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Heat and water loss versus shelter: a dilemma in thermoregulatory decision making for a retreat-dwelling nocturnal gecko

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ABSTRACT

Understanding the interaction between upper voluntary thermal limit (VT_{max}) and water loss may aid in predicting responses of ectotherms to increasing temperatures within microhabitats. However, the temperature at which climate heating will force cool-climate nocturnal lizards to abandon daytime retreats remains poorly understood. Here, we developed a new laboratory protocol for determining VT_{max} in the retreat-dwelling, viviparous *Woodworthia* 'Otago/Southland' gecko, based on escape behaviour (abandonment of heated retreat). We compared the body temperature (T_b) at VT_{max}, and duration of heating, between two source groups with different thermal histories, and among three reproductive groups. We also examined continuous changes in T_b (via an attached biologger) and total evaporative water loss (EWL) during heating. In the field, we measured T_b and microhabitat thermal profiles to establish whether geckos reach VT_{max} in nature. We found that VT_{max} and duration of heating varied between source groups (and thus potentially with prior thermal experience), but not among reproductive groups. Moreover, geckos reached a peak temperature slightly higher than VT_{max} before abandoning the retreat. Total EWL increased with increasing VT_{max} and with the duration of heating. In the field, pregnant geckos with attached biologgers reached VT_{max} temperature, and temperatures of some separately monitored microhabitats exceeded VT_{max} in hot weather implying that some retreats must be abandoned to avoid overheating. Our results suggest that cool-climate nocturnal lizards that inhabit daytime retreats may abandon retreats more frequently if climate warming persists, implying a trade-off between retention of originally occupied shelter and ongoing water loss due to overheating.

KEY WORDS: Costs of thermoregulation, Ectotherm, Evaporative water loss, Retreat-dwelling gecko, Thermal tolerance

INTRODUCTION

Ectotherms, including lizards, are strongly influenced in their use of natural environments by abiotic factors, notably temperature. Global heating is already affecting the distribution of organisms, especially ectotherms (Parmesan et al., 1999; Perry et al., 2005) and is predicted to continue over the coming decades (IPCC, 2013). Some populations of lizard species may have already exceeded their extinction threshold, and although particular concern exists for tropical species (Huey et al., 2012; Sinervo et al., 2010; Thomas

et al., 2004), the vulnerability of cool-climate species must also be considered (Kingsolver et al., 2013). A key aspect of assessing the vulnerability of lizards to climate heating is to understand a species' thermal tolerance limits (Nguyen et al., 2011; Sunday et al., 2014), including the extent to which limits are influenced by prior thermal acclimatisation and by metabolic and hydric states (Beuchat, 1986; Daut and Andrews, 1993; Dayananda et al., 2017). Water availability affects thermoregulatory competencies in ectotherms, resulting in a trade-off between temperature increase and water balance (Davis and DeNardo, 2009; Rozen-Rechels et al., 2019). Water constraints limit growth and activity level, and in lizards are more severe in some reproductive groups such as pregnant females (Lorenzon et al., 1999).

The upper voluntary measure of thermal tolerance, commonly called VT_{max} (voluntary thermal maximum), has been justified as an integral marker of thermal physiology for predicting an organism's vulnerability to warming (Rezende et al., 2011). This parameter denotes the upper temperature limit to the voluntary activity of an organism when other environmental factors are constant. Once this upper set point for activity is reached, the animal responds through behaviours involving an 'organised movement' to seek a cooler microhabitat (Camacho and Rusch, 2017). In diurnal lizards, such movements typically include shuttling between an exposed location and a cooler and shaded microhabitat, or withdrawal to a retreat or crevice (Díaz and Cabezas-Díaz, 2004). Inability to withdraw to a cooler microhabitat will lead to heat stress (e.g. panting), followed by the eventual loss of the righting response (at the critical thermal maximum, or CT_{max}) with death resulting soon afterwards (Camacho and Rusch, 2017; Huang et al., 2006). In diurnal lizards, mean VT_{max} (in °C) typically lies a few degrees above the mean preferred body temperature, and a few degrees below mean CT_{max} (Cadena and Tattersall, 2009; Camacho and Rusch, 2017; Garrick, 1979; Kearney and Predavec, 2000). To date, most research on VT_{max} in squamates has focused on diurnal species (Cadena and Tattersall, 2009; Camacho et al., 2018). The factors that influence when nocturnal rock-dwelling squamates abandon an existing retreat and seek a cooler microhabitat remain poorly understood, including for cool-temperate viviparous species.

In a heterogeneous environment, VT_{max} is likely to be associated with potential costs and benefits. Nocturnal species, which often thermoregulate within a refuge by day, are faced with the dilemma of when to abandon a retreat that offers shelter (Croak et al., 2012; Kearney and Predavec, 2000; Webb et al., 2004). The costs of remaining within the retreat include ongoing heating and evaporative water loss, whereas the costs of leaving include a short-term increase in the risks of predation, overheating and water loss while in the open, as well as the energetic cost of finding a cooler retreat (Huey and Slatkin, 1976; Vickers et al., 2011). The animal may also consider the opportunity cost if the abandoned retreat is taken over by intraspecific competitors, preventing the return of the initial occupant (Cote et al., 2008). In some cases,

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avoidance of predators outweighs the cost of becoming overheated (Downes and Shine, 1998), and risk of predation may be particularly severe for pregnant females due to the physical burden of pregnancy resulting in reduced locomotion (Olsson et al., 2000).

During the time that the nocturnal rock-dweller remains under the warming retreat, it may minimise the risk of overheating by employing physiological and behavioural processes that modify heat exchange with the environment, including changes to evaporative water loss (EWL), which increases with body temperature (Jameson, 1981) and is the sum of respiratory, cutaneous (across the skin) and ocular (from the eyes) water loss (Lillywhite (2006); Guillon et al., 2014). It comprises insensible water loss (passive diffusion of water through the skin and respiratory tracts, and its subsequent loss by evaporation), as well as active water loss through panting and tongue-flicking (Cain et al., 2006). These processes contribute to evaporative cooling (Lillywhite and Navas, 2006). The whole-animal rates of EWL may be affected by body size and shape, which influence the surface area:volume ratio (Cain et al., 2006), as well as by energy-demanding physiological states such as pregnancy, which often involve a preference for warmer temperatures (Dupoué et al., 2015; Lourdais et al., 2017). However, to our knowledge, the variation in VT_{max} within a species (e.g. with acclimatisation to more predictable environments and among adult reproductive groups), the behaviours that occur within retreats as VT_{max} is approached and, in particular, the relationship between VT_{max} and EWL, remain unknown for nocturnal lizards that occupy daytime retreats.

In this study, we examine VT_{max} and its relationship with EWL in a cool-climate viviparous gecko (*Woodworthia* 'Otago/Southland'; Garman 1901) from southern New Zealand. These nocturnally foraging geckos inhabit crevices in rock outcrops by day including under loose rock slabs (superficial retreats). Females in the population at Macraes in coastal Otago (∼600 m above sea level) have a biennial reproductive cycle with pregnancies lasting up to 14 months (Cree and Guillette, 1995). Cryptic basking during the day has recently been seen (especially in females) and may be an adaptation to elevate body temperature during pregnancy (Gibson et al., 2015). Geckos in superficial retreats have been recorded with field body temperatures up to 31°C in spring (Chukwuka, 2020); on the hottest days, geckos are thought to abandon these retreats and move to deep crevices to avoid warmer temperatures (Rock and Cree, 2008). In a thermal gradient, variation exists in selected temperatures based on pregnancy status, sex and population (Rock et al., 2000, 2002), with pregnant females from Macraes having a mean selected temperature (T_{sel}) up to 8°C higher than males, and up to 5°C higher than non-pregnant females.

Given these variations, we predicted that VT_{max} would vary with acclimatisation to captivity (involving a more predictable retreat temperature with less risk of overheating, and with greater availability of standing water) compared with the wild geckos (with more variable thermal opportunities and greater risk of overheating on hot days), a difference that could be relevant to the use of captive-sourced lizards for conservation translocations (Hare et al., 2020). We also predicted that both VT_{max} and EWL would vary among adult reproductive groups (including different sexes and female pregnancy conditions). Additionally, we predicted that geckos have behaviours that minimise overheating within retreats, but that VT_{max} will eventually be reached under loose slabs on hot days in the field. To test these predictions, we developed a protocol for measuring VT_{max} based on escape behaviour (i.e. abandonment of the heated daytime retreat) in this rock-dwelling species. Specifically, we asked the following questions. (1) Do the VT_{max} and the duration of heating vary

between geckos held in long-term captivity under relatively stable thermal and hydric conditions and wild geckos (i.e. collected fresh from the field)? (2) Do these same responses vary among adult reproductive groups? Within the wild geckos, we also asked the following. (3) Do geckos reach high temperatures under the retreat and then thermoregulate for a period before exiting at VT_{max}? (4) Is individual VT_{max} related to the amount of EWL? Finally, for geckos and their field microhabitats, we asked the following. (5) Do pregnant females reach VT_{max} on hot days, and how are their body temperatures during heating related to rock and air temperatures? (6) Do microhabitat temperatures (under either thick or thin rocks) exceed VT_{max} temperatures on hot days in summer?

MATERIALS AND METHODS
Ethical statement
This study was conducted under authorisations from the New Zealand Department of Conservation (53725-FAU) and the University of Otago Animal Ethics Committee (protocols AUP 11/17 and 18/133) and following consultation with the Ngāi Tahu Research Consultation Committee (University of Otago) and Kāti Huirapa Rūnaka ki Puketeraki (guardians from the indigenous Māori community).

Experimental animals
We examined VT_{max} in two source groups of geckos with differences in prior thermal opportunity, captive geckos held in our colony facility with a predictable thermal regime and wild geckos freshly collected from the field with more variable thermal opportunities. For each source group, we included adults in three reproductive groups (males, pregnant females and non-pregnant females). For each source and reproductive group, sample sizes were 7–17 for VT_{max} tested geckos and 5–8 for control geckos; mean snout–vent length (SVL): 74.0–80.0 mm (Table 1).

Captive geckos had been held in captivity for at least 10 years on a seasonally varying photothermal cycle, with some individuals producing healthy offspring each summer. All except two of the captive-held geckos were born in the wild prior to captive-housing. Animals were tested during the austral late summer and early autumn months (January–April) when pregnant females are likely to be at the late-pregnant stage (Cree and Hare, 2016b). The geckos were housed in glass cages (45–60 litres with a mesh lid, two to three geckos per cage) containing retreat sites made with terracotta tiles, including a warm retreat (heated by a 120 W overhead lamp) and cool retreats (∼room temperature). All cages provided plastic climbing structures, and a dish of water and a container of damp sphagnum moss were always available. Room ambient temperature was 16°C by day and 13°C by night in summer, with the warm retreat providing a surface tile temperature of 31±1°C for 10 h day^{-1}, 4 days week^{-1}. This regime allowed the geckos to reach the mean selected body temperatures at 14.00 h previously measured for this population in late summer, namely about 28°C for pregnant females and about 25°C for males (Rock et al., 2000), but without risk of overheating to the probable CT_{max} estimated from lethal temperature data as about 35–37°C (Hare and Cree, 2016). The photoperiod was 15 h:9 h light:dark, with dawn and dusk ramps provided during the photophase. Full-spectrum ultraviolet lighting was provided while the basking lamps were on. We fed the geckos weekly with calcium- and vitamin-dusted live insects (mainly crickets) and fruit. Adults were sexed by the presence (males) or absence (females) of a hemipenial sac and precloacal pores, while pregnancy status of females was assessed by palpating the abdomen gently (Cree and Hare, 2016b).

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Table 1. Summary statistics of sample sizes, morphometrics and measures of evaporative water loss for *Woodworthia* 'Otago/Southland' geckos used in our study

		Reproductive group		
Source group	Parameter	Males	Non-pregnant females	Pregnant females
Captive geckos	N	7	10	8
	Snout–vent length (mm)	78.0±10.9	77.0±1.0	80.0±1.6
	Mass (g)	14.57±0.45	13.72±0.40	14.84±0.39
Wild geckos	N	17 (15)*	15	16 (15)*
	Snout–vent length (mm)	77.1±1.3	74.1±1.8	79.9±1.0
	Mass (g)	9.38±0.38	8.24±0.51	11.42±0.53
	Rate of EWL (mg h^{-1})	36.27±4.41	62.03±11.94	46.92±5.29
	Total surface area (cm^2)	95.77±3.69	94.11±6.11	125.57±5.34
	Mass-specific rate of EWL (mg g^{-1} h^{-1})	3.95±0.51	7.70±1.23	4.17±0.45
	Surface area-specific rate of EWL (mg cm^{-2} h^{-1})	0.39±0.05	0.65±0.09	0.38±0.04

*Number in parentheses for wild geckos refers to the subset of animals that did not urinate or defecate during the VT_{max} trial, and that was used for subsequent calculation of evaporative water loss (EWL; tested for wild geckos only). Values are means±s.e.m.

For the wild geckos, we collected adult geckos from lightly grazed tussock-grassland/pasture near Macraes (~650 m above sea level) in Eastern Otago, New Zealand, during late spring/early summer (November–January). This period corresponds to early/ mid-pregnancy for wild female geckos at Macraes (Cree and Hare, 2016b). Geckos were captured by hand from under rock slabs (with GPS location recorded), marked with a non-toxic marker and placed in cloth bags inside a cool box. We transported the geckos to a University of Otago animal holding facility in Dunedin, taking care to avoid overheating during transit. On arrival, we treated geckos topically with sunflower oil to kill ectoparasitic chigger mites (Cree and Hare, 2010). Housing (in a quarantine room) and husbandry were as above for the captive geckos, except that wild geckos were housed individually in 20-litre (17 cm×28 cm×43 cm) plastic cages with mesh lids. We examined VT_{max} 2–4 days after collection and we returned all individuals to their site of capture soon afterwards.

VT_{max} testing arena
In prior studies, VT_{max} has been tested in nocturnal squamates as the highest temperature reached in a thermal gradient (Cox et al., 2018; Kearney and Predavec, 2000), and in diurnal lizards as the temperature at exit from a warming chamber (Camacho et al., 2018), with movement to a cooler spot in a shuttle box (Cadena and Tattersall, 2009) or with initiation of escape behaviour during heating in a water bath (Virens and Cree, 2019). Here, we developed a new VT_{max} testing protocol for retreat-dwelling geckos with an ecologically realistic heating rate (see below), in a set-up simulating the geckos' natural habitat. We tested geckos for VT_{max} individually within a glass terrarium (85 cm×45 cm×40 cm) lined with paper towels and with a retreat site at each end (35 cm apart; Fig. 1). We made each retreat site using two grey ceramic tiles (25 cm long, 25 cm wide, 0.8 cm thick) that were stacked and separated on three edges by smaller rectangular ceramic tiles in between; two of the supporting tiles faced the walls of the terrarium, and the third faced the other retreat. The internal height of each retreat site was 1.8 cm, which was sufficient to allow the geckos to adopt an on-toes posture allowing the gecko's dorsum to make contact with the upper tile (Penniket and Cree, 2015). For the geckos that were heated to VT_{max}, heating was provided from one of the two 250 W infra-red heat lamps (LHT-008, Manrose) that hung 35 cm above the centre of each tile. We attached a thermocouple probe to the edge of the upper surface of the lower tile, to monitor temperature where the retreat was likely to be coolest during the heating (the centre of the upper tile heated more rapidly). The heat lamp above the retreat chosen by the gecko (see below) was regulated with a rheostat to

generate a heating rate of ~0.10°C min^{-1} at the edge, a rate similar to those measured for rocks on a warm day in the field (Chukwuka, 2020; see also the field heating rates for live geckos, reported below in the Results section). The room air temperature was maintained at 18°C throughout, a typical temperature in the field at Macraes on a sunny afternoon. The unheated retreat remained at room temperature, providing a cool shelter for the geckos to run towards when VT_{max} was reached. We connected a Logitech webcam outside the glass arena with a clear view of the two retreat sites, enabling us to monitor the lower tile temperature by computer from an adjacent vestibule during the heating, and to detect when an animal left the heated retreat. For control animals, the heat lamps were replaced with LED light bulbs (Phillips, E27) that provided no heat but gave the same luminescence as the 250 W heat lamp. We cleaned the cages between VT_{max} testing to remove pheromonal cues from the geckos.

VT_{max} testing procedure
To ensure that the choice of retreat site was voluntary, we placed each gecko at the centre of the cage. The gecko was then allowed an equilibration period of 1 h to familiarise itself with the enclosure, during which time it settled under one of the retreats. The retreat site chosen by the gecko served as the heated retreat while the other became the cool retreat. As the gecko's retreat site was gradually heated from above, the arena was continuously monitored from an adjacent vestibule through the webcam. As soon as the gecko voluntarily left the retreat site, i.e. when the entire body of the gecko
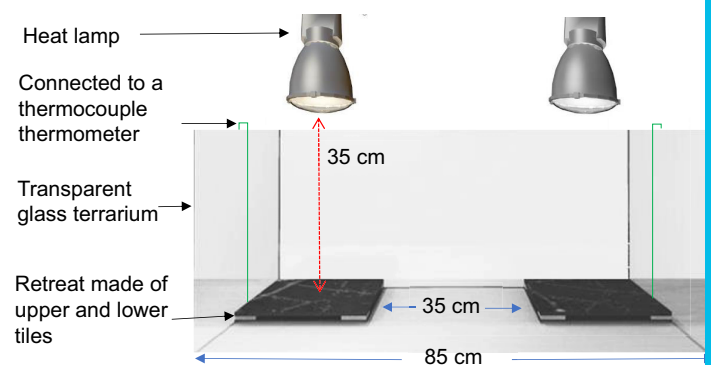
Fig. 1. An illustration of the voluntary thermal maximum test arena for rock-dwelling *Woodworthia* 'Otago/Southland' geckos. The heating rate of the lower tile's coolest edge was controlled to 0.10°C min^{-1} with a rheostat. For the control, heat lamps were replaced with LED light bulbs. Only the lamp or bulb over the occupied retreat was turned on.

was out of the heated retreat and on the paper towel (thus excluding those that climbed on top of the upper heated tiles to bask and then returned to the heated retreat), we re-entered the room and recorded the skin surface temperature over the dorsal abdomen with an infra-red camera to the nearest 0.1°C (FLIR i60, FLIR Systems Inc., USA). This value (i.e. VT_{max}) was measured using skin surface temperature only because, in a previous comparison of values with those obtained from a thermocouple thermometer in the cloaca, there was no significant difference between thermocouple-measured data and skin surface temperature, with an average discrepancy of 0.67±0.16°C (Chukwuka et al., 2019). The emissivity of the camera was set at 0.95 and reflected temperature at the ambient temperature of the room. The time elapsing between the start of heating and the time that the geckos left the heated retreat was recorded as 'duration of heating' in minutes.

For welfare reasons (to prevent inadvertent lethal overheating, as part of our ethical approval), we included an 'intervention point', which was defined as a maximum temperature at the corner edge of the lower tile of 42°C (preliminary trials indicated that this tile temperature was several degrees above simultaneous gecko temperatures, and likely to be above VT_{max}). In the rare cases where the intervention point was reached without the gecko having left the retreat, we re-entered the room to terminate the heating and discarded the data for that animal. To demonstrate that the reason geckos left the heated retreat was because of the heat rather than any other factor, a different set of geckos was used as controls (N=5–10 per reproductive group). For these animals, the LED bulb above the retreat was turned on for 2 h (approximately the time that heated animals took to reach VT_{max}). The control animals' behaviour was monitored with the webcam and skin surface temperature (T_{sk}) was measured and recorded after 2 h or when geckos left the retreat (whichever came first).

For the wild geckos, the VT_{max} testing arena and procedure for heated and control groups were the same as for captive geckos except for the following. Immediately before they were placed in the arena, geckos were weighed to nearest 0.001 g (PM480, Metler), for determination of subsequent mass loss due to evaporation. We attached a temperature-sensitive data logger of ~0.34 g to the dorsal abdomen with a small piece of double-sided tape underneath and a strip of hypoallergenic surgical tape over the top, to monitor skin temperature during heating. The attached data logger, henceforth referred to as a biologger, is a miniaturised Thermocron iButton (DS1922L) modified as described in Virens and Cree (2018). We programmed the biologger to record temperature to the nearest 0.063°C every minute. Geckos were re-weighed immediately after the thermogram was taken; any geckos that urinated or defaecated during heating were excluded from EWL calculations. We estimated EWL (i.e. the sum of pulmonary, cutaneous and ocular water loss; Carneiro et al., 2017) from the mass loss during the period of equilibration and VT_{max} heating (Belasen et al., 2017; Dupoué et al., 2015). Rate of EWL was calculated relative to geckos' body mass and total surface area. To estimate surface area, we measured the SVL and vent–tail length (VTL) with a ruler, and mid-abdominal width and tail-base width with a calliper, and then made the same assumptions about the lizard's body shape as Belasen et al. (2017). Assuming that the trunk of the gecko is a flattened cylinder in shape and that the tail is cone-shaped, the surface area of the trunk (cylinder) was determined using SVL as the height and mid-abdominal dimensions to obtain the circumference. Also, the surface area of the tail (cone) was calculated using VTL as the height and tail-base width as the base circumference. The two values (the surface area of the trunk plus surface area of the tail) were added to

estimate the total body surface area of the gecko (Belasen et al., 2017). For the controls, we reweighed the geckos after 120 min of exposure to LED light.

We did not feed the geckos for 48 h before VT_{max} testing, as digestion can affect temperature regulation in lizards (Van Damme et al., 1991). We tested only two to three animals per day, and each gecko was used only once for either VT_{max} heating or as a control. We monitored the geckos for several days after testing to ensure recovery, and for the colony geckos only, pregnant females were monitored in individual cages until parturition occurred. All the pregnant colony geckos tested for VT_{max} gave birth to at least one viable offspring, except for one gecko that delivered a stillbirth.

Field study of gecko skin temperatures: is VT_{max} reached?

To ascertain whether VT_{max} is reached in the field, forcing the abandonment of retreat, we took both direct and indirect approaches. The direct approach was to attach biologgers to pregnant geckos (N=13) in the field at Macraes to infer body temperature reached on sunny days. Although separate work shows that geckos occupy both thick (thickness ≥4.6 cm) and thin slabs (thickness ≤4.5 cm) during spring (Chukwuka, 2020), by the time of our search for geckos on hot days in summer, no gecko was found under thin slabs. Thus, we limited biologger attachment to geckos found under thick slabs. Biologgers were attached as above to geckos in the early morning hours during late summer (February) to early autumn (March). The under-rock temperature was measured with a Hygrochron iButton stuck to the rock substrate below the superficial slabs. Geckos were returned to their retreats and left undisturbed for up to 3 days. We also measured air temperature and relative humidity using Hygrochron iButtons hung on vegetation close to the rock slab (at ~1.5 m above the ground). Although all but two biologgers were retrieved, some had detached from geckos, and two were not functional. We report data for the five geckos that were recovered from under their original rocks with the biologgers still attached. Mean dimensions of the four rock slabs occupied by the five geckos, as measured with a measuring tape and a calliper, were area=720 cm^2 and thickness=7.5 cm.

For the indirect approach, we established for other rock slabs over a longer period of time, whether the microhabitat temperatures exceeded VT_{max} on hot days in summer. We measured the temperature of microhabitats under both thin and thick rock slabs (N=6 for each rock thickness category), used by geckos from December 2018 to February 2019 using dataloggers (Thermocron iButtons) stuck on the rock with duct tape. For each rock thickness category, we measured the temperatures of the underside of the rock slab, $T_{retreat-top}$ and rock substrate below the rock slab, $T_{retreat-bottom}$ (Rock, 1999) every hour from dawn to dusk. Geckos occupied the chosen rock slabs when we installed the data loggers and were different from those under the rock slabs used for biologger attachments.

Data analysis

Data from biologgers were downloaded using OneWire iButton software (https://www.maximintegrated.com/). All data were analysed in R Core Team (http://www.R-project.org/). We checked for the homogeneity of variances by examining the plot of residuals and Cook's distance. Results were considered significant at P=0.05 and mean values are presented ±s.e.m.

The percentages of geckos that were still under their retreats at 120 min were compared between the heated and control groups with a binomial test. For the heated geckos, we compared the time spent visible at the edge of the heated retreat, VT_{max} value and duration of

heating using generalised linear models (GLM, Gaussian family link) with source and reproductive group as predictor variables. We excluded two geckos (one male, one pregnant female) that left the retreat within 60 min of the start of VT_{max} testing and that were identified as potential outliers in the final model. These excluded geckos had body temperatures less than the preferred body temperature of the corresponding reproductive group (Rock et al., 2000). We included mass of the geckos in initial models as a covariate but removed it from the final model as it was non-significant for temperature-related variables. Furthermore, to understand the magnitude of differences between the means, we calculated effect sizes (Hedge's g) between the measured variables for pairwise comparisons (Ialongo, 2016). The effect sizes were interpreted using a guide of Sawilowsky (2009) as very small (0.01–0.19), small (0.20–0.49), medium (0.50–0.79), large (0.80–1.20) and very large (>1.20).

For the wild geckos used in laboratory VT_{max} testing, we extracted three measurements from the attached biologgers: (i) heating rates within the first 60 min (from the temperature difference over this time interval); (ii) peak skin temperature reached while under the heated tile; and (iii) skin temperature at exit from the heated tile, which corresponds to the definition of VT_{max}. We tested whether peak temperature differed from the VT_{max} value using a generalised linear mixed-effect model with gecko identity as a random effect. We also tested whether the responses i–iii above differed among reproductive groups using a separate GLM. We present representative traces of biologger temperatures during heating for each of the reproductive groups. For EWL in wild adults, we calculated the rate of evaporative water loss per hour for each gecko from the difference in mass before and after the VT_{max} experiment. We then divided the rate of EWL per hour by body mass or total surface area to obtain mass specific- and surface area-specific rates of EWL, respectively. We fitted a GLM to examine the effect of reproductive group on these rates. To understand whether VT_{max} predicted water loss, we fitted a linear regression between total EWL and VT_{max} using the 'lmodel2' package (Legendre and Legendre, 1998), followed by multiple regression of total evaporative water loss with VT_{max} and duration of heating.

For the field study of gecko temperatures on sunny days, we calculated the gecko's heating rate over 60 min to the time when the geckos recorded the highest peak temperature. We calculated the means of these heating rates, as well as the mean of the peak skin temperature. The mean heating rates and peak temperatures in the field study were compared with the wild geckos used in VT_{max} testing in the laboratory using a GLM. Finally, the representative temperature traces for one gecko, its under-rock logger, and the surrounding air temperature were plotted. From the data loggers used to measure the temperatures of other retreats over December 2018 to February 2019, the data were first averaged across the six

replicates. Then we extracted the hourly maximum and mean temperature to give accounts of temperature variations and extreme heat experienced by geckos in these microhabitats (Sheldon and Dillon, 2016). We estimated the disparity between the mean VT_{max} and the maximum hourly microhabitat temperatures for both thin and thick rock slabs in summer. The mean disparity and maximum temperatures were compared among the microhabitat retreats using a GLM model.

RESULTS
Differences in behaviour between heated geckos and controls
Heated geckos in all reproductive groups remained hidden under the retreat for the first 30 min of heating. As heating progressed, geckos positioned their head at the edge of the retreat; some occasionally climbed onto the heated top tile to bask and then withdrew under the heated tile. As heating continued, gular fluttering and lung ventilation became more rapid and, occasionally, the heated geckos flicked their tongue and licked their eyes. Gaping was observed in only two heated geckos (a pregnant and a non-pregnant female, both from the captive group) during heating. As the heated geckos approached VT_{max}, rapid locomotory movements back and forth along the edge of the tile were observed. In contrast, the control geckos were less visible at the edge of their retreats throughout the experiment, and movement (when the geckos were visible at the edge of the retreat) was minimal compared with the heated geckos. Control geckos were also more likely to remain under the retreat (lit but unheated) at 120 min (88%) compared with the geckos from the heated retreats (36%, $P<0.05$, binomial test, $N=34$ for control and $N=73$ for heated groups).

### Time spent visible at the edge of the retreat, VT_{max} and duration of heating
The time spent visible at the edge of the heated retreat differed significantly between captive and wild geckos ($\chi^2=6.23$, d.f.=1, $P=0.01$) with captive geckos spending more time visible (27.34 ±1.82 min) at the edge of the retreat during VT_{max} heating than wild geckos (22.95±1.04 min; Hedge's $g=0.55$). Furthermore, there was a significant effect of reproductive group ($\chi^2=8.99$, d.f.=2, $P=0.01$; Table 2) and a significant interaction between source and reproductive group ($\chi^2=5.96$, d.f.=2, $P=0.05$). The main contributing influence was that pregnant females spent more time at the edge of the retreat compared with non-pregnant females (large effect size; Table 2).

Likewise, mean VT_{max} differed significantly between captive (32.56±0.33°C) and wild geckos (30.65±0.21°C), with the latter group having a mean value 1.91°C lower (Fig. 2; $\chi^2=24.70$, d.f.=1, $P<0.001$; Hedge's $g=1.24$). However, the influence of reproductive group on mean VT_{max} was not significant ($\chi^2=1.69$, d.f.=2, $P=0.42$) and there was no significant interaction between source and

Table 2. Effect sizes* for comparisons among adult geckos used in laboratory studies of voluntary thermal maximum

Parameter	Males:pregnant females	Males:non-pregnant females	Pregnant females:non-pregnant females
Time spent visible at edge of the retreat	0.38	0.39	0.81*
VT_{max}	0.05	0.34	0.28
Time to abandon retreat	0.12	0.02	0.13
Mass-specific rate of EWL[‡]	0.13	1.10*	1.03*
Surface area-specific rate of EWL[‡]	0.05	0.72*	0.87*
Heating rate[‡]	0.57*	0.17	0.56*

*Medium or large effects (Hedge's g). [‡]These variables measured for wild geckos only. VT_{max}, voluntary thermal maximum; EWL, evaporative water loss.
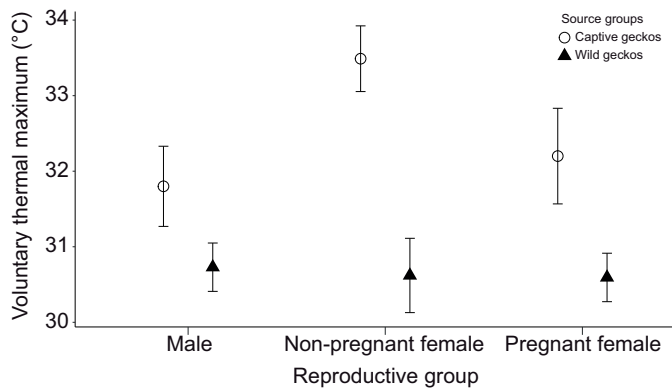
Fig. 2. Mean voluntary thermal maximum of geckos from different sources and different reproductive groups. Effect of source (captive versus wild) was statistically significant (P=0.001). However, there was no influence of reproductive group and no interaction (P>0.05). Sample sizes are 7–17 for each mean value. Skin temperature was recorded using a thermal camera. Values are means±s.e.m.


Fig. 3. Mean duration of heating for geckos from different sources and different reproductive groups, from the start of heating until exit from the retreat. Effect of source group on the duration of heating was statistically significant (P=0.05). However, there was no effect on reproductive group (P>0.05). The interaction was close to significance (P=0.08). Sample sizes are 7–17 for each mean point. Values are means±s.e.m.

reproductive group (χ^2=3.99, d.f.=2, P=0.13). Effect sizes between reproductive groups were correspondingly small or very small (Hedge's g≤0.34).

Considering the duration of heating, we observed a significant effect of source, with a lower mean value in captive geckos (102.21± 4.63 min) than in wild geckos (114.42±3.82 min; χ^2=3.78, d.f.=1, P=0.05; Fig. 3). However, the effect size between the duration of VT$_{\mathrm{max}}$ for the colony and wild geckos was small (Hedge's g=0.47). There was no influence of reproductive group (χ^2=0.26, d.f.=1, P=0.88), with effect sizes between groups being small (Table 2).

Temperature profiles during heating
From the biologger attached to the wild geckos during heating in the laboratory, geckos of all groups heated at mean rates of at least 0.17 ±0.03°C min^{-1} during the first 60 min, which was faster than the coolest part of the retreat. Although there was no significant difference in heating rate among the three reproductive groups (χ^2=2.27, d.f.=2, P=0.32; Fig. 4), the effect sizes between pregnant females and other groups were moderate (Hedge's g>0.55; Table 2). Heating was rapid in the first 60 min and followed by a thermoregulation phase of up to 45 min before exiting the heated retreat (Fig. 5). The wild geckos reached a mean peak temperature of 31.29±0.24°C, which differed significantly from the mean exit temperature of 30.28±0.21°C (χ^2=9.69, d.f.=1, P=0.001). However, there was no significant difference among reproductive groups in either mean peak temperature (χ^2=0.06, d.f.=1, P=0.97) or mean exit temperature (χ^2=1.55, d.f.=1, P=0.46; Fig. 6). The mean time spent by the geckos thermoregulating (from the peak temperature until exit) was statistically similar among the reproductive groups (mean: 7.81±1.06 min, χ^2=0.27, d.f.=1, P=0.87).

Evaporative water loss during heating
Mass-specific and surface area-specific EWL differed significantly among the reproductive groups (mass-specific: χ^2=10.71, d.f.=2, P=0.004; surface area-specific: χ^2=7.92, d.f.=2, P=0.02; Table 1). Mean values were largest in non-pregnant females (effect sizes compared with other reproductive groups were typically large; Table 2). Total EWL increased significantly with increasing VT$_{\mathrm{max}}$ (t_{39}=8.18; r=0.33, P=0.03; Fig. 7A) and with duration of heating (t_{39}=12.23; r=50, P=0.001; Fig. 7B). However, the multiple regression of total EWL with VT$_{\mathrm{max}}$ and duration of heating showed that duration of heating ($F_{1,37}$=9.14, P=0.004) but not

VT$_{\mathrm{max}}$ ($F_{1,37}$=0.02, P=0.88) predicted water loss in *Woodworthia* 'Otago/Southland' geckos (Fig. S1). The control geckos showed a negligible change in body mass (0.01±0.003 g) and thus the EWL of the control group differed significantly from the heated group (0.10±0.01 g; χ^2=27.08, d.f.=1, P<0.001), with a very large effect size (Hedge's g=1.46).

Field study of gecko body temperatures: is VT$_{\mathrm{max}}$ reached?
In the field, the biologgers attached to pregnant geckos showed that daytime body temperatures were above the rock temperature in the morning, with peaks (periods of rapid heating) between 13.50 and 16.30 h on both days, respectively (see Fig. S2 for the representative temperature trace). Periods of rapid warming in skin temperature indicated that the geckos may have been basking openly, or had found warmer parts of the rock than where the iButtons for rock temperature were placed. For these field geckos, the mean heating rate during the most rapid periods was 0.16± 0.01°C min^{-1}, which did not differ significantly from the mean heating rate of geckos tested for VT$_{\mathrm{max}}$ in the laboratory (χ^2=2.18, d.f.=1, P=0.14; Fig. 4). Geckos reached a peak skin temperature in the field (30.40±0.92°C; N=5) that did not differ statistically from the peak temperature of the wild geckos tested for VT$_{\mathrm{max}}$ in the laboratory (χ^2=1.42, d.f.=1, P=0.23). In addition, the time spent thermoregulating at the peak temperature for pregnant female geckos in the field (mean: 6.0±1.30 min) did not differ significantly from the time spent by the wild geckos tested for VT$_{\mathrm{max}}$ in the laboratory (χ^2=0.37, d.f.=1, P=0.53).

The maximum hourly microhabitat temperatures recorded over summer exceeded the VT$_{\mathrm{max}}$ temperature between 11.00 and 12.00 h for all the retreat locations except the thick rock slab $T_{\mathrm{retreat-bottom}}$ (Fig. S3). The maximum thick rock slab $T_{\mathrm{retreat-bottom}}$ remained below VT$_{\mathrm{max}}$ until 14.00 h, but with ∼6°C difference from other maximum hourly microhabitat temperatures. Heating under thin rock slabs and $T_{\mathrm{retreat-top}}$ of thick rock slabs was rapid from 11.00 to 17.00 h (time of day: χ^2=1714.94, d.f.=1, P<0.001). The $T_{\mathrm{retreat-bottom}}$ of thick rock slabs heated more slowly, with a peak temperature of 35.80±0.62°C at 19.00 h (χ^2=81.92, d.f.=3, P<0.001; Fig. S3). However, the disparity between VT$_{\mathrm{max}}$ and all microhabitat temperatures was higher for the thick rock than the thin rock slab $T_{\mathrm{retreat-bottom}}$ (maximum disparity: −13.1°C; χ^2=8.45, d.f.=1, P=0.03) and the rock temperatures were above VT$_{\mathrm{max}}$ from late afternoon to early evening (time of day: χ^2=101.36, d.f.=1, P<0.001; Fig. 8).
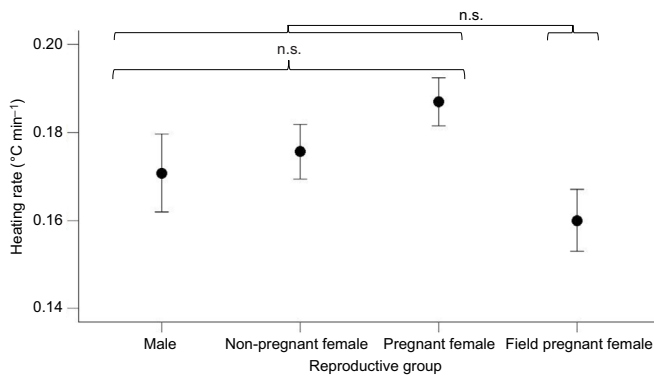
Fig. 4. Mean heating rate for wild geckos of three reproductive groups in the laboratory, and pregnant geckos in the field during late summer to early autumn (February–March). Heating rates were measured over a 60 min period using an attached biologger. For the wild geckos in the laboratory, there was no significant difference in heating rate among the reproductive groups, although medium effect sizes were detected for pregnant females when compared with other reproductive groups (Table 2). Also, a medium effect size (0.66) was found between wild geckos and pregnant females in the field. The brackets indicate groups included in statistical comparisons; n.s., not significant. Sample sizes are N=10–14 for laboratory-tested geckos and N=5 for field pregnant females. Values are means±s.e.m.

DISCUSSION

The upper limit for voluntary thermal tolerance, known as VT_{max}, is gaining attention as an ecologically relevant measure for thermal tolerance of ectotherms (Camacho et al., 2018). However, studies to date have focused on measuring the upper voluntary thermal tolerance experimentally in diurnal species (for a review, see Camacho and Rusch, 2017) or inferred it from the behaviour of nocturnal species in a thermal gradient (Kearney and Predavec, 2000). Our study developed a new protocol for VT_{max} testing in a nocturnal rock-dwelling lizard based on escape movement to avoid warming (Camacho and Rusch, 2017), as opposed to the highest temperature selected in a thermal gradient. Using this protocol for the cool-temperate species *Woodworthia* 'Otago/Southland', we observed that time spent at the edge of the retreat, VT_{max} and duration of heating differed between the wild and captive geckos.

Although the effects of reproductive group on mean VT_{max} and on the duration of heating were not statistically significant, the time spent at the edge of the retreat during heating was higher for pregnant females than other reproductive groups. In the wild geckos, EWL increased with increasing VT_{max} and duration of heating. The attached biologger during VT_{max} heating showed that the geckos initially reached a peak temperature higher than the exit (VT_{max}) temperature, and then thermoregulated for a time before abandoning the heated retreat. The time spent thermoregulating did not differ among wild reproductive groups in the laboratory. In the field, we found that gecko body temperatures were higher than rock and air temperatures on a hot sunny day, and that peak temperature was comparable to the peak temperatures and VT_{max} values (at exit) recorded in the laboratory for wild geckos.

As expected, the VT_{max} values recorded here (means of 32.56°C for captives and 30.65°C for wild geckos) were higher than mean values for selected temperature previously recorded on a thermal gradient for the same species (Rock et al., 2000). Using our new protocol, we also observed behaviours in the heated geckos (such as gaping, rapid gular fluttering and locomotory movements back and forth along the edge of tiles) that were different from the control group, indicating that the reason geckos left the heated slabs was because of heat. Overall, we consider that our method yields more convincing evidence that the values recorded experimentally were the actual VT_{max} values than if measured in a thermal gradient. For instance, on a thermal gradient, a lizard might choose a particular spot and remain at that temperature without increasing its body temperature further or exploring the thermal gradient beyond the chosen spot. However, increasing the heat intensity, when using our testing protocol as opposed to using a thermal gradient, will force the lizards to voluntarily abandon the spot and explore cooler locations within the retreats.

Our study showed three differences between the wild geckos and the captive geckos during VT_{max} testing. Wild geckos (collected fresh from the field) were less visible at the edge of the retreat during heating, had a mean VT_{max} value that was 1.91°C lower and also had a longer duration of heating than for captive geckos. The difference in VT_{max} values may be attributed to differences in the geckos' prior thermal opportunities; this is a short-term beneficial
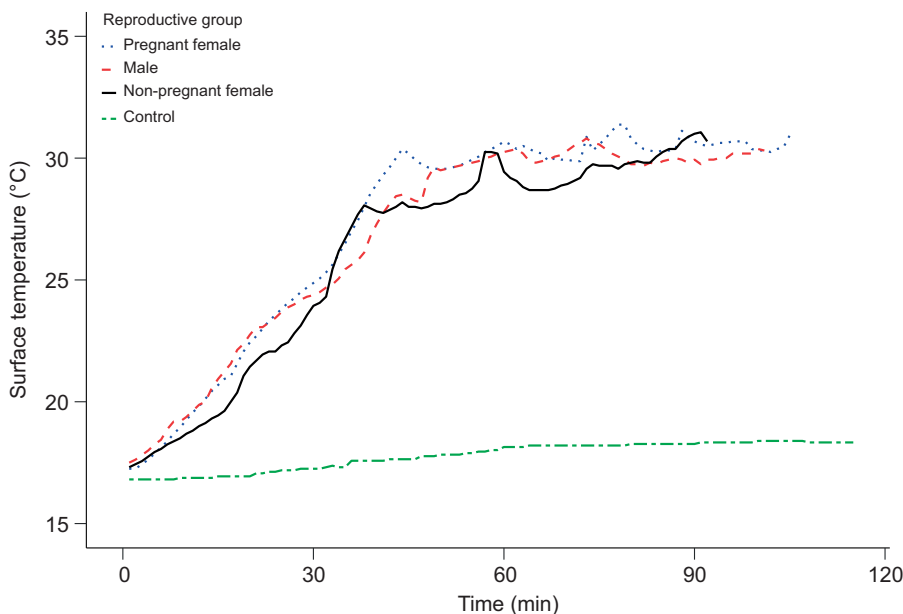

Fig. 5. Representative traces of skin temperature measured with biologgers attached to wild geckos during laboratory voluntary thermal maximum testing. The temperature traces are for individual geckos. The control is a gecko exposed to lit LED light in the same test condition as with the heated geckos but without heat.
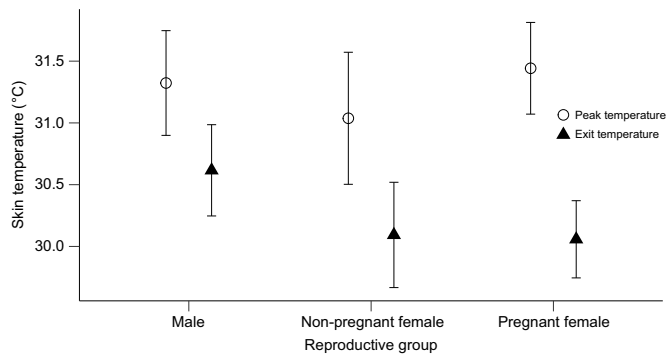
Fig. 6. Mean skin temperature recorded with a biologger attached to the posterior abdomen of wild adult geckos in different reproductive groups during voluntary thermal maximum testing. Overall, peak temperature differed significantly from the exit temperature (P=0.001). However, we found no significant difference among the reproductive groups at either peak temperature or exit temperature. Values are means±s.e.m.; N=10–14 for each reproductive group.

response to predictable thermal opportunities by the captive-held lizards (plasticity) compared with the wild lizards with more variable thermal opportunities, and not genetic adaptation. The
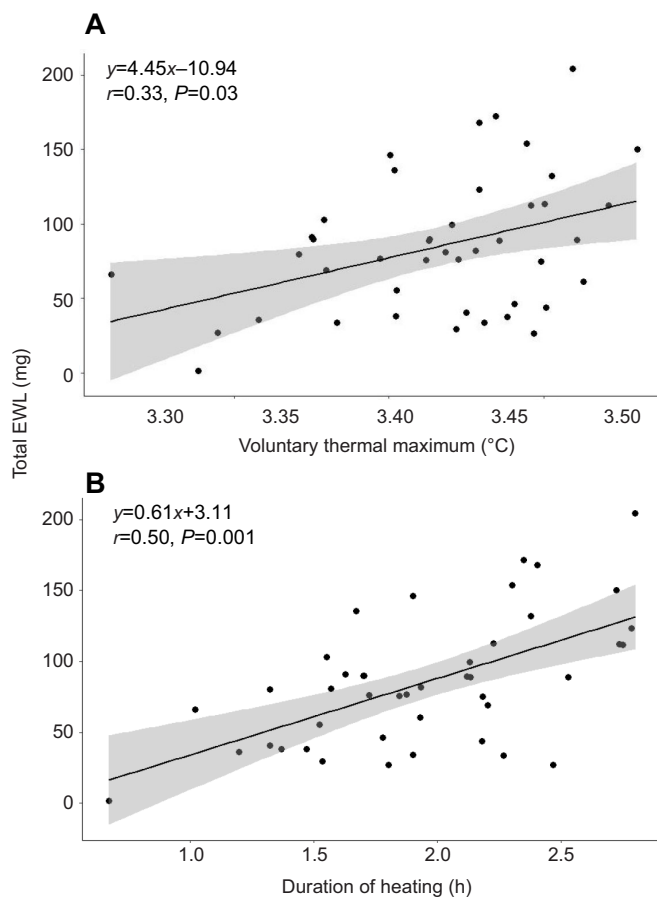
Fig. 7. Regression between evaporative water loss and either voluntary thermal maximum or duration of heating for individual adults of wild geckos in the laboratory. (A) Voluntary thermal maximum; (B) duration of heating. EWL, evaporative water loss. The plot shows a significant positive relationship for both VT_{max} and duration of heating (P<0.05). The grey shading represents the 95% confidence interval of the regression line (continuous black line); N=45.

captive geckos, which had been held in captivity for up to 10 years or were born in captivity, are exposed to a predictable thermal regime in which the heated tile surface reaches up to 31°C for 4 days a week in summer, with no risk of reaching CT_{max}, and in cages in which alternative cooler retreats are immediately adjacent. In contrast, thermal conditions for wild geckos are more variable. Wild geckos are potentially exposed to more extreme and varying heat in the field and get less predictable basking and thermoregulatory opportunity as cloud cover can persist for days. In summer, the field microhabitat temperature under some thin slabs exceeded ~53°C (mean: 42.5±2.57°C) on a hot day (Chukwuka, 2020). Thus, body temperatures experienced in the field are highly variable, even in summer (Rock and Cree, 2008). Although the mechanisms by which previous thermal experiences may affect future thermal tolerance are unknown for our study species, we suggest that the captive geckos may have acclimated to a more predictable retreat temperature different from natural field conditions (Hoffmann et al., 2013; Seebacher et al., 2015). Exposure of ectotherms to wider daily temperature fluctuations with higher maxima has been shown to reduce the optimum temperature (Paaijmans et al., 2013).

Another contributing factor to differences in VT_{max} value between the two source groups may be differences in water availability (and thus the possible hydration states of animals). Captive geckos are held with free-standing water, whereas prior to capture, wild geckos had access only to dew, rain and food as sources of water. Although the wild geckos were held in the laboratory for between 2 and 4 days with free-standing water, differences in prior exposure to moisture or use of the provided water may have affected the hydration state of the geckos. In the lizard *Podarcis* species, experimental dehydration leads to lower selected body temperature, presumably due to the animals' quest to conserve more body water (Sannolo and Carretero, 2019). However, to our knowledge, little is known about VT_{max} of squamates in a dehydrated state. We suggest future testing as to whether VT_{max} or duration of heating are reduced for retreat-dwelling squamates in a dehydrated state.

The longer duration of heating observed in wild geckos from our study suggests that the wild geckos thermoregulated more effectively to keep their body temperature lower than the captive geckos. Time spent under the heated retreat until exit may be prolonged if the geckos are efficient in employing physiological processes to regulate the heating and cooling such as increased cardiac output, enhanced blood circulation to the limbs of the animal and respiratory cooling (Seebacher and Franklin, 2005; Tattersall et al., 2006). Also, lizards may flick their tongue, lick their eyelids or gape to enhance cooling as observed in our study. Effective thermoregulators may also employ other behavioural mechanisms such as postural adjustments, and shuttling around the heated retreat to spot a cool region when faced with the risk of continued heating (Kearney and Predavec, 2000; Stanton-Jones et al., 2018). The time it took our nocturnal retreat-dwelling geckos to abandon their heated retreat and run into the open may depend on their thermoregulatory ability to avoid overheating and the associated costs and benefits.

Differences in perceived predation risk (Martín and López, 1999) and patchiness or distance to alternative (cooler) retreats (Stevenson, 1985) under prior living conditions may also have affected the thermoregulatory strategy in our study. There is no risk of predation to geckos held in our captive colony, and under routine housing the cool retreat is physically closer to the heated slabs than in the wild, allowing the captive geckos to move quickly to a cooler retreat if VT_{max} is reached. Given these differences, the wild geckos may
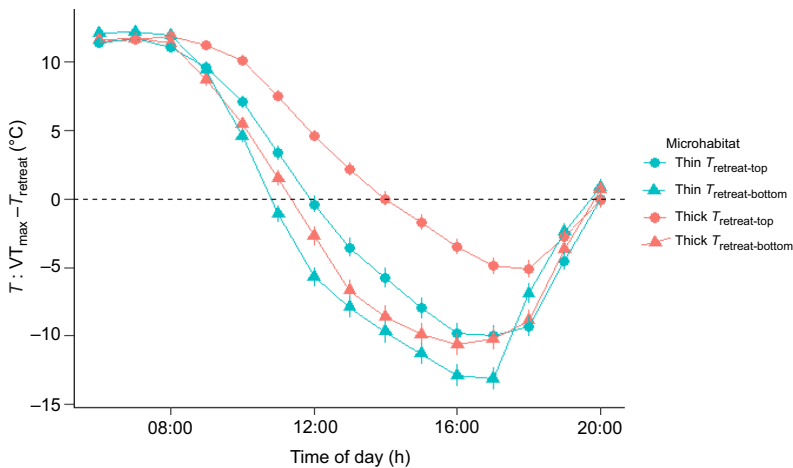
Fig. 8. The mean disparity between VT$_{max}$ and summer maximum temperature for retreats used by geckos at Macraes. Heating was faster under thin rock slabs than thick rock slabs. The mean disparity differed significantly across the microhabitat locations (P=0.03) and with the time of day (P<0.001).

have chosen to incur the costs of thermoregulation under the heated slabs for longer. Nonetheless, there are risks of getting overheated if the animals do not leave the heated retreat once VT$_{max}$ is reached (Camacho et al., 2018), and the decision to move to the open in search of a cooler retreat presumably depends on the cost that the geckos tolerate (Huey and Slatkin, 1976). The lizards may decide to remain under the heated slab if the cost of becoming overheated and/or dehydrated outweighs other costs such as the energetic cost for movement and the cost of predation (Herczeg et al., 2008; Webb and Whiting, 2005). A longer duration of exposure is potentially valuable to our geckos, but if extended beyond the voluntary tolerable limit may result in declines in fitness and upper thermal limits (Kingsolver and Woods, 2016).

Our study failed to support our prediction that VT$_{max}$ and duration of heating would vary across reproductive groups (including different sexes and female reproductive conditions). However, our results in this respect are consistent with those for egg-laying nocturnal squamates such as the marbled gecko (*Christinus marmoratus*) and the ring-necked snake (*Diadophis punctatus*), where no significant effects of sex or reproductive group on upper voluntary temperature were detected (Cox et al., 2018; Kearney and Predavec, 2000). In contrast, Virens and Cree (2019) recorded a higher VT$_{max}$ in post-partum females with medium effect sizes compared with males and pregnant females in a diurnal New Zealand skink (*Oligosoma maccanni*), a sympatric lizard to our study species. We did not test post-partum females in our study and suggest that VT$_{max}$ in this group would be worth testing in future research. However, we did observe that the magnitude of the difference between VT$_{max}$ and the corresponding selected body temperature (range 24–28°C) varied in Otago/Southland geckos with reproductive group, the difference being much smaller for pregnant females (+2°C) than for males and non-pregnant females (+5 to +6°C) in late spring and early summer (Rock et al., 2000). In other words, the high body temperature selected by wild females in early to mid-pregnancy is much closer to VT$_{max}$ than the lower temperatures selected by males and non-pregnant females at the same time, or by pregnant females at the end of embryonic development (Cree and Hare, 2016a). The unwillingness of wild, pregnant females to tolerate heating beyond 2°C above the selected temperature may be because VT$_{max}$ was tested at the stage of embryonic development when pregnant geckos needed to thermoregulate effectively to benefit their embryos (Cree and Hare, 2016a).

The biologgers attached to the wild geckos in the laboratory enabled us to measure heating rates. This non-invasive procedure is an improvement upon the surgical implantation of temperature-sensitive radiotelemetry devices (Rock and Cree, 2008) and gives real-time body temperatures consistent with spot temperatures but over a prolonged period (Virens and Cree, 2018). We found that adult geckos in all reproductive groups maintained a steady heating rate averaging about 0.17–0.19°C min^{-1}. Although the heating rates did not differ significantly, there were medium effect sizes for the difference between pregnant females and other reproductive groups. The result is consistent with the higher selected temperature at the early stage of pregnancy compared with males and non-pregnant females in previous studies (Rock et al., 2000). Also, it is worth noting that the geckos initially reached a higher mean body temperature (by about 1.5°C) during the VT$_{max}$ trial than the temperature at which they eventually left the heated retreat (defined as VT$_{max}$); in other words, 'peak temperature' was higher than 'exit temperature'. The temperature traces from the biologgers show that geckos maintained a temperature within the range of VT$_{max}$ over time, indicating that the geckos thermoregulated for several minutes as they sought cooler locations under the heated retreat or engaged in behaviours that enhanced EWL (Castilla et al., 1999).

An important finding of our study with wild geckos in the laboratory was that total EWL was predicted by the duration of heating but not VT$_{max}$. In other words, geckos that remain longer under the heated retreat lose more water as VT$_{max}$ increases. The mass- and surface area-specific EWL showed large effect size between the non-pregnant female geckos and other reproductive groups, indicating that smaller, non-pregnant females still lose water faster than the larger pregnant geckos and male geckos (Mautz, 1982b). The rate of EWL (cutaneous plus respiratory) increases with increasing body temperature in other reptiles (Camacho et al., 2018; Mautz, 1982a; Sannolo et al., 2018) including in a congener of Otago/Southland geckos (Hare and Cree, 2016). The increase in cutaneous water loss reflects the replenishment of blood flow at the vascular regions of the skin (Smith et al., 1986). Water loss through corneal surfaces of eyes may also occur as geckos were seen licking their eyes, presumably to keep them moist. Our results suggest a tension between thermoregulation and water balance; in other words, water constraints may affect thermoregulation in temperate ectotherms. Thermoregulation may be impaired if the animal is dehydrated, leading to the selection of lower body temperature to minimise further risk of water loss (Crowley, 1987; Sannolo and Carretero, 2019). However, in a fully hydrated state, the activity level is high, and thermoregulation is effective (Rutherford and Gregory, 2003). The severity of water constraint will force lizards to reduce hours of activity to conserve more water (Crowley, 1987), but lizards may also thermoregulate at lower temperature while

frequently retreating to avoid losing more water (Sannolo and Carretero, 2019). Continuous exposure to heat under a heated retreat will distort water balance and have an impact on the physiology of a rock-dwelling lizard (Köhler et al., 2011; Ladyman and Bradshaw, 2003; Rozen-Rechels et al., 2019), but in a warm and humid microclimate, water loss is minimal compared with that in a warm and dry microclimate (Dupoué et al., 2015).

In the field, we found that pregnant female geckos attained a mean peak temperature of 30.4°C, with a mean heating rate of 0.14°C min^{-1}. The mean peak temperature and heating rate observed in the field correspond to the mean VT$_{max}$ and heating rate measured in the laboratory for wild geckos. However, the field body temperature of the geckos was higher than the air and rock temperature, which implies that the geckos may have basked openly (Gibson et al., 2015) or may have chosen the warmest part of the rock to raise their body temperature (Rock and Cree, 2008). Although we cannot be certain that the geckos did not abandon their retreats when the peak temperature was reached, and then return later, the rock slabs were relatively large ones, and we suspect that the geckos may have simply moved to the opposite side of the slabs not receiving direct sun rays. We suggest a future study to have video cameras on both sides of the rock slabs to ascertain if geckos abandon their retreats when experiencing a temperature equivalent to VT$_{max}$ beyond a certain length of time.

Using VT$_{max}$ values for ecophysiological studies depends on the experimental protocols such as experiment set-up and heating rate. VT$_{max}$ testing should be species specific (the same method or protocol for a diurnal species will not be applicable for a nocturnal species) and microhabitat specific, reflecting the natural habitat of the test animals. Also, the heating rate to be used should be ecologically relevant, indicating the animals' field conditions (Hoffmann et al., 2013; Moyen et al., 2019; Terblanche et al., 2007). Measurements of VT$_{max}$ and other thermal tolerance indices in ectotherms should be relevant to present and future field conditions of the animal and also be extended to sensitive life-history stages such as neonates (Hoffmann et al., 2013). Knowing the VT$_{max}$ value is valuable for predictions of vulnerability to climate change because this measure considers the animal's perception of heat. The use of behavioural approaches through postural adjustments under the retreat and by moving away from heated retreats may help ectotherms buffer the impact of climate heating (Huey and Tewksbury, 2009; Sunday et al., 2014); such behaviours may be costly if potential predators are nearby.

Upper thermal tolerance, including VT$_{max}$, is plastic (Gunderson et al., 2017) and can vary with prior conditions that include variation in thermal opportunity (this study). However, whether VT$_{max}$ is repeatable in this species and can change with season remains unclear. Previous research in this species has shown that that preferred temperature varies across the season and among life-history groups (Rock et al., 2000). Repeatability of thermal tolerance varied in other species of lizards; it was low in temperate rock-dwelling cordylid lizards and female *Zootoca vivipara* (formerly *Lacerta vivipara*) (Clusella Trullas et al., 2007; Le Galliard et al., 2003), but high in diurnal female lizard *Agama atra* (Van Berkel and Clusella-Trullas, 2018). For Otago/Southland geckos, consistency in preferred body temperature for similar stages of pregnancy over 20 years suggests that VT$_{max}$ may be repeatable in this species (Cree and Hare, 2016b; Moore et al., 2020; Rock et al., 2000).

In conclusion, our study on a cool-climate viviparous gecko has shown, using a new protocol that is ecologically relevant for testing VT$_{max}$ in retreat-dwelling reptiles, that the upper voluntary thermal limit based on escape behaviour and duration of heating can vary between source groups in a way that may be associated with the prior thermal and/or hydric experience. Reproductive condition had no significant effect on either the VT$_{max}$ or the duration of VT$_{max}$. However, our study reflects the importance of time-dependent effects of exposure in the assessment of thermal tolerance and when making inferences about potential effects of climate change on ectotherms (Kingsolver and Woods, 2016). The positive association between VT$_{max}$ and EWL in wild geckos suggests that wild lizards will abandon their retreats more often under warm, dry conditions than under cool conditions. Taken together, our findings indicate a trade-off between the potential costs (risk of overheating and water loss) and benefits (retaining occupancy of shelter and reducing predation risk) of remaining in a retreat (Belasen et al., 2017; Vickers et al., 2011).

Author contributions
Conceptualization: C.O.C., A.C.; Methodology: C.O.C., J.M.M., A.C.; Software: C.O.C.; Validation: C.O.C., J.M.M.; Formal analysis: C.O.C.; Investigation: C.O.C.; Resources: C.O.C., A.C.; Data curation: C.O.C.; Writing - original draft: C.O.C.; Writing - review & editing: C.O.C., J.M.M., A.C.; Visualization: C.O.C., J.M.M., A.C.; Supervision: J.M.M., A.C.; Project administration: C.O.C., A.C.; Funding acquisition: C.O.C., A.C.

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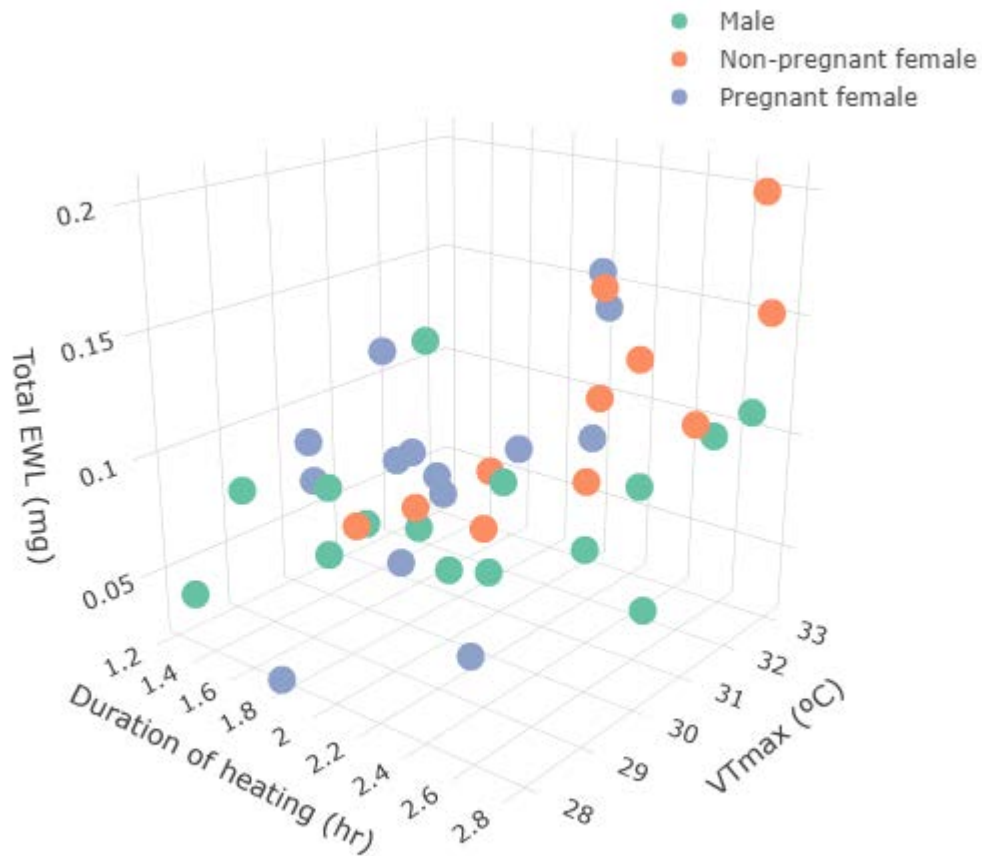
Figure S1: Three-dimensional graph of multiple regression plane of total evaporative loss with VT_{max} and duration of heating as predictor variables. Duration of heating but not VT_{max} predicted total evaporative water loss in *Woodworthia* "Otago/Southland geckos". N = 11=16 for each reproductive group.
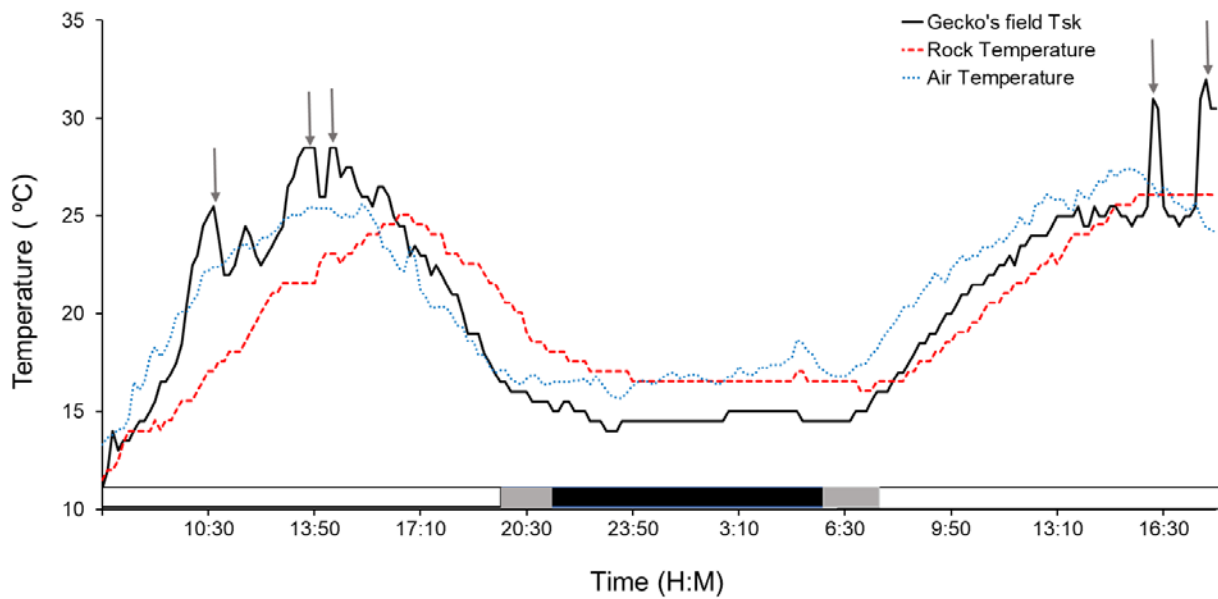
Figure S2: Representative trace of field skin temperature (T_{sk}) measured with a biologger attached to a pregnant *Woodworthia* "Otago/Southland" gecko, along with air and rock temperatures recorded with iButtons. Data were recorded for two days in late summer (February). Arrows indicate peaks in skin temperature attained by the gecko following periods of rapid heating. During these periods, the gecko may have basked openly in the sun or may have located a hotter part of the rock than recorded here. The horizontal bar indicates the photoperiod, with photophase (white bar), dusk and dawn (grey bars) and night (dark bar). The gecko was still under the original retreat when recaptured.
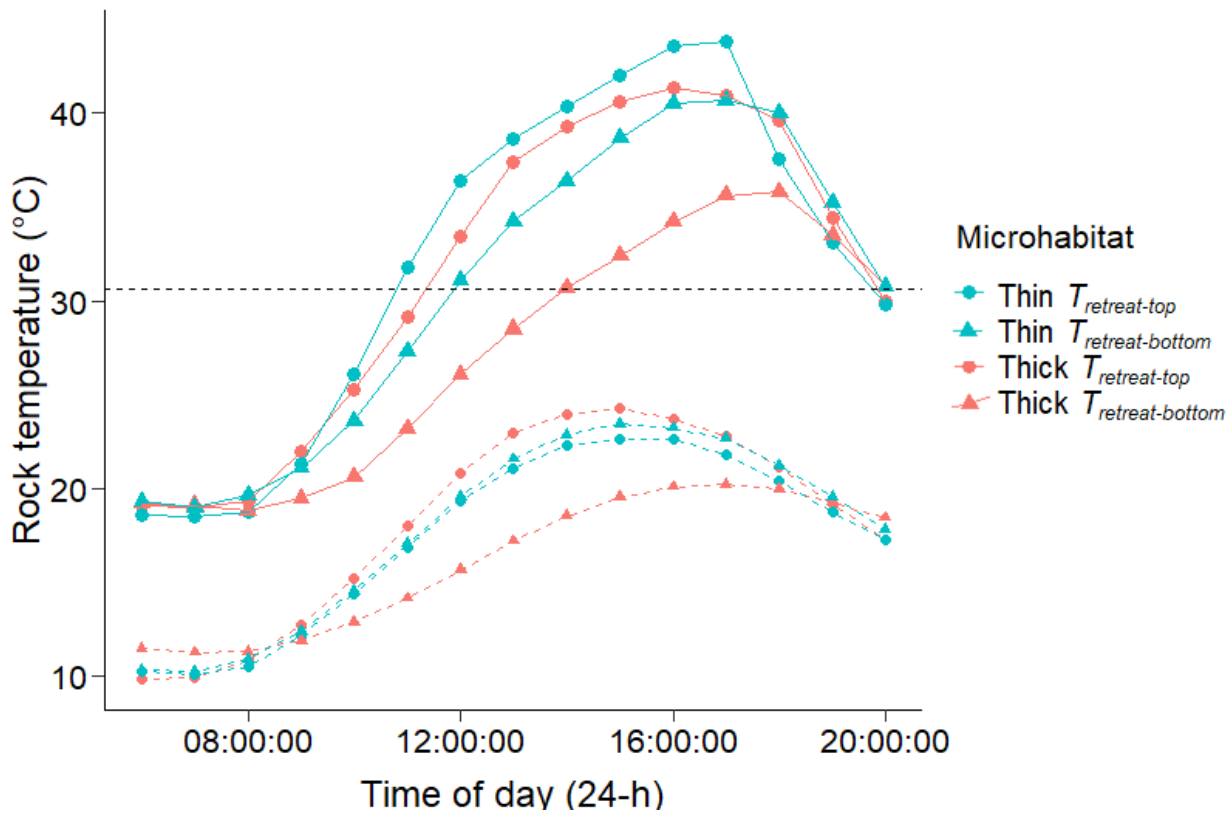
Figure S3. Hourly maximum (solid lines) and mean±se (dashed lines) for microhabitat temperatures of retreats used by Otago/Southland geckos at Macraes in summer (December 2018 – February 2019). The mean microhabitat temperatures differed significantly across locations and with the time of day ($P < 0.001$). Black dashed line is the mean VT_{max} recorded for wild geckos in the laboratory