

Life history traits contribute to decline of critically endangered lizards at Macraes Flat, Otago

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Abstract: Mark–recapture methods were used to determine population abundance and life history of five grand (*Oligosoma grande* Scincidae) and two Otago (*O. otagense*) skink populations over 6 years at Macraes Flat, in southern New Zealand. The population ecology of declining and stable grand skink populations was contrasted and the life histories of grand and Otago skinks were compared. The life histories of both species were similar and characterised by slow maturity and longevity (3–5 and 4–6 years to produce first offspring and longevity up to 18 and 13.5 years in the wild; grand and Otago skinks respectively). With the exception of one grand skink population, all skink populations showed evidence of declines. Annual reproductive output (ARO) was estimated at 1.46 and 1.41 offspring per female per year (grand and Otago skinks respectively). These ARO values were markedly lower than those reported during a previous study at Macraes Flat during the same decade (2.17 and 2.34 respectively). The stable grand skink population excelled (relatively) in all life history traits measured: ARO of 1.66, 30% of newborns persisted 5+ years, adult survivorship averaged 0.84, and 36% of newborns were recruited to the adult population. In contrast, many of the declining populations were seriously deficient in one or more traits. This study raises concerns about the viability of small populations that have dropped below a critical size, beyond which one or multiple life history traits can act to further the decline. It is imperative that conservation managers of k-selected species move outside the ‘improving adult survival’ paradigm and begin to consider other potentially limiting population parameters.

Keywords: Allee effect; apparent survival; fecundity; *Oligosoma*; population; skink

Introduction

Grand (*Oligosoma grande* Scincidae) and Otago (*O. otagense*) skink populations are currently ranked ‘nationally critical’ by New Zealand’s Department of Conservation (Hitchmough et al. 2007; R. Hitchmough, Department of Conservation, Wellington, NZ, pers. comm., 2009). Populations of both species are considered to be in rapid decline throughout their entire range (Whitaker & Loh 1995; Tocher 2006; Norbury et al. 2007). Although declines in abundance have not yet been formally documented, negative forces, most notably habitat destruction and predation pressure, operate over the scattered remaining grand and Otago skink populations (Whitaker & Loh 1995; Whitaker 1996; Houghton & Linkhorn 2002; Berry et al. 2005; Tocher 2006; Norbury et al. 2007). The most influential of these forces is now known to be predation (Norbury et al. 2007; A. Hutcheon, Department of Conservation, Dunedin, NZ, pers. comm., 2008). A large number of exotic predator-species coexist with grand and Otago skinks at Macraes Flat and

collectively they apparently crop individuals of both species at an unsustainable rate (Tocher & Norbury 2005; Tocher 2006; A. Hutcheon, Department of Conservation, Dunedin, NZ, pers. comm., 2008). Management initiatives to assist grand and Otago skinks are currently aimed at eradication of a large suite of mammalian predators, and early signs of population recovery (albeit at a small scale) look promising (G. Norbury, Landcare Research, Alexandra, NZ, pers. comm., 2009).

Grand and Otago skinks conform to a ‘k-selected’ life-history profile: individuals are big-bodied, long-lived, and take at least 3 years to produce their first offspring and tend to only produce 1–3 offspring in each clutch (Cree 1994). There are few existing datasets on skink demographics worldwide (Turner 1977; Cree 1994; Bull 1995; Freeman 1997; Wapstra & Swain 2001; Milne et al. 2002; Chapple 2005). However, in general, for vertebrate species with similar k-selected demographic profiles, population viability has been shown to be more sensitive to adult survival than fecundity (Lande 1988; Russell 1999; Johnson 2002; Doherty et al. 2004), and

even moderate levels of predation on adults can result in population declines (Rodríguez-Estrella et al. 1991; Slooten & Lad 1991; Russell 1999; Johnson 2002; Towns et al. 2007).

The k-selected life-history strategy exhibited by grand and Otago skinks implies they are ill-equipped to persist in an environment ‘unnaturally’ loaded with exotic predators; an environment that now encompasses their entire geographic range (Norbury et al. 2007). In this study, mark–recapture methods were used to determine population abundance trends and life history of five grand and two Otago skink populations over 6 years at Macraes Flat, in southern New Zealand. The population ecology of declining and stable grand skink populations was contrasted and the life histories of grand and Otago skinks were compared. The overall aim of this study was to test the hypothesis that survival, more so than other life history traits, is enhanced in any population exhibiting a positive abundance trend.

Methods

Study populations

Five study sites and their surrounding ‘peripheral’ rock tors were included in this study. Grand skink populations were present at all sites but Otago skink populations only occurred at two (C and D; Fig. 1). (See Tocher (2003) for habitat descriptions of sites A–E in Fig. 1). A predator control operation was carried out over all study populations from May 1999 to 2002, which targeted feral cats (*Felis catus*), but large numbers of ferrets (*Mustelo furo*) were caught as by-catch (Tocher 2006).

Population trends 1996–2002

All five grand skink and two Otago skink populations were sampled three times per skink active season (November–December (spring), February–March (summer), and April–May (autumn)) over 6 years. During each sampling session as many grand and Otago skinks as possible were captured by hand using a noose. From November 1996 to May 1998 sampling sessions lasted 3 weeks. From November 1998 to May 2002 sampling sessions were extended to 5 weeks in an effort to improve number of captures. In total, populations were sampled 18 times over the 6-year study with the exception of population E (a grand skink pastureland site; Fig. 1), which was not visited in November 1996. For any given sampling session, each population was visited over multiple non-consecutive days as weather allowed; the field team rotated around the populations until the sampling session ended.

Captured skinks were marked by toe clipping, weighed, measured, sexed (where possible), and released at the exact point of capture on the same day. Skinks were held individually in white cloth bags inside a cool-bin until they were measured and weighed. At times, individuals were held up to 6 hours, but were more usually held for 2–4 hours. Due to a high natural toe loss, a back-up system using photos of each skink was employed to assign an identity to skinks that had lost toes naturally and were otherwise unable to be accurately identified.

Immigration and emigration patterns

To coarsely quantify immigration and emigration, skinks were captured and marked (through both toe-clipping and temporary marking with a non-toxic marker) at least once per active season on rock tors peripheral to each study

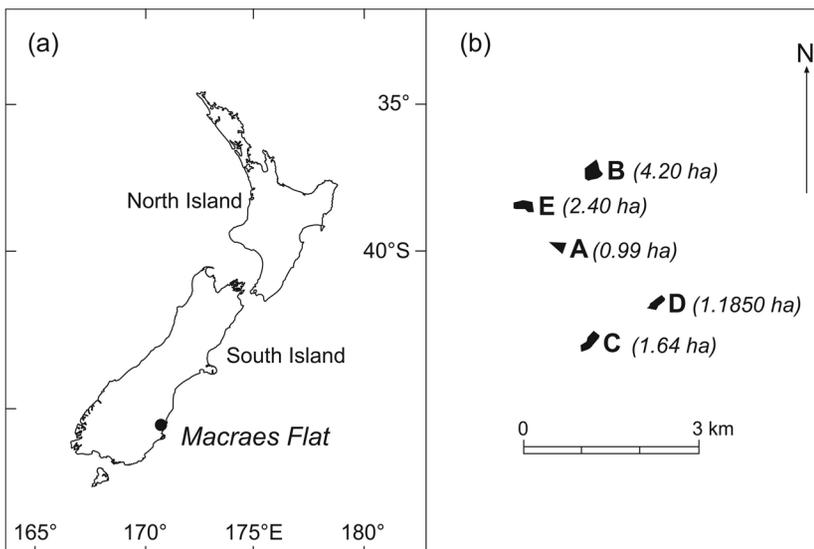


Figure 1. Location (a) and layout (b) of grand (*Oligosoma grande*) and Otago skink (*O. ottagense*) study populations at Macraes Flat, South Island, New Zealand. The area of each study population does not include ‘peripheral rock tors’; these tors surrounded each population but tended not to extend further than 400 m from the centre of each study population (with the exception of site B). Sites A, B and E were grand skink populations; sites C and D had both species present.

site. Peripheral rock tors tended to extend no further than 400 m from the centre of the study population. A skink movement was considered 'definite' if the skink had been captured at a new tor on >2 occasions; 'possible' for ≤ 2 captures at a new tor, or 'temporary' where the vast majority of captures of an individual were from one tor, but infrequent captures (usually 1) were made at a second tor, followed by captures back at the original tor. Net loss per year (over the 6-year study) through emigration was estimated for each population using the formula (total emigration - total immigration)/6 years.

Although searches of peripheral rock tors were less frequent and of shorter duration (on average 2–3 days per study site per year) than the intense capturing carried out within the study populations, there did not appear to be large numbers of uncaptured skinks on peripheral rocks at the end of a sampling period. Nonetheless, data will be biased towards detecting immigration into study populations (also see Houghton 2000).

Age to first reproduction (AFR)

Female skinks captured in their birth year (sexed retrospectively) were followed until they were first recorded with oviductal conceptuses (I assumed skinks were post-vitellogenic in late November when sampling for a season commenced; Cree 1994). AFR was calculated as the number of years between the autumn of their birth year to the autumn of the year I assumed they birthed their first clutch (based on the presence of oviductal conceptuses). All available grand and Otago skink data were used to increase sample sizes (i.e. $n = 4$ and $n = 3$ data points for grand and Otago skinks respectively were collected by G. Loh, Department of Conservation, from 1988 to 1996).

Fecundity: clutch frequency, clutch size and annual reproductive output

Mature-sized females (≥ 82 -mm and ≥ 107 -mm snout to vent length (SVL) for grand and Otago skinks respectively; Cree 1994) were palpated (examined externally by observer gently rolling thumb and index finger over the animal's mid-lower abdomen) from late November to determine reproductive state and to estimate the number of growing embryos and oviductal conceptuses. Although different observers (trained by author) were used every year, measurements over populations in a given year are assumed to be consistent. Observers were advised to take a conservative approach when estimating the number of oviductal conceptuses, so my clutch size estimates are probably underestimates.

Following Cree (1994), data for all captures were pooled together into 'female years' for each site, i.e. a single individual could have been palpated over multiple years generating multiple 'female years' of data. I defined a 'female year' as encompassing from late November

to mid-April for each individual. Non-gravid females that were captured for the first time in any given year after mid-April were excluded from the data set; it was assumed these females may have already birthed and were therefore 'false negatives'. For females that were palpated more than once in the same year, I took the lowest count. Counts were, for the most part, consistent, with occasional records of lower counts for a female occurring later in the season; such discrepancies likely represent lost ova or conceptuses (Holmes & Cree 2006). Skinks at population E during February–May 1997 were recorded as 'gravid' with no embryo count; for these skinks I assumed a count of one.

For each female, clutch frequency was calculated for the years they were captured and averaged for each site. Mean clutch size was calculated by averaging the lowest conceptus count for each female capture (mature-sized females recorded 'empty' or for which no clutch size was recorded were excluded from estimates of average clutch size). Annual reproductive output (offspring per female per year) was then calculated for each population (clutch frequency \times mean clutch size).

Sex ratio

Mature-sized skinks of both species were assigned a sex through examination of their capture history over the 6-year study; males were those skinks almost always (>80% of occasions) recorded as a 'male' and never recorded as gravid. Females were those skinks almost always recorded as 'female' and with gravidity data. Total numbers of mature-sized individual males and females that were captured over the study were counted for each population.

Attrition of newborn cohorts

Newborn grand and Otago skinks are produced during late summer–autumn (Cree 1994). The SVL range of newborn, wild grand skinks was not known, but the newborns were conspicuous by their small size, umbilical scars (and often cords) and ease of capture, and they were often found near spent females and/or other similar-sized small skinks. For the purposes of this study, grand skinks were considered to be 'newborn' if their SVL was ≤ 50 -mm SVL when first captured during their birth year and matched one or more of the above criteria. I acknowledge that using a 50-mm SVL cut-off will have led to the inclusion of an unknown percentage of slower growing skinks born the previous summer.

Newborn Otago skinks are known to range in SVL from 38 to 48 mm (J. Connolly, University of Otago, Dunedin, NZ, pers. comm., 2005). Because newborn Otago skinks are probably larger than newborn grand skinks I elevated the cut-off for Otago skink newborns to ≤ 55 -mm SVL; in the wild, no skinks of <39-mm SVL were ever captured. For both species, I assumed all new (not toe-

clipped) small skinks captured in November–December (spring) were born the previous autumn and excluded these from the newborn dataset (i.e. I assumed they had overwintered successfully). Also, any records of newborns subsequently found outside the study site (apparently resident outside the site) were excluded from ‘attrition’ analyses of newborns within the site ($n = 10$ grand skinks, $n = 1$ Otago skink). All other newborns were assumed to have been born some time between February and May and were ≤ 4 months old.

I then tracked the presence/absence of each newborn cohort through the following years of the study to determine their fate (i.e. apparent survival). Occasionally, individuals that were not detected one year were recaptured one or more years later. For these skinks, their presence in those missing years was inferred. This approach reduced the reliability of the method for later-year cohorts, where there were fewer opportunities to correct mistaken missing records. As such, attrition estimates from the later cohorts may be inflated.

Recruitment

To obtain an estimate of recruitment of newborns into the adult population, newborns captured between November 1996 and May 1998 were tracked until they reached adulthood (defined here as $SVL \geq 78$ mm for grand and ≥ 101 mm for Otago skinks; Cree 1994).

Apparent survival of mature-sized skinks over study duration

Mature-sized skinks first captured over the summer of 1996/97 were tracked through the following years in an effort to estimate adult apparent survival. In total, 131 grand skink adults (over five study populations) and 41 adult Otago skinks (over two populations) were tracked.

Statistical analyses

Abundance was estimated using the program JOLLY and the standard Jolly–Seber model for open populations (Pollock et al. 1990). Rate of population change λ was estimated using the formula described by Pradel (1996) in program MARK: $\lambda(i) = N(i+1)/N(i)$. For instances where the model favoured by MARK did not support a constant λ over the course of the study, λ estimates were taken from the best ‘constant λ model’ and the ΔAIC and AIC_c weight are reported for this model.

To compare clutch size between the five grand skink populations, I collapsed clutch size data to calculate a mean for each skink over the 6-year study. I then calculated 95% confidence intervals (CIs) for the mean for each population; non-overlapping populations were deemed to have different estimates for average clutch size.

Results

Population trends 1996–2002

Grand skinks

Model fitting indicated that λ varied through time for almost all populations over the course of the study (best model based on ΔAIC was $\lambda(t)$ for populations A, C, D and E; Table 1). The only exception was population B, for which the $\lambda(\cdot)$ was favoured, indicating a constant λ of 0.81 and unambiguously indicating a population in decline (95% CIs 0.77–0.86; Table 1, Fig. 2).

For populations A, C and D λ estimates from $\lambda(\cdot)$ models (with high ΔAIC values and thus lowered reliability) ranged from 0.82 to 0.93. The 95% CIs for these λ s were always below 1, consistent with declines (Table 1). Only the pastureland population

Table 1. Models fitted to capture–recapture data collected from five grand skink (*Oligosoma grande*) and two Otago skink (*O. ottagense*) populations at Macraes Flat, South Island, New Zealand, from 1996 to 2002. The model used to generate λ was $\phi(t)p(t)\lambda(\cdot)$ in all cases. Model notation is described in Methods section.

Population	No. skinks	Best model based on ΔAIC	Lambda (λ)	95% CIs for λ	ΔAIC of $\phi(t)p(t)\lambda(\cdot)$	Probable population status (ranking from 1 = worst decline)
Grand skinks						
A	250	$\phi(t)p(t)\lambda(t)$	0.93	0.89 to 0.97	24.05	Decline (6)
B	180	$\phi(t)p(t)\lambda(\cdot)$	0.81	0.77 to 0.86	0	Decline (1)
C	166	$\phi(t)p(t)\lambda(t)$	0.91	0.86 to 0.97	12.40	Decline (5)
D	90	$\phi(t)p(t)\lambda(t)$	0.82	0.78 to 0.89	384.01	Decline (2)
E	186	$\phi(t)p(t)\lambda(t)$	0.97	0.93 to 1.02	41.24	Stable
Otago skinks						
C	151	$\phi(t)p(t)\lambda(t)$	0.90	0.84 to 0.96	12.04	Decline (4)
D	138	$\phi(t)p(t)\lambda(t)$	0.89	0.83 to 0.94	20.41	Decline (3)

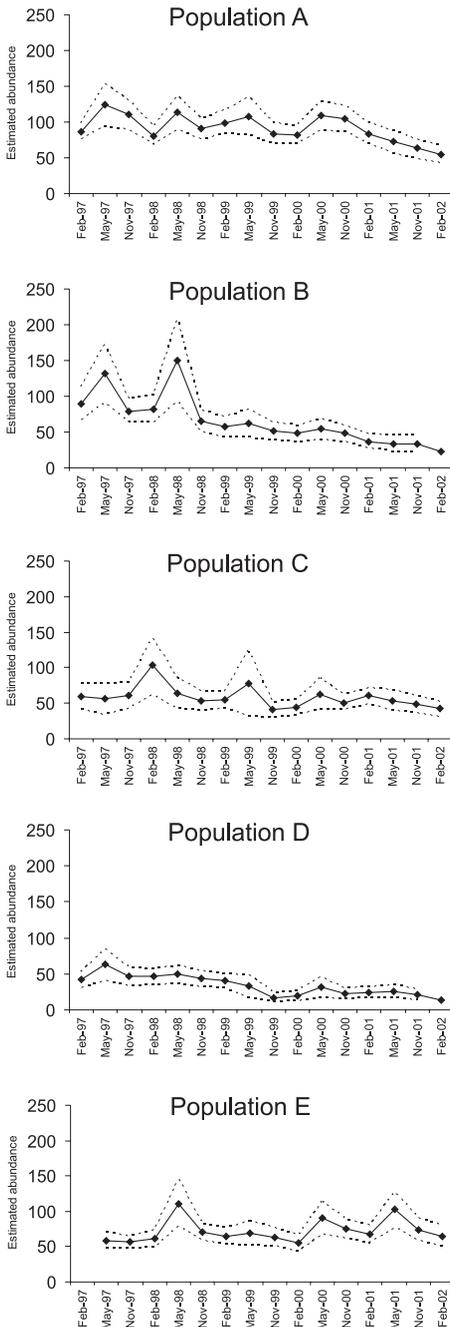


Figure 2. Abundance estimates (with 95% CIs) from program JOLLY for five grand skink (*Oligosoma grande*) populations (A–E) over the course of a 6-year study at Macraes Flat, South Island, New Zealand. Estimates could not be made for the first and last sampling sessions (November 1996 and May 2002).

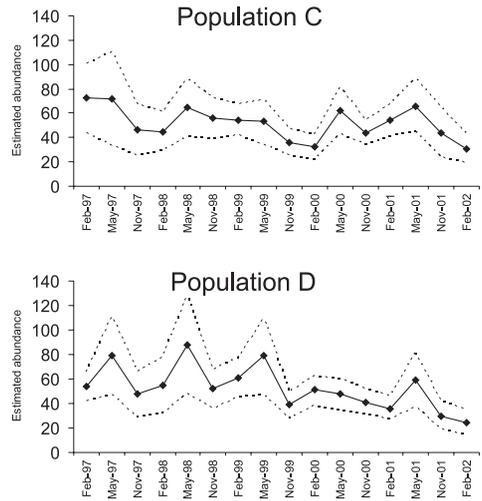


Figure 3. Abundance estimates (with 95% CIs) from program JOLLY for Otago skink (*Oligosoma grande*) populations C and D over the course of a 6-year study at Macraes Flat, South Island, New Zealand. Estimates could not be made for the first and last sampling sessions (November 1996 and May 2002).

(E) appeared stable with a lambda of 0.97 (95% CIs of 0.93–1.02; Table 1).

A visual appraisal of abundance estimates supported lambda estimates showing that four of the five study populations exhibited downward trends over the 6-year study (Fig. 2). Pronounced downward trends occurred in populations A, B and D; and in the case of population B, the abundance estimate dropped approximately 76% from February 1997 to February 2002 (Fig. 2).

Otago skinks

For both populations the lambda estimates from $\lambda(\cdot)$ models (with high Δ AIC values and thus lowered reliability) were consistent with declines (Table 1). A visual appraisal of abundance estimates supported the lambdas and showed downward trends for both study populations over the 6-year study (Fig. 3). The most pronounced downward trend occurred in population D, where the abundance estimates dropped by approximately 64% from February 1997 to February 2002 (Fig. 3). For population C there was some indication that the downward trend in abundance may have been at least partially thwarted over the latter part of the study, but not enough to affect the overall downward trend (Fig. 3).

Immigration and emigration patterns

The majority of individuals (88–92%) of both species captured within the study populations were ‘permanent

Table 2. Immigration and emigration patterns for five grand and two Otago skink study populations at Macraes Flat, South Island, New Zealand, between 1996 and 2002. 'Def.' denotes a definite immigration or emigration event whereby an individual has been recorded at a new location for >2 captures; 'Poss.' denotes a possible immigration or emigration event whereby an individual has been recorded at a new location for ≤ 2 captures; 'Temp.' refers to movements where the vast majority of captures of an individual were from one location, but infrequent captures (usually 1) were made at a second location, followed by captures again at the original location. 'Net loss' is an estimate of overall loss to each population through emigration, per year, calculated using the following formula: (total emigration – total immigration)/6 years.

Populations	Grand skinks (<i>Oligosoma grande</i>)					Otago skinks (<i>O. otagense</i>)	
	A	B	C	D	E	C	D
No. individuals captured inside only	231	160	153	79	168	133	121
No. individuals captured outside only	141	71	84	98	40	51	6
No. individuals captured in & out, i.e. 'movers'	19	20	14	11	18	17	17
% 'movers'	5	8	6	6	8	8	12
% residents (in)	92	89	92	88	90	89	88
Immigrants (Def.)	2	1	0	1	3	3	3
Immigrants (Poss.)	1	4	6	1	2	5	2
Immigrants (Temp.)	0	0	0	2	1	2	0
Total immigrants	3	5	6	4	6	10	5
Emigrants (Def.)	3	2	0	1	0	0	0
Emigrants (Poss.)	12	9	5	3	6	3	9
Emigrants (Temp.)	1	4	3	3	6	4	3
Total emigrants	16	15	8	7	12	7	12
Net loss	2.2	1.7	0.3	0.5	1.0	-0.5	1.2

residents', at least over the time frame of this study (Table 2). Only a small percentage of skinks captured from both inside and outside of the study populations were recorded as 'movers' – either immigrants or emigrants (5–8% and 8–12% of grand and Otago skinks respectively; Table 2).

Very few (0–3) individuals made unambiguous (i.e. definite) movements into or out of the study populations over the 6-year study and these data were too few to investigate emigration/immigration imbalances (Table 2). However, emigration did exceed immigration in six of the seven study populations when all possible immigration movements were tallied and contrasted with all emigration events (Total immigrants and emigrants in Table 2). Although some movements were likely to have been overlooked, especially emigration movements, pooling all movement data in this way generated a conservative estimate of a 'loss' of between 0.3 and 2 skinks per year (c. 4%) from grand skink study populations through emigration. For Otago skinks, population C on average gained 0.5 skinks every year and population D sustained a loss of 1 skink per year (c. 5%; Table 2).

Age to first reproduction

Sample sizes for both species were extremely low, especially given all captures since 1988 were considered

in these analyses. Grand skink females took on average 3.9 years to produce their first clutch (3 years, $n = 6$ females; 4 years, $n = 9$; 5 years, $n = 5$). Otago skinks took longer, averaging 4.8 years (4 years, $n = 2$; 5 years, $n = 2$; 6 years, $n = 1$).

Fecundity: clutch frequency, clutch size and annual reproductive output

Most mature-sized females were found to be pregnant in any given year (on average 85% and 77% of grand and Otago skink females respectively; Table 3). For grand skinks, each mature-sized female carried on average an (inferred) clutch of 1.85, and had a clutch frequency of 0.79, which culminated in an estimate for annual reproductive output (ARO) of 1.46 (offspring per female per year; Table 3). Fecundity estimates were similar for Otago skinks (mean clutch size = 1.74, mean clutch frequency = 0.81, ARO = 1.41; Table 3).

The 'stable' grand skink population (E) had consistently high fecundity measures (i.e. relatively high mean clutch size, mean clutch frequency, and percentage of females pregnant every year) but overall similar fecundity to the most steeply declining population B (Table 3). By way of contrast, a second grand skink population that was in pronounced decline (population D) had consistently

Table 3. Summary of fecundity values and sex ratios taken from five grand and two Otago skink populations from Macraes Flat, South Island, New Zealand, from 1996 to 2002. All populations are in decline except the 'stable' population E. *n* values for mean clutch frequency refer to number of females used in the calculation. *n* values for % female captures pregnant refer to number of female years used in the calculation (see Methods for further definition of female years).

Populations	Grand skinks (<i>Oligosoma grande</i>)					Overall mean	Otago skinks (<i>O. ottagense</i>)		Overall mean
	A	B	C	D	E		C	D	
Sex ratio M:F	1:1	1:1.3	1:1	1:0.8	1:1.1	1:1	1:1.3	1:0.9	1:1.1
<i>n</i> M:F	37:35	25:33	30:30	22:18	25:27	139:143	19:24	18:17	37:41
Mean clutch frequency (<i>n</i>)	0.81(35)	0.91(32)	0.68(29)	0.64(18)	0.87(26)	0.79(140)	0.74(23)	0.9(17)	0.81(40)
Mean clutch size ± SEM)	1.85 ± 0.01	1.88 ± 0.01	1.92 ± 0.02	1.42 ± 0.03	1.91 ± 0.01	1.85 ± 0.05	1.73 ± 0.02	1.76 ± 0.03	1.74 ± 0.09
(<i>n</i>)	(87)	(69)	(49)	(25)	(74)	(304)	(37)	(29)	(66)
% of female captures pregnant (<i>n</i>)	85.3 (102)	92 (75)	80 (60)	67.5 (40)	90.2 (82)	85 (359)	72.5 (51)	83.3 (36)	77 (87)
Annual reproductive output (offspring per female per year)	1.50	1.71	1.31	0.91	1.66	1.46	1.28	1.58	1.41

low fecundity measures. In particular, mean clutch size (a mean of each skink's mean over the 6-year study) was significantly lower for population D than for all other populations (Table 3).

The lowest ARO values for grand skinks were generated for populations cohabiting with Otago skinks (i.e. populations C and D; Table 3). Where grand and Otago skinks cohabited, Otago skinks had a higher ARO at one site (1.58 vs 0.91) and both species had similar AROs at the second site (1.28 vs 1.31 for Otago and grand skinks respectively; Table 3).

The highest average clutch size recorded during this study for grand skinks was 2.4 for population E (the stable population) during the summer of 1998/99. Yearly clutch size averages were usually 2 or less (in 77% of cases) and for the declining grand skink population D, average clutch size estimates never exceeded 1.75. For Otago skinks, the highest average clutch sizes were 2.3 (recorded in population C during the summer of 1999/2000) and 2.2 (recorded in population D during 1998/99). As for grand skinks average clutch size for Otago skinks rarely exceeded 2 (only the cases listed above exceeded 2; 83% of cases were 2 or lower).

Sex ratio

The sex ratio of mature-sized grand and Otago skinks averaged 1:1 M:F and 1:1.1, respectively, when captures over all populations and all study years were pooled (Table 3).

Attrition of newborn cohorts

On average 74% of newborn grand skinks were still alive during Y2 (their second summer; Table 4). This figure dropped to 48% during their third summer, and continued to decline during Y4 and Y5 (Table 4). The stable population E had a consistently high persistence of cohorts compared with the declining populations, with 30% of the 1996/97 cohort persisting to Y6 (SVL range 83–101 mm), compared with 10%, 0%, 0% and 0% for populations A, B, C and D respectively. Population C had the lowest persistence, with no skinks appearing to survive past their fourth summer.

For Otago skink newborns, 64% survived to be recaptured during their second summer, dropping to 41% during the third summer. These figures were remarkably consistent over both Otago skink populations, but lower than grand skink averages. Unlike grand skinks (with the exception of population E), Otago skink newborns that reached their fourth summer apparently persisted well; on average 22% of the 1996/97 cohort was still present in Y6 (SVL range 102–112 mm), a persistence almost three times that of grand skinks (Table 4).

Recruitment

On average 18% of grand skink newborns survived to adulthood (SVL ≥ 78 mm) (Table 5), which was usually (but not always) reached in their fourth summer of life. Similarly, approximately 22% of Otago skink newborns survived to adulthood (SVL ≥ 101 mm) (Table 5), which was attained during their fourth or fifth summer.

Table 4. Percentage of the total number of newborns captured over five cohorts (n) that were recaptured in Years 2–5 (Y2–Y5) from each population (A–E). Y1 was the birth year for each of the cohorts, i.e. the summers of 1996/97, 1997/98, 1998/99, 1999/2000 and 2000/01 for cohorts 1–5 respectively. I assumed 100% of newborns from each cohort survived their capture summer, i.e. Y1 is 100%. Attrition of each cohort was estimated from recapture records in years following birth summer (e.g. for skinks with Y1 over the summer of 1996/97, attrition was tracked over Y2–Y6). For skinks born over the summer of 2000/01, attrition was only tracked to Y2, when the study ended. Hence, attrition of newborn cohorts between Y1 and Y2 is more 'robust' (averaged over five cohorts) compared with attrition values for skinks between Y5 and Y6 (based on a single cohort born over 1996/97; Y6 in table). Mean 'persistence' is calculated for each year across study populations, i.e. on average 74% of 271 grand skink newborns survived to be recaptured some time over their second summer (where they reach SVLs of between 42 and 68 mm). Initial cohort size (in Y1) averaged 11 (range 1–24) for grand skinks and 10 (range 5–15) for Otago skinks at Macraes Flat, South Island, New Zealand.

	Grand skinks (<i>Oligosoma grande</i>)						Otago skinks (<i>O. otagense</i>)				
	SVL (mm)	A	B	C	D	E	Mean persistence (%)	SVL (mm)	C	D	Mean persistence (%)
n (Y1)	79	53	42	25	72			46	50		
Y2	42–68	84	67	80	71	70	74	52–86	64	63	64
Y3	55–84	51	35	48	44	63	48	67–93	43	40	41
Y4	66–90	26	13	18	27	41	25	78–106	26	23	24
Y5	76–93	13	9	0	15	30	13	96–111	27	20	23
Y6	83–101	10	0	0	0	30	8	102–112	14	29	22

Table 5. Recruitment into the adult population of newborns that were captured over the summers of 1996/97 and 1997/98 (SVLs ≥ 78 mm and ≥ 101 mm for grand and Otago skinks respectively; Cree 1994) at Macraes Flat, Otago, New Zealand.

Populations	Grand skinks (<i>Oligosoma grande</i>)						Otago skinks (<i>O. otagense</i>)		
	A	B	C	D	E	Mean	C	D	Mean
Newborns captured between Nov 1996 and May 1998	26	26	11	13	33		12	16	
Newborns to have reached adulthood	4	3	1	2	12		3	3	
% recruitment	15	12	9	15	36	18	25	19	22

Apparent survival of mature-sized skinks over study duration

Annual survivorship for the single cohort followed from 1996/97 was low for both grand and Otago skinks averaging 0.71 and 0.58 respectively over the duration of this study (Table 6). Only 7–15% of adults in declining grand skink populations survived to be recaptured during 2001/02 (corresponding to mean annual apparent survival values of 0.62–0.75; Table 6). The stable population E had the highest survivorship, with 39% of the original cohort left and a corresponding mean annual apparent survival of 0.84 (Table 6). Survivorship was generally much lower for Otago skink mature-sized individuals, with only 5% surviving to be recaptured during 2001/02 (mean annual apparent survival of 0.56–0.59; Table 6).

Adult skinks from all populations of both species had a life expectancy of about 3 years; the only exception is

grand skink population E, where skinks had approximately double that life expectancy (Table 6). The lowest life expectancies were calculated for the Otago skink populations (2.3 and 2.5 years; Table 6).

Discussion

These data raise some real and serious concerns about the viability of small fragmented populations of the critically endangered grand and Otago skinks in what is considered the core habitat for these species. Although grand and Otago skinks at Macraes Flat share identical habitat and are even sympatric at some sites (Towns 1985; Coddington & Cree 1997; Marshall 2000), they do have apparent differences in their life history traits that cause them to respond in different ways to contemporary threats

Table 6. Number of mature-sized skinks first captured at Macraes Flat, South Island, New Zealand, in 1996/97 (Y1) that were subsequently recaptured in the following summers. Skinks were identified by their toe clips. A crude estimate of 'mean annual survival' was calculated by averaging survival of the cohorts from summer to summer, e.g. 22 of 37 skinks from population A (i.e. 59%) survived between 1996/97 and 1997/98, and so on. Life expectancy = $1/(1 - \text{mean annual survival})$. For Otago skink population D, more skinks were captured over 1998/99 than were recorded the previous summer. In this case I assumed survival was 100% but acknowledge with an asterisk my low confidence in the resulting 'mean annual survival' value for this population.

Populations	Grand skinks (<i>Oligosoma grande</i>)					Mean	Otago skinks (<i>O. otagense</i>)		
	A	B	C	D	E		C	D	Mean
1996/97	37	29	21	26	18		20	21	
1997/98	22	22	10	17	16		11	6	
1998/99	21	19	8	17	14		11	9	
1999/2000	13	11	4	5	8		4	3	
2000/01	11	6	4	5	8		3	2	
2001/02	5	2	2	4	7		1	1	
Mean annual survival	0.69	0.62	0.66	0.75	0.84	0.71	0.59	0.56*	0.58
Life expectancy of adults (yrs)	3.3	2.6	2.9	4	6.3		2.5	2.3	

Table 7. Summary of life history traits for declining or stable grand and Otago skink populations (A–E) at Macraes Flat, South Island, New Zealand, from 1996 to 2002. Refer to Tables 1, 2, 3, 5 and 6 for information on how these data were collated.

	Grand skinks (<i>Oligosoma grande</i>)					Otago skinks (<i>O. otagense</i>)	
	A	B	C	D	E	C	D
Population trends							
Lambda	0.93	0.81	0.91	0.82	0.97	0.9	0.89
95% CI for lambda	0.89–0.97	0.77–0.86	0.86–0.97	0.78–0.89	0.93–1.02	0.84–0.96	0.83–0.94
Population abundance trend	Decline	Decline	Decline	Decline	Stable	Decline	Decline
Movements							
Total immigrants	3	5	6	4	6	10	5
Total emigrants	16	15	8	7	12	7	12
Net loss	2.2	1.7	0.3	0.5	1	–0.5	1.2
Fecundity							
Sex ratio M:F	1:1	1:1.3	1:1	1:0.8	1:1.1	1:1.3	1:0.9
Mean clutch frequency (n)	0.81	0.91	0.68	0.64	0.87	0.74	0.9
Mean clutch size (± 1 SEM)	1.85 \pm 0.01	1.88 \pm 0.01	1.92 \pm 0.02	1.42 \pm 0.03	1.91 \pm 0.01	1.73 \pm 0.02	1.76 \pm 0.03
% of female captures pregnant	85.3	92	80	67.5	90.2	72.5	83.3
Annual reproductive output (offspring per female per year)	1.5	1.71	1.31	0.91	1.66	1.28	1.58
Recruitment							
% recruitment	15	12	9	15	36	25	19
Survival							
Mean annual survival	0.69	0.62	0.66	0.75	0.84	0.59	0.56
Life expectancy of adults (yrs)	3.3	2.6	2.9	4	6.3	2.5	2.3

and subsequent conservation management initiatives (Whitaker & Loh 1995; Whitaker 1996; Coddington & Cree 1997; Houghton 2000; Marshall 2000; Tocher 2003; Tocher & Norbury 2005). Preliminary population projection modelling carried out to date that considers these life-history differences predicts faster decline trajectories for Otago skinks (Tocher & Norbury 2005), but both skink species are in urgent need of assistance.

Due to a combination of both exogenous causes (e.g. predation) and endogenous causes (life history traits that limit population growth) populations of both grand and Otago skinks have declined at varying rates over the course of this study. Some populations have shown steep declines in abundance, others have exhibited more moderate declines, and one population was stable. By studying multiple populations I have helped elucidate decline factors for both skink species. Some populations are in decline primarily due to adult survivorship being too low while others have noticeable fecundity constraints (Table 7). Still other populations are showing declines due to a combination of survival and fecundity problems (Table 7). A gross extrapolation of abundance estimates predicts that most populations will be extinct within 10–20 years. The one exception to this is grand skink population E, located in a highly modified pastureland site; this population appeared to be on an upward trajectory throughout the 6-year study, including the period when predators were not under any form of control (1996–1999).

The predator control operation conducted from 1999 to 2002 did little to avert downward population-size trends in other populations. I cannot entirely rule out the possibility that declines were somewhat lessened due to the predator control; any benefit though was apparently subtle and improvement in population size was further hindered by low fecundity of some populations over the time frame of my study (Table 7).

Adult survivorship reported here (0.71 and 0.58 for grand and Otago skinks respectively) is higher than that found previously using sophisticated capture–recapture methodology (approximately 0.54; Tocher 2006). Apparent survival estimates generated by Tocher (2006) included all-aged skinks (including juveniles), which likely produced relative underestimates for adults. Both estimates are much lower than that found for a long-lived skink from Australia, *Tiliqua rugosa*, which was estimated to have an annual survivorship of 80–90% (Bull 1995). Population projection modelling for both grand and Otago skinks has indicated that they also require an adult survivorship of approximately 80% to stabilise declining populations at Macraes Flat (Tocher & Norbury 2005). Given this result, adult survivorship in almost all populations of grand and Otago skinks is alarmingly low and only in the stable population E does adult survivorship reach a level expected to result in population increase (Tocher & Norbury 2005).

Emigration and immigration patterns do not explain

decline patterns over my study populations. Definite emigration and immigration events were rare; the majority of skinks remained resident within the study populations over the 6-year duration of the study. Where I did detect movement, similar levels of immigration and emigration were noted in both declining and the stable population. The steeply declining grand skink population B declined by approximately 10 skinks per year during the course of my study. Although some emigration events may well have been overlooked by my sampling regime on peripheral rocks, I do not believe my estimate of loss through emigration of around one skink per year was out by the factor of 10 required to explain declines in this population. My modest estimates of emigration are supported by a more thorough study conducted by Houghton (2000) who did not find an imbalance of emigration over immigration for any of my study populations over the summers spanning 1997–1999.

A direct comparison between the fecundity data collected during this study and those collected by Cree (1994) reveals disturbing contrasts. Cree (1994) reported annual reproductive outputs (AROs) of 2.17 for grand skinks and 2.34 for Otago skinks. In contrast, my estimates for ARO of 1.46 and 1.41 were between 33 and 40% lower than Cree's estimates. These lower estimates were a result of clutch frequencies being approximately 10% lower and, perhaps more worryingly, my average clutch size estimates being on average 30% lower than those recorded earlier (Cree 1994).

Although I expected some variation in the ability of observers to accurately count developing conceptuses, the lower fecundity measures recorded from 1996 cannot easily be explained through fieldworkers not being skilled enough to detect and count developing conceptuses (palpation, when carefully carried out seems unlikely to cause reproductive failure; Holmes & Cree 2006). For this explanation to have traction all workers from 1996 would need to have been seriously deficient in field-palpation skills, relative to Cree (1994). I believe this to be highly improbable and suggest it is more likely that fecundity has declined in both species at Macraes Flat as time has passed. Nonetheless, underestimation of clutch size by my fieldworkers during this study must remain a possibility. There has been no independent test performed to confirm the validity of the comparison with Cree (1994), and my fieldworkers were advised to take a conservative approach when estimating the number of oviductal conceptuses. Further to this, clutch-size estimates from palpation (even if accurate as to number) do not necessarily translate to viable offspring on the ground. Clutch size can fall during pregnancy potentially worsening the situation for both grand and Otago skinks (Holmes & Cree 2006; A. Cree, University of Otago, Dunedin, NZ, pers. comm., 2008).

I offer three possible explanations for a large drop in ARO since the work of Cree (1994): (1) the influence of ectoparasites (Reardon & Norbury 2004; Holmes & Cree

2006); (2) researcher disturbance; and (3) a combination of demographic stochasticity and Allee effects (Allee et al. 1949; Lande 1993). I believe a change in ectoparasite loading brought about by the introduction of a novel stressor is a plausible explanation for lower fecundity for some skink populations at Macraes Flat. Two species of ectoparasitic mite are known from wild populations of grand and Otago skinks: *Ophionyssus scincorum* and *Odontacarus lygosomae* (Reardon & Norbury 2004). Infestations of the brown mite *O. scincorum* have been associated with pregnancy failures in captive McCann's skink, *Oligosoma maccanni* (Holmes & Cree 2006), a species that coexists with grand and Otago skinks at Macraes Flat. A possible relationship between mite loading and fecundity in Otago and grand skinks requires further investigation.

The notion of researcher disturbance playing some role in grand and Otago skink population declines was first raised by a concerned conservation manager (R. Thomas, Department of Conservation, Dunedin, NZ, pers. comm., 2002). A recent local study has shown disturbance can seriously affect endangered wildlife such as yellow-eyed penguins (*Megadyptes antipodes*; Ellenberg et al. 2007) and I acknowledge the possibility that disturbance through 'research' may have accelerated the deterioration of already pressured (through predation) skink populations. Ectoparasite loading and Allee effects could also be exacerbated by researcher disturbance.

On balance of evidence, population declines at Macraes Flat are unlikely to be caused primarily by researchers especially given declines on different scales have been noted by other researchers at Macraes Flat (Whitaker 1996; Houghton & Linkhorn 2002). Biologists are often faced with a dilemma between obtaining adequate data to document decline (and thus ultimately recruit management funds) versus ensuring appropriate safeguards are in place so that the process is not detrimental. Whenever possible, reducing levels of disturbance is desirable; the grand and Otago skink recovery team have now abandoned toe-clipping in favour of using photo identification of individual skinks as one way of reducing researcher-induced disturbance (G. Norbury, Landcare Research, Alexandra, NZ, pers. comm., 2005).

The third explanation for reduced ARO, and the one I favour, is the combined influence of a so-called 'Allee effect' and stochastic variation in demographic parameters. These two processes have been shown to affect low-density populations, and may contribute to eventual population extinction (Allee et al. 1949; Lande 1993; Liebhold & Bascombe 2003). I postulate that population declines have led to a breakdown in the social fabric of these skink populations leading to the variation in fecundity measures shown in this study. Both species are known to be social; they bask commensally, indicating that monogamy may be a feature of their reproduction (pers. obs., 1997; Marshall 2000; Germano 2007; see also Bull

1988, 1990). I observed that fecundity measures vary between declining populations in an unpredictable way; this 'randomness' implies an acute lack of stability below a critical population size, a notion suggestive of stochastic processes. Perhaps working in tandem, an Allee effect (a relationship between population density and fecundity) can operate when population size is relatively small and may result in some form of reproductive and/or social dysfunction; indeed any component of individual fitness maybe involved leading to the lowered ARO observed here (Allee 1931; Allee et al. 1949).

In conclusion, I present an alarming synopsis of declines in multiple populations of grand and Otago skinks and many of the patterns I observed remain largely unexplained likely due to the unpredictability in vital rates observed in near-extinct populations (Allee 1931; Lande 1993). One result gives hope: a single grand skink population is stable and this population excels in many traits measured (Table 7). As grand and Otago skinks are on an apparent extinction trajectory conservation managers need to explore techniques that will result in enhanced fecundity, newborn recruitment and survival, rather than rely on initiatives that will improve survival alone. Improvements in multiple traits concurrently will likely result in a faster reversal of declines and an expeditious population-size increase beyond the reach of the stochastic forces operating at the current low population sizes.

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