

Maternal and environmental influences on reproductive success of a viviparous grassland lizard

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Abstract: Understanding the factors that drive population persistence and growth is fundamental to both conservation management and evolutionary biology. Internal (maternal) and external (environmental) factors can affect female reproductive output, and in oviparous reptiles both may strongly influence offspring phenotype and quality. However, the link between these effects, their importance for reproductive output and offspring characteristics of live-bearing lizards, and whether population declines are linked to these factors in modified versus native habitats are unknown. We used a common New Zealand skink species, *Oligosoma maccanni* (McCann's skink), found in grazed native and exotic grassland to test whether differences in environmental or maternal characteristics influenced birth date, pregnancy success and offspring phenotype. In both grassland types the date of birth was c. 8 days earlier at lower altitudes (altitudinal range = 564–719 m a.s.l.), and small females were less likely to have successful pregnancies. However, larger females had more weak or deformed offspring, suggesting that reproductive senescence may exist in this species. While other research shows that exotic grasslands do not support as many skinks as native tussock grassland, reproductive success of pregnant skinks (viable litter size) was not affected by habitat modification. However, neonates had greater body condition (mass for length) when from females with higher post-partum body condition, and these females were from the native tussock grasslands. In conjunction with previously published data on McCann's skink, our data suggest that reduced offspring quality may contribute to the lower population numbers in the exotic habitats.

Keywords: grassland; habitat modification; offspring; *Oligosoma maccanni*; phenotype; pregnancy success

Introduction

The persistence (and ultimate survival) of populations and species is intricately linked to factors that control reproductive output, offspring quality and offspring survival, and these are related to maternal and environmental characteristics. Habitat quality influences the reproductive success of many vertebrates, with females from higher-quality territories (e.g. those with more food resources, better retreats) generally having higher body condition, earlier onset of breeding, and ultimately more offspring (e.g. mammals: Ims 1987; Thompson et al. 2007; birds: Martin 1987; Norris et al. 2004; reptiles: Naulleau & Bonnet 1996; Rubenstein & Wikelski 2003). The environment experienced by a female may lead to variation in her growth (and ultimately size), overall condition and physiological state. These factors may in turn influence offspring development and phenotype through 'maternal effects', such as via yolk quantity and changes in hormones (Bernardo 1996; Mousseau & Fox 1998).

The timing of offspring production can also influence offspring survival, with the best time for hatching/birth being when the most resources are available for growth and when enough time remains to find retreats or to migrate before the onset of winter (Olsson & Shine 1998; Warner et al. 2007). In ectothermic species, optimal timing of parturition is confounded by the strong thermal dependence of embryogenesis, with gestation length significantly shorter when developmental temperatures are higher (e.g. Cree & Hare 2010). The thermal environments experienced by embryos of reptiles also result in long-term changes in phenotype, and most of this evidence

is derived from laboratory-based studies (Beuchat 1988; Wapstra 2000; Deeming 2004). These changes in phenotype include differences in size, shape, behaviour and locomotor performance (Blumberg et al. 2002; Hare et al. 2002, 2008). Offspring quality, in species with delayed maturity, is normally inferred by size at hatching (or birth) and locomotor performance. Bigger offspring generally have a greater chance of survival to maturity (Ferguson & Fox 1984; Elphick and Shine 1998, but see Congdon et al. 1999; Warner & Shine 2007) and faster offspring have a better chance of escaping predators, catching prey, and having beneficial social interactions (Garland et al. 1990; Jayne & Bennett 1990; Husak et al. 2006). Thus, environmental factors that influence offspring quality, such as changes in vegetation structure and the resultant thermal environment, may have lasting implications for reptiles.

Urbanisation and pastoralism have dramatically altered the life history of many species, with some seemingly benefiting and reaching high numbers, whereas others are disadvantaged and eventually extirpated from modified areas (Lunney 2001; DeStefano & DeGraaf 2003; Chace & Walsh 2006; McKinney 2008). Habitat loss may pose the greatest danger for threatened terrestrial reptiles with 63% of species in danger of extinction by agriculture alone (Böhm et al. unpubl. data). Within New Zealand the tussock grassland region of coastal Otago has experienced some of the most dramatic declines of abundance and distribution of lizards (Patterson 1984; Towns & Daugherty 1994; Whitaker & Loh 1995). Intensive modification (burning, ploughing and oversowing) of native tussock grasslands for agriculture, predation by introduced mammals, and other activities such as gold-mining have

contributed to this reduction (Towns & Daugherty 1994; Whitaker 1996). Whether the declines in lizard numbers are linked to reduction in reproductive output and potentially detrimental changes in offspring phenotype in modified versus native habitats is unknown.

Our study aimed to determine whether maternal and/or environmental factors explain differences in reproductive success and offspring quality in a viviparous lizard, particularly in response to habitat modification. We assessed maternal (size, condition and tail length) and environmental (altitude, habitat type, vegetation height, rock size) characteristics in relation to birth date, pregnancy success and offspring characteristics. We used the heliothermic lizard *Oligosoma maccanni* (McCann's skink) as it is non-threatened and relatively common, yet numbers are reduced where introduced predators are present and where habitats are modified (Whitaker 1996; Norbury 2001; Lettink et al. 2010). Reproductive cycles of female *Oligosoma maccanni* are also well understood (Holmes & Cree 2006). We used both macro- and micro-habitat scales to explore potential associations.

Materials and methods

Study species and area

Oligosoma maccanni (Lacertilia: Scincidae) generally lives in dry, rocky environments and is most abundant in montane grassland (Gill & Whitaker 2001). It has an annual reproductive cycle in which pregnancy extends from September/October (austral spring) until January/February in the Otago region (mid- to late summer; Holmes & Cree 2006). *Oligosoma maccanni* is territorial (Patterson & Daugherty 1990) and exhibits site philopatry in the short term (at least 2 years; KMH unpubl. data). The minimum size at maturity is 49 mm snout-vent length (SVL; Holmes & Cree 2006) and is estimated to occur at 3–4 years of age in the wild (KMH unpubl. data). Litter size (mean = 2.8 offspring; range = 1–7) increases with maternal body length (Holmes & Cree 2006; this study). In the laboratory, pregnant females thermoregulate to gain as much basking opportunity as possible (Hare et al. 2010), select body temperatures of 26.4°–30.2°C (mean = 28.9°C; Hare et al. 2009), and have a significantly shorter gestation period when higher basking opportunity is available (Cree & Hare 2010). About 85% of pregnant female *Oligosoma maccanni* have viable offspring when held under seemingly optimal conditions in the laboratory. This level of pregnancy failure is within the normal range for captive-housed viviparous lizards (Hare et al. 2010b).

The study site is situated at Macraes Flat, New Zealand (45°28' S, 170°28' E) and includes schist outcrops and pieces of loose schist within grasslands. The district is dominated by grazed introduced grassland of predominantly rye grass (*Lolium perenne*) and white clover (*Trifolium repens*; Bibby 1997). Most of the remaining areas of native tussock grassland are subjected to continued grazing by sheep and cattle, infrequent burning, aerial application of fertiliser and oversowing (Whitaker 1996). The tussock grasslands are predominantly tall narrow-leaved snow tussock (*Chionochloa rigida*) and red tussock (*C. rubra*) with some areas of shrubland including matagouri (*Discaria toumatou*), mānuka (*Leptospermum scoparium*), kānuka (*Kunzea ericoides*), *Coprosma* spp. and *Olearia* spp. (Bibby 1997). The grazed tussock grassland that remains is often confined to narrow strips around rocky

outcrops or on steep slopes that cannot be ploughed, although larger areas of tussock grassland are present on some farms (Whitaker 1996). Livestock often shelter around rock tors, disrupting rock pieces and depositing faecal material (KMH pers. obs.). Differences in food abundance and quality between tussock and exotic grasslands at Macraes Flat exist through variation in invertebrate types and abundance (Tocher 2003) as well as the distribution of fruiting plants (O'Connor 1982; Whitaker 1996).

The collection sites were in grazed areas from altitudes of 564–719 m a.s.l. At the site of capture we recorded altitude, vegetation type (exotic grass, tussock or bushes) and height, and overall rock height and size. Altitude was obtained using a global positioning system device (Garmin GPS 12, USA). The surrounding vegetation (macro-vegetation scale within 500-m radius) was visually scored as introduced pasture or native tussock (whichever constituted >60% of the vegetation). Vegetation within a 2-m radius of the capture locality (rock tor/piece) was visually scored as percentages of introduced pasture, native tussock and shrubs (<10%, 10–50% or >50%) present. Rock height was measured, and rock size was calculated as the minimum width by the maximum width (estimated surface area; m²).

Pregnant female *Oligosoma maccanni* were captured by hand from 35 different altitudes and 41 different rock outcrops. At each site we scored the vegetation as native tussock (54% of females) or exotic (46% of females) grasslands. As native tussock grasslands are more common at high than low altitudes, care was taken to include both native and exotic grasslands in high and low altitude collection sites. At the lower half of altitudes 41% of females were collected from tussock grasslands, whereas at higher altitudes 67% of females were collected from tussock grasslands. This meant that the proportion of pregnant lizards captured from native versus exotic grasslands did not differ significantly between low or high altitudes ($P = 0.06$), ensuring a more balanced design for analyses.

Animal collection and husbandry

Fifty-four late-pregnant *Oligosoma maccanni* were captured from 4 to 9 January 2009 and transported to the laboratory at the University of Otago, allowing complete litters from known females to be obtained. After transportation, mass (± 1 mg), snout-vent length (SVL; ± 1 mm), tail length (± 1 mm) and tail regeneration (y/n) were recorded and the skinks were placed in laboratory housing within 24 h of collection. The females ranged in size, with SVL of 56–78 mm (66.1 ± 0.7 mm SEM) and masses of 3.1–8.6 g (5.9 ± 0.9 g SEM). All females had ectoparasitic mites, which were eliminated using rigorous cage cleaning and vegetable-oil rubs (Hare et al. 2010).

The pregnant females were individually housed in identical 20-L plastic containers, with basking and cool retreat sites. Room air temperature was 15°C during the day and 12°C at night. The thermal regime was standardised among females and provided basking opportunity for 8 h each day, 5 days per week (40 h week⁻¹), which is estimated as available basking opportunity in the wild (Hare et al. 2009; Hare & Cree 2010a). When heat lamps were on, the skinks could choose to bask at their preferred temperature range or remain at ambient room temperatures.

An Arcadia D3 reptile lamp (Croydon, UK) provided UV light for 8 h per day (0900 to 1700 hours NZST). Ceiling-mounted fluorescent lights simulated a summer photoperiod with a 2-h dawn and dusk ramp (15:9 L:D) at 0500 and 1800

hours. Skinks were also provided with moist sphagnum moss and free access to water and were fed three times a week either with live insects dusted with a vitamin mixture or with pureed fruit.

Parturition and offspring phenotype

Gestation length was estimated from a nominal ovulation date of 1 October (based on dissections of wild skinks; Holmes & Cree 2006; Cree & Hare 2010) until the day of the first birth. Pregnancy outcome was ranked as successful (at least one viable offspring) or unsuccessful (no live offspring). Stillbirths were classified as fully developed dead offspring and abortions were classified as underdeveloped, non-viable offspring. On the day of birth all young were weighed to 1 mg, and SVL and tail-length were measured (± 0.5 mm) as potential correlates for offspring quality. The maximal sprint speed of offspring was also measured three times at each of two body temperatures, 15°C and 25°C. These temperatures were chosen as they approximated the preferred body temperature of c. 24–27°C reported for non-pregnant, captive *Oligosoma maccanni* by day (Besson & Cree 2010) and ambient summer air temperatures experienced in the field (15°C; Hare et al., 2009). A paintbrush was used to encourage sprinting in neonates 1–2 days old by touching their tails, and 15-min rest was given between each sprint trial. Speed at each temperature was measured on two consecutive days between 1300 and 1600 hours, with a different experimental temperature each day. The order of experimental temperatures was randomised to control for potential habituation effects. A plastic racetrack (width 0.08 m), with four paired photocells in slots (0.25 m apart and 4 mm high) over 1 m, was used to test speed. The interruption of each successive infrared beam stopped one of the timers. The fastest measure of speed over 0.25 m across the three trials was used in analyses.

Statistical analyses

Data were analysed using version 2.5.1 of the statistical program R (R Development Core Team 2008). Data transformations were performed as required to meet assumptions of normality. For all analyses we used a sequential table model of analysis, including the most significant factors first, to avoid attributing significance to later variables if significance could be explained by earlier variables. Statistical significance was assumed at $P < 0.05$. Data are expressed as mean \pm 1 SEM unless otherwise stated.

We tested whether date of birth for live, viable offspring varied with altitude, using regression analyses (only successful pregnancies were used in these analyses). As altitude was related to date of birth (see Results), it was included as a covariate in the remainder of date-of-birth analyses. Subsequently, general linear models were used to test whether date of birth was related to vegetation and rock characteristics (vegetation type, vegetation height, rock height and rock area, and their interactions) with altitude as a covariate. Body condition was calculated as the residuals from fitted data, using a linear regression of log(mass) on log(SVL) and was only included in models without mass and SVL.

We first tested whether pregnancy outcome (successful or unsuccessful) was related to days held in the laboratory. Days in the laboratory did not influence pregnancy outcome ($F_{1,50} = 0.975$, $P = 0.328$) and was ignored for the remainder of analyses. We then tested whether pregnancy outcome was related to maternal SVL, tail length (potential fat stores),

post-parturition body condition, and/or habitat characteristics (altitude, vegetation and rock characteristics as detailed above) using generalised linear mixed models (GLMM); maternal identity was included as a random factor. We assumed that tail length at capture was equivalent to that from early vitellogenesis, as field conditions over winter at Macraes Flat offer little to no opportunity for basking and growth (Hare & Cree unpub. data). We scored tail regeneration in the same manner outlined in Chapple et al. 2002. We tested whether final litter size (viable offspring only) was related to habitat characteristics (as for pregnancy outcome), using linear mixed effects models (LME), but included maternal SVL as a covariate and maternal identity as a random factor. We also used LME models to test whether females that gave birth to an entire litter within one day had different maternal and/or habitat characteristics (as above) from those that gave birth over multiple days (asynchronous births).

We tested whether offspring size or sprint speed at each temperature were related to maternal characteristics including asynchronous births, litter size, maternal size (SVL, tail length, tail regeneration (y/n), tail regeneration score, body condition and post-partum mass), using LME models. The neonate phenotypic measure (speed, SVL, tail length, mass or body condition) was included as a dependent variable and the maternal characteristic as the independent variable, and maternal identity as a random factor. We then tested whether phenotype of neonates was related to maternal habitat characteristics. The phenotypic measures were analysed in relation to date of birth, altitude, vegetation type and height, and rock height and surface area and their interactions, using GLMM. The phenotypic measure was included as a dependent variable and the habitat characteristic as the independent variable(s), and maternal identity was included as a random repeated variable. Because maternal body condition strongly influenced offspring size (see results), we included this variable as a covariate in all analyses of habitat. Juvenile size measures were also included as covariates in sprint-speed analyses, as morphology influences speed of lizards (Bauwens et al. 1995). Sex was not included in analyses as juveniles are monomorphic and non-lethal methods of sex identification have not been identified.

Results

The females gave birth to 172 live offspring and 17 stillbirths/inviolate offspring. We also noted the apparent consumption of at least six stillbirths (see Hare et al. (2010) for information on consumption of birth products). Live births took place from 12 January to 25 February 2009, between 92 and 142 days after the nominal ovulation date of 1 October 2008 or 6–52 days after collection. Stillbirths took place from 9 January to 25 January 2001, on average 23 ± 4 days after collection. Birth dates overlapped with those seen in the wild, with the first wild neonates of 2009 observed on 29 January (L. Judd, New Zealand Department of Conservation, pers. comm.). Generally, all members of a litter were born within one day (83%), but 13% of birthing events (viable offspring only) occurred over more than one day (1.7 ± 0.6 days); the longest interval between first and last births of a litter was 5 days. Parturition dates across all skinks spanned 50 days and were on average c. 8 days earlier in females from lower altitudes than higher altitudes ($r^2 = 0.176$, $P = 0.005$). No other factors (environmental) or their interactions influenced the date of

birth events ($P > 0.05$ in all cases). Similarly, no factors (environmental or maternal) or their interactions influenced whether a female had all births in one day or exhibited asynchronous birthing ($P > 0.05$ in all cases).

Forty-seven females (87%) gave birth to at least one live offspring, with seven females (13%) having stillbirths or no births. Four females had at least one live offspring and one stillbirth or deformed non-viable offspring. One female had a litter of six stillbirths. Litter size of viable offspring ranged from one to six (3.7 ± 0.2 offspring per female). Litter size increased with increasing maternal SVL ($F_{1,45} = 82.000$, $P < 0.001$) and was not influenced by any other factors or their interactions ($P > 0.05$ in all cases), including no influence of previous tail-loss by females ($F_{2,51} = 19.220$, $P = 0.609$). No habitat characteristics (altitude, vegetation, rock) or maternal size factors influenced pregnancy outcome ($P > 0.05$ in all cases), although there was a trend for smaller females to have fewer viable offspring per individual (Fig. 1). Larger females (SVL = 68.3 ± 2.6 mm, $n = 4$) produced more of the weak and/or deformed offspring.

Neonates ranged in size from 23- to 29-mm SVL (26.6 ± 0.1 mm) and 0.26 to 0.46 g (0.33 ± 0.01 g). Offspring were heavier from mothers with higher maternal post-partum body condition ($F_{2,43} = 2.084$, $P = 0.043$), but this was influenced by interactions with altitude and tussock cover. The post-partum body condition of females was heavier from higher altitudes ($P = 0.019$; 8.9% of total variation), and from areas with >50% tussock present within a 2-m radius around the site of capture ($P = 0.030$; 83.5% of total variation). No other factors (environmental or maternal) or their interactions were related to size measures of females or had an influence on offspring size measures at birth ($P > 0.05$ in all cases; including previous tail-loss by females having no influence on juvenile SVL, $F_{3,122} = 0.610$, $P = 0.609$). Sprint speed of juveniles was faster at ambient temperatures of 25°C than 15°C (0.43 ± 0.01 m s⁻¹ and 0.30 ± 0.01 m s⁻¹ respectively; $F_{1,291} = 160.266$, $P < 0.001$). No other factors (environmental or maternal) explained sprint speed at birth ($P > 0.05$ in all cases).

Discussion

Understanding factors that support successful pregnancies and offspring quality is essential in order to answer fundamental questions in evolutionary ecology and for conservation management of species. In our study, larger *Oligosoma maccanni* had greater pregnancy success. We also found that birth date increased with an increase in altitude. Offspring body condition was lower from females from exotic grasslands, and by association females with lower post-partum body condition.

Maternal effects

Oligosoma maccanni that were greater than 65-mm SVL were more likely to have successful pregnancies. Larger skinks had larger litters, but also a higher incidence of weak/poorly formed offspring (weak offspring were lethargic and later died). Larger skinks are potentially older, and may be undergoing reproductive senescence, although age and size influences on reproductive success are hard to tease apart. For example, larger female sand lizards (*Lacerta agilis*) lay more eggs, but within an age cohort many size classes are present, resulting in variable clutch sizes (Olsson & Shine 1996). However, hatchability of eggs (offspring viability) from older females was not tested (Olsson & Shine 1996). In Blanding's turtle (*Emydoidea blandingii*), body size, and by association clutch size, was similar among age groups, but older females had a higher incidence of nest failures due to developmental problems of embryos (Congdon et al. 2001). For those juvenile turtles that hatched there was no difference in hatchling morphology (Congdon et al. 2001). Conversely, painted turtles (*Chrysemys picta*) had greater offspring quality (more eggs and larger hatchling size) with age (Congdon et al. 2003). The potential for reproductive senescence in *Oligosoma maccanni* and other viviparous squamates deserves further exploration.

Previous tail loss in pregnant *Oligosoma maccanni* did not influence offspring size or litter size. This result is in direct contrast to a study on an Australian viviparous skink

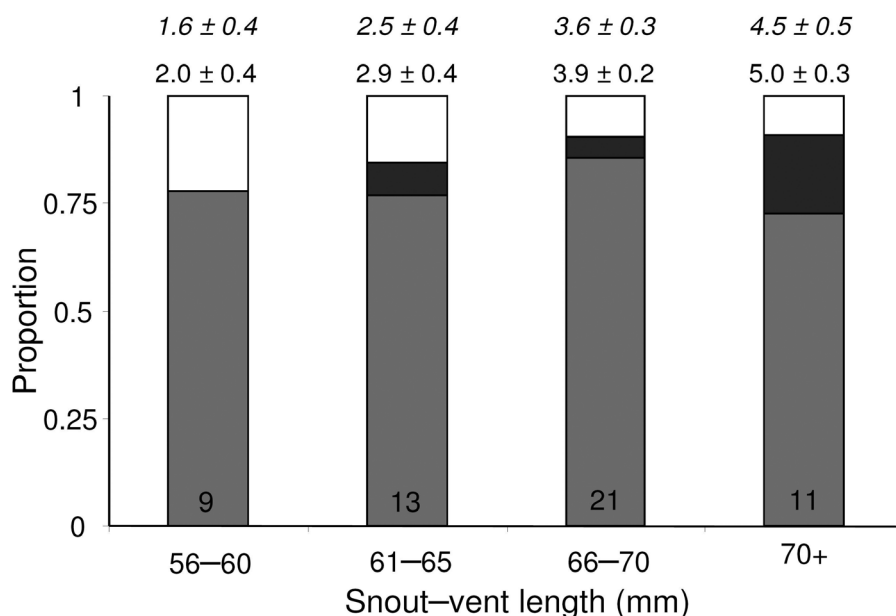


Figure 1. Relationship between maternal size and pregnancy outcome in *Oligosoma maccanni* (McCann's skink). Pregnancy outcome was ranked as successful (light grey; live births only), partially successful (dark grey; at least one viable offspring, and one dead and/or weak offspring), and unsuccessful (white; no viable offspring). The mean litter size (± 1 SE; viable offspring only) for each size group is indicated above the bars for all females included regardless of pregnancy outcome (above; *italics*), and only females that had some viable offspring (below). Sample sizes are shown at the base of bars.

(*Niveoscincus metallicus*), which found reduced litter size and larger offspring from females with previous tail loss (Chapple et al. 2002). Instead, neonate *Oligosoma maccanni* had higher body condition when delivered by females with higher post-partum body condition. Larger neonates are likely to have higher survival (Ferguson & Fox 1984; Elphick & Shine 1998). Interestingly, females had higher post-partum body condition when from areas with more than 50% native tussocks immediately surrounding the rock outcrop (within 2 m). Females also had higher body condition when from higher altitudes, but this cannot be teased apart from the time that females spent in captivity as females from higher altitudes took longer to give birth. Although we have considered female body condition as a maternal effect on offspring, it should be noted that maternal body condition is itself influenced by environment; thus the two categories of 'effect' are not completely independent.

Environmental effects

Birth date for *Oligosoma maccanni* varied widely (over 50 days) and was strongly influenced by altitude, despite there being only a 155-m difference in altitude among collection sites. On average birth occurred c. 8 days earlier at the lowest altitudes. Potential explanations for earlier births from lower altitudes include: (1) earlier ovulation at lower altitudes, (2) shorter gestation length at lower altitudes, or (3) a combination of both. These explanations for earlier births may be driven by slight differences in the thermal quality of high and low altitude habitats. Mean air temperature of Macraes Flat during the gestation period was c. 15°C (NIWA 2005; Hare et al. 2009). In mountainous areas of Otago air temperature cools by 0.7°C with every 100-m elevation (Fitzharris 2003), which equates to c. 1°C difference over the altitudinal range of this study. This small difference in ambient air temperature may enable embryonic development to proceed at lower altitudes even when basking opportunity is not available, as embryonic development is assumed to proceed above 16°C in *Oligosoma maccanni* (based on data for other temperate species; Shine & Harlow 1993; Hare et al. 2009).

Time of birth is important for both parents and offspring. Benefits of early reproduction in reptiles include post-reproductive females gaining higher body condition before producing the next clutch of vitellogenic follicles (Naulleau & Bonnet 1996) and juveniles having more opportunity to increase in size by the end of the activity season (Bauwens & Verheyen 1985). This means that timing offspring production with resource availability and good environmental conditions is vital. High altitudes at Macraes Flat (where the *Oligosoma maccanni* were collected) may have later provision of food items (fruit ripening and insect hatching) than low altitudes, and this deserves further exploration. Also, heavier offspring were obtained from the skinks from higher altitudes, which may offset any potential influence of shorter growing seasons.

Implications of habitat modification for skinks

Habitat modification and introduced predators reduce the population density of *Oligosoma maccanni* (Norbury et al. 2009; Lettink et al. 2010), and habitat modification is associated with offspring body condition, but not reproductive output (this study). Females from native tussock areas have higher post-partum body condition, which has flow-on effects for offspring size. Possible explanations as to why females may have higher post-partum body condition in tussock areas

include: (1) higher food abundance (Whitaker 1996; but see Tocher 2003); (2) greater quality of food (i.e. more diversity in food items; O'Connor 1982; Whitaker 1996; Tocher 2003); (3) reduced time foraging/escaping predators (e.g. through greater habitat matrix; Berry et al. 2005); (4) differences in thermal conditions (e.g. warmer winter retreats; unpubl. data). These and other possible explanations deserve study. Regardless, higher post-partum body condition will result in larger vitellogenic follicles, larger conceptuses and therefore the higher body condition seen in the neonates. Larger neonates are more likely to survive (KMH unpubl. data). Although litter size increases with female SVL, our data also suggest the potential for reproductive senescence in *Oligosoma maccanni*.

Our data on the influence of environmental and maternal conditions on reproduction and offspring phenotype of *Oligosoma maccanni* may be useful as a general guide for management of sympatric species of viviparous skinks for which very little information is available. For example, the critically endangered grand and Otago skinks (*Oligosoma grande*, *O. ottagense*) have undergone dramatic declines and are in fragmented, genetically isolated populations (Whitaker & Loh 1995; Berry et al. 2005). Populations of these two species that persist in modified grassland habitats are not only isolated from dispersal opportunities (Berry et al. 2005), but may also produce offspring of lower quality than those in tussock areas (as shown in this study for *Oligosoma maccanni*), with subsequent lowered survival rates. More attention could be given to the feasibility of maintaining agricultural and conservation values on private land. For example, reproductive success and offspring quality are similar from rocky areas immediately surrounded by native tussock to those of continuous tussock. However, consideration would need to be given to protecting these tussock areas from grazing by stock and rabbits (Whitaker 1996; Norbury et al. 2009), mammalian predators (Norbury 2001; Norbury et al. 2009; Lettink et al. 2010), and to providing 'tussock corridors' that enable migration among isolated populations (Berry et al. 2005).

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