

Nest-site selection and the factors influencing hatching success and offspring phenotype in a nocturnal skink

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Abstract. Nest-site selection in ectothermic animals influences hatching success and offspring phenotype, and it is predicted that females should choose nesting sites that maximise their reproductive fitness, ultimately through the reproductive success of their offspring. We completed nest-site choice experiments on a nocturnal lizard, the egg-laying skink (*Oligosoma suteri*), to determine whether eggs (and subsequent hatchlings) from cooler nests do better at cooler incubation temperatures, and conversely if those laid in warmer nests perform better at warmer incubation temperatures. We provided a simple nest-choice experiment, with oviposition-retreat sites available in either a hot or a cool sector of the enclosure; in the wild females nest under objects. Female *O. suteri* laid eggs both during the day and night, and nested more in the hot than cool sector. Eggs from each clutch were split across three egg incubation temperatures (18°C, 22°C, 26°C) to decouple the impact of initial nest-site choice from the subsequent incubation temperature regime. Whether eggs were initially laid in the hot or cool sector was not related to hatching success, offspring phenotype or offspring locomotor performance. We conclude that offspring phenotype and performance is primarily influenced by the temperature during incubation, rather than the initial thermal environment of the nest location. Thus, female *O. suteri* may select warmer nesting sites to ensure higher incubation temperature and enhanced offspring fitness.

Keywords: incubation temperature, nest-site selection, New Zealand, *Oligosoma suteri*, reptile.

Introduction

In ectothermic animals, nest-site selection exerts a strong influence on egg development and survival, and offspring phenotype and fitness (Shine and Harlow, 1996; Booth, 2006; Refsnider and Janzen, 2010; Refsnider, 2016). In oviparous squamates, females are predicted to select nesting sites that adjust fitness-related aspects of offspring phenotype (Pike et al., 2010), via the incubation temperatures that prevail within these nest-sites (e.g. ‘maternal manipulation’ hypothesis; Shine, 1995; Booth, 2006; Webb et al., 2006; Pike et al., 2011). Some experimental studies have examined nest-site selection in lizards, and the cues that they use when choosing sites (e.g. substrate temperature;

Bull et al., 1988; Warner and Andrews, 2002; Iraeta et al., 2007; Doody, 2009; Mitchell et al., 2013a).

Two confounding factors have complicated studies of nest-site selection in lizards. Firstly, for species with temperature-dependent sex-determination (e.g., Bull et al., 1988; Booth, 2006) it is difficult to determine whether incubation temperature and sex ratio (and the associated sex-specific phenotype) are the primary driver of nest-site choice, or not. Secondly, many studies do not decouple the impact of the initial choice of nest-site from the subsequent temperature regime in the nest during development (Shine et al., 1997; Refsnider and Janzen, 2010; Mitchell et al., 2013b; Refsnider, 2016). Thus, in species without temperature-dependent sex-determination, we have a limited understanding about whether hatchlings differ in the optimal incubation temperature. For instance, little data exists on whether hatchlings from warm nests perform better when also incubated at warmer incubation temperatures, and

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vice-versa for those from cooler nests (e.g. maternal 'matching' hypothesis; Shine et al., 1997; Mitchell et al., 2013b).

We used laboratory experiments to investigate maternal nest-site selection and nesting behaviour of the only endemic oviparous lizard in New Zealand (Cree and Hare, 2016). The aptly named egg-laying skink (*Oligosoma suteri* Boulenger), is a species that lacks temperature-dependent sex-determination (Hare et al., 2002). We investigated whether: (i) females select nesting sites based on substrate thermal cues, and (ii) the thermal cues where nests are laid is related to the hatching success and phenotype of hatchlings across three different incubation temperatures (18°C, 22°C and 26°C). We used a split-clutch experimental design that assigned eggs from each clutch to one of the three incubation temperatures (Hare et al., 2002).

Some female *O. suteri* share nesting sites (Whitaker, 1968) suggesting that a cue for nest site choice is important in this species. Incubation takes up to three months in the wild (Whitaker, 1968), and in captive conditions duration of incubation is strongly and positively correlated with temperature (Hare et al., 2002). Based on our previous studies (Hare et al., 2002, 2004, 2008a; see methods for more details on relevant results), we predicted that female *O. suteri* would select warmer nesting sites. Here we relate our findings to previously published data on the outcomes of the three different incubation regimes on egg survival, offspring survival and offspring phenotype (Hare et al., 2002, 2004, 2008a).

Materials and methods

Animal collection and husbandry

Oligosoma suteri is a medium-sized skink [75–115 mm adult snout-vent length (SVL); Miller et al., 2010] found on rocky beaches in northern New Zealand, from 34° to 37°S (Hare et al., 2008b; Chapple and Hitchmough, 2016). Ovulation occurs in late October, with eggs laid in clutches of 2–5 (mean = 3.6 ± 0.1 eggs) in sand or soil deposits

beneath large stones above the high tide mark in mid-December to early-January (Townes, 1975b; Hare et al., 2002).

These data arise from a much larger study on the possible effects of incubation temperatures on the sex, survival and phenotype of *O. suteri*, as such animal collection and husbandry are outlined in detail elsewhere (Hare et al., 2002). Briefly, in early summer 1999 we collected 60 gravid females from Green Island, Mercury Island group, New Zealand (36°38'S, 175°51'E, 1–2 m a.s.l.). The females were transported to Victoria University of Wellington and housed indoors within identical conditions at ambient air temperatures of 14°C. Housing consisted of transparent plastic boxes (215 × 330 × 110 mm, 7 L) containing a large square of wire mesh (165 × 120 mm) for ventilation and UV light penetration. All females were housed in these conditions from 8 December 1999 until their eventual release. Each enclosure contained moistened, non-fertilised potting mix in the bottom (~20 mm deep), and water was provided *ad libitum*.

To allow for behavioural thermoregulation through indirect basking a heating wire was placed beneath one end of the enclosures, and was on $24 \text{ h} \cdot \text{d}^{-1}$. The result was the provision of two different thermal sectors in each enclosure, a 'hot' sector and 'cool' sector (fig. 1). Each sector was provisioned with a retreat (*Pinus radiata* bark) for females to hide beneath and also to provide two choices for possible oviposition sites (noting that in the wild nests are found in deposits beneath objects; Townes, 1975b; fig. 1). The range of possible temperatures available in the enclosures ranged from 14°C to 30°C ($\pm 0.5^\circ\text{C}$). Temperature of the soil at each end of representative enclosures was measured using thermocouple data loggers with temperatures recorded daily. The preferred body temperature range of *O. suteri* is unknown, but they reach maximum voluntary body temperatures of 25°C in captivity and foraging ceases below 8–10°C (Townes, 1975a).

The enclosures were stacked on shelves with simulated natural lighting (Duro-test® True-lite® power twist) suspended from the ceiling on a 12L:12D light cycle (lights on at 0600 h). Females were fed three times a week with live insects dusted with vitamin supplement powder (Villavet cal-cipup). We also measured the snout-vent length (SVL), tail length (± 0.5 mm) and post-oviposition mass (± 1 mg) of all females for use in analyses.

Oviposition and egg incubation

To minimise potential disturbance to the females, enclosures were checked only twice daily for eggs, once in the morning (0600–0800 h; up to 2 h after lights came on) and once in the evening (1700–1800 h; just as lights turned off), giving us broad 'day' vs. 'night' oviposition timing. We note that we cannot be sure that eggs laid 'overnight' were, in some cases, laid during the 2 h after lights came on. We recorded the location of oviposition and whether eggs were buried beneath the substrate or laid on the surface, and any instances where females were still found curled on top of the nest. To record the location of oviposition we used the two thermal sectors; the 'hot' sector was the warmer

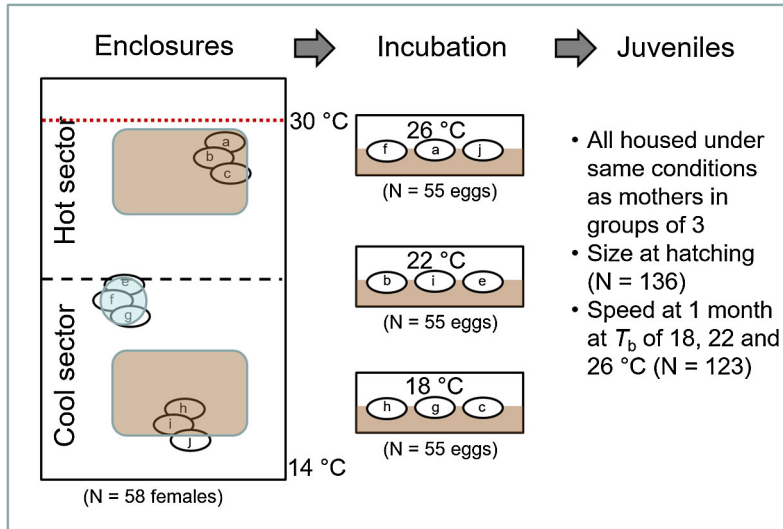


Figure 1. Experimental design showing: Enclosure set up for gravid *Oligosoma suteri* (and resulting juveniles), with minimum and maximum soil temperatures available, and the division into the hot and cool sectors. Three example nests are shown, with individual eggs labelled; the central nest would be classed as 'cool'; upper dotted line indicates approximate placement of the heating wire beneath the enclosures; transparent shapes indicate placement and relative size to enclosure, of bark (rectangle) and water dish (circle), all of which were used to nest under (see main text). Incubation of a random assortment of eggs from each nest among the three different incubation regimes. Juveniles underwent phenotypic measures (T_b = body temperature).

end (max = 30°C and the warmest half of the enclosure directly above the heating wire), and the 'cool' sector was the coolest half of the enclosure (min = 14°C and furthest from the heating wire). Although a gradient in temperatures was likely not possible throughout enclosures due to use of a distinct basking site, we could divide the enclosures into 'hot' and 'cool' sectors, and, as stated above, provide oviposition retreat-sites within each sector (fig. 1). Some females laid under the water dish near the middle of the enclosure ($n = 3$), and these were assigned to the cool sector (fig. 1).

Egg incubation methods are described in detail elsewhere (Hare et al., 2002). Briefly, when experiments were initially undertaken no data were available from natural nests. As such, incubation temperatures were selected over the range of temperatures at which eggs were predicted to be exposed in the wild (Hare et al., 2002), and were also based on successful incubation temperatures of northern tuatara (*Sphenodon punctatus*) populations in artificial conditions (now published in Mitchell et al., 2006), as well as successful skink incubation at similar latitudes (Elphick and Shine, 1999). In 2015, dataloggers placed in nests located on Korapuki Island (also in the Mercury Island Group) found that wild nests range in temperature from 18°C to 32°C, cycling over 24 h (V. Stenhouse, pers. comm).

The females laid 214 eggs and 165 were allocated to an incubation treatment; two eggs were used to determine the stage at oviposition (Hare et al., 2002), 38 were allocated to a study on placentation (J. Stewart and M.B. Thompson unpub. data), and some eggs were non-viable (Hare et al., 2002). At least three eggs from each female were randomly

distributed among the constant incubation regimes (18°C, 22°C and 26°C) so that each clutch was represented at all incubation temperatures. This meant that eggs laid in the cool sector were split between the three incubation temperatures, allowing the decoupling of selected site vs. incubation temperature effects (fig. 1). Clutches with more than three eggs had additional eggs also randomly assigned to the incubation regimes. We acknowledge that compared with constant incubation temperatures, fluctuating temperatures may enhance hatching locomotor performance (e.g., Booth, 2006). However, at the time of our experiments constant incubation temperatures were still the norm. Water was added to the vermiculite daily to keep the developing eggs moist.

From previous studies, we know that female size and initial egg mass do not influence hatching success of eggs (Hare et al., 2002) and that water potential of the vermiculite incubation medium (either -120 kPa or -270 kPa) had no influence on any variables (Hare et al., 2002, 2004, 2008a); these variables are not discussed further here. Eggs were more likely to fail to hatch when from the 18°C incubation regime (Hare et al., 2002); we do not reanalyse or discuss results based solely on incubation temperatures here.

Juvenile husbandry and phenotype

Juvenile husbandry and phenotypic measures are also described in detail elsewhere (Hare et al., 2004, 2008a). Briefly, following hatching juveniles were individually marked by toe-clip, weighed (± 1 mg), and SVL and tail length measured (± 0.5 mm). They were housed under the same conditions as the mothers to standardize post-natal

environment, but in groups of three based on their size and date of hatching. We assumed no agonistic encounters among juveniles for the time of this experiment, based on their small size relative to the enclosure, ample retreat sites and food, and lack of any physical damage. At the conclusion of all studies (outside the scope of this paper) all surviving individuals were translocated to Korapuki Island, Mercury Island Group.

Sprint speed was measured at 1 month of age in post-absorptive individuals at body temperatures of 18°C, 22°C and 26°C. The order in which individuals completed each test temperature was randomized. Individuals were sprinted three times each day at one temperature and given at least 15 minutes rest between each test. A paintbrush was used to encourage sprinting. Speed was measured between 0900 and 1700 h with a different experimental temperature each day. Time of day has no influence on performance of all age groups and both sexes for *O. suteri* (Hare et al., 2008a; Miller et al., 2010). A wooden racetrack (70 mm × 1.5 m), with five paired infrared lights in slots (0.25 m apart and 4 mm high) over 1 m, was used to test sprint speed. The lights transmitted and received an infrared beam horizontally across the track and interruption of each successive infrared beam stops a timer allowing speed to be calculated. Maximum sprint-speed over 0.25 m was taken as a measure of burst speed, as *O. suteri* does not need to perform long sprints to reach cover in its natural boulder-beach environment (Hare et al., 2008a; Miller et al., 2010). Bigger individuals are faster, but leg length has no influence on speed (Hare et al., 2008a; Miller et al., 2010).

Data 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. Statistical significance was assumed at $P < 0.05$. Data are expressed as mean \pm 1 SE unless otherwise stated.

We compared whether gravid females were more likely to oviposit during the day or night, and whether they were more likely to nest in the hot or cool sector using one-tailed binomial tests. We tested whether hatching success within each incubation temperature was related to the thermal

sector in which nests were first laid (i.e. eggs from nests in the hot sector hatched more often at higher temperatures than eggs from nests in the cool sector) by using z-tests for population proportions.

We tested whether the interaction between 'hot' and 'cool' sector nests and incubation regime influenced phenotype (SVL, VTL and mass) at hatching using non-linear mixed-effects models; thermal sector and incubation temperature were the independent variables, and size was the dependent variable with maternal ID included as a random grouping variable. Similarly, we tested for differences in sprint speed at 1 month of age at the three different ambient temperatures using nest location and incubation temperature as independent variables, $\log(\text{speed})$ as the dependent variable, SVL as a covariate, individual ID as a repeated measure.

Results

Female *O. suteri* were just as likely to nest at night (57%; 1800 h to 0800 h) as during the day (43%; 0800 h to 1800 h) ($P = 0.179$). Most females dug a shallow scrape beneath bark in which to lay their eggs (88%), but two (3%) laid their eggs on the surface of the soil. Five females (9%) laid at least one egg on the surface of the soil and the rest within a nest (all in the hot sector). The majority of females laid their eggs in the hot sector (79%), with fewer nesting in the cool (21%) sector ($P < 0.001$). Within each incubation regime, thermal sector where the nest was laid did not influence whether an egg hatched or not ($P > 0.05$ in all cases). For example, eggs incubated at 18°C were not more likely to hatch if laid in the cool sector (70% hatched) than the hot sector (67% hatched) ($z = 0.203$; $P = 0.842$; fig. 2).

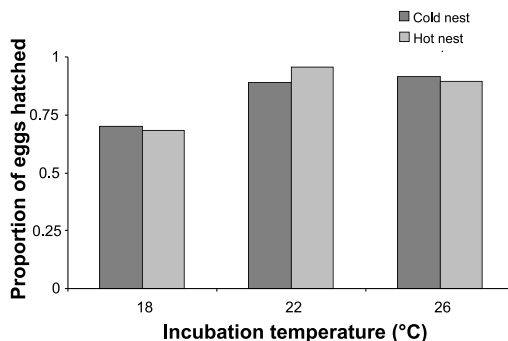
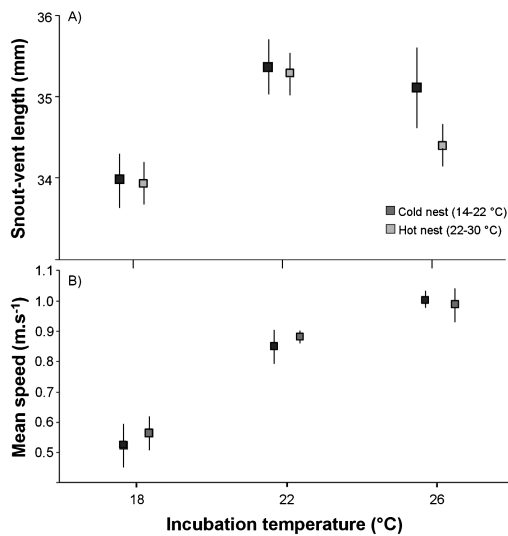


Figure 2. Proportion of *Oligosoma suteri* eggs from nests laid with the hot or cool sector (see fig. 1) that hatched at three incubation temperatures. Sample sizes are presented in table 1.

Table 1. Samples sizes for eggs and the resulting hatchlings from nests of *Oligosoma suteri* laid in the cold or hot sectors of an enclosure, and incubated under one of three constant incubation temperatures.

Incubation temperature	Eggs laid in cold sector				Eggs laid in hot sector			
	18°C	22°C	26°C	All	18°C	22°C	26°C	All
Eggs ($n = 165$)	10	10	10	30	45	45	45	135
Hatched ($n = 136$)	7	8	9	24	30	42	40	112
Speed measures at 1 month ($n = 123$)	4	8	8	20	21	42	40	103

**Figure 3.** Phenotype of *Oligosoma suteri* at 1 month of age which hatched from eggs laid at hot or cool locations (see fig. 1) and randomly distributed among three constant incubation temperatures. (A) size (± 1 SE; snout-vent length used as an example), (B) mean maximum sprint-speed (± 1 SE; ambient running temperature of 26°C shown as an example). Sample sizes are presented in table 1.

Broadly (all data pooled), the thermal sector in which eggs were laid had no influence on SVL ($F_{1,51} = 0.100$, $P = 0.811$), VTL ($F_{1,51} = 0.100$, $P = 0.735$) or mass ($F_{1,51} = 0.232$; $P = 0.632$). Similarly, there was no significant interaction between thermal sector of the nest and incubation regime for any size measures ($P > 0.05$ in all cases; fig. 3a, supplementary fig. S1). At all three ambient temperatures, speed of juveniles at 1 month of age was not related to the thermal sector chosen to nest in by the female ($F_{1,51} = 0.244$, $P = 0.624$) nor its interaction with subsequent incubation temperature ($F_{2,311} = 0.345$, $P = 0.708$; fig. 3b, supplementary fig. S2).

Discussion

We documented the nesting behaviour of *O. suteri*, and demonstrated that although females did not display a preference for the time of day at which they laid their eggs, they nested more in locations where the substrate was warm rather than cool. While variation was evident in the thermal-sector preference of nesting females, hatchlings from nests laid in the cool sector did not perform better under cooler incubation regimes. Rather, incubation temperature appears to be the primary determinant of hatching success and offspring phenotype (Hare et al., 2002).

Oligosoma suteri prefers to nest in warmer substrates

Oligosoma suteri appeared to use substrate thermal cues to select nesting sites, as the vast majority of females (79%) laid their eggs in the warmer section of the housing container. This result contrasts with the nest-site selection of some other nocturnal lizard species. For instance, the leopard gecko (*Eublepharis macularius*), a species with temperature-dependent sex-determination, prefers to oviposit in substrates of intermediate, rather than extreme, temperatures (Bull et al., 1988). However, as *O. suteri* lacks temperature-dependent sex-determination, and nest-site choice is independent of offspring sex ratio, it may have preferentially selected nest-sites that would improve offspring fitness (see Hare et al., 2002, 2004, 2008a).

Our study provides important information on the nesting behaviour of *O. suteri*. Few *O. suteri* nests have ever been found in the wild

(Whitaker, 1968; Towns, 1975a, b), and our laboratory experiment indicates that nests are likely located in warm locations under items within the rocky beaches that the species inhabits (Hare et al., 2008b). Although *O. suteri* is primarily nocturnal, under laboratory conditions it laid eggs both during the day and night, but whether this may also occur in the wild is unknown. Potentially, diel timing of oviposition is linked to when individuals can achieve body temperatures necessary for oviposition/parturition. For example, in laboratory-held *O. maccanni* (a viviparous diurnal skink) females primarily gave birth in the warm sector of the cage (Chamberlain et al., 2010). Similar to most other oviparous lizard species (Booth, 2006; Doody, 2009), the nest depth of *O. suteri* eggs was relatively shallow, and occasionally eggs were placed on the soil surface. Additionally, potentially the females laid their eggs where they were spending most of their time, and further behavioural studies are warranted to discount this possibility.

Hatchlings from cold nests did not differ in their optimal incubation temperature

Hatchling *O. suteri* from nests laid in cool and warm locations exhibited the same optimal incubation temperatures for hatching success, and offspring phenotype and performance. Thus, we found no evidence that hatchlings from nests laid in cooler locations perform better at cooler incubation temperatures (or vice versa). Similarly, Shine et al. (1997) used experimental nest translocations in the field to demonstrate that a female nest choice in the eastern three-lined skink (*Bassiana duperreyi*) did not influence the response of her offspring to differing incubation regimes. Likewise, female nest-site choice in painted turtles (*Chrysemys picta*) is not associated with the thermal reaction norms of her offspring (Mitchell et al., 2013b). Nest-site temperature and subsequent thermal conditions during incubation are often closely linked under natural conditions (Refsnider and Janzen, 2010; Refsnider, 2016). Thus, incubation temperature

during egg development, rather than the initial nest-site selection, is most likely the key determinant of offspring phenotype in *O. suteri* (e.g. Hare et al., 2002).

While incubation temperature influences offspring phenotype in many lizard species (Shine and Harlow, 1996; Booth, 2006; Pike et al., 2011), the effect varies among species (Booth, 2006). In *O. suteri*, higher incubation temperatures (22°C, 26°C) result in increased proxies for biological fitness (hatching success, offspring morphology, locomotor performance and survival; Hare et al., 2002, 2004, 2008a) and, as warmer nest-sites will generally lead to warmer incubation temperatures, this may explain the preference for nesting in warmer substrates observed in the current study. Our results are consistent with suggestions that temperature is a major determinant of the past distribution of *O. suteri* (Hare et al., 2008b), with cold climates currently restricting the species, the only native oviparous lizard in New Zealand (Towns, 1975a, b), to the relatively warmer northern regions of the country.

Acknowledgements. We thank C. Green, N. Nelson, and D. Towns for providing expertise, time and assistance, V. Stenhouse for his personal communication on wild nest temperatures and anonymous reviewers for their useful insights and suggestions. The research was carried out with New Zealand Department of Conservation approval, Victoria University of Wellington Animal Ethics Committee approval, and after consultation with Ngāti Hei, Ngāti Maru and Ngāti Whanaunga. Funding was provided by Victoria University of Wellington.

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Submitted: May 25, 2017. Accepted: June 5, 2017.

Associate Editor: Sylvain Dubey.