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RESEARCH

Thermal and physical characteristics of the nesting habitat of New Zealand's only endemic oviparous lizard

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Abstract: Nest characteristics and nest-site choice determine fitness outcomes for reptile embryos and resulting hatchlings. Little is known about the nesting of *Oligosoma suteri*, New Zealand's only egg-laying lizard. We investigated the physical and thermal environment of nests and available microhabitats, including nest-like sites, with the aim of applying this information to future search efforts and translocation plans. Nests of *O. suteri* were difficult to locate in known nesting habitat occupied by a self-sustaining population; only 0.42 nests were found per person-hour of searching during mid-January on Korapuki Island, and several of these nests were likely communal. All eggs were partially buried in a fine, sandy-silt substrate beneath a rock and were within 2 m of overhanging vegetation. Thermal profiles of these nests and three mock nests chosen with similar physical characteristics result in incubation lengths observed in successful lab-based incubation studies. Our outcomes support lab-based evidence that females select nest sites based on temperature as temperature data loggers deployed at other parts of the beach recorded temperatures that are outside the known successful incubation temperatures. We recommend investigating thermal conditions at proposed translocation sites, including sites outside the species' current range so that predictions can be made regarding population viability should the species need to be moved south due to loss of habitat under future climate change scenarios.

Keywords: nest characteristics, *Oligosoma suteri*, reptile, skink, temperature

Introduction

Availability of nesting habitat, nest-site selection, and fitness of produced offspring are important parameters in determining distributions and population success of oviparous (egg-laying) animals. Nest site selection in oviparous animals is generally a trade-off between concealment from predators and other factors that influence maternal and offspring fitness, e.g., bees (Seeley & Morse 1978); birds (Latif et al. 2012); reptiles (Kolbe & Janzen 2002), but may include other parameters such as indirect oviposition-site choice via mate choice (Refsnider & Janzen 2010). In oviparous ectotherms, maternal care is less common (Ellis & Chappell 1987; Combrink et al. 2016), and multiple studies suggest that nest sites are selected based on the influence of microhabitat on egg development and survival, and offspring phenotype and fitness (Shine & Harlow 1996; Booth 2006; Refsnider & Janzen 2010; Refsnider 2016). Nest predation is a major cause of reproductive failure for many birds as well as reptiles (Latif et al. 2012; Combrink et al. 2016), but an added consideration for reptiles is the influence of thermal and hydric conditions on the eggs and resulting hatchlings (Deeming 2004). Some reptiles lay eggs in rookeries, e.g. tuatara (*Sphenodon punctatus*) and some turtles (Refsnider et al.

2010; Limpus et al. 1983), and some nest communally, laying eggs together in a single nest (Doody et al. 2009). Communal nesting may be a result of limited suitable nest sites or direct fitness benefits, which may include hydric modifications of incubation conditions (Radder & Shine 2007).

Of the 100+ endemic lizard species in New Zealand, only one is oviparous, the egg-laying skink (*Oligosoma suteri*) (van Winkel et al. 2018). While considerable research on the nesting habits of tuatara (the only other endemic oviparous reptile in New Zealand) exists (Refsnider et al. 2010; Cree 2014; Nelson et al. 2018), the nesting habits and habitat of *O. suteri* have received far less attention. Nests of *O. suteri* have rarely been located in the wild despite effort searching areas thought to be their primary nesting habitat: rocky beaches in northern New Zealand (Table 1). Indeed, no details of nest temperature have been recorded despite laboratory studies investigating the effects of incubation temperature on hatchlings (Hare et al. 2002, 2004). Female *O. suteri* lay between one and five eggs (Towns 1975; Hare et al. 2002) between mid-December and mid-January (Towns 1975) with hatching occurring between late-February and mid-April (Whitaker 1968; Towns 1975). Nesting sites in the wild have all been located beneath rocks and boulders above the high-tide line and below permanent

Table 1. Summary of data recorded in publications detailing searches for, and serendipitous discovery of, nests of *Oligosoma suteri* in New Zealand.

Location	Date	No. of nests (no. of sites)	Mean eggs per nest ± 1 SE (range)	Nest description	Notes	Citation
Taranga Island/ Hen and Chicken Group	Early February 1968	14 (9)	5.3 ± 0.9 (1 to 11)	• Average of ~4 m above high tide (range = 2.4 to 6.1 m) • Beneath rocks/stones in damp sand/silt or dry gravel • 85% of nests had entrance back-filled	Additional searching of nearby beach and forest unsuccessful	Whitaker 1968
Cable Bay, Waiheke Island	22 December 1971	0	NA	NA	Females not gravid and no nests located	Towns 1975
Great Island, Three Kings Island Group	9 February 2001	2 (1)	[18 eggs total]	• Nests in close proximity • Beneath boulder in fine brown talus • 10 m above high tide	Nests located while setting pit-fall traps	Parrish & Gill 2003
Rangitoto/Motutapu Island	17–23 December 2015	0	NA	NA	Daily searches for nests on each island. Adult *O. suteri* located but no nests	Stenhouse unpubl. data
Great Barrier Island	25 December 2015 to 1 January 2016	0	NA	NA	No *O. suteri* or nests located	Stenhouse unpubl. data
Korapuki Island, Mercury Island Group	11–18 January 2016	5 (2)	5.6 ± 1.3 (2 to 9)	• beneath rocks in sandy-silt • eggs buried 0-30 mm depth • all at least 5 m above high-tide mark	See text and Table 2 for details	This study
Port Jackson, Coromandel	3–9 January 2016	0	NA	NA	Daily searches and pitfall trapping but no *O. suteri* or nests located	Stenhouse unpubl. data

vegetation (Whitaker 1968; Parrish & Gill 2003; Stenhouse et al. 2018). Some females appear to use cues for selection of nest sites in the wild as communal nesting is common (Whitaker 1968). Indeed, in one study in captivity, the majority of females (79% gravid females) laid their eggs in the warmest portion of their cage (Chapple et al. 2017), suggesting that substrate temperature is a cue for nest-site selection. Hatching success, offspring phenotype and performance is strongly influenced by the temperature during incubation (Hare et al. 2002; 2004).

Populations of *Oligosoma suteri* were once widespread on the mainland and offshore islands of northern New Zealand, but have declined in distribution and number on the mainland due to predation pressure from introduced predatory mammals (Towns & Ferreira 2001); the last recorded observation of *O. suteri* on the mainland was in 2010 at Tapotupotu Bay, Cape Reinga (New Zealand Department of Conservation Herpetofauna Database, data provided 12 November 2018). Furthermore, the species' habitat is likely threatened by sea-level rise resulting from climate change (Ackerley et al. 2013). With the increased investment in mainland sanctuaries, and the knowledge that successful development of embryos is possible in locations outside their current distribution (Stenhouse et al. 2018), translocation may become an important tool in the conservation of this species. However, prior to management outside their current range, it is vital that further data on physiology are obtained (Hare & Cree 2016). In particular, details of nesting requirements and the thermal profiles of a range of microhabitats in their environment may enable selection of suitable locations for translocation, as has been done for tuatara (Besson et al. 2012). This includes use of degree-day models which are useful for predicting timing of events

based on temperature-dependent developmental processes (Hartley & Lester 2003; Schultze et al. 2016). Stenhouse et al. (2018) provide estimated thermal requirements for successful embryonic development at 616 degree-days above a threshold temperature of 13.8°C.

We searched likely nesting habitat of *O. suteri* on the rocky shore of Korapuki Island during summer, with the aim to: (1) determine the search effort required to find nests of *O. suteri* on an island where they are known to breed successfully; (2) characterise the physical and thermal environments of nests of *O. suteri*; (3) compare the thermal characteristics of natural nests with available microsites, including nest-like sites such as those whose occurrence might be used to judge the suitability of a translocation site; (4) use incubation degree-day estimates from laboratory studies to estimate the length of incubation periods required to achieve hatching under a range of potential oviposition dates.

Methods

Study site, nest searches and installation of nest temperature data loggers

Korapuki Island, Mercury Island Group is an 18-ha island that has undergone restoration initiatives, and is the site of a successful translocation of *O. suteri*, with a large self-sustaining population present (Towns & Ferreira 2001; Miller et al. 2011). The study site was situated at the site of the original translocation, a boulder beach with a western aspect (Fig. 1), as the only other population on the island is challenging to reach and still in the establishment phase (Hare et al. 2020).
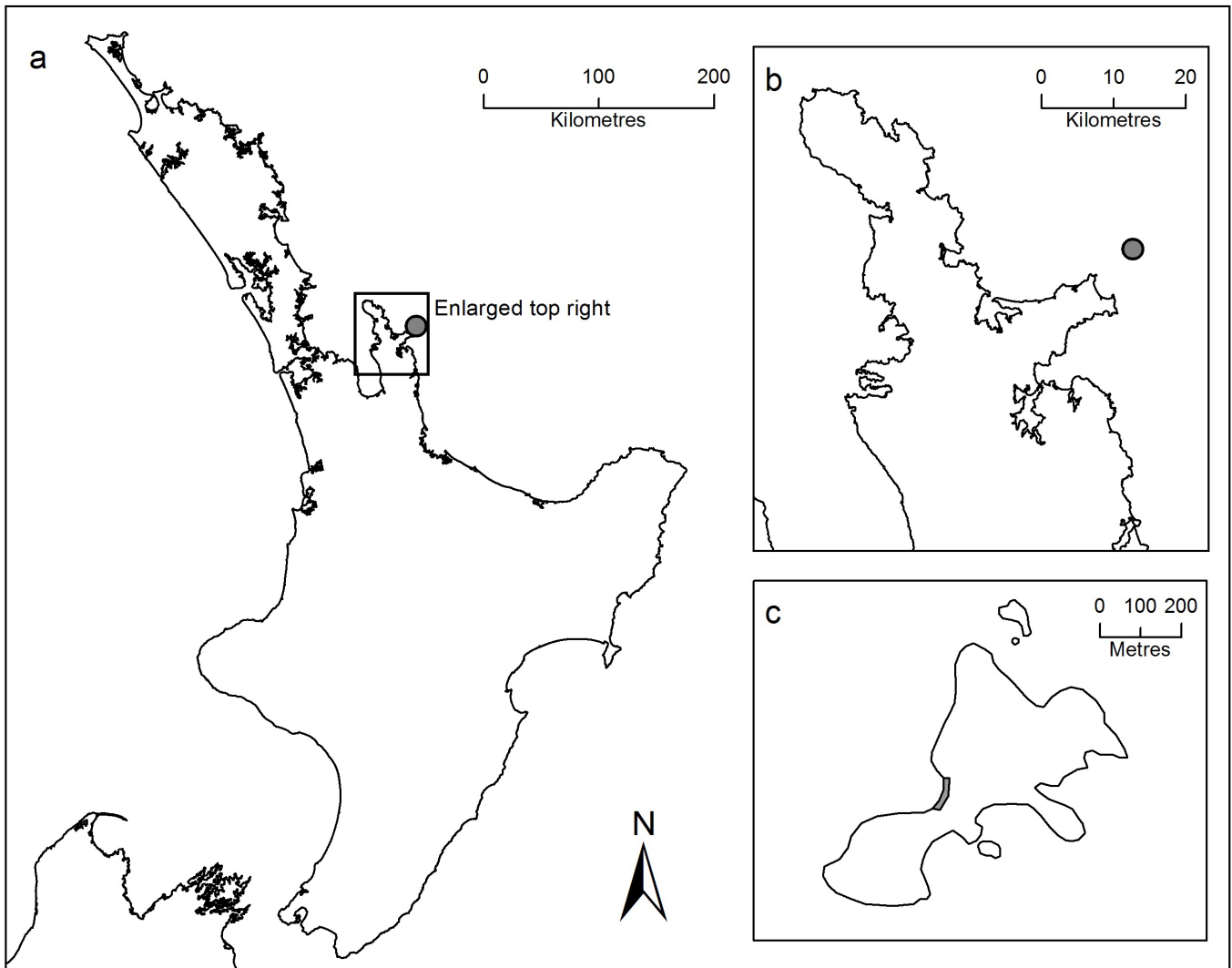
Figure 1 Location of study site on Korapuki Island, Mercury Island Group, off the Coromandel Peninsula, New Zealand. (a) Te Ika a Māui/North Island with Coromandel Peninsula indicated in the box and Korapuki Island by the grey dot; (b) Enlargement of Coromandel Peninsula with Korapuki Island indicated by the grey dot; (c) Enlargement of Korapuki Island, with the study site (boulder beach with a western aspect) indicated by a grey shaded area. Data from NZ coastlines and islands polygons (LINZ 2012).

From 12 to 14 January 2016, areas that met the requirements of likely nesting habitat were identified based on details of previous studies (see Table 1) and searched methodically. Three field workers were assigned areas of the beach where large rocks were present in which to search for nests by lifting stones or debris for timed periods. In general, the objective was to lift every rock within the area that was overlying sandy substrate. However, due to the depth of the rocks in many parts of the beach this was not possible. Instead, rocks were lifted to a depth of approximately 300 mm. Excavation to depths greater than 300 mm was not undertaken to minimise disturbance to the nesting environment and because previous nests were not found at lower depths (see Table 1). Where nests were found, we recorded the number of eggs, substrate type, depth of eggs within the substrate, and the dimensions of the overlying rock (Fig. 2). The rocks around one nest had been disturbed by searching prior to the nest being discovered, which likely altered the thermal environment (Pike et al. 2010). No measurements were made of this nest.

Up to two temperature data loggers (HOBO® pro v.2, Onset; resolution 0.02°C; accuracy: ±0.21°C) were installed in each nest. More than one data logger was placed if eggs were found at a range of depths within a nest, with the sensors of the data loggers located at the extremes of the depths. Additionally, we identified three rocks that had similar dimensions and underlying substrate as the natural nests and used these sites to record temperature in mock nests. The three mock nests were all located within 6 m of the natural nests and data loggers were installed at the top of the substrate beneath the overlying rock (i.e. 0 mm depth).

We also measured the thermal microhabitat across the beach profile, by installing data loggers at depths in the boulder field of approximately 0, 100, and 200 mm at 0, 5, 10, and 15 m from the high tide mark (one logger at each depth-distance combination). All data loggers were shaded from the sun by at least one rock. We chose 200 mm as the maximum depth as daily variation in temperature is greatly reduced below this depth (Geiger et al. 2003). An additional data logger was attached to a tree at a height of 1.2 m in the shade to measure shade air temperature. All data loggers were pre-set to record hourly temperature readings for the duration of the study. Temperature data were collected from 15 January 2016

Figure 2 Photograph (south-eastern aspect) of boulder beach where nests of *Oligosoma suteri* were discovered on Korapuki Island, Mercury Island Group, New Zealand on 13th and 14th January 2016. Nest sites are indicated by white circles. Nests 1 to 4 (inset) were discovered towards the north end of the beach (larger circle) while nest 5 was found approximately 12 m to the south. See Tables 1–3 for more details on nests. The three mock nests were located between nests 1 to 4 and 5 though their locations were not marked. The area searched is indicated by the white arrow. Photos: CK Woolley.

to 31 August 2017, except one beach-profile microhabitat data logger which was re-started on 18 January 2016 prior to the field workers leaving the island. Three beach-profile microhabitat data loggers failed to record any data, and the data logger installed at 0 mm in natural nest three failed on 15 January 2017.

Predictions of accumulated degree-days

Degree-day models are a type of developmental model used to simulate the temperature dependence of developmental processes in order to estimate the timing of an ecological process (Moore & Remais 2014). We calculated accumulated degree-days for each site and soil depth using the hourly temperature output from the data loggers and the equation:

$$dd = \Sigma \, (T - 13.8) \times 0.042 \qquad (1)$$

where dd is degree-days, T is the temperature from the data logger, 13.8 is the minimum development threshold temperature (calculated by Stenhouse et al. 2018), and 0.042 is the hourly fraction of one day. If $T < 13.8°C$, then values of $T - 13.8$ for

that hour were assigned a value of zero (i.e. no development occurred). Accumulated degree-days were calculated for each nest (mock and natural) using six possible oviposition dates: 1 December, 15 December, 1 January, 15 January, 1 February and 15 February (plausible dates from Stenhouse et al. 2018), with incubation length estimated when 616 degree-days were reached.

Statistical analysis

Summary statistics (mean daily maximum, minimum and mean temperatures, and number of degree-days above 13.8°C) were generated for all data loggers to capture the thermal profile from 15 January–30 April 2016 (the remainder of the nesting season when eggs were known to be present). We compared mean daily mean, minimum and maximum temperatures recorded at 0mm below the overlying rock of natural and mock nests for this period using *t*-tests.

As temperature data for a complete nesting season were only available for the season following that when eggs were known to be present, we used a mixed effects model to compare mean daily mean temperatures for the period 15 January–30

April 2016 with the same period in 2017 for data loggers active for these periods. Site type (natural nest, mock nest, or boulder field) and year were fixed factors and data logger id was a random effect.

We then used linear models to assess the effect of depth on mean daily minimum, maximum and mean temperatures at nest sites and in the boulder field for the period 1 December 2016–30 June 2017 (a complete nesting season). Finally, we used degree days to estimate incubation duration for mock and natural nests given a variety of plausible laying dates in this period. All analyses were run in R (v. 3.5.1; R Core Team 2018).

Results

Physical characteristics of nests

Between 12 and 14 January 2016 three people searched c. 380 m^2 for a total of 240 minutes and found five nests of *O. suteri* (0.42 nests person-hour^{-1}; 1 nest 76 m^{-2}). Four nests were located within 2 m of each other and a fifth nest 12 m south (Fig. 2). All eggs were partially buried (up to 30 mm from the surface) in a fine, sandy-silt substrate beneath a rock and were within 2 m of overhanging vegetation (taupata *Coprosma repens*; harakeke *Phormium tenax*). The overlying rocks were between 100 and 270 mm thick (deep) and up to of 600 mm in length (Table 2). The number of eggs within each nest ranged from two to nine; i.e. at least two nests were inferred to have eggs from more than one female based on maximum reported clutch sizes (Cree & Hare 2016).

Thermal character of nests and the microhabitat

Between 15 January and 30 April 2016 the rocky beach ranged in temperature from a mean daily minimum of 17.21 ± 0.23°C to a mean daily maximum of 27.26 ± 0.62°C (both occurring at a depth of 0 mm; Table 3). In the same period, temperatures of natural nests ranged from a mean daily minimum of 19.61 ± 0.22°C to a mean daily maximum of 24.42 ± 0.46°C.

Comparison of temperatures at 0 mm depths in natural and mock nests found that mean daily mean temperatures were around 0.7°C higher in natural vs. mock nests (21.36°C cf. 20.60°C, $t_{3.87}$ = −2.88, p < 0.05) and mean maximum temperatures were almost 2°C higher in natural nests than mock nests (23.66°C cf. 21.77°C, $t_{3.88}$ = −3.18, p < 0.05). Mean daily minimum temperature did not differ between nest types ($t_{3.94}$ = −0.36, p = 0.74).
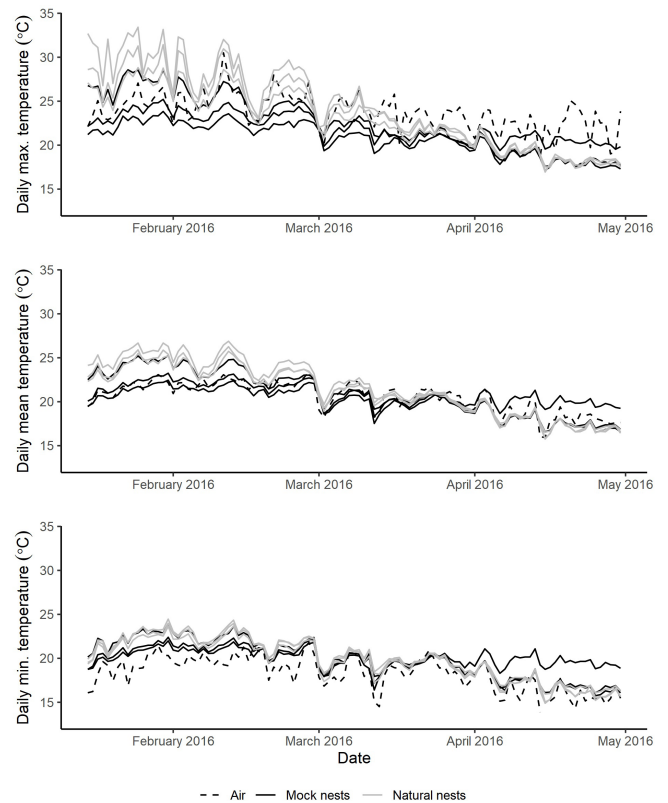

Figure 3 Maximum, mean and minimum daily temperatures at natural (grey lines, *n* = 3) and mock (black lines, *n* = 3) nest sites (soil depth = 0 mm) of *Oligosoma suteri*, and air (dashed lines, *n* = 1, height of 1.2 m, shaded) between 15 January and 30 April 2016 on Korapuki Island, Mercury Island Group. Standard error bars are so small as not to be visible.

Comparison of the time series trend of the three data loggers deployed in nests at 0 mm (nests 1 and 2) with the three mock nests during this period revealed that the natural nests were warmer over the summer months (before March; Fig. 3). As temperatures cooled during March, temperatures of two of the three mock nests closely tracked those of the natural nests while the third mock nest maintained a considerably higher temperature (Fig. 3).

Temperatures differed between the two nesting seasons (comparison of data between 15 January to 30 April) with mean

Table 2. Description of five natural nests of *Oligosoma suteri* and three mock nests on Korapuki Island, Mercury Island Group, New Zealand. In all of the natural nests, eggs were either buried or embedded in a sandy-silt substrate. NR = variables were not recorded. Nest 4 had no variables measured, including no data logger deployed, as the area had been recently disturbed (see main text). Data loggers in mock nests were placed on top of the substrate beneath the overlying rock (Table 3).

Nest type	Nest number	Number of eggs	Depth of eggs in substrate (mm)	Dimensions of overlying rock (mm)		
				length	width	depth
Natural nest	N1	8	0–20	480	300	220
	N2	9	0–20	600	450	100
	N3	5	20–30	300	190	270
	N4	4	NR	NR	NR	NR
	N5	2	20 mm	530	440	220
Mock nest	M1	0	-	480	510	150
	M2	0	-	410	280	140
	M3	0	-	520	430	280

Table 3. Summary statistics and calculated degree-days for locations with data loggers deployed on Korapuki Island, Mercury Island Group, New Zealand between 15 January 2016 and 30 April 2016. Data loggers recorded temperature in four natural nests of *Oligosoma suteri*, three 'mock' nests, the rocky beach, and air temperature 1.2 m above the ground in the shade. Nests and mock nests both had a stone overlying sandy substrate, and the rocky beach example in the table was a jumble of rocks on rocks 10 m from high tide (the only location where no data loggers failed). The depth of data loggers was at the surface of the nest, and the maximum depth of the eggs. T = temperature; dd = degree days. HTM = high-tide mark. Degree-days calculation is in text.

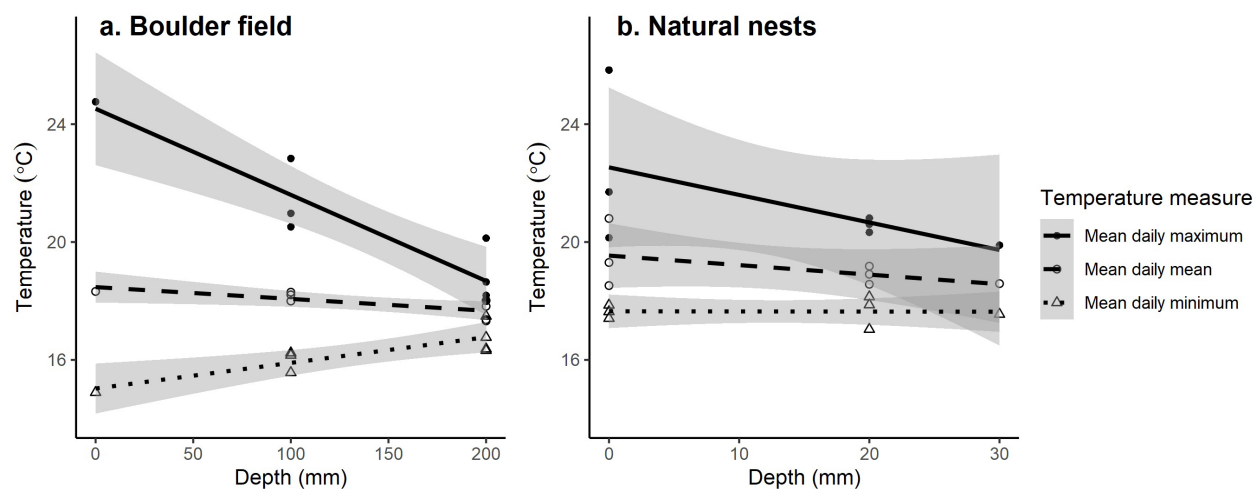| Temperature variable	Natural nests (logger depth)							Mock nests (logger depth)			Rocky beach 10 m from HTM (logger depth)			Air
	Nest 1		Nest 2		Nest 3		Nest 5	M1	M2	M3				
											0 mm	100 mm	200 mm	
	0 mm	20 mm	0 mm	20 mm	0 mm	30mm	20 mm	0 mm	0 mm	0 mm				
Mean daily mean T ± SE	21.16 ± 0.25	21.23 ± 0.27	21.70 ± 0.31	21.61 ± 0.26	21.23 ± 0.28	21.14 ± 0.25	22.28 ± 0.23	20.55 ± 0.10	20.29 ± 0.19	20.98 ± 0.25	20.67 ± 0.29	20.18 ± 0.26	19.21 ± 0.23	20.54 ± 0.17
Mean daily min T ± SE	20.07 ± 0.22	19.71 ± 0.22	19.98 ± 0.24	20.63 ± 0.23	19.61 ± 0.22	20.16 ± 0.22	20.89 ± 0.21	20.00 ± 0.10	19.49 ± 0.17	19.94 ± 0.22	17.21 ± 0.23	18.49 ± 0.23	18.34 ± 0.21	18.22 ± 0.19
Mean daily max T ± SE	22.85 ± 0.33	23.59 ± 0.39	24.42 ± 0.46	23.03 ± 0.32	23.69 ± 0.39	22.53 ± 0.31	24.22 ± 0.28	21.34 ± 0.11	21.45 ± 0.22	22.53 ± 0.32	27.26 ± 0.62	22.69 ± 0.36	20.35 ± 0.26	23.78 ± 0.20
dd	794.27	801.48	851.61	842.20	801.50	791.19	914.49	727.60	700.10	774.81	740.58	688.36	583.47	726.59

Figure 4 Relationships between depth and mean daily minimum, mean and maximum temperatures for dataloggers deployed on Korapuki Island at: a) the boulder field ($n=8$) and (b) natural nests of *Oligosoma suteri* ($n=7$) for the period 1 December 2016–30 June 2017. Grey shading represents 95% confidence intervals. N.B. data for the same loggers are replicated on the same plot to illustrate how depth affects different measures of temperature.

daily mean temperature 0.76°C warmer in 2016 than the same period in 2017 (20.80°C cf. 20.04°C; $t_{16} = -4.21$, $p < 0.001$).

Depth in the boulder field and in the soil of natural nests had varying effects on the three temperature metrics. For the period 1 December 2016–30 June 2017 (a complete nesting season the year following the discovery of eggs), mean daily maximum temperature decreased with depth (estimate = −0.03 ± 0.01, $t_{12} = -4.06$, $p < 0.05$; Fig. 3) and mean daily minimum temperature increased with depth (estimate = 0.01 ± 0.00, $t_{12} = 4.11$, $p < 0.05$; Fig. 4). Mean daily mean temperature did not differ significantly with depth ($t_{12} = -1.60$, $p = 0.135$).

Duration of incubation

Using degree-days, eggs laid on 01 December 2016, 15 December 2016, 01 January 2017, and 15 January 2017 were likely to hatch between 71.0 and 95.8 days following oviposition, and were on average 11.2 days earlier if laid in natural nests compared to mock nests ($F_{1,31} = 10.991$, $p < 0.05$; Fig. 5). If eggs were laid later on 01 February or 15 February 2017, then estimated incubation lengths were much more variable, ranging from 66.9 to 252.3 days.

Discussion

Despite working on an island with a healthy, thriving population of *O. suteri*, the rate of finding nests and number of nests found was low (0.42 nests person-hour^{-1}; c. 1 nest 76 m^{-2}). Based on a low rate of nest discovery, Whitaker (1968) suggested that *O. suteri* may be using other habitat for nesting, but despite searching all parts of the beach and adjacent forest, Whitaker (1968) found no other nesting sites; indeed, all nest sites have to date been located in rocky portions of beaches under rocks/stones (Table 1). As nests of *O. suteri* at our study site appeared to be closely clustered, it is possible that we were unable to locate the core of nesting activity, and further investigation of suitable nesting locations is warranted. Similarly, it may be that we conducted our survey prior to the main nesting

activity period in our study year and we recommend that future surveys consider extending the search period to allow for this possibility.

Nesting beneath rocks by *O. suteri* may provide protection from predation, temperature fluctuations, dehydration and possible erosion by wave action (Whitaker 1968). While beach-nesting is uncommon among skinks, other reptiles that nest on beaches usually do so in sand, e.g. turtles (Hays et al. 1995; Wood et al. 2000), crocodiles (Web et al. 1983; Somaweera and Shine 2013). On the Galápagos Islands, for example, lava lizards (*Tropidurus albemarlensi* and *T. grayi*) preferred to nest in open sand unless sea lions (*Zalophus californianus*) were present, which altered their nesting preference to amongst rocks or vegetation (Burger 1993). Many oviparous reptiles select nest sites based on temperature, compensating for the effects of the physical environment (Ewert et al. 2005; Doody et al. 2006; Doody 2009). Spikes in temperature can increase mortality and alter the physiology of embryos (Hall & Warner 2018). We found that thermal fluctuations (mean daily minimum and maximum temperatures) in natural (and mock) nests were less pronounced than the wider beach profiles (19.61–24.42°C cf. 17.21–27.26°C; Table 3). Coupled with laboratory data on maternal nest-site selection and subsequent offspring performance (Chapple et al. 2017), we provide further evidence that temperature is likely a key factor in nest-site selection for *O. suteri*, considering temperatures elsewhere on the rocky beach reached substantially higher temperatures which may be lethal for embryos of *O. suteri*. However, further study with larger sample sizes, and replication across years and at other sites is warranted; such studies should include variation in aspect, weather, and a greater range of habitat variables to ensure geographic differences are incorporated in models.

Communal nesting in *O. suteri* may be due to a rarity of suitable nesting sites or a direct fitness benefit of laying near other eggs (Radder & Shine 2007). Radder and Shine (2007) showed that eggs of *Bassiana duperreyi* benefited from communal nesting through hydric modifications of tightly packed eggs. While survival of eggs and hatchlings of
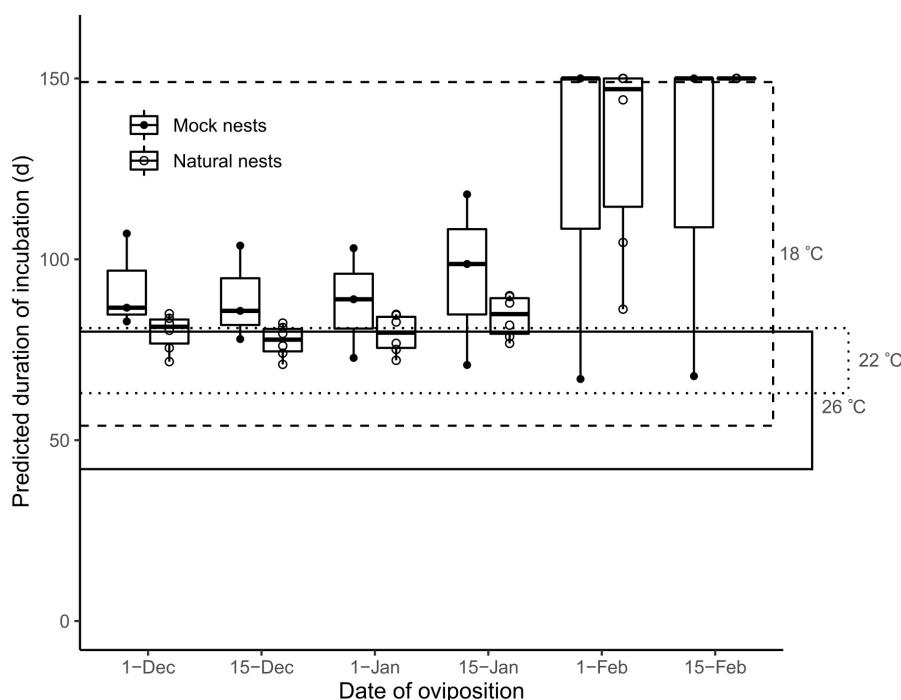

Figure 5 Predicted duration of incubation for eggs of *Oligosoma suteri* within natural and mock nests for a range of estimated oviposition dates in austral summer 2016–17 using an incubation 'duration' of 616 degree days (Stenhouse et al. 2018). The longest known successful incubation time for *O. suteri* is 149 days and the shortest is 42 days (Hare unpubl. data). Predicted incubation lengths longer than 149 days were all greater than 210 days and were rounded down to 150 days for ease of viewing. The range of duration of incubation times for successful incubation of eggs held in the laboratory at 18 (dashed box), 22 (dotted box) or 26°C (solid box) from Hare et al. (2002) is shown on the right.

O. suteri, including long-term phenotypic differences, is not related to small variation in substrate moisture content, large losses in moisture result in egg failure (Hare et al. 2002). While we expect that selection of nest sites and communal nesting is not primarily linked to hydric conditions, we cannot rule it out as a possible factor for nest-site choice. Likewise, despite the compelling links between nest sites and temperature, we cannot discount that nest sites are chosen to reduce predation on eggs (e.g. by birds, crabs, tuatara, and larger lizards), or other possibilities (Refsnider et al. 2010).

Modelling of natural nest temperatures using degree-days indicated that average estimated hatching dates were within the constant artificial incubation temperatures that had the largest hatchlings (22–26°C), and those with physical characteristics suitable for survival (Hare et al. 2004; 2020), which indicates that we captured relevant nesting information for successful nests. However, if we missed the bulk of nesting activity by conducting our survey early with respect to thermal conditions in our study year, then it is possible that later oviposition dates in February might not result in such successful outcomes. Longer, cooler incubation regimes in laboratory studies resulted in many physical characteristics of embryos that reduced survival, such as, small body size and physical abnormalities (Hare et al. 2002, 2004) and likely, lower survival in the wild (Hare et al. 2020).

Across the year, mean temperatures of mock and natural nests were similar, but the warmer temperatures achieved by natural nests in the earlier part of the year resulted in them reaching sufficient degree-days for earlier hatching. In addition, temperatures experienced in nests of *O. suteri* would result in incubation lengths similar to those seen in successful lab-based incubation studies. Mock nests appear to mimic natural nests well, with potential for slightly longer incubation, but in general recorded temperatures were within the environmental tolerances of incubation seen so far in *O. suteri*. Mock nests may therefore be used to test the likelihood of successful incubation at new sites prior to any translocation/ reintroduction of this species, providing valuable information about whether a site is appropriate (Jarvie et al. 2014). The higher temperatures recorded at mock nest 1 during April are not easily explained. It could be that characteristics of the overlying rock or its position on the beach gave this site warmer temperatures during this period.

As *O. suteri* does not have temperature-dependent sex-determination (Cree et al. 2021), and estimated incubation lengths of our mock nests are within the known range for successful hatching and offspring performance, measuring temperatures at nest-like sites may be a useful way to test the suitability of new locations for translocations prior to any movement of animals. Translocations may include locations outside the known distributional range of the species as an action to offset future climate warming, a strategy that appears feasible based on previous thermal modelling (Stenhouse et al. 2018). When selecting from locations outside their known range that have predator control, suitable nesting conditions are likely to be the primary limit to population success for *O. suteri*.

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Author contributions

CKW, VS and NJN conceptualised the research; CKW and VS undertook the field work; CKW and KMH undertook the analysis; all authors were involved in writing the manuscript.

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