

Landscape-scale trapping of stoats (*Mustela erminea*) benefits tokoeka (*Apteryx australis*) in the Murchison Mountains, Fiordland, New Zealand

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Abstract A 15,000 ha low-intensity stoat (*Mustela erminea*) trapping network was established in the Murchison Mountains in 2002, primarily to protect the last natural population of the critically endangered takahe (*Porphyrio hochstetteri*). We compared the productivity and survival of threatened southern brown kiwi or tokoeka (*Apteryx australis*) living in 3 valleys that were covered by this trapping network with those in a nearby valley that was left untreated. Chick survival to 6 months old was significantly higher in the trapped areas (37%) than in the untrapped area (19%). This doubling of chick survival was sufficient to change the rate of population growth, as derived from Leslie matrix analyses, from a projected decline of 1.6% per annum without management to a projected increase of 1.2% per annum with trapping.

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INTRODUCTION

Birds that have evolved on islands in the absence of mammalian predators typically have structural, behavioural or life-history traits that leave them especially vulnerable to predation by introduced mammals (e.g. flightlessness, ground-nesting and low productivity). Since humans and their associated mammalian predators arrived in New Zealand about 750 years ago (Wilmshurst et al. 2011), 51 species of birds have become extinct (Robertson et al. 2013) and many other species have

declined dramatically – currently 57 (68%) of 84 endemic bird species are classified as ‘Threatened’ (BirdLife International 2015).

The first wave of bird extinctions in New Zealand took place soon after the arrival of Maori colonists from Polynesia, who hunted birds, brought dogs/kuri (*Canis familiaris*) and Pacific rats/kiore (*Rattus exulans*) with them, and burned large areas of forest and dry scrub. By the time of first European contact about 250 years ago, 36 bird species were already extinct, including the complete radiation of 10 moa species (Robertson et al. 2013). A second wave of 15 extinctions followed European colonisation as a result of the massive loss of forest

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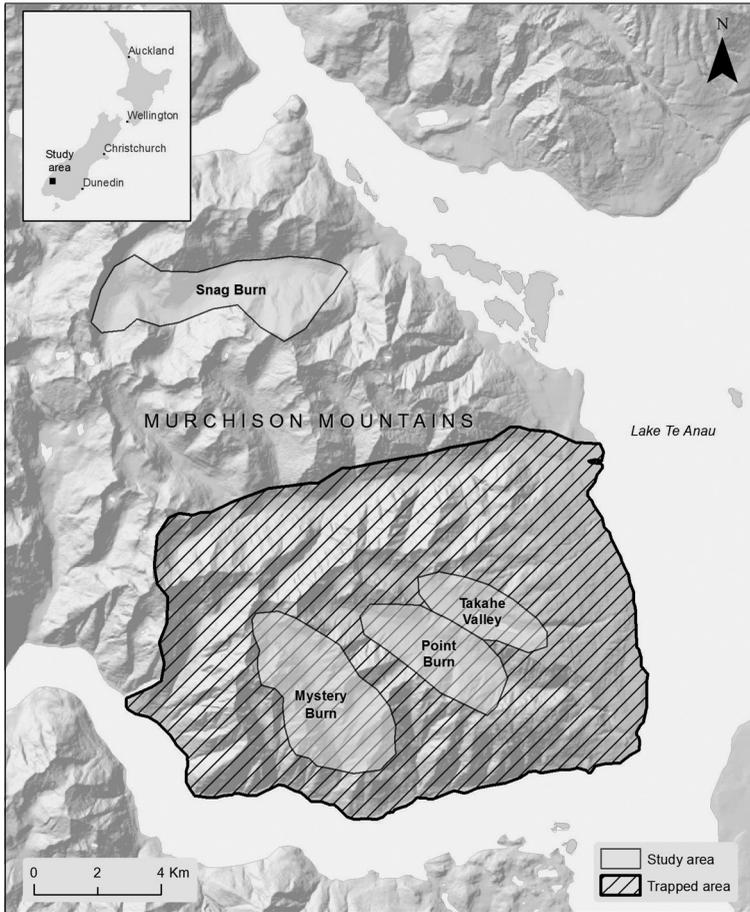


Fig. 1. Map of the Murchison Mountains showing the 4 study sites in relation to the 15,000 ha area in which stoats were trapped.

and wetland habitats, hunting and collecting and, most importantly, the introduction of a new suite of mammalian predators, including cats (*Felis catus*), Norway rats (*Rattus norvegicus*), ship rats (*R. rattus*), ferrets (*Mustela furo*), stoats (*M. erminea*) and weasels (*M. nivalis*).

The southern brown kiwi or tokoeka (*Apteryx australis*) is a flightless, nocturnal bird that is confined to the mountains just south of Haast, in Fiordland from the Hollyford Valley to Preservation Inlet, and on Stewart Island (Heather & Robertson 2015). In 2008, the total population was estimated at c.30,000 birds, of which about half were in Fiordland (Holzapfel *et al.* 2008). The Fiordland population of tokoeka has a threat ranking of 'Nationally Vulnerable' (Robertson *et al.* 2013) based on an assumed decline of 2% per annum (Holzapfel *et al.* 2008), which equates to a 60% decline over 3 generations (45 years).

The main threat to kiwi populations on the mainland of New Zealand is predation by introduced mammals, especially dogs, ferrets, stoats, and cats (McLennan *et al.* 1996; Robertson

et al. 2011; Robertson & de Monchy 2012). In the absence of predator control, only about 6% of kiwi chicks survive to reach adulthood (Robertson *et al.* 2011). Once kiwi reach approximately 1 kg at 6–8 months old, stoats and cats no longer pose a serious risk to them; however, dogs and ferrets kill many subadult and adult birds (McLennan *et al.* 1996; Robertson *et al.* 2011), and are the critical predators in some parts of New Zealand (Robertson *et al.* 2011). In Fiordland, predation of tokoeka chicks by stoats is likely to be the main threat to the long-term viability of the species because cats, dogs and ferrets are scarce or absent, and most of their habitat is protected within Fiordland National Park.

Landscape-scale trapping of stoats has had variable success in protecting kiwi, being very effective in some areas but not others (Robertson & de Monchy 2012). In 2002, a landscape-scale (15,000 ha), but low-intensity stoat trapping programme (1 double-set trap box per 21 ha, checked and re-baited quarterly) was established in the very rugged terrain of the Murchison Mountains to help protect the last natural population of the critically endangered

takahe (*Porphyrio hochstetteri*) (Hegg *et al.* 2012). We investigated whether this stoat trapping programme also affected the population dynamics of tokoeka by comparing their population parameters in 3 valleys in which stoats were trapped with those in an untreated valley about 12 km away.

METHODS

Study area

The Murchison Mountains (45° 14' S, 167° 34' E) are a peninsular range located east of the main divide between the South and Middle Fiords of Lake Te Anau, Fiordland (Fig.1). Following the rediscovery of takahe in the Murchison Mountains in 1948, the entire 51,000 ha peninsula was designated as the Murchison Mountains Special (Takahe) Area. This designation strictly limits public access, despite the area being located in Fiordland National Park.

The Murchison Mountains have an altitudinal range from 204 m at the shore of Lake Te Anau to 1905 m at Mt Lyall. The mountainous area is dissected by rugged forest-clad river systems. The temperate rain forest consists predominantly of silver beech/tawhai (*Lophozonia menziesii*) with red beech/tawhairunui (*Fuscospora fusca*) in the lower valleys. Higher-altitude sites are covered in mountain beech/tawhairauiki (*F. solandri* var. *cliffortioides*) with pockets of southern rata (*Metrosideros umbellata*) on well-drained ridges and spurs. Open areas of the valleys consist of fuchsia/kotukutuku (*Fuchsia excorticata*), mountain ribbonwood/houhere (*Hoheria lyallii*) and mountain holly/hakeke (*Olearia ilicifolia*).

Approximately 60% of the Murchison Mountains area is covered in forest. The remaining area includes low-alpine snow tussock grasslands above the tree-line (c. 1100 m asl) through to high-alpine fellfields (c. 1500 m asl). At lower altitudes, the tall tussock grasses *Chionochloa pallens*, *C. flavescens* and *C. crassiuscula* are in abundance, while at higher altitudes, shorter tussocks, low scrub, cushion plants, lichens, mosses and prostrate herbs predominate. Permanent snow and ice fields and bare rock are found on the higher peaks.

Predator control

A large-scale stoat trapping network covering 15,000 ha or 30% of the Murchison Mountains (Fig.1) was established in 2002, primarily to protect takahe (Hegg *et al.* 2012). The intention was that trap lines would be less than 2 km apart throughout the area; however, this distance was exceeded in some places due to difficult terrain. Traps were serviced quarterly (in August, November, February and May) and baited with a hen's egg and rabbit meat.

From 2002 to 2008, 720 double-set trap boxes were operational (an average density of 1 trap box per 21 ha). Due to their success in helping to protect

adult and young takahe (Hegg *et al.* 2012), a further 1025 double-set trap boxes were added in 2008/09 to cover the entire 51,000 ha peninsula, giving a total of 1745 trap boxes at an average density of 1 box per 29 ha. Since 2015, the trap density has been doubled to an average density of 1 box per 14 ha (Chris Birmingham, *pers. comm.*). This is a slightly lower intensity compared with many other stoat trapping programmes in New Zealand, but is the largest stoat control programme in the world and a remarkable achievement given the very difficult terrain.

Study sites

We monitored tokoeka in 3 treatment sites located in the stoat trapping area. The first site to be monitored was the Mystery Burn (45° 18' S, 167° 35' E), starting in 2003. Monitoring was then extended to the Point Burn (45° 17' S, 167° 38' E) and Takahe Valley (45° 17' S, 167° 39' E) in 2006 and 2007, respectively. The observed pairs were spread over approximately 1400 ha at 700 – 1300 m asl. We also monitored an untrapped area, the Snag Burn (45° 11' S, 167° 32' E), starting in 2004. At this site, pairs were spread over 1600 ha at 400 – 1300 m asl. At all sites, we monitored chick survival until the end of the 2008/09 season, at which time trapping was extended across the entire peninsula and so the non-treatment site became subsumed within the trapped area. We also monitored adult and subadult (>6 months old) survival at all study sites until early 2012.

Field methods

We mainly captured adult kiwi at night by hand or in hand-nets after luring them in by playing recorded calls or imitating their calls with shepherd's whistles. Some adults were caught during the day after locating them with certified kiwi-detection dogs, or finding them sharing a den with their radio-tagged partner. Males were the primary target because they do most of the daytime incubation and so allowed nests to be found.

We sexed birds based on their weight and bill length, and banded them. We also attached a miniature (22 g) Kiwitrac mortality transmitter to the tibia of each male using a plastic hospital baby band and electrical tape (Miles & McLennan 1998). From 2007 onwards, we used transmitters with the additional 'Egg Timer™' function developed by Wildtech NZ Ltd, which reports the length of incubation undertaken since detecting the change in activity patterns of males when they begin incubation.

During the breeding season, we checked males weekly by triangulating their position. If a male was stationary for 3 consecutive weeks, it was considered to potentially be incubating an egg. These males were then checked during the day and either the egg was seen or felt under the

incubating male to confirm breeding. After 'Egg Timer' transmitters were introduced, we used that incubation information in conjunction with nest inspections to confirm breeding activity. Following the failure of some nests as a result of predation or suspected predation by kea (*Nestor notabilis*), we marked nests with a concealed transmitter rather than with flagging tape. A small infrared camera was located near the burrow entrance to detect the first emergence of the chick from the nest burrow. The following day or evening, we caught the chick by hand in the nest or as it emerged. We inspected failed nests to determine the causes of failure.

We fitted each chick with a 10.5 g Kiwitrack tibia-mounted mortality transmitter (Miles & McLennan 1998) at about 8 days old (range 2-10 days). We monitored survival remotely at approximately weekly intervals, and also whilst changing the leg harness every 4-6 weeks. Once juveniles reached 800 g at about 4 months old, we fitted them with a more powerful 13 g mortality transmitter. From 6 months old, when subadults typically weighed about 1000 g and so were safe from stoat predation, we checked on them monthly, and changed their transmitter at 6-month intervals.

Analysis

We developed population matrix models for the trapped and untrapped areas using PopTools, a Microsoft Excel add-in. Age at first breeding was estimated to be 4 years old, based on other kiwi studies (Robertson *et al.* 2011; Robertson & deMonchy 2012), and so we used a 5 x 5 matrix. PopTools calculated an intrinsic rate of population growth, λ , which was then converted to a percentage annual change, r . A sensitivity matrix was also calculated to determine the contribution that a small fixed change to each matrix element made to the overall model, allowing the key factor impacting on population growth to be identified.

Because we followed mainly radio-tagged males, adult productivity was calculated as the number of eggs per radio-tagged male per year. Based on our observations, tokoeka appeared to be monogamous and to have an even sex-ratio. We calculated hatching success from all 105 nesting attempts as the number of chicks hatched relative to the number of eggs laid, regardless of whether the egg was actually seen.

The Kaplan-Meier procedure (Robertson & Westbrooke 2005) was used to calculate the survival rate of chicks from hatching to 1 year old. We also noted survival to 6 months old (183 days) as this is a commonly used metric in kiwi studies because at about this age all but little spotted kiwi (*Apteryx owenii*) weigh approximately 1 kg and become safe from stoat predation. We assumed that chicks were radio-tagged at about 8 days old, when they

were starting to emerge from their nest burrow at night, unless we had more precise information about their age from their stage of development or earlier sightings on cameras. We assumed that 3 untagged chicks that left probe holes at the burrow entrance died at about 8 days old, but the other 5 chicks that died before they could be radio-tagged did so at 4 days old; errors in these estimates made no difference to the overall survival estimates. We compared chick survival in the trapped and non-trapped areas using the Mantel-Haenszel statistic, a log-rank test (Robertson & Westbrooke 2005).

Subadult survival from 6 months old through to 4 years old was based on pooled samples from the trapped and non-trapped areas, with the assumption that these subadults were safe from stoat predation and that risks of natural mortality were similar throughout the entire area. To improve the survival estimates, we retained transmitters on as many subadults as possible after we had completed the direct comparison between trapped and non-trapped areas. We also used a staggered-entry design (Pollock *et al.* 1989) to incorporate 4 subadults that were found during the study either by kiwi-detection dogs or when sharing a burrow with a radio-tagged adult, presumably one of their parents. The ages of these 4 subadults were estimated after comparing their bill length and weight with that of known-aged subadults.

Annual survival of adults and life expectancy (and their 95% confidence intervals) were calculated using the Mayfield method (Robertson & Westbrooke 2005). Data were pooled from the trapped and untrapped areas, and we assumed that the mortality rate was constant over time. Because adult mortality has been shown to be the most critical factor in the demography of kiwi populations (Robertson & de Monchy 2012), we improved the survival estimate by retaining transmitters on as many adults as possible for 3 years after completing the direct comparison between trapped and non-trapped areas.

RESULTS

A total of 53 adult males and 22 adult females were captured between May 2003 and March 2012; 3 of these birds (2 males and 1 female) were initially caught as chicks or subadults, and were followed through to adulthood. The higher number of males captured was an artefact of deliberately aiming to catch and radio-tag males rather than a reflection on the sex ratio of the population. Our comparison of breeding productivity and chick survival (Table 1) is confined to the 5 breeding seasons from 2004/05 to 2008/09, when we were able to follow radio-tagged birds in both trapped and untrapped areas. Data on the survival of subadults and adults from before

and after the chick study period were, however, used in our population models.

Productivity

Between 2004/05 and 2008/09, 45 different radio-tagged adult males were followed through a total of 129 complete breeding seasons – an average of 2.9 breeding seasons per male. The sample was split reasonably evenly between trapped areas (24 males over 67 breeding seasons) and the untrapped area (21 males over 62 seasons) (Table 1). Of the 45 males, 34 (76%) were recorded breeding at some stage during the study; however, a significantly higher proportion of males was recorded breeding in the trapped areas than in the untrapped area (92% *cf.* 57%, respectively: $z = 2.69$, $P = 0.007$).

We recorded 105 nesting attempts during the study – 56 in the trapped area and 49 in the untrapped area (Table 1). Overall, 51 pairs (65%) had a single nest each year, and 27 (35%) had 2 nests; none had 3 nests. Birds in the trapped areas were half as likely to re-nest within a season compared with those in the untrapped area (24% *cf.* 48%, respectively: $z = 2.20$, $P = 0.028$), which partially offset the higher percentage of breeding pairs observed in the trapped areas. Because this species has a fixed clutch size of 1 egg (131.0 × 80.8 mm, $n = 7$), this translates into 0.84 eggs associated with each adult male per year in the trapped areas and 0.79 eggs per adult male in the untrapped area. Hatching success was 46% in the trapped areas and 47% in the untrapped area, which, assuming an equal sex ratio among adults (Robertson & deMonchy 2012), gives an overall annual productivity of 0.1940 chicks per adult, or 0.388 chicks per pair, in the trapped areas, and 0.1855 chicks per adult, or 0.371 chicks per pair in the untrapped area (Table 1).

Chick survival

In the trapped area, we recorded 26 chicks between 2004 and 2009, of which 3 died before radio-tagging. Of the 23 remaining chicks, 7 (30%) were killed by stoats, 4 died of unknown causes, 1 was killed by a kea, 1 died from a yolk sac infection and 1 disappeared, leaving at least 9 (35%) of the original 26 to survive to become subadults (> 6 months old). The Kaplan-Meier estimate of survival was 36.7% to 6 months old, and 32.6% to 1 year old (Table 1).

In the untrapped area, we recorded 23 chicks between 2004 and 2009. Five of these chicks died before radio-tagging. Of the 18 radio-tagged chicks, 11 (61%) were killed by stoats and 3 died of unknown causes, leaving 4 (17%) of the original 23 chicks to survive to become subadults. The Kaplan-Meier estimate of survival was 17.4% to 6 months old and 13.0% to 1 year old (Table 1).

Survival of chicks to 6 months old was significantly higher in the trapped areas than in the untrapped area (Mantel-Haenszel log-rank statistic,

Table 1. Life history parameters and population growth rates of tokoeka in trapped and untrapped areas in the Murchison Mountains, Fiordland. Data within each of the 2 columns were specifically measured for that treatment, while data shared across the 2 columns were pooled from the trapped and untrapped areas. Adult sex ratio is assumed to be even, and age at first breeding is assumed to be 4 years, following Robertson & deMonchy (2012).

| Variable | Trapped | Untrapped |
|-----------------------------|---------|-----------|
| No. adult transmitter years | | 213 |
| No. adult deaths | | 8 |
| Annual adult survival (%) | | 96.24 |
| Life expectancy (years) | | 26.6 |
| Adult male breeding seasons | 67 | 62 |
| % adult males bred | 67.00 | 53.23 |
| No. eggs | 56 | 49 |
| No. eggs per adult per year | 0.8358 | 0.7903 |
| % eggs hatched | 46.43 | 46.94 |
| Chicks per adult | 0.1940 | 0.1855 |
| No. chicks radio-tagged | 26 | 23 |
| Chick survival (0-183 days) | 0.3665 | 0.1739 |
| Survival (0-1 year) | 0.3258 | 0.1304 |
| Survival (1-2 years) | | 0.9167 |
| Survival (2-3 years) | | 0.9000 |
| Survival (3-4 years) | | 1.0000 |
| Lambda | 1.0121 | 0.9838 |
| Population growth rate | 1.21% | -1.64% |

$\chi^2 = 4.28$, $P = 0.039$). The survival curves in the 2 treatments diverged after 18 days (Fig. 2), which is at about the stage when chicks permanently left the nest.

Subadult survival

Of the 18 subadults monitored between 2004 and 2011, 14 were first caught as chicks and 4 were caught as subadults. Survival was initially rather poor, with only 86% surviving the period from 6 to 12 months old. The 2 deaths resulted from the birds falling into deep cavities – one bird was retrieved alive from a hole but was treated in the analysis as though it had died because it would not have escaped without assistance; however it was added back into the monitored sample of subadults once it had been rescued and deemed fit to be released. From 12 months of age onwards, survival of subadults was 90-100% per annum (Table 1). One bird was killed by another kiwi at 14 months old, and another died

Table 2. Leslie matrices and corresponding sensitivity matrices for the tokoeka populations in A, trapped areas and B, untrapped areas in the Murchison Mountains, Fiordland. In the Leslie matrices the top right-hand figure is the number of chicks hatched per adult, the subdiagonal figures from left to right represent annual survival of birds aged 0–1, 1–2, 2–3 and 3–4 years, and the bottom right-hand figure is the annual survival of adults. In the corresponding sensitivity matrix, the magnitude of each number reflects the importance that a set change to each variable would make to the overall population growth rate – the higher the value the greater the influence of that variable. In both sensitivity matrices, adult survival is clearly the key factor affecting the growth rate of the kiwi populations.

A. Trapped areas

| Leslie matrix | | | | |
|--------------------|--------|--------|--------|--------|
| 0 | 0 | 0 | 0 | 0.1940 |
| 0.3258 | 0 | 0 | 0 | 0 |
| 0 | 0.9167 | 0 | 0 | 0 |
| 0 | 0 | 0.9000 | 0 | 0 |
| 0 | 0 | 0 | 1.0000 | 0.9624 |
| Sensitivity matrix | | | | |
| 0 | 0 | 0 | 0 | 0.2141 |
| 0.1275 | 0 | 0 | 0 | 0 |
| 0 | 0.0453 | 0 | 0 | 0 |
| 0 | 0 | 0.0462 | 0 | 0 |
| 0 | 0 | 0 | 0.0415 | 0.8358 |

B. Untrapped area

| Leslie matrix | | | | |
|--------------------|--------|--------|--------|--------|
| 0 | 0 | 0 | 0 | 0.1855 |
| 0.1304 | 0 | 0 | 0 | 0 |
| 0 | 0.9167 | 0 | 0 | 0 |
| 0 | 0 | 0.9000 | 0 | 0 |
| 0 | 0 | 0 | 1.0000 | 0.9624 |
| Sensitivity matrix | | | | |
| 0 | 0 | 0 | 0 | 0.1057 |
| 0.1504 | 0 | 0 | 0 | 0 |
| 0 | 0.0214 | 0 | 0 | 0 |
| 0 | 0 | 0.0218 | 0 | 0 |
| 0 | 0 | 0 | 0.0196 | 0.9203 |

of unknown causes at 25 months old. By the time the birds reached 3 years of age, the sample size was reduced to just 6 birds because of these 2 deaths and the failure of transmitters or transmitter harnesses. Three radio-tagged subadults graduated to become adults at 4 years old.

Adult survival

Over 217 transmitter years for 53 adult males and 4 adult females, 8 deaths were recorded – 3 birds drowned in fast-flowing mountain streams, possibly resulting from the collapse of snow bridges, and 5 apparently died of other natural causes. This translates into an annual survival of 96.2% (95% CI: 93.2–98.4%) and a life expectancy of 26.6 years (95% CI: 15–62 years) (Table 1).

Population models

Leslie matrices were developed for the trapped and untrapped areas (Table 2). We assumed that any difference between treatments was due to differences in productivity and chick survival rates, because these were the only variables potentially affected by stoats. In both Leslie matrices, the survival rates of adults and subadults over 1 year old were pooled across treatments to increase the sample size and reduce stochastic variation. The population in the trapped areas was projected to be increasing by 1.21% per annum ($\lambda = 1.0121$) whereas the population in the untrapped area was projected to be declining by 1.64% per annum ($\lambda = 0.9838$) (Table 1). Sensitivity analysis showed that adult survival was the key factor affecting the growth of both populations (0.84–0.92), followed by productivity (0.11–0.21) and survival to 1 year old (0.13–0.15); annual subadult survival rates from 1 to 4 years old had minimal influence on population growth (0.02–0.05).

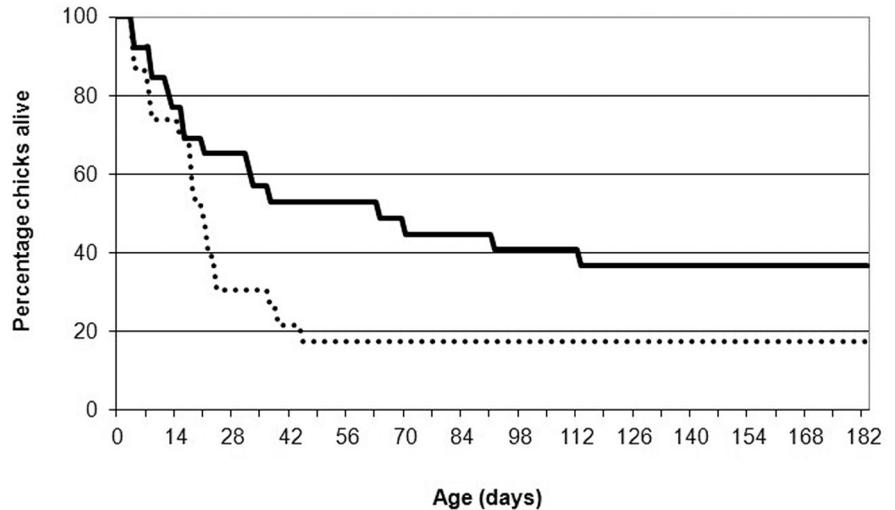
DISCUSSION

There has been a huge reduction in both the range and numbers of unmanaged kiwi populations on the mainland of New Zealand, including tokoeka in Fiordland (Holzapfel *et al.* 2008). It is believed that the decline in tokoeka on the mainland of Fiordland is the result of recruitment failure, primarily as a result of predation of chicks by stoats.

The low-intensity, but extensive stoat trapping programme in the Murchison Mountains was designed primarily to protect takahe. We showed that it also significantly increased the survival of tokoeka chicks to 6 months old compared with a nearby untrapped area. This doubling of chick survival resulted in a projected population increase of 1.21% per annum, compared with a decline of 1.64% per annum in the untrapped area. It should be noted that measurement errors were associated with the various input parameters in the matrices, so the real outcome may not be as clear-cut as this, or the differences may be greater; however, there is support from other studies that these input and outcome values are likely to be reasonably accurate.

The overall productivity figures of approximately 0.41 eggs per adult per year was similar to the 0.48 eggs recorded for rowi (*Apteryx rowi*) and 0.35 for Haast

Fig. 2. Survival of tokoeka chicks to 6 months old (183 days) in trapped areas (solid line) and an untrapped area (dotted line) in the Murchison Mountains, Fiordland.



tokoeka (*Apteryx australis* 'Haast'), both of which also lay 1-egg clutches (Robertson & deMonchy 2012). The number of apparent non-breeders in the untrapped area was extraordinarily high, but this may indicate that a number of breeding attempts failed before nests were detected; for example, one bird was not known to have bred in the 5 seasons over which he was radio-tagged but was found with a brood patch on one occasion. The introduction of 'Egg-TimerTM' transmitters in 2007, which successfully recorded the start of incubation at about one-third of nests based on changes in the behaviour of the male, did not increase the rate of observed breeding attempts, however. The low breeding rate in the untrapped area was compensated for by the much higher rate of re-nesting within a season by the birds that were known to have bred, but it is not clear why this happened.

Hatching success was similar in the trapped and untrapped areas (46% and 47%, respectively), and also similar to that of rowi (48%) but lower than for Haast tokoeka (62%) (Robertson & deMonchy 2012). If significant numbers of early nest failures went undetected, the actual hatching success in the Murchison Mountains may have been lower than we recorded, however. Kea were involved or implicated in a number of nest failures, but this impact was reduced once we stopped marking nests with flagging tape and by ensuring that we did not approach nests while kea were nearby.

The survival of chicks to 6 months old in the trapped areas (37%) was near the middle of a range of values (15–67%) recorded for kiwi chicks in other landscape-scale stoat trapping programmes in New Zealand (Robertson & de Monchy 2012). As in all other studies, stoats were still implicated in the majority of chick deaths, despite the trapping

efforts. Chick survival in the untrapped area (17%) was similar to the 11% recorded in unmanaged parts of Northland (Robertson *et al.* 2011) and the 19% recorded in Tongariro Forest in the season before a 1080 operation in September 2011 (Hugh Robertson *et al.*, *unpubl.*). Stoats were implicated in the majority of deaths of chicks in all 3 studies.

Subadult survival from 6 months to 4 years of age (71%) was in the range of the few values (61–81%) observed or estimated elsewhere (Robertson & deMonchy 2012), but annual adult survival (96.2%) was lower than the 96.7–97.9% observed in 4 of the 5 kiwi sanctuaries, and the 98.4% observed in 63 adult bird years between 2001 and 2005 at a lowland site in the Clinton Valley, 50 km away (Hannah Edmonds, *unpubl.*). This low survival rate was unexpected given that there are no predators of adult kiwi in the Murchison Mountains. It is possible that the harsh conditions, which may have led to several birds drowning when snow bridges collapsed into mountain streams, made up for the lack of predators. Another possibility is that this was an ageing population with a disproportionately high number of very old birds, and few young adults, due to poor recruitment in the decades before stoat trapping began. The low number of breeding birds in the populations may also reflect a senescent population of birds, but to date no research has run long enough to show the effects of old age in wild kiwi.

As expected, sensitivity analysis revealed that adult survival was the key factor affecting the population dynamics of these kiwi populations. Adult survival rates in the Murchison Mountains cannot be increased through conservation management because most, if not all, deaths were from natural causes – unless rejuvenating the population reduces

senescence-related mortality. Rather, the easiest variables for conservation managers to manipulate are hatching success (a component of productivity) and chick survival. Kea are a natural predator of tokoeka eggs, but our initial nest-marking technique probably increased their predation pressure in both the trapped and untrapped areas, resulting in poorer population prognoses than normal. Chick survival rates were significantly higher in the 3 valleys with low-intensity landscape-scale trapping than in the nearby untreated Snag Burn Valley. This single variable tipped the balance between populations that were projected to decline without management to ones projected to increase with trapping. By artificially manipulating chick survival rate in the Leslie matrix and holding all other variables constant, the population of tokoeka in the Murchison Mountains had a positive trajectory if chick survival to 6 months old is above 27.5%. This is considerably higher than the 19% figure calculated by McLennan *et al.* (1996) for brown kiwi (*Apteryx mantelli*), but this is a much more productive species with many 2-egg clutches and a higher rate of re-nesting (Robertson *et al.* 2011).

It is an ongoing challenge for conservation managers to control populations of introduced predators to suitably low levels over sufficiently large areas on the mainland of New Zealand to allow flightless, ground-nesting and low-productivity species, such as kiwi and takahe, to survive and, better still, to regain some of the ground they have lost over the last 125 years since mustelids were introduced. This ambitious, landscape-scale predator trapping programme in the Murchison Mountains, which was aimed primarily at protecting the last remaining natural takahe population, has now been expanded to cover the entire 51,000 ha peninsula. Our results show that this trapping programme should have useful secondary benefits to tokoeka, improving their conservation outlook.

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