

Predator control allows critically endangered lizards to recover on mainland New Zealand

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Abstract: Two conservation tools have been developed over the last 10–15 years for species on the New Zealand mainland that are vulnerable to introduced mammalian predators: landscape-scale predator trapping networks, and eradication of predators within mammal-proof exclosures. We tested whether these tools would allow population growth of critically endangered grand skinks (*Oligosoma grande*) and Otago skinks (*O. otagense*) over three years. Skink populations were subjected to one of three predator treatments: (1) near-eradication inside a mammal-proof fence; (2) suppression by trapping within a 2100-ha area; and (3) unmanaged predator populations. Monitoring by non-invasive photo-resight methods, and data analysis using program MARK, showed that the greatest increase in abundance of both species occurred at the centre of the predator trapping treatment and inside a mammal-proof fence. For grand skinks, there was little or no change in population size at the trapping periphery. At the unmanaged sites, the grand skink population underwent a catastrophic decline whereas the Otago skink population was stable. A grouping analysis showed that the unmanaged grand skink treatment was clearly distinguished from the other predator treatments based on survival rate. Results suggest that: (1) predation by introduced mammals is a key driver in the decline of these skinks, and episodic predation events may be a component of this process; and (2) use of mammal-proof fences or intensive predator control over a large enough area should allow skink populations to recover.

Keywords: conservation; episodic; fence; *Oligosoma*; Otago; predation; recovery; resight; skink; survival

Introduction

Modern conservation efforts in New Zealand have largely focused on the transfer of vulnerable species to, or their retention on, pest-free offshore islands (Saunders & Norton 2001; Connolly 2008; Bellingham et al. 2010). Such methods inevitably exclude species for which there is no equivalent island habitat (Connolly 2008). Over the last 10–15 years, new mainland-specific conservation methods have been developed for New Zealand species that are vulnerable to introduced predators; these comprise the protection of extensive habitat areas by landscape-scale pest-trapping networks (Innes et al. 1999) and the eradication of pests inside pest-proof exclosures (Scofield et al. 2011). Despite the growing popularity of pest-proof exclosures worldwide (Hayward & Kerley 2009), the population response of fauna to these management actions is rarely reported (with some notable exceptions: Moseby & O'Donnell 2003; Richards & Short 2003; Gallacher & Hill 2006; Blick et al. 2008; Watts et al. 2011) and there has been no direct comparison between the efficacy of landscape-scale pest-control techniques and pest-proof fencing to date.

Grand skinks (*Oligosoma grande*) and Otago skinks (*O. otagense*) are two of New Zealand's largest and most critically endangered reptiles (Tocher 2003; Hitchmough et al. 2010). They are saxicolous, being associated with deeply fractured schist rock outcrops (Towns 1985). While broadly syntopic, sharing the same geographical range, grand skinks are more commonly found on ridge tops whereas Otago skinks tend to be associated with gullies (Towns 1985). As yet no equivalent

habitat has been identified on New Zealand's offshore islands. Both species were once found over much of Central Otago, from Lake Hawea in the west to Macraes Flat in the east (Whitaker & Loh 1995). Their apparent decline to about 8% of their presumed former range (Whitaker & Loh 1995) has left both species in relict populations in native tussock grasslands at the extreme east and west of their former range.

Molecular evidence has indicated that while grand skink populations were discontinuous across their range prior to human colonisation, recent declines have been dramatic and probably of anthropogenic origin (Berry & Gleeson 2005). Estimates of total remaining numbers of each species range from 1400 to 5000 (Patterson 1992; Whitaker & Loh 1995; Whitaker 1996; Coddington & Cree 1997). Localised extinctions of both species have been recorded across much of their current range since the mid-1970s (Whitaker & Loh 1995).

The loss of these skink species from the more xeric regions of Otago has been attributed to a history of extremely abundant populations of introduced rabbits (*Oryctolagus cuniculus*) and the diverse suite of introduced mammalian predators that prey upon them (Tocher 2006). In this region rabbits are primary prey for feral cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*Mustela erminea*), and weasels (*Mustela nivalis*), while lizards are secondary prey (King 2005). Other known mammalian predators of lizards within Otago include European hedgehogs (*Erinaceus europaeus*), ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*) and mice (*Mus musculus*) (King 2005; Spitzen - van der Sluijs et al. 2009; Tocher 2009), all of which may also function as competitors of grand and Otago skinks

given that they are all partially insectivorous and frugivorous.

Potential introduced avian threats to grand and Otago skinks include magpies (*Gymnorhina tibicen*), little owls (*Athene noctua*), and starlings (*Sturnus vulgaris*), as well as self-introduced Australasian harriers (*Circus approximans*). In addition to predation, other agents of decline have also been suggested or implicated including vegetation degradation (Whitaker 1996; Tocher 2003), ectoparasites (Reardon & Norbury 2004), demographic stochasticity, and small population effects (Tocher 2009).

Predation by cats and ferrets has been specifically implicated in the decline of grand and Otago skinks at Macraes Flat in eastern Otago (Middlemiss 1995). The effects of trapping of cats and ferrets on the survival of grand and Otago skinks at Macraes Flat were subsequently tested in a 6-year study (Tocher 2006). However, none of the targeted populations of skinks showed evidence of recovery, but instead continued to decline. While Tocher (2006) failed to find evidence that skink survival was influenced by selective predator removal she noted that her statistical power was low. Concern about the rate and magnitude of these declines resulted in the establishment of a concerted skink recovery programme by the Department of Conservation.

In this study, we reassessed predator impacts on remnant grand and Otago skink populations by testing whether the eradication of five mammalian predator species within mammal-proof fences would allow recovery of remnant grand and Otago skink populations, and whether the same result could be achieved by suppression through landscape-scale predator trapping. The success of either management technique would

then implicate mammalian predation as a key factor in the decline of these species.

Methods

Study area

The study sites were in and around reserve land near the township of Macraes Flat (45°25' S, 170°28' E) in eastern Otago (Fig. 1). The area contains extensive rock outcrops of Haast schist at an altitude of 400–600 m. The vegetation is a mosaic of close-cropped introduced grasses, native tussock (*Chionochloa rigida*, *C. rubra*), and mixed shrublands with mānuka (*Leptospermum scoparium*) as the dominant woody species (Bibby 1997). Golden speargrass (*Aciphylla aurea*) and mountain flax (*Phormium cookianum*) are common on the steeper slopes (Bibby 1997).

We used the same general study-site localities as Tocher (2006) (Table 1) because they represented the largest known extant skink populations, and they provided a context for the effectiveness of our new management. Detailed descriptions of the sites are given in Tocher (2003, 2006). Each site (170–630 m in diameter) contained a series of clustered schist outcrops (spread over 1.3–8.6 ha). Site boundaries were defined by where the outcrops became disjunct.

Study design

We conducted the study over three austral-summer periods from January 2006 to March 2008 at six sites (Table 1,

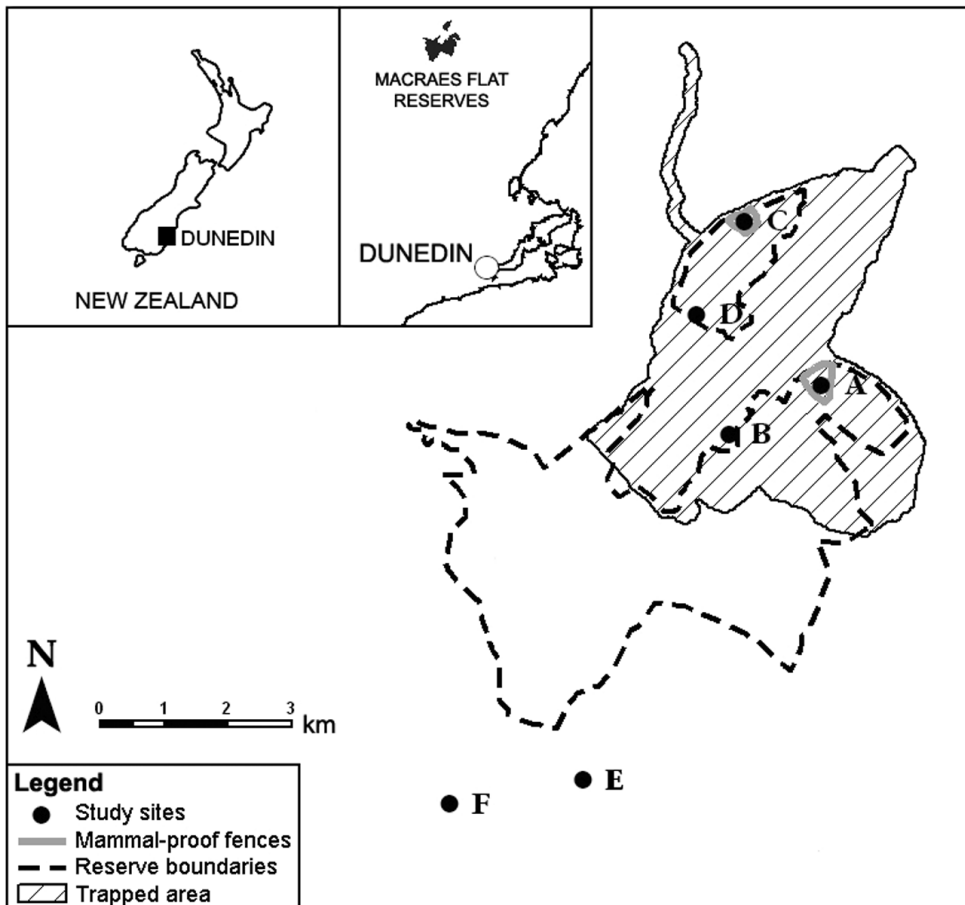


Figure 1. Locations of skink study sites A–F at Macraes Flat, eastern Otago, South Island, New Zealand.

Table 1. Experimental treatments and monitored grand and Otago skink (*Oligosoma grande*, *O. otagense*) populations at each site at Macraes Flat, eastern Otago, New Zealand.

Site	Species	Experimental designation	Number of surveys in austral summer			Site in Tocher (2006)
			2006	2007	2008	
A	Grand and Otago	Mammal-proof fence	5	5	9	D
B	Grand and Otago	Trapping core	5	4	6	C
C	Grand	Trapping periphery then mammal-proof fence	5	4	6	B
D	Grand	Trapping periphery	5	3	4	A
E	Otago	Unmanaged	5	4	5	F
F	Grand	Unmanaged	5	4	2 + 6 ^a	G

^a Surveys pre- and post-stoat sighting.

Fig. 1). Abundance and survival of grand and Otago skinks were measured in populations subjected to three predator management treatments: (1) near-eradication of predators inside a mammal-proof fence (Site A); (2) suppression of predator populations by a landscape-scale trapping network (details below) in which two levels of protection were considered: trapping core (i.e. protected by multiple trap lines surrounding the site) (Site B), and trapping periphery (i.e. protected by a single trap line on one side and multiple trap lines on other sides) (Sites C and D); and (3) no mammal management (Sites E and F) (Fig. 1). All sites had incursions of mice and rabbits. Despite ongoing eradication attempts inside the mammal-proof fence, low rabbit numbers and intermittent low mouse populations remained. A second mammal-proof fence was completed at Site C in July 2007 (i.e. the predator management treatment changed at this site partway through the study). Due to the heterogeneous spread of the remnant skink populations at Macraes Flat there was no Otago skink population at the trapping periphery.

Predator eradication and suppression

We targeted five species of introduced predators (cat, ferret, stoat, weasel, and hedgehog) using 12 trap and bait combinations. We used six trap types: Conibear 220 (Woodstream Corporation, St Lititz, Pennsylvania, USA), Victor® Soft Catch leg-hold (Woodstream Corp.), Timms® possum trap (KBL Rotational Moulders, NZ), DOC 150 and 250 (Curtis Metal Products, NZ) and Mark VI Fenn traps (FHT Works, Worcester, UK) and three bait types: hen's egg, gutted rabbit or hare (*Lepus europaeus*) segments, and fish-based cat food wrapped within loose-weave cloth. We deployed 400 traps, on average every 100 m along 42 km of trap line that covered about 2100 ha of skink habitat and included the study sites A, B, C and D (Fig. 1).

The mammal-proof fences (Xcluder Pest Proof Fencing Limited, Cambridge, NZ) were 1.8 m high, made of 6 × 12 mm stainless steel mesh with a subterranean skirt at the base and a metal rolled hood barrier at the top (fenced areas were 18 ha at Site A, and 9 ha at Site C). To eradicate predators within the fences we used toxins and the aforementioned traps. To poison rabbits and hares, we used hand-laid carrot impregnated with sodium monofluoroacetate (1080), and magnesium phosphide fumigant (Magtoxin® granules). Rodents were poisoned with brodifacoum-baited cereal pellets (Pestoff® 20R) and ongoing monitoring for rodents was undertaken through the use of ink-based tracking tunnels (Site A: $n = 77$, Site C: $n = 42$)

(sensu Blackwell et al. 2002). In order to remove any residual predators inside the mammal-proof fences we maintained kill traps (i.e. our trap suite excluding Victor® Soft Catch leg-hold) for the duration of the study (Site A: $n = 24$, Site C: $n = 18$). Total predator eradication was achieved 14 months after the fence was closed at Site A (total within-fence captures: one stoat and three hedgehogs) and 4 months after fence closure at Site C (one hedgehog).

Skink monitoring protocol

In order to minimise potential adverse effects of handling on skink behaviour (Germano 2007), and to improve robustness of population estimators (Williams et al. 2002), we used a multi-session, non-invasive photo-resight methodology that accounted for variable detection probabilities and resight heterogeneity. The photo-resight methodology is an established technique in herpetology (e.g. Perera & Pérez-Mellado 2004; Sacchi et al. 2007; Gebauer 2009; Knox 2010) and has been shown to be less error prone than toe coding (Sacchi et al. 2007).

For consistency, and to maximise the probability of seeing skinks, we carried out photo-resight surveys in warm sunny conditions with low wind strength (as in Roughton 2005). Surveyors attempted to photograph both lateral sides of all visible skinks, with a preference for the nose to foreleg region, which encompassed easily distinguished blotched and/or curvilinear black and gold markings. The best images of the left and right sides of each individual were coded and archived to form a photographic library against which subsequent images could be visually compared.

We found that patterning was exceptionally stable across years in both species but that stippling tended to develop with age. Recognisable changes in scale colouration between years were seen in less than 2% of the population. Visual identification for both species typically involved examining an image profile consisting of 750 scales. The maximum number of scale changes in any such profile over the course of the study was seven. At mammal-proof-fenced Site A, where no adult skink immigration was possible, no new mature grand skinks were identified after the first year of monitoring, nor any mature animals of either species after the second year. Therefore, the risk of misidentification due to pattern change was likely to be very low or absent.

No time limits were imposed for each survey; although each surveyor had to cover all of the required rock outcrops of a site (typically 3–5 h per survey day with 3–4 observers per site). To minimise observer bias between sampling occasions,

we alternated assignment of surveyors to outcrops each session. We attempted to survey each site in the same month every year.

We conducted 3–9 surveys (photo–resight sessions) at each site during each austral summer (primary sessions: 2006–2008, Table 1). In 2006, five surveys were conducted at each site. In 2007, poor weather conditions allowed for fewer surveys. Preliminary analyses of data showed that detection probabilities were variable between sites. Some sites showed apparent increases in mean abundance estimates but these had very large confidence intervals. In order to improve resolution at the sites that exhibited large confidence intervals (e.g. Site A), we increased survey effort in 2008. As the timing of the photo–resight sessions straddled the birth season, skinks born during the monitoring period were removed from the statistical analyses to avoid violating the requirement of population closure (Williams et al. 2002).

Photo–resight data analysis

We analysed the photo–resight data using the robust design model with the Huggins closed population estimator in Program MARK (version 4.3; White & Burnham 1999) to obtain abundance and survival estimates (Huggins 1989, 1991). We assumed that surveys had no impact on skink behaviour so probabilities of first capture were set equal to recapture probabilities, i.e. $p = c$. We allowed annual survival to vary between primary periods (years; Williams et al. 2002). Our field observations suggested that some skinks were hypervigilant, consequently we made capture heterogeneity one of our candidate models. Heterogeneous capture probabilities can be accounted for by assuming the population consists of a mixture of subpopulations with different capture probabilities (Pledger 2000) that may be caused by different skink and/or observer behaviour. For our heterogeneity models we assumed two mixture groups. Four models were thus tested for each site: (1) constant capture probability: $p(\cdot) = c(\cdot)$; (2) constant capture probability and additive heterogeneity: $p(+h) = c(+h)$; (3) capture probability with a day effect and additive heterogeneity: $p(t+h) = c(t+h)$; and (4) capture probability with a day effect only: $p(t) = c(t)$.

We scaled survival into annual equivalents, as intervals between primary periods varied from 329 to 367 days. Emigration and immigration parameters were set to zero (i.e. $\gamma'(0) \gamma''(0)$) as we had no conceptual framework by which to separate temporary emigration from decreased survival over such a short time frame. Additionally, permanent emigration will always confound survival estimation; the statistical consequence of this is to lower survival estimates as all emigration is treated as mortality.

Model interpretation

Model selection was based on the corrected Akaike Information Criterion (AICc, an adjustment to the AIC to account for bias due to small sample size; Burnham & Anderson 2001). We used AICc to compute model weights to rank models and accepted the top model when it had an AICc model weight of >0.9 . If this criterion was not fulfilled, we applied model averaging across all estimable models. For model-averaged confidence intervals of population size we used a logarithm-based confidence interval incorporating minimum numbers alive (White et al. 2001).

Overall population growth rate

We derived the overall population growth rate as the ratio of the

abundance estimates. Ninety-five percent confidence intervals were obtained by first calculating them on the natural logarithm scale to account for the asymmetric nature of growth rates (i.e. they can range from zero to infinity, with 1 indicating a stable population size), then the limits were back-transformed onto the real scale. The delta method (Seber 1982; Powell 2007) was used to determine the appropriate variances for estimated quantities when moving between the real and log scale.

Site-grouping analysis

To look for crude similarities in survival between groups of sites, we generated a reduced model with constant survival, site-specific detection probabilities year-varying (but constant within year), and no interval scaling: $S(\cdot) p(\cdot) = c(\cdot)$. This model was built in program MARK (version 5.0), which allows missing encounter history data to be represented and therefore sites differing in number of secondary photo–resight sessions can be compared. Models with alternative site groupings were then compared to reflect the response scenarios we thought plausible.

For analysis of grand skink data, the five models were: (1) no survival differences between sites: (A,B,C,D,F); (2) all sites different: (A)(B)(C)(D)(F); (3) all sites within the trapping network or mammal-proof fences the same, but unmanaged site different: (A,B,C,D)(F); (4) sites mammal-proof-fenced throughout the study or at the trapping core the same, sites at the trapping periphery the same, and unmanaged site different: (A,B)(C,D)(F); and (5) site mammal-proof-fenced throughout different, all other managed sites the same, unmanaged site different: (A)(B,C,D)(F).

For analysis of Otago skink data, the models were: (1) no survival differences between sites: (A,B,E); (2) all sites different: (A)(B)(E); (3) sites at the trapping core or within a mammal-proof fence the same, unmanaged site different: (A,B)(E); and (4) mammal-proof fence different, trapped and unmanaged sites the same: (A)(B,E).

Results

Predator trapping

The predator trapping programme removed similar numbers of predators each year (range: 1084–1350 animals, Table 2). Hedgehogs were most commonly caught followed by cats and ferrets.

Table 2. Number of each predator species removed from the predator-trapping network at Macraes Flat, eastern Otago, New Zealand, during each study year.

Species	Calendar year			Total
	2006	2007	2008	
Cat (<i>Felis catus</i>)	219	212	204	635
Ferret (<i>Mustela furo</i>)	144	126	153	423
Hedgehog (<i>Erinaceus europaeus</i>)	899	634	761	2294
Stoat (<i>Mustela erminea</i>)	68	92	82	242
Weasel (<i>Mustela nivalis</i>)	20	20	2	42
Total	1350	1084	1202	3636

Table 3. Grand skink (*Oligosoma grande*) annual survival at Macraes Flat, eastern Otago, New Zealand, and derived overall population growth rates with 95% confidence intervals. The model presented is either the top model with a model weight of >0.9 or a model average of the estimable models. Model notation is described in the Methods section.

Site	Model	Regime 2006	Survival 2006–2007 (95% CI)	Regime 2007	Survival 2007–2008 (95% CI)	Overall population growth rate 2006–2008 (95% CI)
A	$p(t+h) = c(t+h)$	Mammal-proof fence	0.81 (0.70–0.90)	Mammal-proof fence	0.71 (0.60–0.81)	1.32 (1.25–1.40)
B	$p(.) = c(.)$	Trapping core	0.72 (0.53–0.85)	Trapping core	0.69 (0.52–0.82)	1.48 (1.44–1.53)
C	$p(t+h) = c(t+h)$	Trapping periphery	0.62 (0.48–0.74)	Mammal-proof fence	0.74 (0.61–0.85)	1.21 (1.09–1.34)
D	$p(t) = c(t)$	Trapping periphery	0.64 (0.55–0.72)	Trapping periphery	0.64 (0.55–0.72)	1.08 (1.04–1.11)
F	$p(.) = c(.)$, $p(t) = c(t)$ model average	Unmanaged	0.18 (0.11–0.29)	Unmanaged	0.62 ^a (0.39–0.80)	0.15 (0.10–0.21)

^aAnnualised survival prior to stoat sighting in 2008 (see Results).

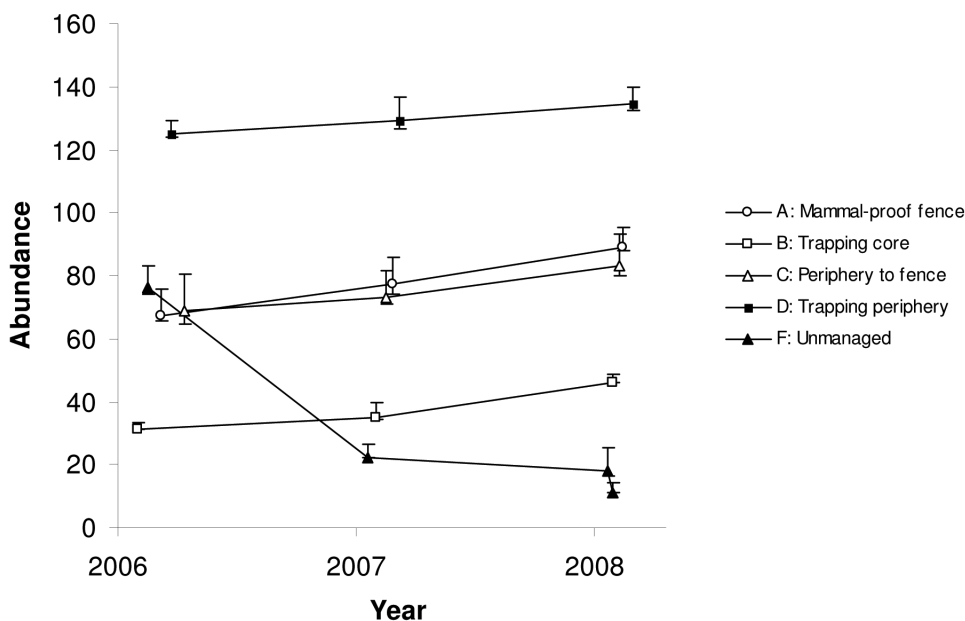


Figure 2. Grand skink (*Oligosoma grande*) abundance at Macraes Flat, eastern Otago, New Zealand (\pm 95% confidence intervals). Note: Site F has two results in 2008 representing pre- and post-stoat predation estimates.

Grand skink abundance and survival

Substantial increases in grand skink abundance were recorded within the mammal-proof fence and in the trapping core (Sites A and B, Fig. 2). Overall population growth rates were 1.32 and 1.48 (Table 3) from estimated initial populations of 67 and 31 individuals, respectively (population growth rates of 1 indicate stability, <1 decline, >1 increase). The trapping periphery (Site D) showed only marginal positive growth. Unequivocal declines of large magnitude were recorded at the unmanaged Site F where the skink population declined by 85% (derived growth rate = 0.15), from 76 to 11 skinks over the three years.

The error component of the survival estimates overlapped between all sites except for the unmanaged Site F in 2006–2007, which was substantially lower than all other estimates (Table 3). This low survival estimate parallels the decline in abundance seen at this site over the same period (Fig. 2).

While differences in survival between managed sites were equivocal, the highest survival estimates were recorded for grand skink populations protected by mammal-proof-fencing and core-trapping regimes (Table 3).

While monitoring skinks at Site F in 2008, we observed a stoat actively searching for prey on the rocks that contained skinks. We assumed that the stoat was targeting skinks as these were the most likely prey items in the immediate habitat. The robust design model assumes that each monitoring session is closed to migration, births and deaths. Predation of skinks would violate this assumption. Consequently, the monitoring data for that day were discarded and a new session (primary period) began 5 days later. We took advantage of this natural experiment because the 2 days prior to the stoat sighting were sufficient to establish abundance and survival estimates, which could be compared before and after the sighting (Fig. 2). The estimated probability of survival between the pre- and post-

stoat periods was 0.55 (95% CI 0.31–0.77) (equivalent to an annualised survival estimate of 0.05), which suggests 45% of the population did not survive between the pre- and post-stoat periods. A comparison of the pre- and post-stoat monitoring photographs revealed that three of the 11 sighted skinks remaining after the stoat observation had lost (autotomised) their tails over the 5-day period.

Otago skink abundance and survival

Substantial increases in Otago skink abundance were recorded within the mammal-proof fence and in the trapping core (Sites A and B, Fig. 3). Derived population growth rates were 1.67 and 1.92 (Table 4) from initial populations of 62 and 37 individuals, respectively. There was no evidence of change in abundance at the unmanaged Site E. Differences in survival estimates due to management treatment were equivocal, although the mammal-proof-fenced site consistently had the highest point estimate of survival (Table 4).

Site-grouping analysis

For grand skinks, the grouping analysis showed unambiguously that unmanaged Site F was distinguished from the other four sites based on survival (Table 5). The model-averaged survival

rates of skinks at Site F were substantially lower than those at all other grand skink sites (Site F: $\hat{S} = 0.22$, 95% CI 0.14–0.32; cf. Site A–D: $\hat{S} \sim 0.70$, 95% CI $\sim \hat{S}$ 0.62–0.81). The top two models described three similar grouping structures (broadly paralleling our perceived intensity of predator management) and commanded 74% of the AICc weightings (Table 5).

For Otago skinks, the pattern in the grouping analysis was somewhat weaker with even the worst model being relatively plausible (Table 6). Unlike grand skink survival, the unmanaged site was not clearly distinguished in terms of Otago skink survival but appeared to be similar to the trapping core.

Discussion

Skink response to management

Our study found that control of mammalian predators, either by way of near-eradication inside a pest-proof fence or suppression within the core of an intensively trapped area, could enable localised recoveries of similar magnitude in grand and Otago skink populations. This is likely the first proven example of successful mainland management for endangered New Zealand lizards.

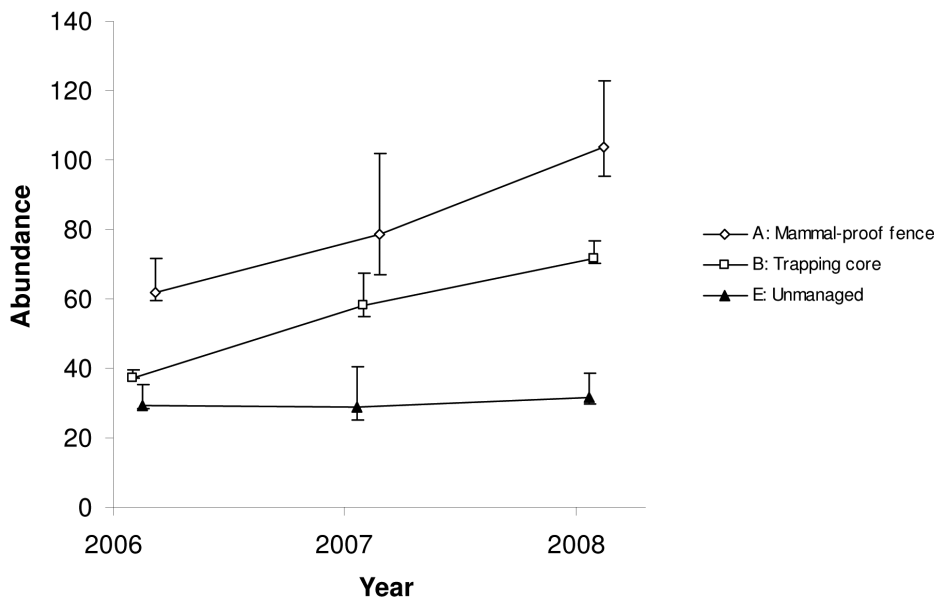


Figure 3. Otago skink (*Oligosoma otagense*) abundance at Macraes Flat, eastern Otago, New Zealand (± 95% confidence intervals)

Table 4. Otago skink (*Oligosoma otagense*) annual survival at Macraes Flat, eastern Otago, New Zealand, and derived overall population growth rates with 95% confidence intervals. The model presented is either the top model with a model weight of >0.9 or a model average of the estimable models. Model notation is described in the Methods section.

Site	Model	Regime 2006–2008	Survival 2006–2007 (95% CI)	Survival 2007–2008 (95% CI)	Overall population growth rate 2006–2008 (95% CI)
A	$p(t+h) = c(t+h)$	Mammal-proof fence	0.83 (0.67–0.92)	0.94 (0.50–1.00)	1.67 (1.35–2.07)
B	$p(.) = c(.), p(t) = c(t)$ model average	Trapping core	0.78 (0.61–0.89)	0.70 (0.56–0.81)	1.92 (1.79–2.07)
E	$p(.) = c(.)$	Unmanaged	0.82 (0.54–0.95)	0.58 (0.37–0.76)	1.06 (0.91–1.24)

Table 5. Model ranking of groupings for grand skink (*Oligosoma grande*) sites from a reduced model of survival. Brackets define sites considered as singular groups. Model notation is described in the Methods section.

Model $p(.) = c(.)$	AICc	Δ AIC	AIC weight	Number of parameters	Deviance
(A)(B,C,D)(F)	7667.57	0.00	0.40	18	9153.14
(A,B)(C,D)(F)	7667.90	0.33	0.34	18	9153.47
(A,B,C,D)(F)	7669.44	1.86	0.15	17	9157.02
(A)(B)(C)(D)(F)	7670.45	2.88	0.09	20	9151.98
(A,B,C,D,F)	7731.93	64.35	0.00	16	9221.53

Table 6. Model ranking of group effects for Otago skink (*Oligosoma otagense*) sites at Macraes Flat, eastern Otago, New Zealand, from a reduced model of survival. Brackets define sites considered as singular groups. Model notation is described in the Methods section.

Model $p(.) = c(.)$	AICc	Δ AIC	AIC weight	Number of parameters	Deviance
(A)(B,E)	3666.86	0.00	0.53	11	4087.65
(A)(B)(E)	3668.71	1.85	0.21	12	4087.46
(A,B,E)	3669.38	2.52	0.15	10	4092.20
(A,B)(E)	3669.85	2.99	0.12	11	4090.64

While both predator management techniques delivered benefits to the skink populations, the mammal-proof fence emerged as a distinct group in the top model of site-grouping analyses for both species, with survival estimates highest under this form of protection. Therefore, mammal-proof fencing may have an advantage over the trapping core, despite the trapping core having higher observed population growth rates for both species. Given the uncertainty in the survival estimates, it may be several years before this anomaly is resolved.

Little if any recovery of the grand skink population was observed at the trapping periphery, possibly because of higher predator densities at the edges of the trapping network. Unfortunately, the heterogeneous spread of the remnant skink populations at Macraes Flat meant there was no Otago skink population near the periphery of the trapped area for comparison.

When wildlife managers are presented with two viable yet competing protection strategies, an assessment of their relative value must be undertaken regarding efficacy, longevity, placement, cost, flexibility, and goal. Mammal-proof fencing may at first glance appear the better option as the prospect of predator infiltration is lower. However, fences need ongoing maintenance and eventual replacement. Trapping has a much higher risk of predator incursion, high daily and ongoing commitment costs but low replacement costs, and the advantage in the long term of spatial flexibility. Climate and habitat may change over time, in which case trapping networks can be easily shifted but mammal-proof fences cannot. The downside of a trapping network, from our study, appears to be that in order to confer adequate protection for a population at the trapping core an extensive area must be buffered by trapping, which may actually give little advantage to the populations within its outer margins. If management at Macraes Flat was to change from the current dual-species focus to an ecosystem-level approach then the relative benefits of these methods would have to be reappraised.

Predator activity

Our unmanaged sites offer insight into a potentially important process that may be exacerbating the decline of grand and Otago skinks. Although there was no change in the abundance of Otago skinks at their unmanaged site we observed a catastrophic decline of grand skinks at their unmanaged site. The population declined in 2006–2007 and again in 2008. The latter decline coincided with the sighting of a stoat hunting skinks on the study rocks; the subsequent appearance of skinks with fresh tail loss and the disappearance of nearly half the remaining population within a 5-day period was something never previously observed in many years of surveying. It seems plausible that stoat predation was the cause of this decline. A similar episodic phenomenon was seen by K. Gebauer (University of Otago, pers. comm.) during a grand skink telemetry study at Macraes Flat in 2010. Over a few days several study animals went missing, carcasses were retrieved, and a radio transmitter from one skink was found in a cat scat.

We hypothesise that such episodic predation events in which rare secondary prey are specifically targeted in a localised and intermittent manner may be an important part of a stepwise extinction process with grand and Otago skinks. We speculate that because of the short time frame and intense nature of such episodic predation, it is rarely observed during annual or even seasonal monitoring regimes. Not surprisingly, the sporadic nature of this phenomenon has meant that it has been largely anecdotal in all but the most severe cases (e.g. Taborsky 1988).

Hedgehogs were the most frequently caught mammals during our study. Although hedgehogs are primarily insectivorous omnivores, their predatory impacts on lizards are beginning to be understood (Jones et al. 2005; Spitzen-van der Sluijs et al. 2009). Given their high abundance and ubiquitous distribution, even if only a small proportion of hedgehogs consumed skinks the cumulative effects of their predation could be substantial.

Introduced avian predators and mice are likely to prey on grand and Otago skinks to some degree, and both were present at the sites where skink populations recovered. This suggests that neither of these two groups had strong deleterious effects over the course of the study. However, the 3-year term of our study is a short ecological time frame and is unlikely to account for year-to-year fluctuations in mouse abundance. Mice have been implicated in the suppression of some lizard populations in New Zealand (Newman 1994). A significant tussock seed masting event at Macraes Flat may enable rodent numbers to increase dramatically, leading to predation (Wilson & Lee 2010) that could potentially erode skink population gains in non-rodent-irruption seasons.

We did not measure site-specific predator activity before we applied the treatments. However, Tocher (2006) established that predator activity was similar across treatment and control sites before her predator trapping began, thereby suggesting a ubiquitous predator presence regardless of site. We retained the same study sites as Tocher (2006) and our catch rate of predators was consistent across years.

Although this experiment focused on removing predators, we are mindful that a hyperpredation process (Smith & Quin 1996; Courchamp et al. 2000) may exist in which introduced primary prey abundance determines introduced predator numbers and thereby the rate of predation on native skinks as secondary prey. Indeed, such processes have been demonstrated for other native lizard species in New Zealand grassland systems (Norbury 2001). Under this scenario, long-term suppression of the primary prey (in this case rabbits, and perhaps also mice) could conceivably yield a positive response in grand and Otago skinks via a general reduction in predator numbers. This may be a productive avenue for future research.

Divergence in species-specific survival rates

Our empirical findings suggest that Otago skink populations have higher growth rates and generally higher survival rates than grand skinks. Compared with Tocher (2009), our estimated survival rates for Otago skinks in predator controlled areas were much higher ($\hat{S} = 0.70\text{--}0.94$ cf. $\hat{S} = 0.58$), whereas those for grand skinks were similar ($\hat{S} = 0.69\text{--}0.74$ cf. $\hat{S} = 0.71$).

Despite superficially similar habitat requirements, distribution, diet, and natural history, grand and Otago skinks appear to differ in a number of other characteristics. In this study, Otago skinks were much less detectable and their activity more idiosyncratic than grand skinks. Otago skink resight probabilities were typically about 0.4 (range: 0.23–0.67) whereas grand skinks' were about 0.6 (range: 0.50–0.67). Otago skinks have a more extensive, gully-based distribution (Towns 1985) and from our study seem to be capable of more rapid population growth. They also have an association with fruit-bearing plants and shrubs of Macraes Flat, which are now more often found in gully systems due to their loss elsewhere as a result of agricultural development (M. Thorsen, DOC, pers. comm.). Grand skinks by comparison have an affinity for ridge-top rocks, with less cover, fewer protective bluffs, and greater proximity to pastoral development, which may be associated with increased predator numbers due to higher rabbit abundance. We suspect that grand skinks because of such habitat selection, lower population growth rates (this study), and more limited distribution are at present the more vulnerable of the two species. It is therefore questionable whether the two species should be treated as a single management unit as is currently the case. Nevertheless, given the punctuated declines

and lack of population recovery observed at our unmanaged sites, both skink species appear susceptible to extinction.

Management implications

Cost–benefit analysis has shown that trapping at Macraes Flat for grand and Otago skink protection is more cost efficient than mammal-proof fencing for areas greater than 10 ha (Hutcheon et al. 2011). As a result, by 2009 we had increased the landscape trapping programme at Macraes Flat to approximately 800 traps deployed across 4500 ha of reserve and neighbouring farms. Given the diversity and abundance of mammalian predators in the Macraes Flat ecosystem, we advocate that all mammalian predators be controlled.

The Grand and Otago Skink Recovery Programme is now at the stage of integrating the fencing and trapping techniques to accelerate population recovery by translocating skinks from mammal-proof-fenced areas to vacant habitat at the trapping core. Consequently, investment in the response monitoring of such populations remains crucial both for quantifying the outcome and for supporting future decision-making.

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References

- Bellingham PJ, Towns DR, Cameron EK, Davis JJ, Wardle DA, Wilmshurst JM, Mulder CPH 2010. New Zealand island restoration: seabirds, predators, and the importance of history. *New Zealand Journal of Ecology* 34: 115–136.
- Berry O, Gleeson DM 2005. Distinguishing historical fragmentation from a recent population decline – shrinking or pre-shrunk skink from New Zealand? *Biological Conservation* 123: 197–210.
- Bibby CJ 1997. Macraes Ecological District: a survey report for the Protected Natural Areas Programme. Unpublished MSc, University of Otago, Dunedin, New Zealand. 203 p.
- Blackwell GL, Potter MA, McLennan JA 2002. Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story? *New Zealand Journal of Ecology* 26: 43–51.
- Blick R, Bartholomew R, Burrell T, Burns KC 2008. Successional dynamics after pest eradication in the Karori Wildlife Sanctuary. *New Zealand Natural Sciences* 33: 3–14.

- Burnham KP, Anderson DR 2001. Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28: 111–119.
- Coddington EJ, Cree A 1997. Population numbers, response to weather, movements and management of the threatened New Zealand skinks *Oligosoma grande* and *O. otagense* in tussock grassland. *Pacific Conservation Biology* 3: 379–391.
- Connolly TA 2008. The potential for re-invasion by mammalian pests at Maungatautari Ecological Island. Unpublished MSc thesis, University of Waikato, Hamilton, New Zealand. 119 p.
- Courchamp F, Langlais M, Sugihara G 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* 69: 154–164.
- Gallacher DJ, Hill JP 2006. Effects of camel grazing on the ecology of small perennial plants in Dubai (UAE) inland desert. *Journal of Arid Environments* 66: 738–750.
- Gebauer K 2009. Trapping and identification techniques for small-scaled skinks (*Oligosoma microlepis*). DOC Research & Development Series 318. Wellington, Department of Conservation. 24 p.
- Germano JM 2007. Movements, home ranges, and capture effects of the endangered Otago skink (*Oligosoma otagense*). *Journal of Herpetology* 41: 179–186.
- Hayward MW, Kerley GIH 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation* 142: 1–13.
- Hitchmough RA, Hoare JM, Jamieson H, Newman D, Tocher MD, Anderson PJ, Lettink M, Whitaker AH 2010. Conservation status of New Zealand reptiles, 2009. *New Zealand Journal of Zoology* 37: 203–224.
- Huggins RM 1989. On the statistical analysis of capture experiments. *Biometrika* 76: 133–140.
- Huggins RM 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47: 725–732.
- Hutcheon A, Norbury G, Whitmore N 2011. Response monitoring and cost–benefit analysis drives adaptive management of critically endangered skinks. *Kino* 18: 14–15.
- Innes J, Hay I, 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.
- Jones C, Moss K, Sanders M 2005. Diet of hedgehogs (*Erinaceus europaeus*) in the upper Waitaki Basin, New Zealand: Implications for conservation. *New Zealand Journal of Ecology* 29: 29–35.
- King CM ed. 2005. The handbook of New Zealand mammals. 2nd edn. Melbourne, Oxford University Press. 610 p.
- Knox CD 2010. Habitat requirements of the jewelled gecko (*Naultinus gemmeus*): effects of grazing, predation and habitat fragmentation. Unpublished MSc, University of Otago, Dunedin, New Zealand. 94 p.
- Middlemiss A 1995. Predation of lizards by feral house cats (*Felis catus*) and ferrets (*Mustela furo*) in the tussock grasslands of Otago. Unpublished MSc, University of Otago, Dunedin, New Zealand. 120 p.
- Moseby KE, O'Donnell E 2003. Reintroduction of the greater bilby, *Macrotis lagotis* (Reid) (Marsupialia: Thylacomyidae) to northern South Australia: survival, ecology and notes on reintroduction protocols. *Wildlife Research* 30: 15–27.
- Newman DG 1994. Effects of a mouse, *Mus musculus*, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. *New Zealand Journal of Zoology* 21: 443–456.
- Norbury G 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. *Journal of Applied Ecology* 38: 1350–1361.
- Patterson GB 1992. Development of Otago skink and grand skink population census and monitoring techniques. Science & Research Internal Report 133. Wellington, Department of Conservation. 23 p.
- Perera A, Pérez-Mellado V 2004. Photographic identification as a noninvasive marking technique for lacertid lizards. *Herpetological Review* 35: 349–350.
- Pledger S 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* 56: 434–442.
- Powell LA 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109: 949–954.
- Reardon JT, Norbury G 2004. Ectoparasite and hemoparasite infection in a diverse temperate lizard assemblage at Macraes Flat, South Island, New Zealand. *Journal of Parasitology* 90: 1274–1278.
- Richards JD, Short J 2003. Reintroduction and establishment of the western barred bandicoot *Perameles bougainville* (Marsupialia: Peramelidae) at Shark Bay, Western Australia. *Biological Conservation* 109: 181–195.
- Roughton CM 2005. Assessment of methods to monitor Otago skink and grand skink populations, New Zealand. DOC Research & Development Series 211. Wellington, Department of Conservation. 26 p.
- Sacchi R, Scali S, Fasola M, Galeotti P 2007. The numerical encoding of scale morphology highly improves photographic identification in lizards. *Acta Herpetologica* 2: 27–35.
- Saunders A, Norton DA 2001. Ecological restoration at Mainland Islands in New Zealand. *Biological Conservation* 99: 109–119.
- Scofield RP, Cullen R, Wang M 2011. Are predator-proof fences the answer to New Zealand's terrestrial faunal biodiversity crisis? *New Zealand Journal of Ecology* 35: 312–317.
- Seber GAF 1982. The estimation of animal abundance and related parameters. 2nd edn. London, Charles Griffin. 654 p.
- Smith AP, Quin DG 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77: 243–267.
- Spitzen - van der Sluijs AM, Spitzen J, Houston D, Stumpel AHP 2009. Skink predation by hedgehogs at Macraes Flat, Otago, New Zealand. *New Zealand Journal of Ecology* 33: 205–207.
- Taborsky M 1988. Kiwis and dog predation: observation in Waitangi State Forest. *Notornis* 25: 197–202.
- Tocher MD 2003. The diet of grand skinks (*Oligosoma grande*) and Otago skinks (*O. otagense*) in Otago serral tussock grasslands. *New Zealand Journal of Zoology* 30: 243–257.
- Tocher MD 2006. Survival of grand and Otago skinks following predator control. *The Journal of Wildlife Management* 70: 31–42.
- Tocher MD 2009. Life history traits contribute to decline of critically endangered lizards at Macraes Flat, Otago.

- New Zealand Journal of Ecology 33: 125–137.
- Towns DR 1985. The status and prospects of the rare New Zealand lizards *Leiopisma grande* (Gray), *Cyclodina whitakeri* (Hardy), and *Leiopisma otagense* (McCann) (Lacertilia: Scincidae). In: Grigg G, Shine R, Ehmann H eds Biology of Australasian frogs and reptiles. Chipping Norton, Surrey Beatty in association with the Royal Zoological Society of New South Wales. Pp. 481–489.
- Watts CH, Armstrong DP, Innes J, Thornburrow D 2011. Dramatic increases in weta (Orthoptera) following mammal eradication on Maungatautari – evidence from pitfalls and tracking tunnels. New Zealand Journal of Ecology 35: 261–272.
- Whitaker AH 1996. Impact of agricultural development on grand skink (*Oligosoma grande*) (Reptilia: Scincidae) populations at Macraes Flat, Otago, New Zealand. Science for Conservation 33. Wellington, Department of Conservation. 33 p.
- Whitaker AH, Loh G 1995. Otago skink and grand skink recovery plan (*Leiopisma otagense* and *L. grande*). Threatened Species Recovery Plan 14. Wellington, Department of Conservation. 25 p.
- White GC, Burnham KP 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl.): S120–S138.
- White GC, Burnham KP, Anderson DR 2001. Advanced features of Program MARK. In: Field RJ, Warren RJ, Okarma H eds Proceedings of the Second International Wildlife Management Congress. Bethesda, Maryland, USA, The Wildlife Society. Pp. 368–377.
- Williams BK, Nichols JD, Conroy MJ 2002. Analysis and management of animal populations: modelling, estimation, and decision making. Academic Press, San Diego. 817 p.
- Wilson DJ, Lee WG 2010. Primary and secondary resource pulses in an alpine ecosystem: snow tussock grass (*Chionochloa* spp.) flowering and house mouse (*Mus musculus*) populations in New Zealand. Wildlife Research 37: 89–103.

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