

## Assessing and comparing population densities and indices of skinks under three predator management regimes

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Published online: 22 September 2016

**Abstract:** Introduced mammalian predators threaten populations of endemic New Zealand skinks. Their effects on skink populations have been not often quantified on the mainland and are known primarily from skink population increases on islands from which mammals have been eradicated. Estimating skink population density with capture–recapture trapping is time-consuming and costly. Counting skinks in artificial retreats in specific weather conditions may be a useful and relatively quick way to index population density, but needs calibration for different habitats and species. In 2007 and 2009, we estimated the population density of small terrestrial skinks (McCann’s skink *Oligosoma maccanni*, southern grass skink *O. aff. polychroma* clade 5 and cryptic skink *O. inconspicuum*), based on spatially explicit capture–recapture (SECR) in pitfall traps in three mammal-management treatments at Macraes Flat, Otago. The treatments were eradication of large predators and near-eradication of rodents inside a mammal-resistant fence, suppression of mammalian predator populations through continuous trapping (two locations within an extensive area), and no mammal management. We tested for relationships between the estimated population densities and dawn and late-morning counts of skinks in artificial retreats. Skink density (three species combined) ranged from c. 1200 per ha at the experimental control site to c. 4000 per ha at the fenced site. These treatment differences in skink density may be the combined effect of predator management and pre-existing differences due to habitat characteristics and farming practices. Skink counts done in late morning (2009) were related to estimated skink densities but did not differ significantly between treatments. Skink counts done at dawn (both years) were not related to densities. Counts, but not densities, were significantly higher at locations with a more northerly aspect. We recommend further investigation of the utility of skink counts in artificial retreats for monitoring skink density at this location, with careful control of ambient temperature during sampling, and of aspect, habitat and device placement.

**Keywords:** artificial cover object; artificial retreat; count; lizard; mammal-proof fence; monitoring; New Zealand; pitfall trap; SECR; spatially explicit capture recapture

## Introduction

Endemic New Zealand skinks are threatened by introduced mammalian predators, including feral cats (*Felis catus*), mustelids (*Mustela* spp.), European hedgehogs (*Erinaceus europaeus*), and rodents (rats *Rattus* spp. and house mice *Mus musculus*) (King 2005). When humans arrived in New Zealand in c. AD 1280 (Wilmshurst et al. 2008), bats were the only terrestrial mammal. Populations of many skink species have recovered after rats or mice were eradicated from offshore islands (Newman 1994; Towns & Broome 2003; Towns et al. 2003; Monks et al. 2014). More recently, studies on the New Zealand mainland have shown that removing or excluding mammals can increase the survival and/or abundance of skinks (*Oligosoma* spp.) (Lettink et al. 2010; Reardon et al. 2012; Jones et al. 2013; Norbury et al. 2013, 2014).

Predatory mammals are managed with both exclusion fencing and extensive trapping in mixed grassland–shrubland habitat near Macraes Flat in eastern Otago, South Island, to protect remnant populations of the endangered grand skink (*Oligosoma grande*) and Otago skink (*O. otagense*) (Reardon et al. 2012). Several smaller skink species (southern grass skink *O. aff. polychroma* clade 5 (formerly called common skink), McCann’s skink *O. maccanni* and cryptic skink *O.*

*inconspicuum*; nomenclature based on Hitchmough et al. (2013) and Bell (2014)) are common in this region. In 2006, we used artificial retreats (also known as cover boards or artificial cover objects) to sample these small skinks in three different predator management treatments at Macraes Flat (Wilson et al. 2007). We counted more skinks in retreats inside a mammal-resistant fence (c. two skinks per grid of 16 retreats) than at a site with no mammal management (c. 0.7 skinks per grid) at dawn on a single morning in late March 2006.

In the same study, we estimated skink population sizes based on capture–recapture (CR) of skinks found in the retreats, expressed as numbers of skinks per grid of retreats (Wilson et al. 2007), but these estimates were low relative to results of earlier studies in nearby locations, in which skinks were captured in pitfall traps (Patterson 1985; Dixon 2004). We may have underestimated skink numbers by failing to sample part of the population, possibly because home ranges were small relative to the 5-m spacing between devices (see Lettink et al. 2011), large or dominant individuals defended the retreats against intruders (Batson et al. 2015), or sampling was done in sub-optimal conditions (Hoare et al. 2009; Lettink et al. 2011). We did not calculate skink population density (numbers per ha) because we lacked spatial data describing skink movements and home ranges, as most recaptured individuals were found

repeatedly in the same retreat. We recommended using pitfall traps spaced closely together (3 m apart) to increase the chance of skinks moving among them. Skink population density could then be estimated on the basis of spatially explicit capture–recapture (SECR) (Efford 2004; Borchers & Efford 2008; Efford & Fewster 2013), a relatively new analytical method that estimates spatial detection parameters on the basis of recapture locations of individual animals.

Because CR studies are time-consuming and costly, more rapid index methods are frequently sought to assess the relative abundance of cryptic animals for research and monitoring (e.g. Bailey et al. 2004; Hoare et al. 2009; Lettink et al. 2011). Counts of individuals are often used, requiring the assumptions that counts are consistently (usually linearly) related to population density and that the probability of detecting an animal is constant over time and space (Pollock et al. 2002; Bailey et al. 2004; Conn et al. 2006). Lettink et al. (2011) found that when southern grass skinks were counted in artificial retreats in certain ‘optimal’ weather conditions in grassland in the Eglinton Valley (Fiordland), the counts provided an index of skink population size. That is, skink counts in retreats on days with optimal conditions were linearly related to population sizes estimated with CR in pitfall traps at eight trapping grids, and counts were highly repeatable between days. They recommended calibration of this relationship for other habitats and other skink species.

Here we estimate skink density on the basis of SECR in pitfall traps at Macraes Flat, in the same three mammal-management treatments as in our earlier study, and test for a relationship between density estimates and counts of skinks in artificial retreats. The pitfall trapping and retreat counts were done in 2007 and 2009, about 1 and 3 years, respectively, after the predator management treatments were implemented. We also test for changes in skink counts since our earlier study (in 2006; Wilson et al. 2007), and for effects of northerly and westerly aspect on skink counts and densities. The mammal-management treatments were: (1) eradication of large predators and near-eradication of rodents inside a mammal-resistant fence; (2) suppression of mammalian predator populations through continuous trapping (two locations within an extensive area); and (3) no predator management (an experimental control site outside the conservation area).

## Methods

### Study site and species

This research was done near Macraes Flat, eastern Otago (45°27' S; 170°26' E; 400–600 m a.s.l.), on reserve land managed by the Department of Conservation’s Grand and Otago Skink (GAOS) Recovery Programme. The vegetation has been highly modified by farming practices, including burning, top-dressing with fertiliser, over-sowing, grazing by livestock, and browsing by introduced herbivores, primarily rabbits (*Oryctolagus cuniculus*), but no burning or fertilising had been done within the reserve for more than 10 years prior to our study (Whitaker 1996). Tall-tussock grassland now predominates (narrow-leaved snow tussock *Chionochloa rigida* and silver tussock *Poa cita*, with hard tussock *Festuca novae-zelandiae* in dry places and red tussock *C. rubra* in damp places). Inter-tussock vegetation is a mixture of indigenous and exotic grasses, forbs, subshrubs and mosses. There are also extensive schist rock outcrops and, especially in stream

gullies, patches of seral shrubland (matagouri *Discaria toumatou*, mānuka *Leptospermum scoparium*, kānuka *Kunzea* spp., *Coprosma* spp. and *Olearia* spp.).

Southern grass 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 79 mm, 73 mm and 75 mm, respectively (Jewell 2008).

### Predator management treatments and lizard sampling

Two regimes for managing mammalian pests were in place at Macraes Flat: near-eradication in mammal-resistant (i.e. mammal-proof, except for house mice) fenced enclosures; and suppression of predatory mammals, except for house mice, through extensive trapping. We worked in an 18-ha mammal-resistant enclosure (Xcluder™ Pest Proof Fencing, Cambridge, NZ) that was completed in June 2005, with mammals eradicated 14 months later, except for occasional incursions by rabbits and mice (Reardon et al. 2012). Continuous lethal trapping of feral cats, feral ferrets (*Mustela furo*), stoats (*M. erminea*), weasels (*M. nivalis*), Norway rats (*Rattus norvegicus*) and hedgehogs from 2100 ha surrounding this mammal enclosure was implemented by January 2006 (Reardon et al. 2012). The predators caught most frequently during 2006–2008 were hedgehogs, cats and ferrets (Reardon et al. 2012). Between September 2008 and January 2009, the trapped area was permanently extended to 4660 ha, with some traps placed within 1 km of our experimental control site.

We sampled skinks 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-resistant fence; (2) removal: immediately outside the fence, within the area where mammals are removed through extensive trapping as described above; (3) removal 2: the central core of the mammal removal area, more than 1 km from sites 1 and 2; and (4) experimental control: no mammal management or restrictions on agricultural use, more than 5 km from sites one to three (but within 1 km of predator traps in 2009, see above).

Sites (1), (3) and (4) correspond to sites A, B and E in Reardon et al. (2012). Livestock were excluded from sites (1), (2) and (3) with fences. We sampled all four sites in March 2006 (Wilson et al. 2007), March 2007 (with artificial retreats at all four sites but pitfall traps at sites (1) and (2) only) and March 2009.

### 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, which were dominated by tussock grasses. Within each treatment, a generalised random tessellated stratified design (GRTS; Stevens & Olsen 2004) was used to position six sampling points (at least 30 m apart) across each habitat type; one small trapping grid was placed at each point (described in detail below). A sampling design with traps in scattered clusters can be effective where the density of the target population varies spatially, if spatial methods such as SECR are used

to model variation in capture probability that results from the edge effects on small trapping grids (Efford & Fewster 2013). We later removed some grids from analyses because they were grazed by sheep (two removal grids, inadvertently established outside livestock fences and therefore with much less vegetation cover than other grids in fence, removal and removal 2), and in 2009 also because the pitfall traps were disturbed (one removal grid with bait missing from 75–88% of traps on days 3–5 and some trap covers disturbed, probably by rabbits or brushtail possums *Trichosurus vulpecula*) or their contents preyed upon (one experimental control grid with two skink tails in traps and one cover disturbed, probably by rodents or mustelids, and only two live captures). The resulting number of grids was 46 in 2007 and 44 in 2009.

### Estimating the population density of skinks: field methods for SECR in pitfall traps

We designed our methods to maximise skink recapture rates for SECR analysis by: (1) spacing pitfall traps only 3 m apart, (2) attempting to reduce trap-shyness by adding cover inside pitfall traps and minimising handling of skinks by not weighing or sexing them, and (3) combining data from many small trapping grids for analysis. In 2007, we established a grid of 16 pitfall traps at five of the six (because of difficulty fitting grids into some narrow gullies) gully sampling points and all of the ridge sampling points in each of the fence and removal treatments (21 pitfall grids). In 2009, we established grids of pitfall traps at all sampling points in all four treatments (44 pitfall grids). Pitfall traps, arranged in four rows and four columns with 3-m spacing, were set out 1–2 weeks before trapping began on 25 March 2007 and 22 March 2009, and were removed after each trapping session. In some narrow gullies we used other grid configurations, usually three rows of five or six traps. Pitfall traps were 100-mm diameter, 750-ml plastic pots, each with drainage holes and a 150 × 150 mm raised plywood cover. Soil or plant litter was placed in each trap to provide cover for captured animals (Lettink et al. 2011). Traps were baited daily with one cm<sup>3</sup> of canned pear and checked each morning on 5 consecutive sampling days, concurrently at all treatments.

Each new, unmarked skink caught in a pitfall trap was marked by clipping one toe on each of two feet, and released after recording its SVL, species and any unusual features. Naturally missing toes were incorporated into our identification system and at most one additional toe was clipped. In 2009, we also used xylene-free silver paint pens to dot the head of each new capture to facilitate identification of recaptures, as naturally missing toes were common. Recaptured animals were released quickly after recording their toe-code. Otago skinks, which are nationally endangered (Hitchmough et al. 2013), were released promptly with no marking or measuring.

### Estimating the population density of skinks: analytical methods

The population density of skinks (skinks per ha) was estimated in each treatment and habitat type with SECR models (Efford 2004; Borchers & Efford 2008; Efford & Fewster 2013). We assumed that populations were closed during each 5-day trapping session (i.e. that no reproduction, mortality, immigration or emigration occurred during these periods). Spatial detection models, representing daily capture probability as a function,  $g$ , of the distance between a trap and the centre of a skink's home range (Efford 2004), were fitted to the capture data by maximising the full likelihood. The function took the

form of a half-normal function with width  $\sigma$  m. Two spatial detection parameters were estimated:  $g_0$ , the probability of capture (per day) in a trap located at the centre of the home range (i.e. at 0 m), and  $\sigma$  (m). Skink home range centres were assumed to be spatially randomly distributed according to a Poisson point process with a density parameter (Efford 2016) estimated from the capture data.

We modelled the density of southern grass skinks, McCann's skinks and cryptic skinks combined, in each treatment–habitat combination, with separate SECR models for 2007 and 2009. Species were combined to maximise sample size and to remove effects of any species identification errors (five such errors were detected in 2007 only). Density was modelled as an additive function of treatment and habitat, by treating each grid as a 'session' and treatment and habitat as session covariates (with a different level for each treatment and habitat) in package *secr* (version 2.5.0; Efford 2016) in program R (version 2.15.3; R Core Team 2016). For each year, we compared alternative models for all sessions (grids) combined in which  $g_0$  was constant (i.e. the null model) or an additive function of time (sampling day), alternative behavioural responses to capture, and/or either species, habitat or size (adult or juvenile based on SVL; Wilson et al. 2007). We also compared models in which  $\sigma$  was a function of species or habitat, only in combination with species or habitat models, respectively, for  $g_0$ . In time models,  $g_0$  varied between the 5 days of the capture session (e.g. owing to weather conditions). Four alternative types of behavioural responses to capture (Efford 2016) were considered (Table 1):

$b$ , a permanent response in which an animal's probability of capture increased (a trap-happy response) or decreased (trap-shy) after its first capture

$bk$ , a trap-specific permanent response in which an animal became trap-happy or trap-shy in relation to a particular trap (e.g. Royle et al. 2011)

$B$ , a transient behavioural response (Markovian response) in which an animal became trap-happy or trap-shy only if it had been captured on the preceding capture occasion (day)

$Bk$ , a trap-specific transient behavioural response.

We did not use a continuous size variable (SVL) as in Lettink et al. (2011) because SVL ranges differ between the three skink species, and including both species and SVL generated an unwieldy number of complex alternative models. Models were compared on the basis of Akaike's Information Criterion adjusted for small sample size (AIC<sub>c</sub>; Burnham & Anderson 2002). We took estimates of  $g_0$ ,  $\sigma$  and skink densities from the best-supported model for each year; or when more than one model was supported ( $\Delta$ AIC<sub>c</sub> < 8), we used model-averaging (Burnham & Anderson 2002) to calculate weighted estimates from models with weight > 0.01.

To evaluate model goodness-of-fit, we tested whether our top-ranked SECR models could generate capture data similar to ours; if not, we may have failed to model some source of variation in capture probability. We used function *sim.secr* to generate 100 capture histories from each of the five best-supported models (those with the lowest AIC<sub>c</sub>) from 2007 and 2009. Many of these models had little support, but we included them in order to observe effects of alternative



**Table 1.** Additive SECR models of variation in density  $D$  and spatial detection parameters  $g_0$  and  $\sigma$ , fitted to capture data of skinks at Macraes Flat, Otago. Data from 2007 and 2009 were modelled separately.  $D$  was a function of treatment + habitat in all models. At most one of  $b$ ,  $bk$ ,  $B$  or  $Bk$  were included in a model, and at most one of species, habitat, and size class. Species and habitat models for  $\sigma$  were fitted only in combination with species or habitat models, respectively, for  $g_0$ .

Parameter	Factor	Levels	Values
$D$	treatment	2 (2007)	fence, removal
		4 (2009)	fence, removal, removal 2, experimental control
	habitat	2	gully, ridge
$g_0$	null	—	—
	species	3	southern grass, McCann's, cryptic
	habitat	2	gully, ridge
	size class	2	adult, juvenile
	time	5	days 1–5 of capture session
	$b$	2	0 (first capture) or 1 (captured previously)
	$bk$	2	0 (first capture) or 1 (captured previously)
	$B$	2	0 (not captured on previous day) or 1 (captured on previous day)
$Bk$	2	0 (not captured on previous day) or 1 (captured on previous day)	
$\sigma$	null	—	—
	species	3	southern grass, McCann's, cryptic
	habitat	2	gully, ridge

behavioural response parameters on model fit. For each model, we compared mean numbers of individuals caught and mean numbers of recaptures in the 100 simulated capture histories to our actual capture histories from pitfall trapping.

### Counting skinks in artificial retreats

A grid of 16 artificial retreats was established 10 m from each grid of pitfall traps, arranged in four rows and four columns, but with 5-m spacing between retreats for consistency with our previous study (Wilson et al. 2007). In 2007, artificial retreats were set up at all four treatments, although pitfall trapping was done only at fence and removal. Retreats were set out 3–4 weeks before trapping began and removed after it was completed each year. Artificial retreats were three-layer stacks of  $40 \times 28$  cm sections of Onduline roofing material (distributed by Composite Insulation, Christchurch, NZ) with separators to create 1 cm gaps between the layers (Lettink & Cree 2007; Wilson et al. 2007). In exposed locations, rocks were placed on the retreats to prevent displacement by wind. We measured the aspect of each grid of retreats in 2009, and calculated northerly and westerly aspects, each as  $0$ – $180^\circ$  where  $180^\circ$  indicated due north or due west, respectively. These calculated aspects were used as indices of sunshine during the day and afternoon, which could affect skinks' use of retreats (Walker et al. 2014).

Lizards occupying artificial retreats were counted on the first or second day of pitfall trapping in 2007 and 2009, beginning at dawn when lizards were cold and inactive. In 2009, lizards in and on retreats were also counted 4 days later, in late morning when the sun was high and skinks were active. We checked retreats concurrently at all treatments, inspecting each layer and quickly searching the vegetation underneath. In 2007, lizards in retreats were captured and measured but not marked. In 2009, we marked each lizard found during the dawn retreat check with two head dots and measured it; in the late-morning check we did not capture warm, active lizards

but just recorded species and any resightings on the basis of dotted heads. We obtained hourly minimum and maximum temperatures during retreat checks from the nearest climate stations at Middlemarch, c. 25 km southwest of our study area but at lower altitude (200 m a.s.l.), and Ranfurly, c. 40 km northwest and at similar altitude (400 m a.s.l.) (The National Climate Database, NIWA). No rain fell during counts.

### Testing for relationships between skink density and counts in artificial retreats

We tested whether estimated skink density at each grid predicted the number of skinks counted in retreats at each grid. We selected this analysis, instead of testing whether skink counts predicted densities, because (1) density might be expected to influence counts, rather than the reverse, (2) the continuous variable representing estimated densities was likely to be a more robust predictor than discrete counts with a small range of values, and (3) the discrete counts made a suitable Poisson response variable. However, we also conducted exploratory analyses of whether skink counts predicted densities (linear models with both variables  $\log_e$ -transformed).

We fitted a separate generalised linear mixed-effects model for Poisson-distributed data, with a log link, for each of two response variables: the number of skinks counted at each retreat grid at (1) dawn in 2007 and 2009 and (2) late morning in 2009. We fitted grid as a random effect because the same grids were remeasured in 2 years in (1), and to account for overdispersion in (2). Explanatory variables fitted as fixed effects were treatment, skink density (individuals per ha) estimated at each pitfall trap grid in that year, habitat, and its interaction with density. Additional fixed effects in the dawn count model were year (2007 or 2009 as a categorical variable) and the time when counts were finished at each treatment in each year (minutes), which could affect whether skinks remained inactive in retreats while these were checked. We did not include temperature as it was correlated with year ( $r = 0.63$ ). We also

did not include aspect variables, which were likely to be related to both density and counts, and could therefore obscure any relationship between these two variables. Skink density at each grid was derived in secr as the number of individuals captured there, divided by the grid's estimated effective sampling area determined by  $g_0$  and  $\sigma$  (Borchers & Efford 2008). Prior to analysis, we  $\log_e$ -transformed densities to achieve normality and reduce the leverage of outlying estimates. We rescaled continuous variables to have mean 0 and standard deviation 0.5 by subtracting the mean and dividing by two standard deviations; placing input variables onto a common scale in this way aids interpretation of model coefficients (Gelman 2008) and improves numerical stability. We concluded that collinearity of variables would not substantially increase variance estimates, on the basis of variance inflation factors (function vif in the faraway package in R; Allison 1999; Hair et al. 2010). A fixed effect was considered statistically significant ( $P < 0.05$ ) when the 95% CI of its coefficient excluded zero. Models were fitted in the lme4 package (Bates et al. 2015) in R version 3.2.5.

### Testing for a temporal trend in dawn skink counts in artificial retreats, and for effects of aspect

We used a repeated-measures analysis to test for changes over time in dawn counts from 2006 (Wilson et al. 2007), 2007 and 2009 (this study), by fitting a single generalised linear mixed-effects model for Poisson-distributed data, with a log link. The response variable was the number of skinks counted at each retreat grid at dawn in each year. For this analysis, we used only grids that were measured in all years. Grid was a random effect, because each was remeasured repeatedly over time. The fixed-effect predictor variables were year (as a continuous variable), treatment, the interaction between year and treatment, habitat, northerly and westerly aspects of each retreat grid, two-way interactions between these last three variables (Walker et al. 2014), and the time when counts were finished at each site in each year (as above). We rescaled variables, tested for collinearity, and determined statistical significance as described above.

The above model allowed us to test for effects of aspect on dawn skink counts in artificial retreats. We used a similar model, without the variables year or finish time (nor a habitat

$\times$  westerly aspect interaction, with which the model failed to converge), to test for effects of aspect on late-morning counts done only in 2009. Finally, we used a linear mixed-effects model to test whether aspect affected skink densities. The response variable was  $\log_e$  (skink density), derived as above (see 'Testing for relationships between skink density and counts in artificial retreats'). Predictor variables were treatment, year (categorical), habitat, northerly and westerly aspect, and two-way interactions between these last three variables.

When presenting results of our mixed-effects models, we calculate the magnitude of important effects by unscaling relevant model coefficients. We provide marginal  $R^2$  (variance explained by fixed effects only) and conditional  $R^2$  (variance explained by both fixed and random effects) as measures of model goodness-of-fit (Nakagawa & Shielzeth 2012).

## Results

### SECR model selection and estimation of skink population densities

We caught 763 individual skinks (946 captures) of the target species in pitfall traps in 2007 and 1164 skinks (1467 captures) in 2009. Most captures were of southern grass skinks and McCann's skinks; only 16 cryptic skinks were caught in 2007 and 50 in 2009, most at the fence treatment and all in gully habitat. We also captured two juvenile Otago skinks and three *Woodworthia* 'Otago/Southland' geckos (taxonomy in Nielsen et al. 2011). Daily maximum air temperature during pitfall trapping sessions ranged between 21.4–30.9°C and 19.6–28.4°C in 2007, and 11.9–22.1°C and 13.2–23.7°C in 2009, at the Middlemarch and Ranfurly climate stations, respectively (see Methods).

Only two of our alternative SECR models were supported by the capture data in 2007 ( $AIC_c$  weights = 0.7 and 0.3) and only one in 2009 ( $AIC_c$  weight = 1.0) (Tables 2, 3). All of these top-ranked models had  $g_0$  varying by day and positive (trap-happy) behavioural responses to capture. In 2009, a permanent trap-specific behavioural response ( $bk$ ) had unequivocal support. In 2007, the best-supported model (on the basis of  $AIC_c$ ) had a transient behavioural response ( $B$ ), but a permanent trap-specific behavioural response ( $bk$ )

**Table 2.** The five best-supported SECR models estimating skink density at Macraes Flat, Otago, based on captures in 2007. Models of spatial detection parameters  $g_0$  and  $\sigma$  are shown; density was modelled as a function of treatment + habitat in each case.  $\Delta AIC_c$  shows the difference in  $AIC_c$  score between each model and the best model. For all other models, not shown here,  $\Delta AIC_c > 275$  and model weight = 0. Some models with weight  $\leq 0.01$  are included here for comparison with 2009 models and to illustrate effects of alternative behavioural response parameters on density estimates. The behavioural response parameters are  $b$ , a permanent change in capture probability after an animal's first capture;  $bk$ , a trap-specific permanent response;  $B$  a transient response to capture on the preceding occasion (day); and  $Bk$ , a trap-specific transient response. Estimated density (and SE) at the fence treatment in gully habitat and the mean number of recaptures in simulations based on the model (% of actual recaptures) are also shown.

$g_0$ model	$\sigma$ model	Parameters	Log(likelihood)	$\Delta AIC_c$	Model weight	Density (SE) at fence, gully	Simulated recaptures (% of actual, i.e. 183)
<i>time</i> + $B$	constant	10	-2213.6	0.0	0.70	4774 (484)	82
<i>time</i> + $bk$	constant	10	-2214.5	1.8	0.29	4360 (432)	81
<i>time</i> + $Bk$	constant	10	-2217.7	8.2	0.01	4101 (366)	95
<i>time</i>	constant	9	-2224.1	19.0	0.00	3965 (337)	106
<i>time</i> + $b$	constant	10	-2224.1	21.0	0.00	4250 (1348)	90

**Table 3.** The five best-supported SECR models used to estimate skink density at Macraes Flat, Otago, based on captures in 2009. Models of spatial detection parameters  $g_0$  and  $\sigma$  are shown; density was modelled as a function of treatment + habitat in each case.  $\Delta AIC_c$  shows the difference in  $AIC_c$  score between each model and the best model. For all other models, not shown here,  $\Delta AIC_c > 370$  and model weight = 0. Some models with weight 0 are included here for comparison with 2007 models and to illustrate effects of alternative behavioural response parameters on density estimates. Behavioural response parameters  $b$ ,  $bk$ ,  $B$  and  $Bk$  are as defined in Tables 1 and 2. Estimated density (and SE) at the fence treatment in gully habitat, and the mean number of recaptures in 100 simulations based on the model (% of actual recaptures), are also shown.

$g_0$ model	$\sigma$ model	Parameters	Log(likelihood)	$\Delta AIC_c$	Model weight	Density (SE) at fence, gully	Simulated recaptures (% of actual, i.e. 303)
<i>time + bk</i>	constant	12	-3849.1	0.0	1.0	3500 (327)	67
<i>time + Bk</i>	constant	12	-3872.2	46.2	0.0	3267 (264)	87
<i>time + b</i>	constant	12	-3893.3	88.4	0.0	2157 (283)	179
<i>time + B</i>	constant	12	-3893.9	89.7	0.0	3331 (294)	92
<i>time</i>	constant	11	-3895.7	91.2	0.0	3072 (227)	103

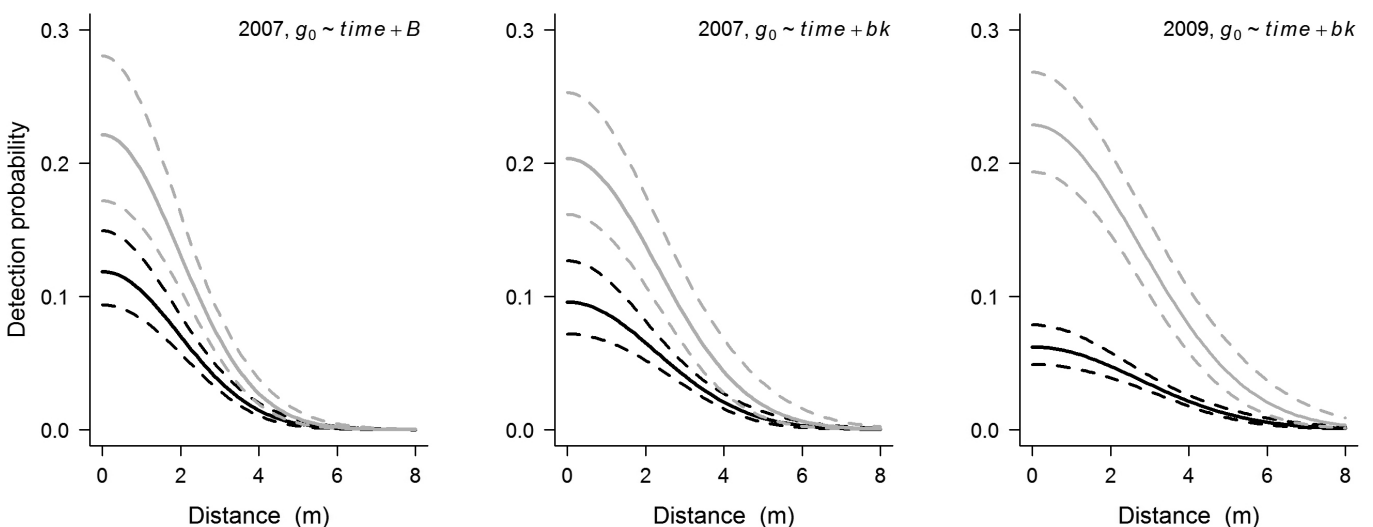
was also supported ( $\Delta AIC_c = 1.8$ ). A transient trap-specific behavioural response had much weaker support ( $Bk$ ,  $\Delta AIC_c = 8.2$ ,  $AIC_c$  weight = 0.01). Other models, including those with  $g_0$  or  $\sigma$  as a function of habitat, species, or skink size class, were clearly inferior according to the  $AIC_c$  criterion ( $\Delta AIC_c \geq 19$  in both years). We based estimates of skink density and the spatial detection parameters  $g_0$ ,  $\sigma$  on the single supported model in 2009, and on model-averaged estimates from the two supported models in 2007.

The estimated probability ( $g_0$ ) of capturing a skink for the first time, in a trap near the centre of its home range, was c. 0.1 in 2007 and 0.06 in 2009 on the days of highest capture probability (day 1 in 2007 and day 2 in 2009; Fig. 1). These probabilities increased approximately two-fold in 2007 and four-fold in 2009 for an animal caught previously (Fig. 1). Capture probabilities declined close to 0 as distance from the home range centre approached 8 m (Fig. 1; estimated  $\sigma$  was 2.0 m and 2.7 m in 2007 and 2009, respectively). Estimated

$g_0$  also varied considerably between days of each 5-day trapping session, ranging between 0.013–0.112 in 2007 and 0.017–0.062 in 2009.

The estimated density of small skinks (all three species combined) ranged from c. 1200 per ha at the experimental control site (estimated in 2009 only; 1179 (95% CI 936–1485) in gullies and 1298 (1030–1636) on ridges) to c. 4000 per ha at the fence treatment (3500 (2915–4202) to 4700 (3815–5790) across habitats and years; Fig. 2). Estimated densities were similar between the removal (3571 (2958–4311) to 4047 (3273–5004)) and fence treatments and between years. Estimated density at removal 2 (2317 (1906–2816) in gullies and 2550 (2102–3094) on ridges, in 2009) was intermediate between the fence and removal treatments and the experimental control. Density was also similar between gully and ridge habitats in all treatments.

Evaluations of model goodness-of-fit showed that the five best-supported models from each year predicted the



**Figure 1.** Fitted spatial detection functions for skinks (southern grass skinks, McCann's skinks, and cryptic skinks combined), showing the probability of capture (per day) as a function of a trap's distance (m) from an animal's home range centre, on the trapping day when capture probability was highest (day 1 of 5 in March 2007 and day 2 of 5 in March 2009), on study plots at Macraes Flat. Black lines represent an animal's first capture and grey lines represent subsequent captures, according to the  $g_0$  model shown. The two best-supported SECR models are shown for 2007 and the best-supported model for 2009. Dashed lines show 95% confidence limits.

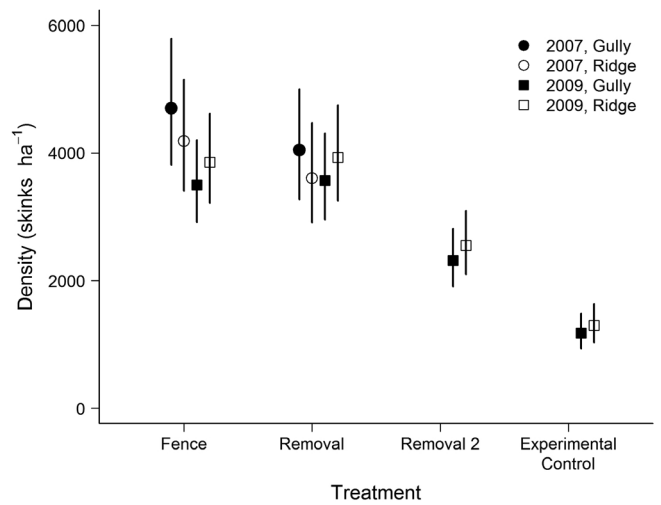
numbers of individual skinks caught almost exactly, but mean simulated recaptures differed from actual numbers of recaptures. Simulations based on the best-supported models in both years tended to underestimate recaptures, with mean simulated recaptures 67–82% of actual recaptures (Tables 2, 3). The *time + Bk* model, which ranked third in 2007 and second in 2009, generated a much better match between simulated and actual recaptures in both years (95% in 2007 and 87% in 2009). These simulations show that our best-supported SECR models predicted too few recaptures and suggest that some variation in recapture probability was not modelled correctly.

**Skink counts in artificial retreats**

We found 68 skinks in artificial retreats in 2007 and 443 in 2009, 149 in dawn counts and 294 new unmarked individuals in late-morning counts. Geckos (16 in 2007 and 76 in 2009) were also found in retreats, as were 13 introduced whistling tree frogs (*Litoria ewingii*) (in 2009 only; frogs were not marked and some may have been recaptures). Air temperatures at nearby climate stations ranged from 3.8–11.5°C (mean hourly minima–maxima) during dawn counts and 11.9–20.6°C during late-morning counts (Table 4). The dawn count in 2009 took longer than expected and was not finished until 10:30 hours at one site, but despite this later completion time, the mean maximum hourly temperatures during the 2007 and 2009 counts were similar (Table 4).

**Relationship between counts of skinks in artificial retreats and estimated skink density**

Counts of skinks in retreats in late morning in 2009 were related to estimated skink density ( $\log_e$  transformed) from SECR in pitfall traps ( $P < 0.05$ , marginal  $R^2 = 0.73$ , conditional  $R^2 = 0.82$ ; Table 5; Fig. 3). For every 10-fold increase in density, late-morning counts were predicted to increase 2.4 fold in gully habitats and 1.1 fold on ridges; this interaction between habitat and density was not statistically significant ( $0.05 < P < 0.1$ ). However, dawn skink counts in 2007 and 2009 were not significantly related to estimated skink density ( $P > 0.1$ , marginal and conditional  $R^2 = 0.26$ ). Neither late-morning counts nor dawn counts differed significantly between treatments, and no other coefficients in these two models differed significantly from zero ( $P > 0.05$ ; Table 5). Exploratory analyses with density as the response variable and counts as



**Figure 2.** Estimated densities of skinks (southern grass skinks, McCann’s skinks, and cryptic skinks) in gully and ridge habitats at two sites with different mammal-management regimes at Macraes Flat in March 2007, and at four sites (fence, removal, removal 2 and experimental control) with three different levels of mammal management in March 2009. Error bars show 95% CIs.

a predictor variable (both  $\log_e$  transformed) also indicated a weak relationship between density and late-morning skink counts ( $0.05 < P < 0.1$ ), and no relationship ( $P > 0.1$ ) between density and dawn counts.

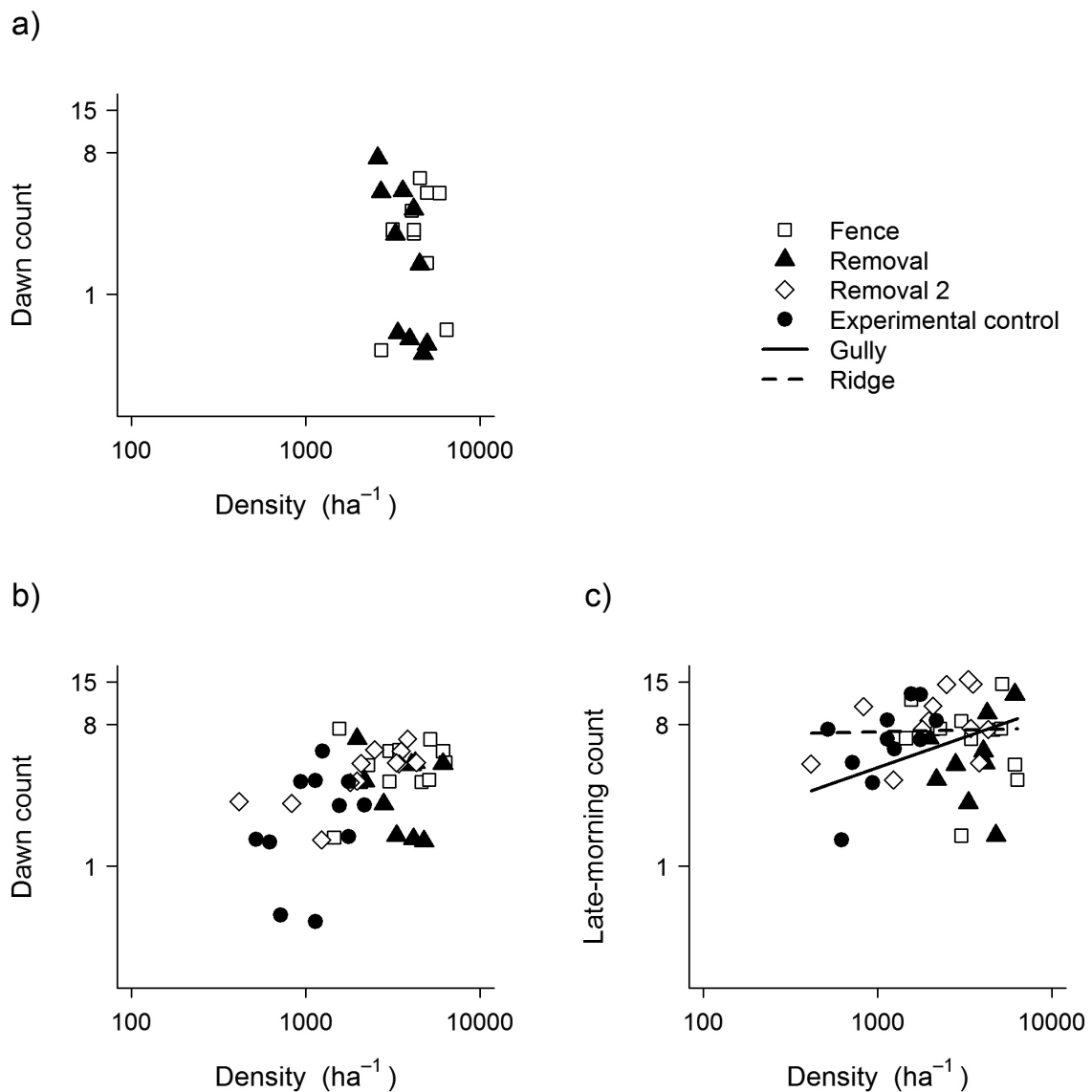
**Lack of temporal change in dawn skink counts in artificial retreats and effects of aspect**

Dawn skink counts did not change significantly between 2006 and 2009 ( $P > 0.1$ ; marginal and conditional  $R^2 = 0.28$ ; Table 6; Fig. 4). Dawn counts were positively related to northerly aspect ( $P < 0.05$ ), increasing by an estimated 13% and 14% for each additional 20° north in gully and ridge habitats, respectively. Dawn counts were also higher in the fence (2.6 times higher, on average;  $P < 0.01$ ) and removal (2.2 times;  $P < 0.05$ ) treatments compared with the experimental control, results that contrast with the lack of significant treatment effects

**Table 4.** Temperatures during dawn counts of skinks at Macraes Flat, Otago, in 2006 (Wilson et al. 2007), 2007 and 2009, and late-morning counts in 2009, based on hourly minima and maxima recorded at the nearest climate stations (Middlemarch, c. 25 km southwest of our study area but at lower altitude (200 m a.s.l.), and Ranfurly, c. 40 km northwest and at similar altitude (400 m a.s.l.); The National Climate Database, NIWA). Counts were done 22–28 March. In 2009, late-morning counts were done 4 days after dawn counts. Time is reported as New Zealand Standard Time (NZST) to avoid confusion resulting from changes to the duration of daylight time (NZDT) since 2007–08. Start and finish times were not recorded separately per treatment in 2006.

Year	Dawn or late-morning	Start times per treatment (NZST)	Finish times per treatment (NZST)	Hourly air temperatures minima–maxima (°C)		Mean maximum hourly temperature (°C)
				Middlemarch	Ranfurly	
2006	Dawn	06:00	08:30	3.8–7.4	4.3–6.3	5.6
2007	Dawn	06:05–06:10	08:15–08:45	5.7–8.7	6.7–10.8	8.1
2009	Dawn	06:00–06:10	08:30–10:30	6.3–11.5	4.3–8.1	7.6
2009	Late morning	09:55–10:15	10:55–11:30	11.9–16.4	14.6–20.6	17.5



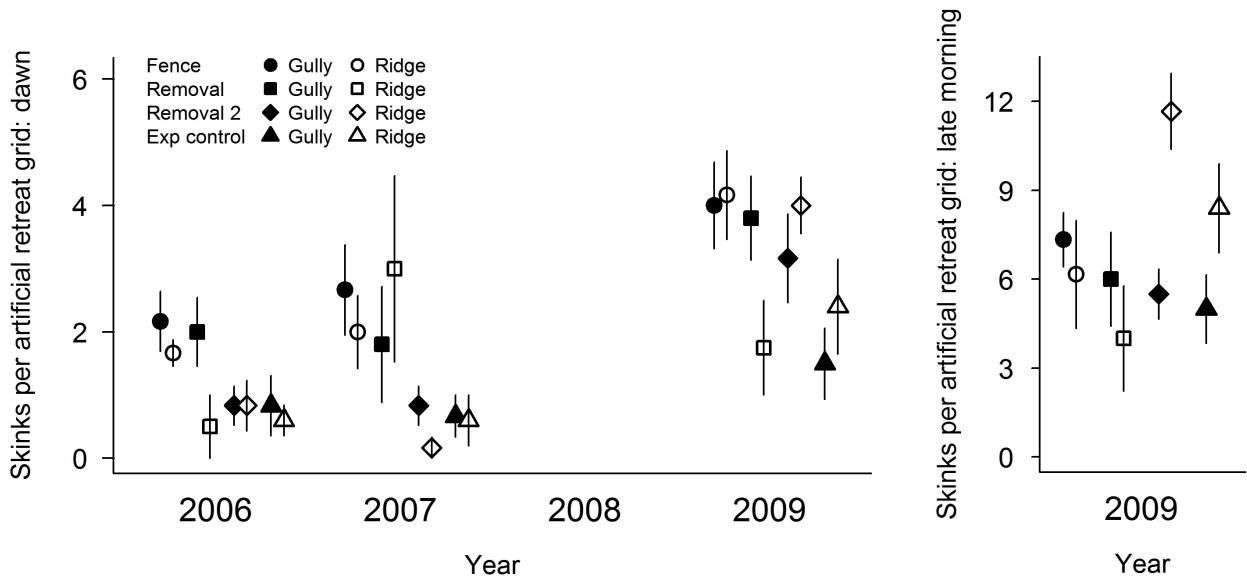


**Figure 3.** Relationships between estimated skink densities (southern grass skinks, McCann’s skinks, and cryptic skinks) and (a) dawn counts in 2007, (b) dawn counts in 2009, and (c) late-morning counts in 2009. Counts have been ‘jittered’ to reduce over-plotting, by adding a small random amount (0.4–0.6) to each; therefore, counts <1 represent zeroes. Lines in (c) show fitted  $\log_e(\text{density})$  effects in gully and ridge habitats.

**Table 5.** Fixed-effect coefficients and their 95% CIs of generalised linear mixed-effects models testing whether skink density predicts numbers of skinks counted in artificial retreats at (1) dawn in 2007 and 2009 and (2) late-morning in 2009 only, at Macraes Flat, Otago. Bold type shows coefficients that differ significantly from zero ( $P < 0.05$ ). The intercept represents the experimental control treatment, gully habitat, and (for dawn counts only) the year 2007. Continuous variables were rescaled to have mean 0 and standard deviation 0.5 by subtracting the mean and dividing by two standard deviations (Gelman 2008). ‘×’ represents an interaction term and ‘—’ indicates a coefficient not included in the model.

Coefficient	Dawn counts (2007 and 2009)	Late-morning counts (2009)
Intercept	0.14 (-0.61–0.89)	<b>1.88 (1.5–2.25)</b>
Treatment fence	0.93 (-0.26–2.12)	-0.19 (-0.67–0.29)
Treatment removal	0.75 (-0.11–1.61)	-0.47 (-1.01–0.07)
Treatment removal 2	0.59 (-0.42–1.61)	0.14 (-0.27–0.55)
Habitat ridge	0.01 (-0.28–0.3)	0.22 (-0.06–0.5)
$\log_e(\text{density})$	0.32 (-0.15–0.79)	<b>0.54 (0.08–0.99)</b>
Finish time	0.33 (-0.5–1.16)	—
Year 2009	0.37 (-0.14–0.88)	—
Habitat ridge × $\log_e(\text{density})$	-0.12 (-0.76–0.53)	-0.5 (-1.09–0.08)





**Figure 4.** Mean number of skinks (southern grass skinks, McCann’s skinks, and cryptic skinks) per grid of 16 artificial retreats (with 5-m spacing) at Macraes Flat, in gully and ridge habitats at four sites with three different levels of mammal management, named fence, removal, removal 2 and experimental control. Left-hand panel shows counts done at dawn in March 2006, 2007 and 2009. Right-hand panel shows counts done in late morning in March 2009. Error bars show standard errors. Note different vertical-axis scales.

**Table 6.** Fixed-effect coefficients and their 95% CIs of generalised linear mixed-effects models testing for (1) temporal change between years in dawn skink counts in artificial retreats, and effects of other factors in 2006, 2007 and 2009, and (2) effects of northerly and westerly aspect variables and other factors on late-morning skink counts in 2009. Bold type shows coefficients that differ significantly from zero ( $P < 0.05$ ). The intercept represents the experimental control treatment in gully habitat. Continuous variables (including year) were rescaled to have mean 0 and standard deviation 0.5 by subtracting the mean and dividing by two standard deviations (Gelman 2008). ‘×’ represents an interaction term and ‘—’ indicates a coefficient not included in the model.

Coefficient	Dawn counts (2006, 2007, 2009)	Late-morning counts (2009)
Intercept	-0.01 (-0.52–0.49)	<b>1.87 (1.5–2.24)</b>
Treatment fence	<b>0.94 (0.41–1.47)</b>	-0.17 (-0.59–0.24)
Treatment removal	<b>0.81 (0.19–1.43)</b>	-0.33 (-0.81–0.14)
Treatment removal 2	0.46 (-0.23–1.16)	0.35 (-0.07–0.78)
Habitat ridge	-0.34 (-0.79–0.11)	0.04 (-0.33–0.41)
Finish time	0.4 (-0.41–1.21)	—
Year	0.33 (-1.09–1.75)	—
Degrees north	<b>0.43 (0.05–0.81)</b>	<b>0.54 (0.13–0.94)</b>
Degrees west	0.14 (-0.31–0.59)	0.25 (-0.18–0.69)
Treatment fence × year	-0.01 (-0.97–0.94)	—
Treatment removal × year	0.21 (-1.3–1.72)	—
Treatment removal 2 × year	1.25 (-0.28–2.78)	—
Habitat ridge × degrees north	0.02 (-0.88–0.92)	-0.22 (-0.91–0.46)
Habitat ridge × degrees west	0.46 (-0.64–1.56)	—
Degrees north × degrees west	-0.13 (-1.19–0.92)	0.12 (-0.9–1.14)

in the previous model (above), without count data from 2006. Finish times, habitat and interactive effects on dawn counts were not statistically significant ( $P > 0.1$ ).

Late-morning counts were also positively related to northerly aspect ( $P < 0.01$ ; marginal  $R^2 = 0.66$ , conditional  $R^2 = 0.76$ ; Table 6), increasing by an estimated 10% in gullies and 4% on ridges, for each additional 20° north. There were no other statistically significant relationships between explanatory

variables and late-morning counts ( $P > 0.1$ ). Skink density was not significantly related to aspect variables ( $P > 0.1$ ; marginal  $R^2 = 0.53$ , conditional  $R^2 = 0.72$ ; Table 7), but density was higher in the fence, removal and removal 2 treatments compared with the experimental control ( $P < 0.01$ ). There were no other statistically significant relationships between explanatory variables and densities ( $P > 0.1$ ).

## Discussion

### Skink population density in relation to predator management at Macraes Flat

Suppressing mammalian predators can lead to population increases for small terrestrial lizards (southern grass skinks, McCann's skinks, and geckos *Woodworthia* spp. combined; Norbury et al. 2013) and larger endangered skinks (grand skinks and Otago skinks; Reardon et al. 2012) at Macraes Flat. The gradient in our skink density estimates, from c. 1200 per ha at the experimental control site to c. 4000 per ha at the fence and removal treatments may therefore result in part from variation in predator management. However, because we lack baseline data from before predator management was implemented, we cannot exclude the possibility that the gradient is due partly to pre-existing differences between our study sites. Pre-existing differences are likely because the predator management treatments were applied selectively to known locations of relict grand skink and Otago skink populations (Reardon et al. 2012). The suitability of the habitat for small skinks may vary between sites owing to dissimilarities in vegetation, historical farming practices, and the availability of basking sites and refugia from predators. Repeating the SECR pitfall trapping at regular intervals in future might enable separation of the effects of pre-existing site differences and predator management on skink density.

Grand and Otago skinks at Macraes Flat increased in abundance to a similar degree whether mammalian predators were excluded with predator-resistant fences (2-year population growth rates 1.3 and 1.7 for the respective species; Reardon et al. 2012) or suppressed with extensive trapping (1.5 and 1.9). Likewise, population densities of small skink species were similar in our fence treatment and our removal treatment, just outside the fence. Because the fence is at most a partial barrier

to the movement of small skinks, which can pass through the mesh, immigration and emigration may equalise densities between these two treatments.

An influence of predation on the variation in skink densities between alternative predator management treatments at Macraes Flat is supported by comparison with earlier

**Table 7.** Fixed-effect coefficients and their 95% CIs for a linear mixed-effects model testing for effects of northerly and westerly aspect variables and other factors on skink density ( $\log_e$ -transformed) estimated in 2007 and 2009 at Macraes Flat, Otago. Bold type shows coefficients that differ significantly from zero ( $P < 0.05$ ). The intercept represents the experimental control treatment in gully habitat in the year 2007. Continuous variables were rescaled to have mean 0 and standard deviation 0.5 by subtracting the mean and dividing by two standard deviations (Gelman 2008). '×' represents an interaction term.

Coefficient	$\log_e(\text{density})$ in 2007 and 2009
Intercept	7.27 (6.85–7.7)
<b>Treatment fence</b>	<b>0.57 (0.15–0.98)</b>
<b>Treatment removal</b>	<b>0.93 (0.52–1.34)</b>
<b>Treatment removal 2</b>	<b>0.87 (0.44–1.3)</b>
Habitat ridge	0.14 (-0.2–0.48)
Year 2009	-0.14 (-0.35–0.08)
Degrees north	0.25 (-0.11–0.61)
Degrees west	0.07 (-0.41–0.56)
Habitat ridge × degrees north	-0.49 (-1.27–0.29)
Habitat ridge × degrees west	-0.51 (-1.44–0.42)
Degrees north × degrees west	-0.59 (-1.54–0.35)

**Table 8.** Previous estimates of density of southern grass skinks, McCann's skinks, cryptic skinks and northern grass skinks, with species trapped in the same sampling areas combined.

Skink species	Location	Habitat	Predator control	Density (per ha)	Reference	Notes
Southern grass and cryptic	Rock and Pillar Range, eastern Otago	Tussock grassland	None	770 and 1670	Patterson 1985	Densities estimated before parturition, and calculated after parturition
Southern grass	Kaitorete Spit, Canterbury	Shrubland	None	200–400	Freeman 1997	
McCann's	Kaitorete Spit, Canterbury	Duneland	None	1050–1850	Freeman 1997	
Southern grass and McCann's	Macraes Flat, eastern Otago	Tall tussock grassland	None	575 and 2250	Dixon 2004	Densities on two different trapping grids
Southern grass	Eglinton Valley, Southland	Grassland	Stoats; periodically possums and rats	3600–9200	Lettink et al. 2011	
Southern grass and McCann's	Macraes Flat, eastern Otago	Tall tussock grassland	Trapping of cats, mustelids and rats began during study	950–1060	Jones et al. 2013	Six experimental pens with different numbers of hedgehogs
Northern grass	Wellington	Abandoned cemetery	None	2220	Barwick 1959	
Northern grass	Pukerua Bay, near Wellington	Coastal shrubland and grassland	None	4900	Towns & Elliott 1996	

studies. Our population density estimates of c. 1200–4000 small terrestrial skinks per ha fall within the range of other estimates for these species (Table 8). In South Island studies, skink densities were generally highest where some predator species were managed (point estimates c. 2400–9200 per ha; our study and Lettink et al. 2011). However, a high density of northern grass skinks (*Oligosoma polychroma*) was also recorded at a North Island location without predator control (4900 per ha; Towns & Elliott 1996). There is no evidence that cumulative effects of predation have reduced the density of northern grass skinks in that North Island population since it was sampled from 1982 to 1988, as capture rates remained stable from 1984–2006 (Hoare et al. 2007). In earlier studies at Macraes Flat, before or coincident with the start of predator trapping, skink densities were lower and more similar to those at our experimental control site (575–2250 per ha; our study; Dixon 2004; Jones et al. 2013).

These comparisons between studies are complicated by climate and habitat differences, the presence of other sympatric skink species at some locations, and different field and analytical methods. In most previous studies, skink density on trapping grids was calculated on the basis of estimated population size divided by grid area, usually with the addition of a buffer strip. Buffer strip widths were based on what was known of species' movements or home range sizes. Lettink et al. (2011) used SECR to estimate a suitable buffer strip width based on capture data, and Jones et al. (2013) did not add a buffer strip because their skinks were constrained within experimental enclosures. As far as we know, SECR has been used in only one other previous New Zealand skink study, which mapped population density contours of 100–700 speckled skinks (*Oligosoma infrapunctatum*) per ha in a patchy environment in the Buller Valley, South Island (Efford & Fewster 2013).

### Behavioural responses of skinks to capture

Positive responses to particular baited detection devices have been observed in wolverines returning repeatedly to camera traps (Royle et al. 2011) and black bears returning to barbed-wire hair-collection corrals (Howe et al. 2013). As far as we know, similar responses to particular live-capture traps have not been published. Modelling the spatial behavioural response of wolverines increased a population density estimate relative to a simpler model (Royle et al. 2011). As expected, our best-supported models, which included positive behavioural responses by skinks, also increased skink density estimates relative to models without these factors. Only the prevailing type of trap-happy behaviour was ambiguous in our best-supported models, with a permanent trap-specific response (*bk*) clearly supported by our SECR data in 2009, but either a transient response affecting only the next capture occasion (*B*) or a permanent trap-specific response (*bk*) supported in 2007.

In earlier studies, permanent trap-shy behavioural responses (*b*) have been inferred for southern grass skinks and McCann's skinks captured in retreats (Wilson et al. 2007) and pitfall traps (Jones et al. 2013) at Macraes Flat, and also for southern grass skinks captured in pitfall traps in the Eglinton Valley (Lettink et al. 2011). Our spatial capture probability parameter ( $g_0$ ) estimates of c. 0.06–0.1 on the day of highest capture probability for skinks caught for the first time and >0.2 for previously-captured skinks, encompass the 0.16 per day estimated for speckled skinks caught in pitfall traps (with behavioural responses and daily variation not modelled; Efford & Fewster 2013). The support for a trap-specific, trap-happy

response (*bk*) in both years of our study suggests that while capture and recapture rates in pitfall traps were low in these populations, some individual skinks repeatedly returned to the same trap. However, some variation in recapture probability was not explained by our most highly-ranked models, as actual recapture rates exceeded simulated mean recapture rates based on the models. Jones and Bell (2010) found that female skinks had a higher recapture rate than males and suggested that gravid females requiring nutrition were attracted to the bait. Although females were not gravid during our early-autumn trapping in late March (Jewell 2008), if their differential attraction to food persisted then sex (which we did not assess in order to minimise handling of skinks) could be another important source of heterogeneity in capture probability. Species and age (indicated by body length) of skinks also seem likely sources of variation in capture probability, but these models were not supported. However, Lettink et al. (2010, 2011) found positive relationships between SVL and capture probabilities of McCann's skinks and southern grass skinks, and it is possible that our categorical skink size-class variable masked differential capture probabilities for the smallest or largest animals. Finally, heterogeneity in capture probability could also arise from some unmeasured characteristic of traps or their surroundings (Royle et al. 2013; Efford 2014), such as proximity to cover (Lettink & Seddon 2007) or aspect.

Unmodelled heterogeneity in capture probability is likely to bias our density estimates, but without substantially altering relationships between estimates for different treatments. The density estimates in our best-supported models exceeded those in other highly-ranked models. For example, choosing the *time + Bk* models (ranked third in 2007 and second in 2009, and with better matches between actual recaptures and simulated recaptures from best-supported models) would lower density in gully habitats at the fence treatment by 13% compared with our model-averaged estimates in 2007 (4101 vs. 4700) and by 7% compared with our best-model estimate in 2009 (3267 vs. 3500). These reductions in density are small relative to the between-year differences in our estimates.

### Relationship between counts of skinks in artificial retreats and skink population density

In grassland in the Eglinton Valley, counts of southern grass skinks in artificial retreats were good predictors of skink population density, but only when counts were done under 'optimal' daytime conditions (i.e. ambient temperatures 12–18°C and insignificant rainfall; Hoare et al. 2009; Lettink et al. 2011). In our study at Macraes Flat, counts of skinks in retreats also did not consistently predict skink density. Late-morning counts (when most skinks were warm and active) were positively related to density. However, late-morning counts did not differ significantly between treatments, whereas density was clearly higher where predators were excluded or removed, compared with the experimental control site. Hourly temperature ranges recorded at climate stations near Macraes Flat, and the lack of rainfall during the late morning counts, were similar to the optimal weather conditions recommended for the Eglinton Valley (Hoare et al. 2009; Lettink et al. 2011), although temperatures during our sampling period (up to 20.6°C at one climate station) may sometimes have exceeded the optimal range. Importantly, local temperatures, which we did not record, may have differed from climate station records. Temperatures recorded at climate stations during our dawn counts (when most skinks were cold and inactive) were below (maximum 11.5°C) the optimal range determined for



the Eglinton Valley (Hoare et al. 2009; Lettink et al. 2011). Although dawn skink counts were not positively related to skink density in 2007 and 2009, they did (when combined with data from 2006) reflect differences between the mammal management treatments.

Aspect may modify the relationship between retreat occupancy and skink density in the complex ridge and gully systems at Macraes Flat, but it is likely to be relatively uniform in the flatter Eglinton Valley landscape. The higher skink counts at north-facing locations during both late-morning and dawn, but not significantly higher densities near the same locations, suggest that microhabitat differences may affect occupancy of individual retreats by skinks seeking warm refuges and basking sites. Extensive spatial variation in retreat usage by skinks at Macraes Flat would violate the assumption of equal detection probability at different locations, necessary for retreat counts to be useful density indices (Pollock et al. 2002; Bailey et al. 2004). The different designs of artificial retreats in the Macraes Flat and Eglinton Valley studies may also have affected results. Our smaller, three-layer retreats offered 2.5 times less surface area for basking, but a greater variety of refuge characteristics, compared with the larger, single-layer Eglinton Valley retreats. We found 32% of skinks in dawn counts and 62% of skinks in late-morning counts between the retreat layers, instead of under or on the retreats. Finally, relationships between skink counts and densities in our study could have been further weakened by differences in habitat and skink density between adjacent paired grids of retreats and pitfall traps.

On the basis of the rather equivocal relationship we found between late-morning skink counts in artificial retreats and skink population density, and the factors discussed above that could affect this relationship, more investigation is needed to determine whether skink counts in retreats have the potential to index skink density at Macraes Flat. Stringent control and recording of local ambient temperature during sampling is needed, in addition to improved control of aspect, habitat and device placement. We recommend that skink counts be done in daytime in weather close to the optimal conditions determined for the Eglinton Valley (discussed above; Hoare et al. 2009; Lettink et al. 2011). Also, instead of pairing retreat grids and pitfall trap grids, retreats could be placed close to pitfall trap locations after trapping is completed, and checked 3 weeks later. In such a design, trapping could be done in February (late summer) and retreat counts in March (early autumn), so that both procedures can be scheduled on days when temperatures are likely to be intermediate and rainfall absent (Hoare et al. 2009; Lettink et al. 2011). To maximise repeatability between surveys, pitfall traps should be placed permanently or at marked positions. Artificial retreats used for monitoring should not be left in place long-term, as they may lead to patches of atypically high skink density (Souter et al. 2004; Lettink & Cree 2007; Batson et al. 2015) or competitive exclusion of small individuals (Batson et al. 2015). Future investigations of artificial retreats for monitoring skinks should use consistent device layouts, and we suggest that both pitfall traps and artificial retreats be spaced 2 m apart in a 5 × 5 formation (Lettink et al. 2011). For Macraes Flat, this change means that new skink counts in retreats cannot be compared with counts from the present study. New density estimates will be comparable with our estimates and they may have improved precision if increased skink capture rates result from the placement of additional pitfall traps (25 vs the 16 in this study) within a similar grid area.

### Lack of temporal change in dawn skink counts during 2006–2009

The lack of significant change in dawn skink counts during 2006–2009 does not necessarily imply no skink population density changes in some predator-management treatments during this period as we found that dawn skink counts were not a useful density index. We know that suppressing top mammalian predators increased the average density of small lizards by about 130 per ha over 3 years, from an experimental study at Macraes Flat and Central Otago (Norbury et al. 2013), and that variation in counts of southern grass skinks in artificial retreats in the Eglinton Valley corresponded to changes in predator abundance during a 5 year period (O'Donnell & Hoare 2012). Our density estimates establish a baseline, 1–3 years after a mammal-resistant fence and mammal trapping programme were implemented, for testing long-term effects of mammal management on skink populations at Macraes Flat. Additional years of density estimation, paired with daytime skink counts under controlled conditions as discussed above, will reveal any time trends in these two variables and any temporal relationship between them.

### Acknowledgements

We thank Amélie Augé, Trent Bell, Ursula Brandes, Ryan Clark, Morgan Coleman, Stephanie Hicks, Kate Ladley, Beatrice Lee, Peter Lei, Sean LeMoine, Lena Ohnheiser and James Smith for fieldwork, the Department of Conservation (DOC) for permission to capture lizards, and DOC staff at the Redbank Base for accommodation and logistical assistance. Murray Efford gave advice and assistance with use of secr for density estimation. We also thank Marieke Lettink, Chris Jones, Adrian Monks, Susan Walker and Debra Wotton for valuable suggestions, and Murray Efford, Jo Monks, Paul van Dam-Bates, Leah Kearns and an anonymous reviewer for very helpful comments on earlier versions of the manuscript. This research was approved by the Animal Ethics Committee of Landcare Research (approval no. 06/02/02) and funded by the Ministry of Business, Innovation and Employment.

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Received 25 August 2015; accepted 27 June 2016