

# Sampling skinks and geckos in artificial cover objects in a dry mixed grassland–shrubland with mammalian predator control

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**Abstract:** Introduced mammalian predators threaten populations of endemic New Zealand lizards but their effects on lizard populations have not been quantified on the mainland. We trialled the use of artificial cover objects (ACOs) for sampling small terrestrial lizards (the skinks *Oligosoma maccanni*, *O. nigriplantare polychroma* and *O. inconspicuum*, and gecko *Hoplodactylus maculatus*) in three experimental mammal-management treatments: a mammal-proof fence, two sites in an intensive mammal-removal area, and an experimental control site with no mammal removal. These predator control regimes were established in 2005–2006 to protect endangered grand skinks (*O. grande*) and Otago skinks (*O. otagense*) at Macraes Flat, North Otago. We (1) counted skinks and geckos found under ACOs on a single day and compared these counts between treatments, and (2) estimated lizard population sizes ( $N$ ) based on capture-mark-recapture (CMR) of lizards under ACOs in daily and weekly sampling sessions. Our results provide baseline data of the abundance of the small lizard species shortly after implementation of predator management. Single-day counts of skinks were significantly higher inside the mammal fence compared with the experimental control. No consistent differences were found between the other treatments. Significantly more skinks were counted in gully habitats than in ridge habitats.  $N$ , counts of skinks from the first day of CMR, and the total number of individuals caught were correlated, but these relationships must be validated with independent data. Few geckos were caught unless ACOs were placed near rock outcrops. Only two skinks but 25% of geckos moved between adjacent ACOs (5-m spacing). The recapture rate of skinks was low; captures declined when ACOs were checked daily but not when they were checked weekly. Because of potential biases of these methods, we propose to compare counts in ACOs and  $N$  based on CMR in ACOs with  $N$  based on CMR in pitfall traps with 3-m spacing.

**Keywords:** ACO; artificial refuge; capture-mark-recapture; *Hoplodactylus maculatus*; index; *Oligosoma inconspicuum*; *Oligosoma maccanni*; *Oligosoma nigriplantare polychroma*; predator removal; program MARK

## Introduction

Introduced mammalian predators – feral cats (*Felis catus*), mustelids (*Mustela* spp.), European hedgehogs (*Erinaceus europaeus*), and rodents (rats *Rattus* spp. and mice *Mus musculus*) – threaten populations of endemic New Zealand lizards (King 2005). On offshore islands, lizard populations may recover when mammals are removed (Newman 1994; Towns & Broome 2003). On the mainland, however, effects of mammals on lizard populations have not been quantified because of the difficulty of removing or excluding all mammalian predators.

A mammal-proof fence around an 18-ha enclosure was built by the Department of Conservation near Macraes Flat in eastern North Otago, to protect

remnant populations of the critically endangered grand skink (*Oligosoma grande*) and Otago skink (*O. otagense*) (Reardon 2006). This mammal enclosure was completed in June 2005 and all mammals were eradicated by January 2006 except for a few mice and rabbits (*Oryctolagus cuniculus*). Continuous removal of mammalian predators from the surrounding area (1200 ha), primarily through intensive trapping, was fully implemented by January 2006 (Reardon 2006). Abundance and survival of grand and Otago skinks within these mammal management areas are assessed with intensive annual photographic identification of individuals (Reardon 2006).

Several other species of small lizards are comparatively abundant at Macraes Flat: the common skink (*Oligosoma nigriplantare polychroma*),

McCann's skink (*O. maccanni*), cryptic skink (*O. inconspicuum*) and common gecko (*Hoplodactylus maculatus*). Green skinks (*O. chloronoton*) are present but uncommon. We aimed to trial a method of indexing the abundance of these more common lizard species to obtain baseline measurements soon after initiating predator control and to document any subsequent changes in population size. We wanted a reliable, low-cost sampling method that could be implemented annually after the busy summer field season.

The abundance of small ground-dwelling lizards is commonly assessed by means of capture-mark-recapture (CMR) in non-lethal pitfall traps (e.g. Freeman 1997). This method requires consecutive days of warm or sunny weather when the animals are active and likely to encounter traps. It is particularly costly at Macraes Flat, where the sky is often overcast and field teams must wait for suitable pitfall-trapping conditions. Another method of surveying reptiles and amphibians, by recording the number occupying artificial retreats or artificial cover objects (ACOs) placed on the ground (e.g. Reading 1997; Monti et al. 2000), has only recently been used in New Zealand (Lettink & Cree 2007). Because ACOs are expected to be occupied by inactive lizards seeking shelter overnight and in cold or overcast conditions, as well as by active lizards (M. Lettink, University of Otago, pers. comm.), this method may require only a single day of sampling and is less reliant on good weather.

We therefore investigated whether a large enough number of small lizards would occupy ACOs at Macraes Flat to permit statistical comparison between the predator management treatments. We compared counts of lizards in ACOs inside the mammal-proof fence, at two sites outside the fence but within the predator removal area, and at an experimental control site outside the conservation area, with no predator removal.

The relationship between the number of animals counted in a survey and the actual population size ( $N$ ) depends on the probability of detecting an animal. Using counts as abundance indices, therefore, requires the strong assumption that detection probability is constant between the sites or sampling occasions that are to be compared. However, temporal and individual heterogeneity in probability of capture are typical of many animal populations (White et al. 1982). The chance of detecting lizards is also likely to vary between different habitats because usage of artificial refuges may depend on the availability of natural refuges (e.g. Hyde & Simons 2001; Lettink & Patrick 2006). Many other factors may affect detection probability, including the density of lizards; e.g. territorial behaviour or interspecific interactions may affect the number of individuals that can simultaneously occupy an ACO (e.g. Langkilde et al. 2003).

However, the four sites we compared were

superficially similar, with only the experimental control site subject to low levels of grazing and occasional burning. In addition, we standardised habitats by stratifying sampling between gullies and ridges within each site. We also expected detection probability to be related to weather, since the utility of ACOs as refuges for ectothermic lizards is likely to depend on ambient temperature (M. Lettink, pers. comm.). Therefore, we sampled lizards simultaneously at all sites in order to standardise weather and temperature at time of capture.

We also tested whether population size of lizards could be estimated based on CMR sampling of lizards in ACOs in the subsequent days and weeks. Whether ACOs are suitable capture devices for lizard CMR sampling depends on the degree to which they meet the underlying assumptions of CMR. One key assumption is that each animal has an equal and constant probability of capture, although various statistical models have been developed to relax this assumption (Otis et al. 1978). Possible behaviours such as long-term occupancy and defence of ACOs by individual lizards could exacerbate the degree of unequal catchability when these devices, in contrast to pitfall traps, are used for CMR. For example, red-backed salamanders (*Plethodon cinereus*) found under wooden boards were more likely to be adults compared with those found under rocks and logs (Marsh & Goicochea 2003). Large salamanders may have preferred boards to natural cover and defended them against small conspecifics (Marsh & Goicochea 2003).

Most published population estimates based on CMR use the closed-capture models of Otis et al. (1978). The alternative models can give very different estimates of  $N$ , and model selection with program CAPTURE (Otis et al. 1978) often performs poorly when data are sparse (Otis et al. 1978; Menkens & Anderson 1988; Hallett et al. 1991). We therefore used model-averaging (Burnham & Anderson 2002) in program MARK (White & Burnham 1999) to combine information about population size from a set of closed-capture models in order to reduce bias resulting from choosing the wrong model. Alternative models incorporated heterogeneity in capture probability due to combinations of five factors: habitat, size class, species, behavioural response to capture, and time. The contributions of the different sources of heterogeneity were weighted according to the models' Akaike weights (Burnham & Anderson 2002). The models we used were analogous to those of Otis et al. (1978), with the addition of heterogeneity based on individual covariates (Huggins 1989; Alho 1990). Because few researchers have compared the results of CAPTURE and MARK (McKelvey & Pearson 2001; Conn et al. 2004; cf. Conn et al. 2006), we also compared the results of model selection in program CAPTURE (Otis et al. 1978) to MARK's model rankings.

We expected the abundance of lizards to differ between the experimental control site and the two predator-reduction treatments, because of long-term differences in burning and grazing regimes outside and inside the conservation area. We did not expect, however, to find large differences between the two predator-removal treatments as the mammal-proof fence had been in place for less than a year, including a single lizard breeding season in summer 2006. The goals of this study were (1) to obtain single-day counts of lizards in ACOs and compare these between the predator management treatments, (2) to test whether CMR of lizards found in ACOs could be used to estimate population size  $N$ , and (3) to develop an experimental design and field protocol for annually counting lizards in ACOs at Macraes Flat.

## Methods

### Study site and management of mammalian pests

This research was done near Macraes Flat, eastern North Otago (45°27' S; 170°26' E), at the site of a 2400-ha reserve operated by the Department of Conservation's Grand and Otago Skink (GAOS) Recovery Programme. The vegetation has been highly modified by farming practices, including burning, oversowing, grazing by livestock, and browsing by introduced herbivores, primarily rabbits (Whitaker 1996). No burning or fertilising has been done within the reserve for many years (Whitaker 1996). Tall-tussock grassland now predominates (narrow-leaved snow tussock *Chionochloa rigida* together with *Poa cita*, and *Festuca novae-zelandiae* in dry places and red tussock *C. rubra* in damp places). Intertussock vegetation is a mixture of indigenous and exotic grasses, forbs, subshrubs and mosses. There are patches of seral shrubland (matagouri *Discaria toumatou*, mānuka *Leptospermum scoparium*, kānuka *Kunzea ericoides*, *Coprosma* spp. and *Olearia* spp.), especially in stream gullies.

Two intensive regimes for managing mammalian pests are in place at Macraes Flat: an 18-ha mammal-proof enclosure and continuous mammal removal. The mammal-proof enclosure (Xcluder™ Pest Proof Fencing, Cambridge, NZ) was completed on 12 June 2005, and the first attempt at eradicating remaining mammals finished on 9 July 2005. No cats, mustelids or rats have since been detected within the fenced area. Three hedgehogs were caught in January–February 2006, mice have been detected occasionally since April 2006, and a few rabbits remained as of June 2006. Continuous removal of cats, ferrets (*Mustela furo*), stoats (*M. erminea*), weasels (*M. nivalis*), rats (*Rattus norvegicus*), and hedgehogs from 1200 ha surrounding the mammal enclosure began in November 2005 and was fully implemented by January 2006. Trapping along 56

km of trap lines has been supplemented with spotlight hunting, tracking by dogs, and lures. Livestock have been excluded with fences.

### Study species

Common skinks, McCann's skinks and cryptic skinks are diurnal heliotherms that obtain heat from direct sunlight. Where the three species are sympatric, they tend to use dry grassy, dry rocky, and damp, densely vegetated microsites, respectively (Patterson & Daugherty 1990; Whitaker et al. 2002). Maximum snout-to-vent lengths (SVL) are 77 mm, 73 mm, and 70 mm, respectively (Gill & Whitaker 1996). Common geckos are primarily nocturnal thigmotherms that obtain heat from the substrate (Cree 1994). They occupy creviced schist outcrops in tussock grasslands, and also inhabit shrublands and forest (Whitaker et al. 2002). The geckos at Macraes Flat are 'Otago/Southland large' geckos (SVL up to 90 mm) within a *Hoplodactylus maculatus* species complex (Whitaker et al. 2002).

### Predator management treatments

We sampled lizards at four sites (each approximately 16–25 ha) within three different predator management treatments, as follows (we later refer to the four sites as 'treatments'):

- (1) Fence: within the mammal-proof fence.
- (2) Removal: immediately outside the fence, within the mammal removal area.
- (3) Removal 2: the central core of the mammal removal area, more than 1 km from sites 1 and 2.
- (4) Experimental control: no mammal control or restrictions on agricultural use, more than 5 km from the other sites.

### Sampling points

Each site (treatment) was stratified into two habitat types: gullies and ridges. Gullies were valleys along streams, usually steep on one side and gradually sloping on the other. Ridges were the surrounding higher elevation land, which was relatively flat with occasional schist rock outcrops. Gullies generally had a higher density of shrubby vegetation compared with ridges.

Within each treatment we chose sampling points at least 30 m apart, six in gully habitat and six in ridge habitat. Points were selected in a generalised random-tessellated stratified design (GRTS; Stevens & Olsen 2004), which assures that samples are distributed more or less evenly throughout each stratum. Points were selected from two-dimensional polygons on ridges, or along one-dimensional streambeds in gullies, drawn on geo-referenced photographic maps with ArcView software (Environmental Systems Research Institute (ESRI), Redlands, California).

## Abundance of lizards

### *Artificial cover objects (ACOs)*

Lizards were sampled with ACOs consisting of a three-layer stack of Onduline roofing material (distributed by Composite Insulation, Christchurch, NZ) cut into 40×28-cm sections. Onduline was first used for lizard and invertebrate ACOs by M. Lettink (Lettink & Patrick 2006; Lettink 2007; Lettink & Cree 2007). It is a lightweight, corrugated composite of plant fibres saturated with bitumen that is easy to handle and appears to have thermal properties suitable for lizard shelters (M. Lettink, pers. comm.). To create gaps between the layers, we glued pieces of pine dowel (1-cm diam.) to the underside of the top two layers (Lettink & Patrick 2006). In exposed locations, rocks were placed on top of ACOs to prevent displacement by wind.

### *Daily sampling*

At each sampling point, we established a grid of 16 ACOs in four rows and four columns with 5-m spacing. This grid size was chosen so that counts of lizards on the first day of a sampling session were likely to be non-zero on most grids in the Fence and Removal treatments, based on preliminary trials in December 2005 (see below). Grids on ridges were aligned north–south; grids in gullies were aligned parallel to the stream, on the more gently sloping side. A few grids in steep, narrow gullies had three rows, two with five ACOs and one with six. We placed ACOs on as flat a surface as possible with minimal vegetation underneath. When an ACO could not be placed 5 m from its neighbours because of rocks, tussocks, shrubs, or creeks, it was put in the closest suitable position.

ACOs were left in position for 4 weeks to allow lizards to become accustomed to their presence (Lettink & Cree 2007), and were then checked daily for 5 days beginning on 28 March 2006. We checked each treatment simultaneously and quickly, beginning at dawn (before sunrise) and finishing within about 2 hours. Most lizards were cold and inactive and therefore easy to capture during this time. Each ACO layer was lifted and any lizards were removed; when multiple lizards were found within one ACO they were held in cotton bags until they could be processed. We numbered lizards on the abdomen with a xylene-free silver or white liquid pen. Numbers remained visible, but not always clearly legible, for 5 days. After the ink was dry and species, SVL, snout-to-tail length, and any unusual features were recorded, each lizard was released into the layer of the ACO in which it had been found.

### *Weekly sampling*

Checking the ACOs daily appeared to result in a declining capture rate. Captures of geckos in ACOs at

Birdlings Flat also declined with daily checks (Lettink & Efford, unpubl.), and in the USA, more red-backed salamanders were found under wooden boards checked weekly or every 3 weeks compared with boards checked daily (Marsh & Goicochea 2003). Therefore, after completing daily sampling on 1 April, we checked the ACOs in the Fence and Removal treatments weekly for 5 weeks (six capture occasions), beginning on 13 April. Lizards were marked permanently by clipping one toe on each of two feet (one toe on one foot for geckos). The ACOs were removed after these checks in order to leave the habitat relatively unmodified in the long term.

We found common and McCann's skinks under discs cut from pine logs used for sampling invertebrates in March in a related study. Therefore, we checked the pine discs in addition to ACOs in the weekly capture session. A pine disc (c. 35-cm diameter and 10 cm thick; Bowie & Frampton 2004) was placed at each corner of a 20×20-m square, outside each 15×15-m grid of ACOs. Surface vegetation was removed by scraping with a spade, so that discs were placed on bare soil. Pine discs were set out during the week of 16 January 2006, checked for invertebrates on 28–29 March, and removed after the weekly lizard sampling.

### *Preliminary daily sampling protocol in December 2005*

We ran a preliminary trial of the sampling protocol on 12.5×5 grids of 25 ACOs with 5-m spacing. Three grids were placed in gully habitats and three in ridge habitats in each of the Fence and Removal treatments. Smaller 4×4 grids were established on 16–25 November 2005 and then enlarged on 9 December. We expected the ACOs to attract geckos and, to a lesser degree, skinks, based on the results of Lettink (2007) and Lettink & Cree (2007). To increase the likelihood of catching geckos, we placed two of the ridge grids in each treatment close to schist rock outcrops. The remaining grids were positioned arbitrarily at least 30 m apart.

We checked ACOs daily for 6 days beginning on 17 December, sampling the two treatments sequentially each day. On the first day ('day 0'), lizards were counted but not marked; on subsequent days they were numbered on the abdomen as described above. On day 0, the sun was high and skinks were active while we sampled the last grids (gully grids in the Fence treatment); we therefore started and finished earlier on subsequent mornings. Beginning on day 0, we baited the ACOs with 1 cm<sup>3</sup> of canned pear under each layer. On the following days, we baited only the top two layers, to encourage lizards into these layers where they were more easily captured. However, as the bait was often found partly eaten with no lizards present, it did not appear to increase the number of lizards caught. For this reason and because bait might

also attract mammalian predators, we did not use bait in subsequent sampling.

## Analytical methods

### *Counts of skinks*

Analyses of single-day counts were done for skinks only, all species combined, because few geckos were caught except in December 2005. Counts of skinks (including escapees) found in grids of ACOs on the first day of both daily sampling sessions (28 March 2006 and 17 December 2005) and the weekly sampling session (13 April) were compared between predator treatments and habitats with generalised linear models in GenStat (GenStat Committee 2002). The counts were assumed to follow a Poisson distribution with a dispersion parameter estimated by the model (i.e. allowing for the variance to be unequal to the mean). The most parsimonious model was chosen by including or excluding Treatment or Habitat terms or their interaction in order to minimise Akaike's information criterion (AIC; Akaike 1974). The statistical significance of differences between each predator treatment and the experimental control and between gully and ridge habitats was tested with approximate *t*-tests, based on the best model (GenStat Committee 2002). When there was a significant interaction between Treatment and Habitat (tested by comparing differences between gully and ridge habitats between the experimental control and each other treatment), data from each habitat were modelled separately to test for significant treatment effects.

### *Power analysis of count data*

We did a simple power analysis to predict how the number of ACO grids used would affect our ability to detect a difference in mean skink counts between treatments. We generated artificial count data from a Poisson distribution with the dispersion estimated from the March count data, within the design used in March, i.e. four treatments and two habitats. We varied the number of ACO grids per treatment-habitat combination from four to ten. In three treatments, the mean number of lizards per grid was set to 0.5, which was the lowest value we estimated in March. The difference between this mean and the mean of the fourth treatment was varied from 0 to 2.5, with an increment of 0.5. A generalised linear model (as described above), with Treatment and Habitat terms and an interaction term, was applied to the simulated data as above. This process was repeated 1000 times for each difference between means and each number of grids. Statistical power of each combination was recorded as the percentage of statistically significant tests ( $P < 0.05$ ) for treatment effects.

### *Lizard population size*

The population sizes ( $N$ ) of lizards at each sampling session were estimated with closed-capture models in program MARK (White & Burnham 1999). Skink and gecko data were analysed separately because of the behavioural and habitat differences between these taxa. A large enough sample of geckos for population estimation was obtained only in the December 2005 session.

Although the assumption of population closure was more valid for the daily sampling period (5 days) than for the weekly sampling period (5 weeks), several factors supported making this assumption for both periods. First, most lizard reproduction occurs in summer and would have been minimal in autumn (Patterson & Daugherty 1990; Cree 1994) during weekly sampling. Second, geckos and common skinks can survive at least 4 years in the presence of predators (Townes & Elliott 1996); mortality during the 5-week sampling period was therefore likely to be low, although possibly higher outside than inside the mammal enclosure. Finally, the home ranges of common skinks, at least, are thought to be very small (13.7 m<sup>2</sup>; Barwick 1959). A larger home-range estimate of >330 m<sup>2</sup> for McCann's skinks was based on the assumption that a lower recapture rate of this species compared with other species was the result of emigration from a trapping area of that size (Patterson 1985).

We used maximum likelihood estimation in program MARK to model several sources of heterogeneity in detection probability. Data from all four treatments were combined to jointly estimate detection probability (White 2005), i.e. we assumed that detection probability, but not population size, was equal between treatments. We fitted Huggins-Alho models (Huggins 1989, 1991; Alho 1990) of capture probability as an additive function of (1) three individual covariates (habitat, species and size class), (2) a behavioural response to previous capture, and (3) time (i.e. variation between capture occasions). Because the population estimate  $N$  includes animals never captured, for which covariates are unknown, it cannot be estimated as a parameter of these models. Instead, model likelihood is calculated by conditioning on the captured animals, and  $\hat{N}$  is then calculated as a derived parameter from the estimated capture probabilities (Huggins 1989, 1991; Alho 1990). The full model of capture probability  $p$  was

$$\text{logit}(p) = \beta_0 + \beta_1 \times \text{Hab} + \beta_2 \times \text{Size} + \beta_3 \times \text{SpM} + \beta_4 \times \text{SpC} + \beta_5 \times x + \beta_6 \times t_1 + \beta_7 \times t_2 + \beta_8 \times t_3 + \beta_9 \times t_4,$$

which is similar to the models tested by Conn et al. (2006) for captures of mice. Logit denotes the transformation

$$\text{logit}(p) = \log_e \left( \frac{p}{1-p} \right),$$

which was used to linearise the relationship between  $p$  and the dependent variables, as in a logistic regression. In this equation, the ratio

$$\frac{p}{1-p}$$

is the odds of a ‘success’ (MacKenzie et al. 2005), i.e. the probability of capturing an individual animal relative to the probability of not capturing it. The parameters  $\beta_i$  were estimated by MARK. The variables *Hab*, *Size*, *SpM*, *SpC*, and  $t_i$  were categorical variables or dummy variables (Table 1). We used discrete size classes instead of individual animal lengths, as in Conn et al. (2006), because our recapture rates were low and Huggins–Alho estimates can be unstable when either samples or some capture probabilities (e.g. for animals of a certain size) are small (Alho 1990; Pollock 2002). We classified lizards as adults or juveniles based on the minimum SVL at which each species attains maturity (Patterson & Daugherty 1990).

We ranked the fit of alternative models with and without the habitat, size class, species, behavioural response, and time variables, based on Akaike’s information criterion adjusted for small sample size (AICc; Akaike 1974; Hurvich & Tsai 1989). The variable *Size* was omitted in analyses of data from the December sampling trial, when SVL was not measured. Gecko data were analysed from the December sampling session only. The skink species variables (*SpM* and *SpC*) were omitted in analyses of gecko data.

The models described above were additive combinations of the traditional closed-capture models  $M_x$  where  $x$  represents different sources of heterogeneity in the capture probability of animals (Otis et al. 1978). Our full model corresponded to an  $M_{t\text{bh}}$  model, where  $t$  indicates time,  $b$  a behavioural response to capture,

and  $h$  individual heterogeneity. An alternative way to model individual heterogeneity is with mixture models, in which the population is assumed to comprise two or more types of individuals with different capture probabilities (Norris & Pollock 1996; Pledger 2000). Although these models are available in program MARK, our data were too sparse for them to be fitted.

We used model-averaging to combine information about  $\hat{N}$  from the entire set of candidate models, according to their Akaike weights, which are calculated based on the differences in AICc between each model and the best model (Burnham & Anderson 2002). Over-parameterised models, in which parameters were identified as singular, or standard errors of estimates were zero or very large (Cooch & White 2006; Conn et al. 2006), were first deleted from the model set. Confidence limits (95%) for model-averaged  $\hat{N}$  were calculated as suggested by White et al. (1999) – a formula that takes into account the total number of individuals caught (i.e.  $M_{t+1}$  in the notation of Otis et al. (1978)), as follows:

$$\left[ M_{t+1} + \frac{(\hat{N} - M_{t+1})}{C}, M_{t+1} + (\hat{N} - M_{t+1}) \times C \right],$$

$$\text{where } C = \exp \left( 1.96 \sqrt{\log_e \left[ 1 + \frac{\text{var}(\hat{N})}{(\hat{N} - M_{t+1})^2} \right]} \right),$$

We compared MARK’s model rankings to the results of model selection in program CAPTURE (Otis et al. 1978). Model selection was applied separately to the data from each treatment within each capture session.

**Table 1.** Variables used in alternative models of the capture probability of lizards.

Purpose	Name	Values	
		1	0
Habitat	<i>Hab</i>	Ridge	Gully
Size class <sup>1</sup>	<i>Size</i>	Adult	Juvenile
Species <sup>2</sup>	<i>SpM</i>	McCann’s skinks	Common or cryptic skinks
Species <sup>2</sup>	<i>SpC</i>	Cryptic skinks	Common or McCann’s skinks
Behavioural response to capture	$x$	Caught previously	First capture
Time	$t_i$ <sup>3</sup>	Capture occasion $i$	Other occasions

<sup>1</sup> Based on the minimum SVL at which each species attains maturity (Patterson & Daugherty 1990).

<sup>2</sup> Species variables were used in analyses of skink data only.

<sup>3</sup>  $i = 1 \dots T-1$  where  $T$  was the number of capture occasions in a capture session. All  $t_i$  were 0 for capture occasion  $T$ .

## Results

### Lizards caught

We marked more than 350 individual lizards in the three sampling sessions (Table 2); common skinks and McCann's skinks accounted for 85% of all lizards captured. Escapes were uncommon (10) except when skinks were active at the end of sampling on day 0 in December (8). A few cryptic skinks were caught in all sessions, only in gullies and primarily at the Fence treatment. Most geckos were caught in December 2005, and most of these (17 of 20 marked individuals) were caught at the ridge grids established near rock outcrops. Only four geckos were caught in the daily sampling session in March–April 2006, and only one gecko was caught in the weekly sampling session beginning in April 2006. A few other vertebrates were found under ACOs: two mice at Removal 2, and one mouse and an introduced whistling frog (*Litoria ewingii*) at the experimental control site. Individual skinks caught on more than one capture occasion were always under the same ACO, with the exception of two McCann's skinks that moved between adjacent ACOs in the weekly session. In contrast, about 25% of geckos moved between adjacent ACOs.

Checking ACOs daily appeared to result in a skink capture rate that declined with time (Fig. 1a, c). This pattern suggests a behavioural response to capture and/or to disturbance of ACOs. When ACOs were checked weekly, the number of skinks caught varied between capture occasions but did not decline consistently over successive occasions (Fig. 1b). At least some of the variation between capture occasions appeared to be related to recent weather conditions. In particular, the number of captures peaked on 28 April, 2 days after heavy rains that flooded some gullies (six ACOs at Fence and four at Removal were washed away and were replaced the day before they were checked). Also, the low capture rate toward the end of the weekly sampling may have occurred because cold autumn

weather made skinks inactive and in need of warmer shelter than ACOs provided.

The proportion of animals caught more than once relative to those caught only once was higher in geckos than in skinks ( $\chi^2_1 = 7.3$ ,  $P = 0.007$ ; Fig. 1c, d) in the trial daily checks of ACOs in December, suggesting a weaker behavioural response to capture by geckos than by skinks.

### Single-day counts of skinks

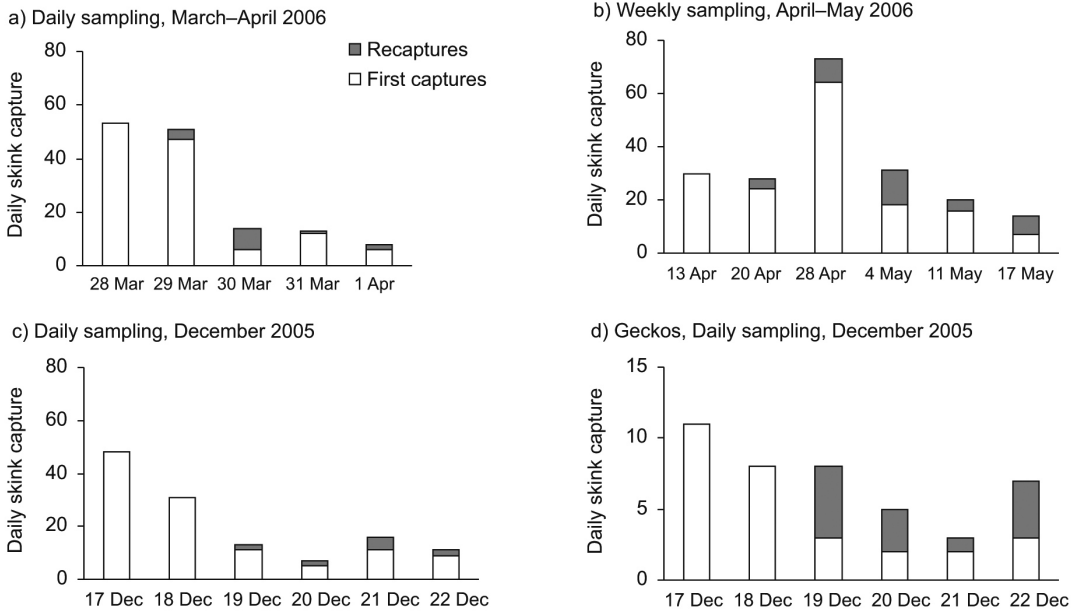
On 28 March, the first day of the daily sampling session, the estimated number of skinks per grid of 16 ACOs varied from 2.5 in gullies in the Fence treatment to 0.5 on ridges at the experimental control (Fig. 2a). The difference between the Fence and experimental control treatments was significant ( $t_{43} = 2.6$ ,  $P = 0.009$ ). There was no significant difference between numbers of skinks in the other predator removal treatments and at the experimental control ( $t_{43} < 1.5$ ,  $P > 0.14$ ) and no other significant differences between predator treatments (based on 95% CIs). Significantly more skinks were found in gully habitats than in ridge habitats ( $t_{43} = 2.1$ ,  $P = 0.032$ ). The most parsimonious model of skink counts retained both Treatment and Habitat factors but not their interaction ( $\Delta\text{AIC} = 0.6$ ).

On 13 April, the first day of the weekly sampling session, fewer than 0.7 skinks were found per grid of ACOs (Fig. 2b). Neither Treatment nor Habitat factors were included in the best model of skink counts. However, when skinks found under pine discs were included in the counts, significantly more skinks were found outside than inside the enclosure, on ridges ( $t_{10} = 3.4$ ,  $P = 0.007$ ; Fig. 2c) but not in gullies, and there was a significant interaction between Treatment and Habitat ( $t_{20} = 2.2$ ,  $P = 0.038$ ).

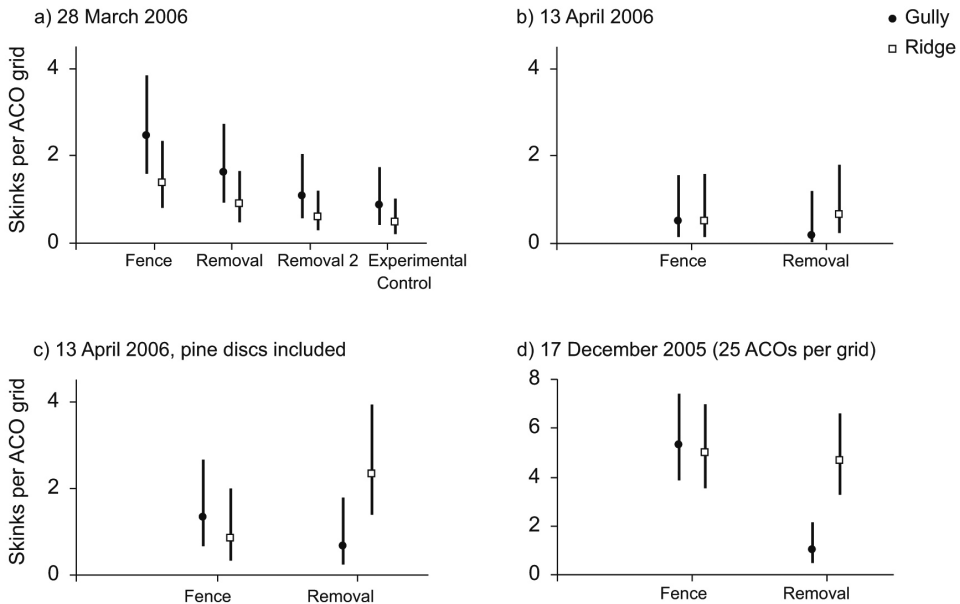
On 17 December 2005, the first day of the trial sampling session (day 0), the estimated number of skinks per grid of 25 ACOs varied from 5.3 in gullies inside the fence to 1.0 in gullies outside (Fig. 2d). Significantly more skinks were found inside than

Table 2. Numbers of individuals caught ( $M_{t+1}$ ) and numbers of recaptures of skinks in a daily capture session from 28 March to 1 April 2006, a weekly capture session in April–May 2006, and a daily capture session in December 2005, and of geckos in a daily capture session in December 2005. (December figures do not include animals caught on the first day of sampling (day 0) and not marked.)

Treatment	Skinks						Geckos	
	March 2006		April–May 2006		December 2005		December 2005	
	Individuals	Recaptures	Individuals	Recaptures	Individuals	Recaptures	Individuals	Recaptures
Fence	58	8	87	22	34	10	6	7
Removal	35	4	73	15	33	1	12	6
Removal 2	21	2						
Experimental control	10	1						



**Figure 1.** Number of first captures and recaptures of lizards on each day of capture-mark-recapture sampling under ACOs at Macraes Flat. (a) Daily sampling of skinks on 48 grids of 16 ACOs, (b) weekly sampling of skinks on 24 grids of 16 ACOs, (c) daily sampling of skinks on 12 grids of 25 ACOs, (d) daily sampling of geckos on 12 grids of 25 ACOs. In (c) and (d) animals were marked on the second and subsequent days only.



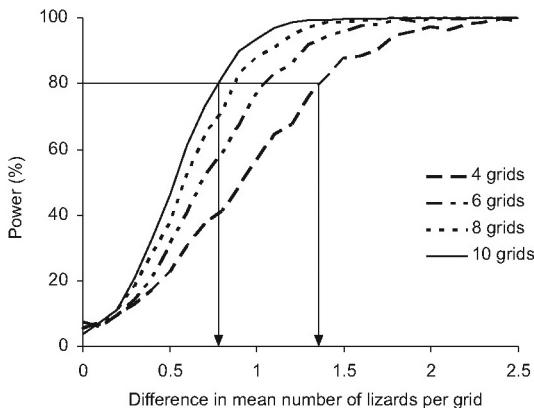
**Figure 2.** Estimated number of skinks (common skinks, McCann's skinks, and cryptic skinks) per grid of 16 ACOs based on counts on three mornings at Macraes Flat, in gully and ridge habitats at four sites with different levels of mammal control. In (c) skinks found under four pine discs at each grid are included; in (d) there were 25 ACOs per grid. Each graph is based on the best-fitting model for those data. Error bars show 95% confidence intervals.



outside the enclosure ( $t_8 = 4.0$ ,  $P < 0.001$ ). The best model included Treatment and Habitat and a significant interaction term ( $t_8 = 3.3$ ,  $P = 0.001$ ), which indicated that the difference between inside and outside was mostly due to a difference between gully grids (Fig. 2d). The estimated number of geckos on 17 December varied from 1.5 per grid on ridges to 0.3 in gullies (not shown). The difference between habitats was not significant ( $t_{10} = 1.4$ ,  $P = 0.153$ ) although the best model for geckos retained a Habitat factor ( $\Delta\text{AIC} = 0.6$ ) but not a Treatment factor ( $\Delta\text{AIC} = 1.9$ ).

### Power analysis of count data

The power analysis predicted that a sampling design with 10 ACO grids per treatment–habitat combination would have 80% power to detect a mean difference of at least 0.8 skinks counted per grid between one treatment and the other three, at a significance level of 0.05 (Fig. 3). That is, when a difference between one treatment and the other three of at least 0.8 exists, the generalised linear model would show a significant Treatment effect ( $P < 0.05$ ) 80% of the time. In contrast, four grids per treatment–habitat combination would give 80% power to detect a mean difference of 1.4 skinks per grid. The design we used with six ACO grids per treatment–habitat combination had 80% power to detect a difference of about 1.1 skinks per grid, whereas the actual difference between Fence and the average of the other treatments in March 2006 was 1.17 skinks per grid.



**Figure 3.** Predicted statistical power to detect between-treatment differences in the mean number of skinks per grid of ACOs, with four to ten grids of 16 ACOs, in each of four treatments. Arrows indicate the differences between one treatment and the other three that were detected in 80% of 1000 simulations with four and ten grids.

### Estimates of lizard population size

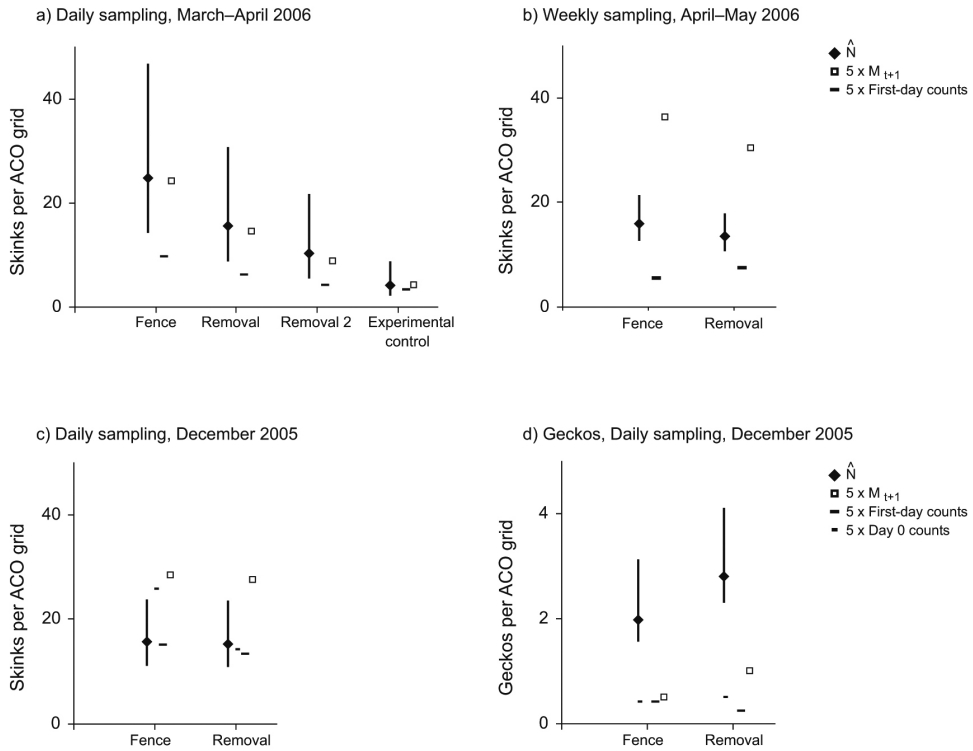
Model-averaged estimates of skink population size ( $\hat{N}$ ) based on daily captures in March 2006 were 24.7 at Fence and 15.6 at Removal, 10.4 at Removal 2, and 4.2 at the experimental control, per 15×15-m grid of ACOs, on average (Fig. 4a; sample sizes in Table 2). These estimates were much less precise than those based on weekly captures, which were 16.0 at Fence and 13.5 at Removal; i.e. both were similar to the daily estimate at Removal (Fig. 4b). Estimates of skink population sizes based on the trial daily sampling session in December 2005 were also similar: 15.7 at Fence and 15.4 at Removal, per 20×20-m grid (Fig. 4c). Although these grids covered 178% of the area of the 15×15-m grids used later, we preferred not to reduce  $\hat{N}$  arbitrarily based on the difference in areas without knowing more about the home ranges and movements of the animals. Model-averaged estimates of gecko population size in December 2005 were 2.0 at Fence and 2.8 at Removal, per 20×20-m grid (Fig. 4d).

### Factors affecting the capture probability of lizards

All the top models (those with the lowest AICc within each set of models) of skink capture probability included Time, and the top model for daily captures from March 2006 also included Habitat (Appendix). Models with Akaike weights  $> 0.1$  included Habitat, as well as Size and Species in the daily March captures, and Size in the weekly captures. In contrast, for geckos in December 2005 the top model included only Habitat but not Time, and one model with Akaike weight  $> 0.1$  also included a behavioural trap response.

Models with different sets of parameters often gave very different estimates of  $\hat{N}$ . For example, estimates for the Fence treatment with daily captures in March ranged between 61 and 333 (Appendix). Including a behavioural response tended to lower  $\hat{N}$  and including time or individual covariates tended to increase  $\hat{N}$ .

We deleted several models that combined both time variation and a behavioural response, in which the estimated SEs of  $\hat{N}$  were much larger than  $\hat{N}$  (more than 1.7 times as large; Appendix). Capture rates were low toward the end of all our capture sessions (Fig. 1), so that few data remained to model either behavioural responses or individual heterogeneity at these times. Because adding a behavioural component tended to reduce  $\hat{N}$ , we were concerned that deleting over-parameterised models may have led to positive bias in the model-averaged  $\hat{N}$ . For the daily skink captures in March, the collective Akaike weight of the six deleted models was 26%, suggesting that some may have been plausible. One deleted model ranked third, with a weight of 0.13. If this model was left in the model set,  $\hat{N}$  was reduced by  $< 1\%$ , but CIs increased by a factor of  $> 1.4$ .



**Figure 4.** Model-averaged estimates of population sizes ( $\hat{N}$ ) at Macraes Flat of (a) skinks (common skinks, McCann's skinks, and cryptic skinks) per grid of 16 ACOs, based on daily sampling within the four predator treatments, and (b) weekly sampling within the Fence and Removal treatments, and (c) skinks and (d) common geckos per grid of 25 ACOs, based on daily sampling within the Fence and Removal treatments. On a scale  $5\times$  that shown on the vertical axes, numbers of individuals captured ( $M_{t+1}$ ) and counts of skinks from the first day of capture-mark-recapture are also shown; (c) and (d) also show day 0 counts of skinks and geckos, respectively, when they were not marked. Error bars show 95% confidence intervals on  $\hat{N}$ .

One model was deleted from each of the model sets of daily captures of skinks and geckos in December; their highest Akaike weight was 0.08 and including them increased  $\hat{N}$  by up to 2.6% and increased CIs by at least  $3\times$ . In the weekly captures, the only deleted model with  $\hat{N}$  of the same order of magnitude as most other models ranked sixth with a weight of 0.04. Including this model increased  $\hat{N}$  by 7.5% and CIs by a factor of 13. However, we also deleted three other weekly capture models with  $\hat{N}$  inflated more than 100 times compared with most models and SEs 100 times greater still, which had Akaike weights between 0.11 and 0.04. Evidently, it was not possible to simultaneously estimate so many sources of variation in capture probability from our data. Although the effects on  $\hat{N}$  of omitting these models are unknown, it is encouraging that all the model-averaged  $\hat{N}$  were similar in the Fence and Removal treatments in March–May, except for the relatively high estimate for the Fence treatment based on daily sampling in March.

### Models selected by program CAPTURE

For skinks sampled daily, program CAPTURE selected the  $M_{tb}$  or  $M_b$  models, followed by  $M_{th}$  and  $M_{bh}$ . For skinks sampled weekly, program CAPTURE selected model  $M_{th}$  for Fence, and  $M_{tb}$ , with  $M_{th}$  second, for Removal. These model rankings indicate variation in capture probability due to time, behavioural responses to capture, and individual heterogeneity. In contrast, CAPTURE selected the  $M_0$  or  $M_{th}$  models for geckos, suggesting that geckos did not show strong behavioural responses to capture, but that variation in trappability with time and between individuals was present.

## Discussion

### Comparison of count indices between treatments

Comparing the estimated number of skinks per grid of ACOs between treatments, based on Poisson regression of single-day counts, led to the conclusion that skink

abundance was higher inside the fence than at the experimental control but did not differ significantly between the Fence and Removal treatments. These conclusions were consistent with our predictions, which were based on agricultural practices in the experimental control site and newly implemented predator management regimes at the other sites. However, when pine discs were included in the April counts, significantly more skinks were found on ridges outside than inside the fence. Whether this result reflects a true difference between treatments in skink abundance on ridges cannot be known without further sampling; instead it may be evidence that the count indices are not suitable for detecting small differences in density. In December, skink counts were significantly higher on our grids inside than outside the fence, but because some grids used in December were placed subjectively, this result cannot be extrapolated to the entire Fence and Removal treatment areas.

Power analysis of the count data showed that our sampling design was sufficient to detect an average difference of 1.1 skinks counted per grid, between one treatment and the other three, with 80% power. If higher power is desired, more ACO grids per treatment-habitat combination could be added. One reason to require higher power in future sampling sessions may be to look for small differences between the Fence and Removal treatments, in order to measure benefits of the predator enclosure to the relatively common skink species.

#### Utility of ACOs for capture-mark-recapture of small skinks and geckos

Our results demonstrate two potential weaknesses in the use of ACOs for CMR of small skinks. First, the rare movement by skinks between ACOs suggests either that the 5-m spacing we used was too large so that most home ranges spanned at most one ACO, or that skinks occupying ACOs defended them from other individuals. Both these factors would tend to increase the heterogeneity of capture probabilities between individuals, and could make some individuals untrappable. In addition, without information about inter-trap movements or home range sizes, it was not possible to estimate animal density ( $D$ ), i.e. the number of individuals per unit of area (Efford 2004; Efford et al. 2004). Second, behavioural responses of skinks to capture may lead to low recapture rates that both generate small samples and make estimation of  $N$  difficult with conventional analytical methods. Most researchers estimate  $N$  with program CAPTURE (McKelvey & Pearson 2001), which lacks models that combine a behavioural response with other sources of heterogeneity, i.e.  $M_{tb}$ ,  $M_{bh}$ , and  $M_{tth}$ . The commonly used 'jackknife' estimator  $M_h$ , although relatively robust to other sources of variation in capture probability (Otis et al. 1978), tends to overestimate  $N$  if trap-shy

responses result in few recaptures, because this pattern is interpreted as indicating a large population (McKelvey & Pearson 2001). Conversely,  $M_b$  underestimates  $N$  if other sources of heterogeneity are present (Otis et al. 1978). When the sample size is small (less than c. 100) and capture probabilities are low (less than c. 0.1), model selection in program CAPTURE may perform poorly so that the wrong model is chosen (Otis et al. 1978; Menkens & Anderson 1988; Hallett et al. 1991). AICc in MARK, may, however, be better at selecting models with a behavioural component when a behavioural response is present (Conn et al. 2004). These problems are not unique to ACOs, as common and McCann's skinks caught in pitfall traps may also exhibit trap-shyness or low recapture rates (Patterson 1985; Towns & Elliott 1996; Dixon 2004).

As geckos moved between adjacent ACOs more often than skinks did, the spacing of ACOs may have been more appropriate for sampling geckos. Geckos also seemed to have a weaker behavioural response to capture compared with skinks, as shown both by the relatively high recapture rate of geckos and by the top models selected by CAPTURE, i.e.  $M_0$  for geckos captured daily, versus  $M_{tb}$  or  $M_b$  for skinks captured daily and  $M_{tb}$  or  $M_{th}$  for skinks captured weekly. ACOs may prove more useful than pitfall traps for CMR of geckos in habitats where geckos are abundant, because geckos can climb out of pitfall traps (Towns & Elliott 1996; Wotton 2002). Finally, geckos appear to be less likely than skinks to defend ACOs against their congeners, since up to 14 geckos, but only one or two skinks, occupied individual ACOs at Birdlings Flat (Lettink & Cree 2007.). At Macraes Flat it may be possible to obtain sufficiently large samples of geckos by placing grids next to rock outcrops. Geckos that primarily occupy shrubs or trees can be sampled with ACOs designed for arboreal placement (Francke 2005).

#### Capture-mark-recapture estimates of lizard population size

Our model-averaged estimates of  $N$  are less likely to be biased than estimates based on any single closed-capture estimator, because model averaging accounted for several sources of variation in capture probability, weighted based on differences in AICc. Conn et al. (2006) found that model-averaged estimates with individual covariates yielded satisfactory population estimates for most known-size populations of mice. Both the declining rate of captures with time in our daily capture sessions and model selection by program CAPTURE indicated that behavioural response to capture was an important source of variation. However, since many of our models that included a behavioural response to capture were deleted because they were over-parameterised, model-averaging may not have adequately incorporated the effect of the behavioural

response, which considerably lowered  $\hat{N}$ . Our model-averaged estimates of  $N$  may therefore have been biased upwards.

In our analyses, capture probabilities were estimated by simultaneously analysing data from all treatments within each capture session. This approach was necessary so that small datasets, such as that from the experimental control, could be analysed, but it required the assumption of equal capture probabilities in all treatments (White 2005). This assumption may not always be valid. For example, if trap saturation occurs in large populations, detection probability may be inversely related to population size (Conn et al. 2006). When enough data are available, variation between treatments in capture probability can be tested explicitly by building a Treatment factor into the capture-recapture models in program MARK (Conn et al. 2006). Trap saturation was not a problem in our study, and because the habitats in the four treatments were superficially similar, we had no reason to suspect a difference in capture probability between treatments. In any case, we did not have enough captures at the Removal 2 or experimental control sites to test for such a difference.

Although we expected that assuming closure of skink populations during the 5-week period of weekly sampling would be reasonable (see Analytical methods), the increase in captures after heavy rain and flooding suggests an influx either of skinks from outside our grids, or of skinks on the grids needing shelter. Lack of closure would lead to a further positive bias in  $\hat{N}$  (Otis et al. 1978). However, since our estimates based on weekly and daily sampling correspond closely, especially at Removal, any biases resulting from the two approaches may have been small or similar. The consistency of the two sets of estimates with each other despite the different problems inherent in each method lends support to both.

Notwithstanding the expected positive biases discussed above, our skink population estimates are somewhat low compared with earlier estimates of skink numbers in tussock grassland. Dixon (2004) estimated there were 23–90 McCann's and common skinks per plot on two 20×20-m plots in tall tussock grassland in the Macraes Flat conservation reserve, based on pitfall trapping on grids of 36 traps with 4-m spacing. Patterson (1985) estimated there were up to 45 common and cryptic skinks (with abundance estimated separately for the two species) per plot on eight 20×20-m plots in lightly grazed tussock grassland in the Rock and Pillar Range in Central Otago, trapped on grids of 49 pitfall traps with 3-m spacing. If both trap-shyness and other sources of capture heterogeneity occurred in these earlier studies,  $N$  may have been overestimated by the  $M_{th}$  (jackknife) estimator (McKelvey & Pearson 2001) used by Dixon (2004), and underestimated by the  $M_{tj}$

(Zippin) estimator (Otis et al. 1978) used by Patterson (1985). Our estimates of  $N$  within the reserve (i.e. at all sites but the experimental control) correspond to 15–44 skinks per grid if results on our 15×15-m grids are adjusted based on total area for comparison with 20×20-m grids.

We have not stated lizard population estimates as densities because we do not know the size of the area sampled by a grid of ACOs. Although individual lizards were almost always recaptured under the same ACO, they may have been drawn to the covers from a large surrounding area. Alternatively, it is possible that an unsampled population of lizards existed between the ACOs, because home ranges were small or ACOs were defended against intruders. A practice common in CMR studies is to base density estimates on an 'effective trapping area' including the trapping grid plus a marginal strip equal to the radius of an average home range (Dice 1938), but our knowledge of skink home ranges (see Analytical methods) is inadequate for this approach. Another method is to set the width of the marginal strip equal to one-half the grid spacing; this calculation yields a grid area of 400 m<sup>2</sup> for the daily March sampling, 625 m<sup>2</sup> for the weekly April–May sampling that included the pine discs, and 625 m<sup>2</sup> for the December sampling. These values should be treated with caution until more is known of the movement patterns of the lizards.

The large SEs on  $\hat{N}$  in the models we deleted suggest this parameter may not be identifiable, i.e. cannot be estimated accurately from the CMR data, perhaps largely because of the behavioural trap response. Counts may therefore perform better than  $\hat{N}$  for comparing the abundance of lizards between treatments, although aspects of lizard behaviour such as territoriality may also weaken the utility of counts. An alternative, but labour-intensive, way to measure effects of predator control on lizards is to use CMR and open-population modelling to estimate their survival, which is more robust than  $\hat{N}$  to variation in capture probability (e.g. Pollock 1982).

### Relationship between counts and population sizes

Although count indices are commonly used to estimate wildlife population sizes, they should be so used only when one is confident that detection probability does not vary in a systematic way (Conn et al. 2006). This relationship ensures the counts will be proportional to population size. Although we standardised habitats and protocols, our one-day counts are vulnerable to effects of weather, which are likely to affect the diurnal movements of skinks and their use of artificial shelters. Our outlying observation of a high number of skinks at the Fence treatment on day 0 in December, when the sun was high and skinks were active, illustrates this problem, as do the high counts after heavy rain on 28

April. Differences between skink species in weather-related or seasonal changes in ACO use might also affect total lizard counts. Therefore, although using single-day counts of lizards to compare between treatments may be valid, using them to compare between different times (e.g. examining trends in annual counts to look for long-term effects of predator control) needs further testing.

The constancy of the relationship between single-day counts and  $\hat{N}$  can be tested by using the relationship observed between counts and  $\hat{N}$  in one trapping session to predict  $\hat{N}$  from first-day counts in a subsequent trapping session and then estimate  $\hat{N}$  from the associated CMR data (e.g. Slade & Blair 2000). In contrast, the strong relationships between counts from the first day of CMR, number of individuals captured ( $M_{t+1}$ ), and model-averaged population estimates in each treatment we observed in the daily sampling (Fig. 4a) were not surprising because the three variables were not independent. The first-day counts would have strongly influenced  $M_{t+1}$  because many lizards were caught on the first day, and  $\hat{N}$  is often linearly related to  $M_{t+1}$  when sample sizes are small (McKelvey & Pearson 2001). On the other hand, the negative relationship between counts and both population estimates and  $M_{t+1}$  obtained from weekly sampling in the Fence and Removal treatments (Fig. 4b) emphasises that counts cannot be expected to distinguish small differences in population size (Slade & Blair 2000).

### Recommendations for future sampling of skinks at Macraes Flat

The consistency between our predictions and conclusions based on the count indices suggests single-day counts may be useful indices of population size, when similar habitats are compared simultaneously so that weather and other conditions are identical. We propose to continue counting skinks in ACOs in late March each year, and to compare the relationships between these one-day counts and associated population estimates to our present results. Because of the poor precision of  $\hat{N}$  based on daily sampling, we prefer to use weekly sampling, although unusual weather events may weaken the assumption of population closure. We suggest that for CMR, ACOs should be placed 3 m apart (not 5 m), so that the home range of one skink is likely to encompass several ACOs. Closer spacing should reduce individual capture heterogeneity (Otis et al. 1978; Conn et al. 2006), and if skinks move between different ACOs on successive capture occasions we may be able to estimate their density (individuals  $m^{-2}$  or  $ha^{-1}$ ; Efford 2004; Efford et al. 2004). However, as this change in protocol would mean that counts, population estimates, and the relationship between the two will not be directly comparable between 2006 and 2007, it may be preferable to retain the present configuration for

the time being. We also propose to compare  $\hat{N}$  based on captures in ACOs, with  $\hat{N}$  based on CMR in pitfall traps arranged in grids with 3-m spacing, adjacent to the ACO grids. By comparing capture probabilities and sources of heterogeneity between the two methods, we will be able to explore likely biases in  $\hat{N}$  based on either method.

Finally, we emphasise that count indices are probably not suitable for comparing very different habitats, e.g. with large differences in vegetation types or in the amount of protective cover available for lizards. The considerable variation in the capture rate of skinks over time (Figs. 1a, b) suggests counts should also not be used to compare abundance between different times of year or periods of different weather. ACOs used for monitoring should not be left in place for the long term because they may enhance the habitat and create hotspots of unrepresentatively high lizard density (Souter et al. 2004; Lettink & Cree 2007).

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**Appendix.** Sets of models for each capture session, showing  $\Delta\text{AICc}$  (the increment in AIC compared with the best-fitting model, which has  $\Delta\text{AICc} = 0$ ), Akaike weights, number of parameters, and  $\hat{N}$  and its SE for the Fence treatment only. Models deleted from each set of candidate models before model averaging are also listed. Only models with weights  $> 0$  are shown. Model parameters are shown in Table 1; 'Behav' means a behavioural response to capture. In models denoted '.', capture probability was modelled as a constant.

a) Daily captures of skinks in March 2006

Model	$\Delta\text{AICc}$	Weight <sup>1</sup>	Parameters	$\hat{N}$	SE
Time + Habitat	0.0	0.49555	6	300.6	146.4
Time + Size + Habitat	1.9	0.18905	7	305.4	150.6
Time + Species + Habitat	2.3	0.15331	8	328.2	158.6
Time	3.9	0.07016	5	200.4	47.5
Time + Species + Size + Habitat	4.2	0.06158	9	333.9	163.0
Time + Species	7.5	0.01184	7	217.3	67.7
Time + Behav + Size	7.6	0.01108	7	92.0	53.6
Time + Species + Size	9.4	0.00448	8	220.1	70.1
Time + Behav + Species + Size	11.4	0.00166	9	97.3	84.1
Behav	14.2	0.00041	2	61.1	2.2
Behav + Habitat	14.2	0.00041	3	61.5	2.5
Behav + Size	16.2	0.00015	3	61.1	2.2
Behav + Size + Habitat	16.2	0.00015	4	61.5	2.5
Behav + Species + Habitat	17.5	0.00008	5	61.6	2.6
Behav + Species	18.0	0.00006	4	61.1	2.3
Behav + Species + Size + Habitat	19.4	0.00003	6	61.6	2.6
Behav + Species + Size	19.9	0.00002	5	61.2	2.3

<sup>1</sup> Model weights were calculated after the models below were deleted from the model set.

Deleted models	$\Delta\text{AICc}$	Weight	Parameters	$\hat{N}$	SE
Time + Behav + Habitat	2.0	0.13121	7	277	470
Time + Behav + Size + Habitat	3.9	0.05152	8	209	265
Time + Behav + Species + Habitat	4.3	0.04325	9	965	4965
Time + Behav	5.9	0.01863	6	262	2467
Time + Behav + Species + Size + Habitat	6.2	0.01622	10	425	1089
Time + Behav + Species	9.3	0.00353	8	$2.2 \times 10^5$	$1.9 \times 10^7$

(b) Weekly captures of skinks in April–May 2006

Model	$\Delta\text{AICc}$	Weight <sup>1</sup>	Parameters	$\hat{N}$	SE
Time	0.0	0.31174	6	199.1	28.1
Time + Habitat	0.8	0.20902	7	203.3	30.2
Time + Size	1.6	0.14074	7	202.0	29.8
Time + Size + Habitat	2.3	0.10015	8	206.7	32.0
Time + Species	3.4	0.05694	8	199.7	28.5
Time + Species + Habitat	4.4	0.03415	9	203.4	30.3
Time + Behav + Species	4.6	0.03089	9	112.8	22.3
Time + Species + Size	4.9	0.02696	9	202.7	30.2
Time + Behav + Species + Habitat	5.0	0.02499	10	110.3	19.0
Time + Behav + Species + Size + Habitat	5.2	0.02362	11	109.0	16.4
Time + Behav + Species + Size	5.2	0.02332	10	111.2	18.7
Time + Species + Size + Habitat	5.8	0.01747	10	206.8	32.1

<sup>1</sup> Model weights were calculated after the models below were deleted from the model set.



Deleted models	$\Delta AICc$	Weight	Parameters	$\hat{N}$	SE
Time + Behav	1.4	0.11294	7	$1.1 \times 10^5$	$8.9 \times 10^6$
Time + Behav + Habitat	2.3	0.07439	8	$1.6 \times 10^5$	$1.7 \times 10^7$
Time + Behav + Size	3.4	0.04298	8	$4.0 \times 10^4$	$5.2 \times 10^6$
Time + Behav + Size + Habitat	4.2	0.02894	9	575	3599

## c) Daily captures of skinks in preliminary trials in December 2005

Model	$\Delta AICc$	Weight <sup>1</sup>	Parameters	$\hat{N}$	SE
Time	0.0	0.65619	5	97.2	26.3
Time + Habitat	1.7	0.27999	6	97.9	27.3
Behav	6.3	0.02875	2	41.4	5.1
Behav + Habitat	7.2	0.01831	3	41.4	5.2
Behav + Species	8.8	0.00797	4	42.7	6.2
Behav + Species + Habitat	8.9	0.00766	5	44.4	8.0
.	13.5	0.00078	1	104.0	28.7
Habitat	15.1	0.00034	2	104.8	29.7

<sup>1</sup> Model weights were calculated after the models below were deleted from the model set.

Deleted models	$\Delta AICc$	Weight	Parameters	$\hat{N}$	SE
Time + Behav + Habitat	3.8	0.08792	7	101	309
Time + Behav + Species + Habitat	6.7	0.02092	9	1988	3344

## d) Daily captures of geckos in preliminary trials in December 2005

Model	$\Delta AICc$	Weight	Parameters	$\hat{N}$	SE
Habitat	0.0	0.42001	2	13.0	4.0
.	1.3	0.22325	1	11.2	2.6
Behav + Habitat	1.8	0.17177	3	10.9	3.6
Behav	3.2	0.08573	2	10.1	2.8
Time + Habitat	4.5	0.04441	6	12.7	3.8
Time	5.7	0.02484	5	11.0	2.5

Deleted models	$\Delta AICc$	Weight	Parameters	$\hat{N}$	SE
Time + Behav + Habitat	6.4	0.01694	7	30	87
Time + Behav	6.9	0.01304	6	$2.1 \times 10^4$	$3.1 \times 10^6$