks during their vulnerable period. Our aim was to measure how predation risks change as juveniles mature, and to identify when their mortality rates decline to adult levels. The study was conducted as part of a wider investigation of predator impacts on kiwi in North Island forests.

Methods

Study area

The study was undertaken from 1992 to 2002 at Lake Waikaremoana (582 m a.s.l.), Te Urewera National Park (212 072 ha), in the south-eastern corner of the largest remaining tract of indigenous forest in the North Island. The catchment of Lake Waikaremoana is

steep and almost entirely covered in old-growth forest, with mixed beech (*Nothofagus* spp.)/podocarp associations on the lower slopes, and near-pure beech stands above 700 m a.s.l. Common sub-canopy species include tree ferns (*Dicksonia* and *Cyathea* spp.), tawari (*Ixerba brexioides*), *Quintinia* spp., *Olearia* spp., *Drachophyllum pyramidale* and *Cyathodes* spp. *Blechnum* ferns predominate at ground level. Evidence of human impacts is scarce, except around the lake itself. The shoreline is fringed by grassland and regenerating vegetation, growing on what was lakebed, exposed in the late 1940s when the water level was lowered permanently by about 4 m for hydroelectric development. In a few places the regenerating shrublands extend further inland, on sites that were formerly occupied, cultivated, or farmed by the Ruapani and Tuhoe people.

Although the vegetation in the catchment is structurally intact, the endemic avifauna is not. It has been depleted by centuries of coexistence with kiore (*Rattus exulans*) followed by decades of exposure to feral pigs (*Sus scrofa*), feral cats (*Felis catus*), possums (*Trichosurus vulpecula*), ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), weasels (*Mustela nivalis*), stoats, ferrets (*M. furo*), and the occasional stray dog (*Canis familiaris*). Mice *(Mus musculus)*, rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus*) and red deer (*Cervus elaphus scoticus)* have lived in the catchment for the last 40–120 years, and hedgehogs (*Erinaceus europaeus)* have recently reached the eastern shoreline of Waikaremoana.

Survival rates of kiwi and growth rates of juveniles

The survival rates of 53 adult and 126 juvenile kiwi were measured by radio-tagging individuals and recording their fates. Nine of the juveniles became adults during the study. Adults were tracked for an average of 1087 days (range 17–3264 days) and juveniles for 115 days (range 1–800 days). Most of the juveniles were of known age and origin because they had been tagged in their natal nests, 4–7 days after hatching. A few were first caught as sub-adults, 14–20 months old. These individuals ($n = 8$) were dispersing, and may have hatched outside of our study area.

All radio-tagged kiwi were monitored at least once a week to determine whether they were alive. The radio signals varied in strength as the birds moved, so it was possible to determine remotely whether an individual was active or stationary by listening to its transmitter at night. Those thought to be stationary were located the following day to establish their status. Adults were usually handled just once each year when their transmitters needed replacing. Juveniles were weighed and measured at least once a fortnight in their first six months of life, then about once every three months over the following two years.

Cause of death and predator identification

Kiwi found dead were examined carefully to ascertain whether they had died of natural causes or been killed by a predator. Natural deaths resulted from: entanglement in vines; falling into holes; fly-strike; deformities; fatal injuries from fighting other kiwi; septicaemia following incomplete adsorption of the yolk sac; intestinal blockages; and 'old age', preceded by the formation of cataracts and (in females) the cessation of laying. Some of the kiwi that 'fell' into holes were probably being chased at the time, so up to 27% of 'natural' deaths may have been caused indirectly by predators.

Predators were blamed for a kiwi's death if one or more of the following criteria was 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 (McLennan *et al.,* 1996). The evidence was unequivocal, except in one instance, when the kiwi may have been scavenged rather than killed.

Predator identity was ascertained from sign on or near carcasses, using the following criteria:

***Stoats*.** Puncture injuries on neck, minimal or no feather loss. Victim often not consumed, or only partly consumed; legs sometimes dismembered; brain often removed through an opening in the back of the skull; ribs and neck vertebrae of young kiwi (< 4 weeks old) sometimes eaten; prey remains usually cached in a deep cavity in tree roots, logs, or underground caverns, or taken to an occupied stoat nest; assorted remains of other prey (mainly rats) often present in caches.

***Ferrets*.** Neck vertebrae, skull, bill, skin, and feathers usually eaten; pelvis, leg bones, feet and claws discarded. Ribs always chewed down to stubs, thoracic vertebrate sometimes also eaten. Prey item not cached, but instead dragged or carried to a sheltered place under overhanging ferns, logs or stream banks. Faeces usually deposited on or near prey remains.

***Cat*.** Carcass plucked; remains surrounded by feathers, often in a relatively open site.

***Pig*.** Skin rolled down the body, from head to feet; prey remains with the appearance of an inverted sock.

***Possum*.** Carcass not eaten; puncture injury to skull or neck; evidence of a prolonged struggle; clumps of possum fur in vicinity of carcass; fur under the victim's claws.

Predation risk

Predation risk was determined for each of seven different age classes, beginning with dependent chicks, and ending with juveniles greater than 130 days old.

The first age class spanned the 30-day period from

hatching through to independence, when chicks are brooded, and therefore guarded, for at least some of the time by the adult male. Brooding occurs only in the nest itself. Newly-hatched chicks are brooded for most of their first 4–6 days of life, except for a few hours of each night when the male leaves to feed. At about day 5, chicks start to make their own unaccompanied foraging trips out of the nest. The trips are brief (< 1 hour) to begin with, but then increase rapidly in duration and distance over the following week. From about day 13 onwards, chicks usually spend the entire night away from their nest, but they continue to return to it at dawn, and spend the day there with the adult male. This pattern continues through to about day 20, when most chicks become fully independent and leave their nests for good. A few remain to day 30. From thereon, chicks have no contact with their parents, except in chance encounters.

The six age classes following on from the onset of independence each covered a period of 20 days, except the last one, which extended from 131 days through to adulthood. For each age class, the percentage daily rate of mortality attributable to predators (M_p) was calculated as:

$$M_p = N_i \times 100 / \Sigma_i \text{ days of exposure}$$

where N_i is the number of kiwi killed by predators in the ith age class, and 'days of exposure' was the total number of 'kiwi-days' accumulated by all of the individuals in the ith age class. For convenience, the term 'daily mortality rate attributable to predators' is abbreviated here to 'predation risk'.

Sources of data

Data from all months, years, and parts of the Waikaremoana catchment were pooled and used in the analyses. Nineteen chicks that were raised entirely in captivity then released at Waikaremoana were excluded from the sample. Fifty-six chicks lived in areas where mustelids and cats were being intensively trapped; 42 were in non-treatment areas; 20 moved from a trapped area into a non-trapped area, or vice-versa; and 8 were first caught as dispersing juveniles in a trapped or non-trapped area. Some of the chicks hatched in months and/or years when stoats were either especially numerous or scarce, and some hatched in seasons when their growth rates may have been slowed by a shortage of food. In short, predation risk varied with locality and season, and no two juveniles would have experienced identical levels of risk during their life. The same is true of the adults.

The pooled sample therefore gives average values of predation risk for a wide range of conditions. Our interest here is not so much in the values themselves (which will vary from place to place and year to year) but in the way that they change as chicks grow, and

how they compare with those of adults living in the same locality at the same time.

Results

Growth and weight of kiwi

At hatching, chicks weighed 320–390 g. Chicks lost weight during their first 10–15 days of life as they consumed residual stores of yolk. Thereafter weight changes were positive, and remained so until the birds
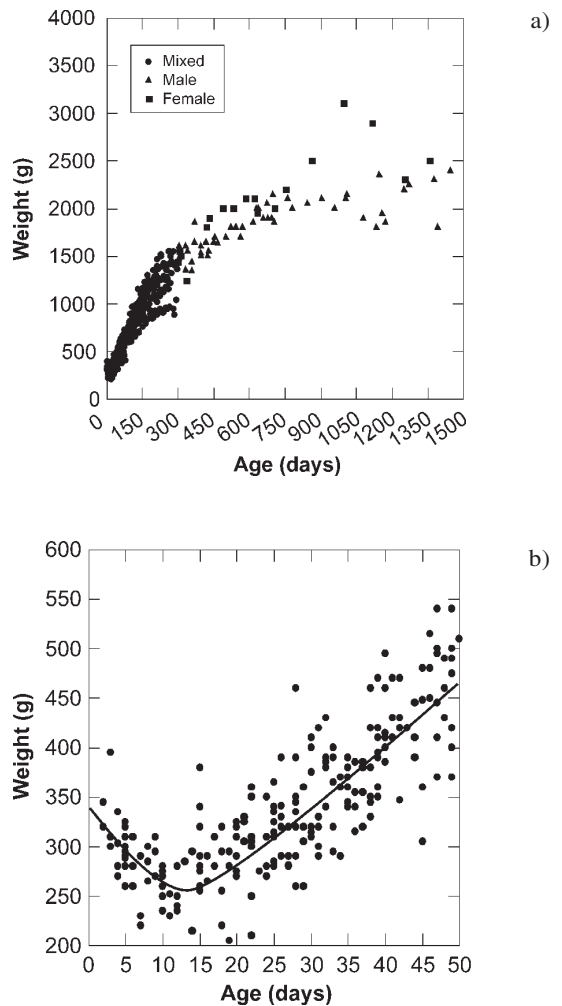

Figure 1. Relationship between weight (g) and age (days after hatching) in North Island brown kiwi. a) the entire period of development, with gender identified for individuals > 300 days of age; b) the first 50 days of development.

attained average adult weight [2038 ± 16 g (S.E.) for 34 males and 2662 ± 32 g for 22 females] 750–1050 days after hatching (Fig. 1). The equations below describe the shape of the growth curves for males and females respectively, with age accounting for 95% of the variation in the sample in each case:

$$\text{Weight (g)} = 339 + 3.872 \, (\text{age in days}) - 0.002 \, (\text{age}^2),$$

and

$$\text{Weight (g)} = 294 + 4.613 \, (\text{age}) - 0.002 \, (\text{age}^2).$$

With the exception of the first 15 days, absolute rates of growth declined steadily throughout development, from a high of 6.3 g day^{-1} at day 30 to about 0.9 g day^{-1} at day 500. The same trend was evident in bill length, with the fastest rates of growth occurring in the first few weeks of life (Fig. 2). From the onset of incubation, growth in kiwi is presumably sigmoid in form, though it is not evident in Fig. 2. The inflection point, where the absolute rate of growth peaks then begins to decline, seems to occur in late incubation or at about the time of hatching, when only about 10% of total growth has been accomplished.

Males and females grew at the same rate from hatching through to adulthood, but females continued to grow after males had reached maturity (Table 1) and so eventually reached a heavier adult weight. The bills of females also grew slightly but significantly faster than those of males, mainly in the period from 200–1400 days (Table 1). Bill growth in females continued for 1300–1400 days, whereas it stopped in males when they reached an age of about 950–1000 days.

Predation risk

Adults

Kiwi were considered to be adults when their weight exceeded 1820 g, the mean weight, less one standard deviation, of paired, breeding males. Five adults were killed by predators in 72 802 tracking days giving daily and annual mortality rates (attributable to predation) of 0.0068% day^{-1} and 2.49% year^{-1} respectively. Ferrets were definitely responsible for three of the deaths, and a possum for another one. A feral pig ate one adult, though it was not clear if it killed it in the first place. No adult kiwi were killed or injured by stoats or cats.

Juveniles

Predators killed 32 of 111 radio-tagged chicks/juveniles. It is likely that predators were partly responsible for the loss of nine untagged chicks that disappeared from their nests before they were old enough to fledge, and for the loss of one tagged chick whose body could not be recovered from an inaccessible cavern.

In young kiwi, predation risk changed significantly throughout the first 130 days of development (Fig. 3). Dependent chicks had a relatively low predation risk (a value between 0.18% day^{-1} and 0.51% day^{-1}) presumably because they were less active than fledged chicks, and were protected by the brooding male for at least some of the time. At the onset of independence (day 30) predation risk increased to about 0.70% day^{-1} and remained high until day 90. Thereafter, predation risk declined sharply: by about 50% between

Table 1. Weight and bill growth rates (mean ± SD; *n* in brackets) of kiwi at Lake Waikaremoana, in relation to age (days after hatching) and gender. The sample sizes for mass and bill growth differ within each sex because, on some occasions, one of the parameters was not measured on some individuals. Within each age class, growth rates did not differ significantly between sexes. Overall, however, the rates of bill growth in females were significantly faster than in males (0.137 ± 0.09 and 0.097 ± 0.081 mm day^{-1} respectively; student's *t* = 3.55, *P* < 0.005).

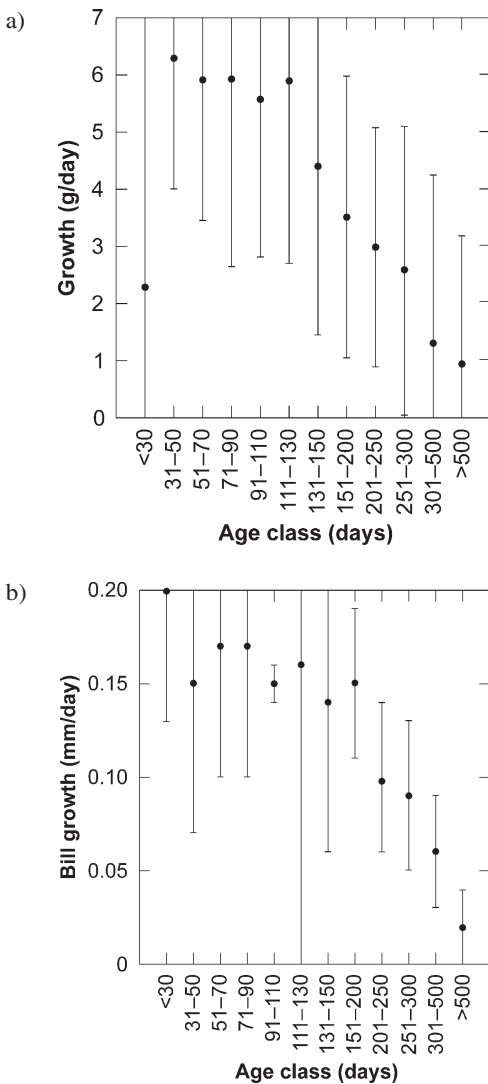| Parameter	Sex	Age (days)				
		0–50	51–100	101–200	201–300	>300
Weight (g day^{-1})	♂	4.3 ± 4.4 (31)	6.1 ± 2.9 (29)	4.6 ± 2.6 (31)	2.8 ± 2.4 (16)	1.1 ± 2.5 (44)
	♀	4.8 ± 4.5 (22)	5.9 ± 2.6 (26)	4.5 ± 3.4 (36)	2.9 ± 2.1 (16)	0.9 ± 2.5 (12)
Bill (mm day^{-1})	♂	0.17 ± 0.07 (23)	0.17 ± 0.08 (25)	0.14 ± 0.07 (25)	0.08 ± 0.04 (14)	0.03 ± 2.5 (47)
	♀	0.17 ± 0.08 (15)	0.17 ± 0.04 (25)	0.16 ± 0.11 (35)	0.11 ± 0.03 (15)	0.04 ± 0.02 (15)

a)

b)

Figure 2. Growth rates (± SD) of kiwi as measured by a) weight (g day $^{-1}$) and b) bill length (mm day $^{-1}$) in relation to age, as measured in days after hatching.

day 91 and day 110, and by another 50% between day 111 and day 130. From day 130 onwards, juveniles had negligible predation risk (0.008% day^{-1}), similar to that of adults (0.007% day^{-1}).

Predation risk in relation to chick mass

Stoats were definitely responsible for 28 (88%) of the 32 confirmed predation losses. Only two (7%) of their victims exceeded 700 g at the time of death, and none exceeded 800 g, suggesting that chicks cease to be
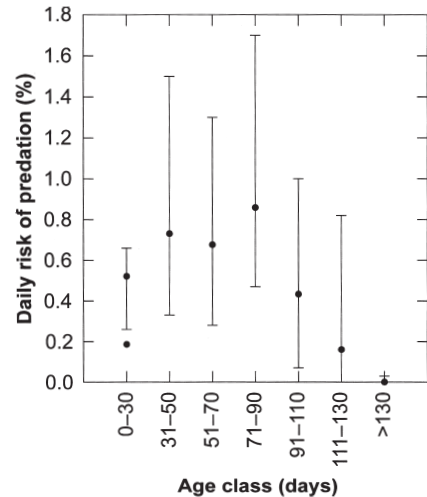

Figure 3. Daily mortality rates (± 95% confidence intervals) of young kiwi in relation to age. Two points are shown for dependent kiwi less than 31 days old. The lower estimate is derived solely from confirmed predation losses; the upper estimate includes the probable predation loss of nine untagged chicks that disappeared from their nests before they were old enough to fledge.

vulnerable to stoats once they reach this weight (Fig. 4). Ferrets were responsible for the deaths of two juveniles (445 g and 900 g) and a cat for another one (320 g). We could not determine with confidence whether a cat or a mustelid caused the remaining death (580 g).

On the basis of exposure, kiwi heavier than 800 g (n = 31) were expected to suffer 20.3 fatalities, significantly more than the one observed (Kolmolgorov-Smirnov goodness-of-fit test; $D = 0.591$, $P < 0.001$). The distribution of kills amongst juveniles up to 800 g conformed to the random expectation (Kolmolgorov-Smirnov goodness-of-fit test; $D = 0.074$, $P > 0.05$) even though predation losses in the 601–700 g category appeared to be unusually high. The risk of being killed by stoats therefore declined abruptly as juveniles increased in weight from 750 g to 800 g, and the status of individuals changed from 'vulnerable' to 'safe' over just two or three weeks.

Discussion

Growth and development of kiwi

North Island brown kiwi have a mode of development that is near the extreme end of precociousness. The chicks hatch fully-feathered, with their eyes open.
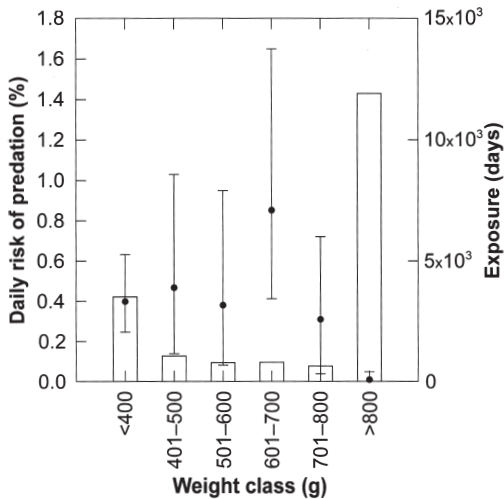
Figure 4. Daily mortality rates ± 95% confidence intervals (left axis) and number of days that juveniles were exposed to predators (right axis) in each of six different weight classes.

They receive no food from their parents, apart from a residual store of yolk, absorbed from the egg just prior to hatching. The chicks begin to make foraging trips out of the nest within a week of hatching, and become independent (fledge) at 10–16% of adult weight. After fledging they have no further contact with their parents, and, in this respect, differ from the offspring of all other extant ratites [emus and cassowaries, Casuariiformes; rheas, Rheiformes; and ostriches, Struthioniformes (Handford and Mares, 1985)] and most other precocial species. In terms of development, their closest non-congeneric counterparts appear to be the Megapodidae, whose young are on their own from the time they hatch (Ricklefs, 1968).

    Among birds, the young of large species generally require more time to attain adult size than those of small species, and young which are fed by their parents grow more rapidly than those which feed themselves (Ricklefs, 1968). North Island brown kiwi conform to these general trends, but are remarkable for their slow rates of growth and prolonged period of juvenile development. In Galliformes and Rallidae (precocial species with young that feed themselves) values of the growth rate constant K_G derived from the Gompertz equation (see Ricklefs, 1967 and 1968) are typically about 0.025 in species with an adult body size of 2500 g (Ricklefs, 1973). The K_G value for kiwi in this study was 0.006[1] derived from growth rates that are similar to those recorded in other parts of its range (H. Robertson, Department of Conservation, Wellington, *pers. comm.*). Kiwi therefore grow at about 1/4th of the rate predicted by allometric regression,

and, incredibly, take longer (511 days) to grow from 10% to 90% of asymptote weight[2] than do emus (adult weight of 30–45 kg; O'Brien, 1990) and ostriches (100–150 kg; Folch, 1992). Kiwi also grow about three times slower than the megapods, whose K_G values (about 0.016) conform to allometric predictions (Ricklefs, 1973). Kiwi are well known for being distinctive, mainly because many of their reproductive and physiological parameters more closely resemble those of mammals than birds (Reid and Williams, 1975; Calder, 1978). Mammals typically grow more slowly than birds (Taylor, 1965) so clearly kiwi are mammal-like in this respect too. Indeed, relative to adult weight, kiwi appear to be the slowest growing of all known birds.

    So why do kiwi grow and develop so slowly when life-history theory (West *et al.*, 2001) predicts they should grow at the fastest rate possible within physiological constraints? We believe the answer lies in their unusual evolutionary history, which, we suggest, has been driven mainly by energetic considerations rather than predator avoidance.

    Growth rates are subject to contrasting selective pressures. Slow growth reduces daily energy demands, but (usually) prolongs development. Fast growth is beneficial if it reduces predation risk, as in North American passerines (Remes and Martin, 2002), but is both energetically and physiologically demanding. Among other things, it increases the risks of nutrient deficiency during development, which can have permanent and profound effects on metabolism, disease resistance, sexual attractiveness in adulthood, and lifespan (Lindstrom, 1999; Metcalfe and Monaghan, 2001).

    Kiwi had few selective pressures for fast growth throughout their long evolutionary history. For some 80% of the Tertiary period, the landscape was dominated by infertile, long-lived vegetation types with low levels of productivity (Lee *et al.*, 2001). Kiwi 'avoided' New Zealand's diverse array of large, diurnal, avian predators (Holdaway *et al.*, 2001) by being

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[1] Conversion factors for the Gompertz equation, derived from the appendix in Ricklefs (1967), were linearly related to age over the range of 15 to 800 days, with an asymptote (A) of 2000 g. The slope (dW_t/dt) of the regression was 0.00222, giving a K_G value of 0.006, derived from the equation $K_G = 2.72 \times dW_t/dt$. It should be noted that the period following hatching in which chicks absorb yolk and lose weight was ignored in the calculation, to improve the fit of the curve. If it had been included, the K_G value would have been even lower still.

[2] The time interval for growth from 10 to 90% of the asymptote was calculated by the formula

$$t_{10-90} = (C_{90} - C_{10})/ \, dW_t/dt$$

where C_{90} and C_{10} are conversion factors for the Gompertz equation (Ricklefs, 1967)

nocturnal, cryptically-coloured and secretive. They had few, if any, nocturnal predators to contend with. The largest owl (*Sceloglaux albifacies*), at 600 g, was still too small to prey on young kiwi; it fed mainly on lizards, and small birds weighing 100–250 g (Worthy, 2001). So benign were the forests at night that young kiwi could fledge at one-tenth of adult weight and wander without parental protection; and adult females, burdened at times with a 450-g egg, could still walk about without additional predation risk (Gould, 1986). Life-history traits were free to develop, almost without compromise, in ways that minimised energy requirements for maintenance, growth and reproduction. And in kiwi, they developed as a package: flightlessness; low metabolic rate; small clutch size; slow growth, prolonged juvenile development; relatively small body size; and a very long adult lifespan. The exceptionally large and energy-rich eggs of kiwi (Reid, 1971) are undoubtedly an exception to the overall pattern, but, paradoxically, females probably produce them at little additional energetic cost. Females draw as much as half of the energy needed for each egg from stored reserves, accumulated gradually in the months before laying (McLennan, 1988), and the actual process of yolk deposition is prolonged, at 25–30 days (Calder, 1979). Overall, the ratio of clutch weight to female weight in brown kiwi (31%) is much higher than that in weka (about 20%) and takahe (*Porphyrio mantelli*) (about 6%), but is similar to or lower than that in many other relatively large species with precocial young, e.g. blue duck (*Hymenolaimus malacorhynchos*) (58%), shelduck (*Tadorna tadornoides*) (60%), black swan (*Cygnus atratus*) (30%) and pheasant (*Phasianus colchicus*) (38%).

Safe size and prey/predator size ratio

Juvenile kiwi ceased to be vulnerable to stoats when they attained a weight of 800 g, 97–166 days after hatching. For individuals that go on to become breeding adults, the first five months of existence would normally comprise just 2% of total life (20 years); and it seems incongruous that a species with such a brief period of vulnerability should now be threatened with extinction in mainland habitats (McLennan *et al*., 1996).

The differences in the shapes of the curves in Fig. 3 and Fig. 4 suggest that it was weight itself, or one of its correlates (such as strength), that conferred safety. Age was related to predation risk only because it took time for juveniles to reach the safe weight of 800 g. Even so, the shape of Fig. 4 is puzzling, and we cannot explain why such a small increase in juvenile weight (from 750 to 800 g) should so profoundly reduce vulnerability. We expected instead that risk would decline gradually, on the basis that the stoats themselves vary in size.

Male stoats are 57% heavier on average than females (mean = 324 g and 207 g respectively) and young of the year are generally lighter than fully-mature adults (King, 1990). If 800-g kiwi juveniles are safe when they are 2.5 times heavier than the average male stoat, then 520-g juveniles should be safe from most female stoats, assuming that the prey-to-predator size ratio is similar for both sexes. Whatever the exact ratio, juvenile kiwi must 'outgrow' small stoats to begin with, and then the larger ones later on; the process probably takes weeks, rather than days. (The expected trend is evident in Fig.4 if the measurement relating to juveniles in the 601-700 g class is dismissed as an outlier. Mortality in this class was influenced substantially by four deaths in an isolated and late-season predation event that occurred in one year only. A single animal may have been responsible for all of the deaths. However, in our view, the event cannot be dismissed simply because it was rare).

The same reasoning applies to ferrets, which are also sexually dimorphic (Daniel and Baker, 1986). Ferrets undoubtedly encounter adult kiwi much more often than they kill them. If ferrets, like stoats, are incapable of killing kiwi 2.5 times heavier than themselves, then only male ferrets exceeding 900–1000 g would be capable of killing adult kiwi. Males of this size are common in agricultural and coastal landscapes, but are relatively rare in North Island forests (Clapperton, 2001). Ferret predation on kiwi is episodic in forest habitats (McLennan *et al.,* 1996) perhaps because, for most of the time, males big enough to kill adults either settle for easier prey or are simply not there.

Robustness of the estimate of safe-size

Despite our findings, juveniles heavier than 800 g do not have a zero risk of stoat predation all of the time. In Northland, for example, stoats have killed two kiwi weighing about 800 g, and another weighing 1160 g (H. Robertson, Department of Conservation, Wellington, *pers. comm.*). In Tongariro forest, a stoat was blamed for the death of a juvenile that was raised to a minimum weight of 1000 g in captivity before being released into the wild (M. Potter, Massey University, *pers. comm.*).

In any locality, safe-size will vary with stoat size. None of the stoats caught during our study at Waikaremoana exceeded 430 g (McLennan *et al. unpubl.*) but males as heavy as 500 g have been recorded infrequently elsewhere (L. Robbins, Massey University, *pers. comm.*). Such animals must be capable of killing 1100-g juveniles, and may be responsible for all of the fatalities referred to above.

Sex ratio of remnant populations

One of the features of remnant kiwi populations is that

there is no consistent bias in adult sex ratio, in part because both sexes have similar rates of adult mortality (McLennan *et al*., 1996). The results of this study also show that there is no gender filter early on in life; both sexes grow at identical rates during their first 20 weeks, so have the same chance of reaching the safe size of 800 g. Kiwi therefore differ from most other threatened forest birds, in which differential predation on nesting females causes effective population size to decline more quickly than actual population size (e.g. Wilson *et al.,* 1998; Innes *et al*. 1999).

Slow growth as a factor influencing predation risk

Our results suggest that slow juvenile growth is the main reason why brown kiwi fail in the presence of uncontrolled stoat populations. If kiwi grew at the same rate as the megapods ($K_G = 0.016$), they would take approximately 44 days, rather than 110 days, to reach the safe size of 800 g (i.e. to grow from 10% to 40% of asymptote weight). With daily rates of predation loss of 0.85% per day, a 66-day reduction in exposure would decrease predation losses from 61% (about current levels) to 31%, and increase recruitment rates to levels that allowed populations to maintain themselves (McLennan *et. al*., 1996). In kiwi then, it is rates of development, rather than *K* selection *per se*, that determine vulnerability to mammalian predators. The same may be true of other New Zealand birds.

The demise of little spotted kiwi

Little spotted kiwi (*Apteryx owenii*) is the smallest of the four (Baker, *et al.,* 1995) or five (Holdaway *et al.,* 2001) species of kiwi. They were widespread and abundant on the western side of the South Island at the start of the 20th century, but have since declined, and are now probably extinct on the mainland (Heather and Robertson, 1996). Their decline was much faster than that of the larger kiwi; in the space of just a few decades, they changed from being the most abundant of all kiwi, to the rarest. Our results suggest that it was the little spotted kiwi's small size, and patterns of growth, that contributed to its rapid demise.

As mature adults, both male (1150 g) and female (1325 g) little spotted kiwi exceed 800 g, and are therefore probably too large for most stoats to prey upon. The juveniles grow for at least 30 months (Heather and Robertson, 1996) so appear to develop at much the same rate as brown kiwi. In little spotted kiwi, the safe size of 800 g is 70% of average male weight, whereas in brown kiwi it is 39% of male weight. If both species 'scale' at the same rate (i.e. they take the same time to accomplish the same proportion of total growth), little spotted kiwi would take 309 days to reach safe-size, compared with 110 days in brown kiwi.

An additional 199 days of exposure to stoats is highly significant. If average predation rates were at the low end of the scale (e.g. 0.5% per day), an annual cohort of chicks would halve in number every 137 days and 79% of the chicks would be killed before they reached an age of 300 days. With a higher rate of predation (say 0.8% per day), the halving time would decline to 86 days and predation mortality over 309 days would increase to 90%. Of course, some juveniles would die for other reasons, so total mortality in both instances would be close to 100%.

It therefore appears likely that catastrophic recruitment failure led to the extinction of little spotted kiwi in mainland forests. In each locality, the process of decline probably lasted about 40–50 years, beginning with the arrival of stoats, and ending with the deaths of the last adults. The occasional juvenile that defied the odds and reached adulthood would have done little to arrest the decline, but may have prolonged the time to extinction.

Amongst the larger kiwi, differences in rates of decline are also correlated with variations in body size and exposure times during the juvenile phase of development. Thus, great spotted kiwi (*Apteryx haastii*) in sub-alpine areas of north-west Nelson are faring much better than brown kiwi in the North Island (25–30% difference in comparative size) and slightly better than their smaller counterparts in lowland forests (15% difference in mean size; McLennan and McCann, 2002). However, it is not yet clear whether these correlations are causal, or merely a consequence of regional and habitat differences in predator abundance.

Implications for conservation managers

When stoats were released in the mid-1880s, conservationists rightly expressed concerns about their probable impacts on flightless birds (King, 1984). Yet if they had known then that the larger kiwis would be vulnerable to stoats for just 2% of their life, they might have been less vociferous in their opposition. At one level then, the results show how difficult it is to predict the potential impact of any novel predator in a system, and how even incredibly brief periods of intense predation can at times lead to extinction. The results also suggest it is unwise to assume that closely-related species have similar predation risks: vulnerability, and ultimately population persistence, can change markedly with seemingly small and inconsequential differences in biology (such as time to reach safe size).

As McLennan *et al.* (1996) point out, the decline of North Island brown kiwi in mainland forests can be halted by ensuring that 20% of young kiwi survive the three-year journey to adulthood. In practice, this means nursing chicks through their first 20 weeks of life, by

reducing their exposure to stoats (Basse *et al.,* 1999), then leaving them to look after themselves for the next 20–40 years. This form of management has now been applied for 8 years at Waikaremoana. We will describe elsewhere how kiwi have responded to it at a population level.

Acknowledgements

References

Baker, A.J.; Daugherty, C.H.; Colbourne, R.; McLennan, J.A. 1995. Flightless brown kiwis of New Zealand possess extremely subdivided population structure and cryptic species like small mammals. *Proceedings of the National Academy of Science, USA 92:* 8254-8258.

Basse, B.; McLennan, J.A.; Wake, G.C. 1999. Analysis of the impact of stoats, *Mustela erminea,* on northern brown kiwi, *Apteryx mantelli,* in New Zealand. *Wildlife Research 26:* 227-237.

Beauchamp, A.J.; van Berkum, B.; Closs, M.J. 1998. The decline of the North Island weka (*Gallirallus australis greyi)* at Parekawa Bay, Bay of Islands. *Notornis 45:* 31-43.

Calder, W.A. 1978. The kiwi. *Scientific American 239:* 102-110.

Calder, W.A. 1979. The kiwi and egg design*:* evolution as a package deal. *Bioscience 29:* 461-467.

Clapperton, B.K. 2001. Advances in New Zealand mammalogy 1990–2000: Feral ferret. *Journal of the Royal Society of New Zealand 31:* 185-203.

Daniel, M.; Baker, A. 1986. *Collins guide to the mammals of New Zealand.* Collins, Auckland,

N.Z.

Folch, A. 1992. Family Ostrich. *In:* del-Hoyo, J.; Elliot, A.; Sargatal, J. (Editors), *Handbook of birds of the world* Vol. 1, pp. 76-83. Lynx-Edicions, Barcelona, Spain.

Gould, S.J. 1986. Of kiwi eggs and the Liberty Bell. *Natural History 90:* 20.

Handford, P.; Mares, M.A. 1985. The mating systems of ratites and tinamous: an evolutionary perspective. *Biological Journal of the Linnean Society 25:* 77-104.

Heather, B.; Robertson, H. 1996. *The field guide to the birds of New Zealand.* Viking, Auckland, N.Z.

Holdaway, R.N. 1999. Introduced predators and avifaunal extinction in New Zealand. *In*: MacPhee (Editor), *Extinctions in near time*, pp. 189-237. Kluwer, New York, U.S.A.

Holdaway, R.N.; Worthy, T.H.; Tennyson, A.J.D. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology 28:* 119-187.

Innes, J.; Hay, R.; Flux, I.; Bradfield, P.; Speed, H.; Jansen, P. 1999. Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biological Conservation 87:* 201-214.

King, C.M. 1984. *Immigrant killers.* Oxford University Press, Auckland, N.Z.

King, C.M. 1990. Stoat. *In:* C.M. King (Editor), *The handbook of New Zealand mammals,* pp. 288-312, Oxford University Press, Auckland, N.Z.

Lee, D.E.; Lee, W.G.; Mortimer, N. 2001. Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany 49:* 341-356.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution 14:* 343-347.

McLennan, J.A. 1988. Breeding of North Island brown kiwi, *Apteryx australis mantelli,* in Hawke's Bay, New Zealand. *New Zealand Journal of Ecology 11:* 89-97.

McLennan, J.A.; Potter, M.A. 1992. Distribution, population changes and management of brown kiwi in Hawke's Bay. *New Zealand Journal of Ecology 16:* 91-102.

McLennan, J.A.; McCann, A. 2002. Genetic variability, distribution and abundance of great spotted kiwi (*Apteryx haastii*). *In:* Overmars, F. (Editor), *Some early 1990s studies in kiwi (Apteryx* spp.) *genetics and management,* pp. 35-55. Science and Research Internal Report 191, Department of Conservation, Wellington, N.Z.

McLennan, J.A.; Potter, M.A.; Robertson, H.A.; Wake, G.C.; Colbourne, R.; Dew, L.; Joyce, L.; McCann,

A.J.; Miles, J.; Miller, P.J.; Reid, J. 1996. Role of predation in the decline of kiwi, *Apteryx* spp., in New Zealand. *New Zealand Journal of Ecology 20:* 27-35.

Metcalfe, N.B.; Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution 16:* 254-260.

O'Brien, R.M. 1990. *Dromaius novaehollandiae* Emu. *In*: Marchant, S.; Higgins, P.J. (Editors), *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1a, ratites to petrels,* pp. 47-58, Oxford University Press, Melbourne, Australia.

Reid, B.; Williams, G.R. 1975. The kiwi. *In:* Kuschel, G. (Editor), *Biogeography and ecology in New Zealand,* pp. 301-330. Junk, The Hague, The Netherlands.

Remes, V.; Martin, T.E. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution 56:* 2505-2518.

Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology 48:* 978-983.

Ricklefs, R.E. 1968. Patterns of growth in birds. *Ibis 110:* 419-451.

Ricklefs, R.E. 1973. Patterns of growth in birds II. Growth rate and mode of development. *Ibis 115:* 177-201.

Reid, B. 1971. Composition of a kiwi egg. *Notornis 18*: 245-249.

Taylor, St. C.S. 1965. A relationship between mature weight and time taken to mature in mammals. *Animal Production 7:* 203-220.

West, G.B.; Brown, J.H.; Enquist, B.J. 2001. A general model for ontogenetic growth. *Nature 413:* 628-631.

Wilson, P.R.; Karl, B.J.; Toft, R.J.; Beggs, J.R.; Taylor, R.H. 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation 83:* 175-185.

Worthy, T.H. 2001. A fossil vertebrate fauna accumulated by laughing owls (*Sceloglaux albifacies)* on the Gouland Downs, northwest Nelson, South Island. *Notornis 48:* 225-233.