

Extreme variation in body temperature in a nocturnal thigmothermic lizard

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Nocturnal lizards inhabiting cool temperate environments potentially experience a wide range of body temperatures (T_b). We used radio telemetry to characterize field T_b in a nocturnal diplodactylid gecko (*Hoplodactylus maculatus*) from a high-latitude (45°S), sub-alpine site in southern New Zealand. Variation in T_b within days (diel), among days and among different reproductive groups of this viviparous species (pregnant females, non-pregnant females and males) was measured with temperature-sensitive transmitters. We found that surgical implantation of transmitters did not have a significant effect on selected temperature on a laboratory gradient (T_{sel}). Field T_b values were examined in concert with T_{sel} and microhabitat temperature in late summer, revealing marked fluctuations of up to 30 °C in T_b both within and between days. When weather conditions allowed, all reproductive groups exhibited some degree of thermoregulation, with T_b generally elevated at least 4 °C above microhabitat temperature and within the bounds (central 50%) of T_{sel} at the warmest times of day on most days. Considerable thermoregulation occurred early in the day, particularly for pregnant females, and is likely to have involved some degree of direct solar basking. Temperature telemetry revealed both extreme variability in T_b and complexity of thermoregulatory behaviour in a primarily nocturnal, thigmothermic lizard.

Key words: thermoregulation, telemetry, reproductive condition, microhabitat temperature, gecko, Diplodactylidae

INTRODUCTION

The thermal biology of nocturnal thigmothermic reptiles has received little attention compared with that of diurnal heliotherms. Studies focusing on the thermal strategies associated with retreat site selection (e.g. Autumn et al., 1994; Schlesinger & Shine, 1994; Webb & Shine, 1998; Kearney & Predavec, 2000; Kearney, 2001; Rock et al., 2000, 2002) have revealed that a surprisingly wide range of temperatures is often available within the microhabitats of nocturnal reptiles. Retreat sites can constitute a diverse microhabitat for thigmothermic basking, affording nocturnal reptiles significant diel variability in body temperature, T_b (Dial, 1978; Werner, 1990; Schlesinger & Shine, 1994; Autumn & De Nardo, 1995; Rock et al., 2002; Rock & Cree, 2003). Such variability would be expected to be greatest in thigmothermic species inhabiting regions with highly stochastic climates. However, variation in T_b is difficult to characterize in reptiles living in thermally variable environments, often necessitating prohibitively long periods of field work. In such environments, temperature telemetry has been a valuable tool for characterizing thermoregulation (e.g. Charland & Gregory, 1990; Shine & Lambeck, 1990; Blázquez, 1995; Whitaker & Shine, 2002). Various techniques for attaching transmitters exist (e.g. external harnesses, forced ingestion, surgical implantation), but, for results to have the greatest validity, care must be taken to assess the effect of the transmitter on the animal's thermoregulation. Forced ingestion of transmitters, for instance, leads to selection of elevated T_b in *Nerodia s. sipedon* (Lutterschmidt & Reinert, 1990). Wang &

Adolph (1995) demonstrated that, in *Sceloporus occidentalis*, surgical implantation of transmitters did not affect thermoregulatory patterns after three days recovery. However, the effect of implantation surgery on thermoregulation must be ascertained on a species-specific basis, though most recent studies have failed to do this.

In this study we use telemetry to examine variation in thermoregulation for a population of nocturnal common geckos from the *Hoplodactylus maculatus* species complex (Daugherty et al., 1994) from the cool high latitudes of southern New Zealand. By day, common geckos are predominantly thigmothermic and inhabit crevices under rock slabs on exfoliating schist tors, the predominant rock outcrops of this region of the southern South Island. Extensive observations of field T_b in different populations from this area have included either spot T_b measurement and/or copper models to predict operative temperatures, and describe generally low body temperatures (Werner & Whitaker, 1978; Spencer & Grimmond, 1994; Rock et al., 2000, 2002). For the Macraes Flat population used in this study, daily means of diurnal spot T_b measurements are known to vary from 15 to 24 °C across the spring–autumn activity season. Night-time T_b values have not been so well assessed, but appear to be generally low, with means of 10 °C in a small summer sample (Rock et al., 2002).

Common geckos are viviparous, and females in certain southern populations, including Macraes Flat, have an unusual reproductive cycle in which gestation lasts approximately 14 months and offspring are produced biennially (Cree & Guillette, 1995). This means that three reproductive groups exist simultaneously in the popula-

tion: pregnant females, non-pregnant (spent or vitellogenic) females and males. As in many reptiles, sex and female reproductive condition affect aspects of thermoregulation, including indices of thermoregulatory effort in the field (Rock et al., 2002), as well as selected temperature (T_{sel} , measured on a thermal gradient in the lab; Rock et al., 2000). The effect of reproductive condition on thermoregulation in *H. maculatus* from southern New Zealand is among the most marked reported for reptiles, and the temporal and microhabitat variation in the thermal environment is dramatic. For example, mean T_{sel} can be as much as 8 °C higher for pregnant females than for non-pregnant females or males, and often 10 °C higher than the available temperature in the warmest microhabitat (Rock et al., 2002). Somewhat surprisingly, studies of spot field T_b do not demonstrate such large divergence between reproductive conditions/sexes (Rock et al., 2000, 2002). To characterize field T_b on a fine temporal scale (to include variability in thermal environment within and between days), we surgically implanted temperature-sensitive radio transmitters into common geckos. Measurements of T_{sel} were compared pre- and post-surgery to control for the effect of the transmitter implantation on thermoregulation. Environmental temperature was recorded on an adjacent tor, providing continuous reference data for estimating the effectiveness of thermoregulation. To assess the effect of reproductive physiology on thermoregulation, we included adults of both sexes and both pregnant and non-pregnant females.

MATERIALS AND METHODS

Geckos were studied at Macraes Flat (500–700 m asl, 45°27'S) during late summer/early autumn (February–March), a time of year when significant differences in T_{sel} occur among reproductive conditions and when opportunities for thermoregulation are abundant (Rock et al., 2000). Males and females were differentiated visually by presence or absence of a hemipenial sac, and female reproductive condition was determined by palpation of the abdominal region (reliability of technique confirmed by Cree & Guillette, 1995; Rock & Cree, 2003; Wilson & Cree, 2003). A total of five males, four non-pregnant females and four pregnant females were collected. Sample sizes of this protected species were restricted to the minimum required to yield statistically significant results, as indicated by power analyses. Individuals were identified by toe-clipping and numbering with xylene-free paint.

Measurement of T_{sel}

We measured T_{sel} one day prior to transmitter implantation (within 24 h of capture) and five days post-implantation. This procedure allowed us to 1) assess the effects of implantation on thermal biology and 2) evaluate the current thermal preferences of each reproductive group relative to T_b achieved in the field. Measurements of T_{sel} were made on a thermal gradient at three times of day (1000, 1400 and 1700) according to a previously described method (Rock et al., 2000). We defined the range of T_{sel} as the central 50% of all

temperatures around the median value, i.e. the interval encompassing the second and third quartiles of the sample, after Hertz et al. (1993).

Implantation surgery

Epoxy-resin-coated transmitters with an internal aerial (SOPT-2011®, Wildlife Materials Inc., Carbondale IL) were selected for use as the crevice-dwelling habit of *H. maculatus* prevents the use of external transmitters or whip antennas. Weighing approximately 1.2 g (about 18 x 8 x 6 mm), which is $\leq 10\%$ of average gecko body mass, transmitters were not expected to significantly alter feeding, movement or thermoregulation (Wang & Adolph, 1995). Before implantation, each transmitter was calibrated to ± 2.5 °C against an Ever Ready reference thermometer warmed progressively in a water bath from 0 to 40 °C. Geckos were anaesthetized by exposure to halothane, and, using aseptic technique, the transmitters were inserted through a small (approximately 10 mm) incision made on the latero-ventral surface of the lower abdominal region. To make sufficient space for the transmitter inside female geckos, the right-side oviduct of pregnant females or right-side ovary of non-pregnant (vitellogenic) females was removed by cauterization. Loss of an embryo or follicle is not unrealistic biologically, as these geckos, which have a maximum clutch size of two, sometimes produce a clutch of one (Cree & Guillette, 1995). In pregnant females, both ovaries (and hence both corpora lutea, a likely source of progesterone during pregnancy) remained intact. In males, transmitters were also positioned on the right side of the body cavity to minimise interference with the digestive tract, but no reproductive structures were removed. Incisions were sutured in two layers (through the muscle and then skin), and coated with a skin glue. The only fatality from surgery was a single male that did not recover from anaesthesia (all other geckos recovered and were fully active within four hours). Following implantation, animals were allowed to recuperate for four days in disinfected plastic bins supplied with retreat sites and with food and water *ad libitum*. Ambient temperature was maintained at 21 °C, with a basking area under a heat lamp maintained at 25 °C for 6 h per day, and L:D cycle equivalent to that at the field site (about 14:10). Geckos were monitored to ensure that there were no post-operative complications and that incisions healed. Five days after surgery T_{sel} was measured for all geckos at the same times of day as before surgery.

Measurement of field T_b by telemetry

Rather than releasing geckos at their individual capture sites and risk being unable to retrieve them from deep inaccessible crevices, we released all the geckos on a specially prepared tor site. The chosen tor, which had no deep crevices, had many loose rock slabs of varied thickness (3–15 cm) and solar exposure, providing a wide choice of thermally varied microhabitats. It was surrounded by natural vegetation, providing ample food resources. No resident geckos were found on the tor at the time of site preparation, although geckos had been

noted there previously, indicating that it was suitable habitat. To prevent the geckos' escape, the tor and surrounding vegetation were enclosed with a solid sheet metal fence sunk at least 4 cm into the ground and braced against wind damage. The fence was "gecko-proofed" by crimping the top third of metal inwards and coating the inside of the 45° angle with petroleum-based grease. The final fence height was approximately 60 cm, forming an enclosure about 7 m in diameter.

We planned to record T_b data automatically by using a radio-receiver connected to a data logger (Falcon Five receiver and DL-2000 data logger, Wildlife Materials Inc., Carbondale IL), programmed to monitor T_b frequencies at approximately hourly intervals for 10–15 days (estimated life of the batteries remaining upon release). However, because of technical difficulties in telemetry equipment function (the signal often appeared to be compromised by a combination of weather conditions and the depth and angle of rock above the transmitter/gecko), we recorded data on only nine days. This was mostly done manually, without the help of the data logger, such that on only five days were we able to acquire data at hourly intervals for a significant part of the day for all individuals (see Results); we focus most of our analyses on data from these days. At the completion of the study, all geckos but one were recaptured, euthanased and dissected to remove the transmitters and to assess any internal trauma from the implant that might have affected thermoregulation. Embryos or follicles from the left oviduct or ovary were removed and measured (wet mass and diameter of the largest vitellogenic follicle or embryonic stage and wet mass) for comparison with measurements for right-side embryos or follicles removed during surgery.

Measurement of environmental temperature

As part of a long-term monitoring study, environmental temperature was recorded at two-hour intervals with a Stowaway data logger (Onset Computer, MA, USA) positioned within gecko microhabitat on a neighbouring tor (<400 m away with the same exposure). An external probe directly monitored the temperature of the underside of a thin loose slab of rock on the top of the tor, where geckos had previously been found. The temperatures recorded at this site (hereafter referred to as T_{top}) are considered to represent some of the highest temperatures available to geckos thermoregulating by thigmothermy in retreat sites at Macraes Flat (for further details see Rock et al., 2000, 2002). A subset of microhabitat temperature data was analysed for the days when T_b was successfully monitored with temperature telemetry.

Statistical analyses

Statistical analyses were performed using DataDesk 4.1 (1993) and SAS 6.12 Statistical Package (SAS, 1996). Significance was set at $P \leq 0.05$ and means are reported ± 1 standard error. Paired t-tests were conducted to test for differences in T_{sel} before and after surgery. We tested the effect of reproductive condition over time on mean T_b using repeated measures ANOVA to compare T_b at the five times of day during which data were available for all indi-

viduals. Separate ANOVAs were performed for each of the five key days of data logging.

RESULTS

Implantation surgery and its effect on T_{sel}

No mortalities were observed in the field and 11 of the 12 geckos released on the fenced tor were recaptured. However, a dead foetus was found within the enclosure late in the experiment and palpation of females on recapture revealed it was from an individual previously categorized as pregnant; thus the sample size for pregnant females was reduced from four to three. Implantation surgery did not appear to have an adverse effect on the remaining females. Embryos removed from the right oviducts of pregnant females at surgery were at early stage 40, with a mean mass (combined with associated yolk and placental membranes) of 0.65 ± 0.05 g. Neonates dissected from the left oviduct of pregnant females after the study ended were at late stage 40 with a mean wet mass of 0.92 ± 0.14 g; residual yolk mass averaged 0.08 ± 0.02 g. Non-pregnant females were all vitellogenic: follicles removed from the right ovary during implantation surgery and from the left ovary at the end of the study approximately 25 days later averaged 6.67 ± 0.33 and 6.0 ± 0.58 mm in diameter, and 0.18 ± 0.03 and 0.14 ± 0.04 g in wet mass, respectively. Dissection of geckos after the experiment revealed no evidence of internal trauma from the transmitters in males or females, although several transmitters had shifted slightly laterally or anteriorly in position.

To maximize statistical power when assessing whether surgery had a significant effect on thermal preference, selected temperatures of the three reproductive conditions were pooled for each time of day. We found no significant difference in T_{sel} measured before and after surgery at any time of day: mean values ranged from 22.2 ± 1.0 °C to 26.4 ± 0.9 °C before surgery and from

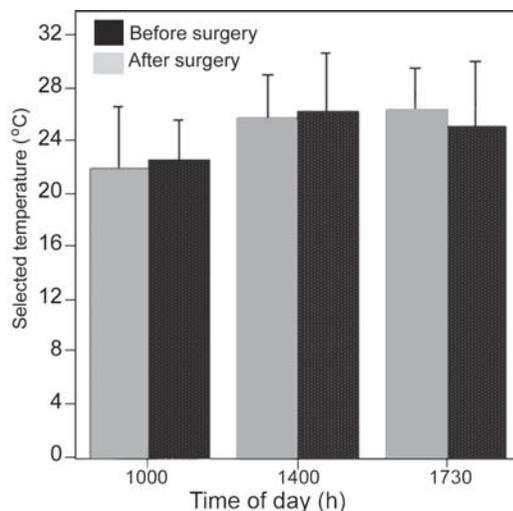


Fig. 1. The effect of implantation surgery on T_{sel} of common geckos. Values are means \pm standard error for T_{sel} , measured at three times of day, one day before and five days after surgery ($P > 0.05$ for each time of day).

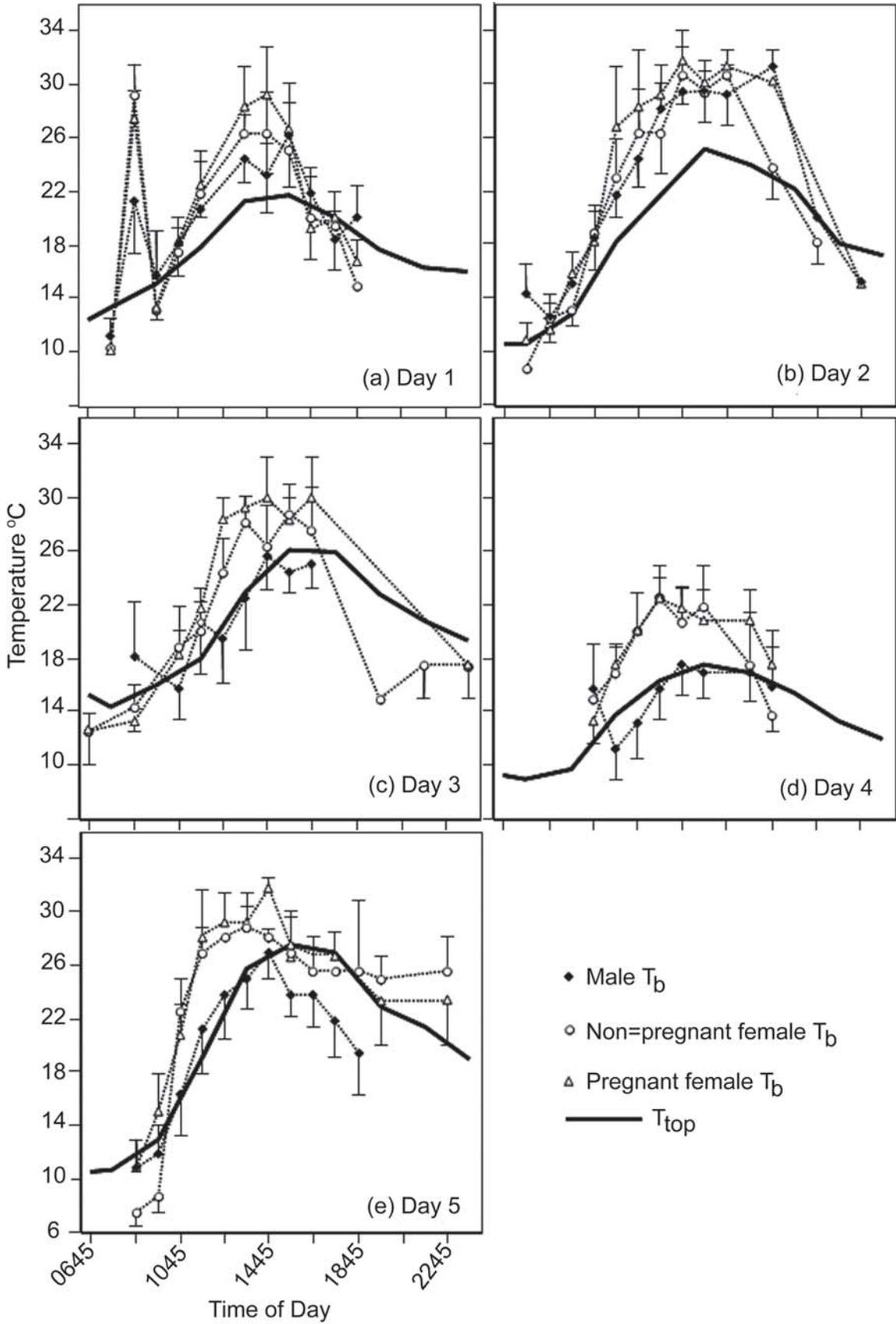


Fig. 2. Diel variation in T_b across five days, where values represent means for each reproductive group for times of day when data were collected for all individuals (symbols connected by dashed lines). An estimate of maximum microhabitat temperature for a thermoregulating gecko under a rock (T_{top} ; see Materials and Methods) is represented by a solid line. To show diel variation in T_b most clearly, most night-time temperatures are excluded from the graphs. To further aid clarity of interpretation only one-way error bars are given: to maintain representation of the spread of data the negative error bar is shown for the lowest plotted mean, whereas positive error bars are given for the other means at each time point.

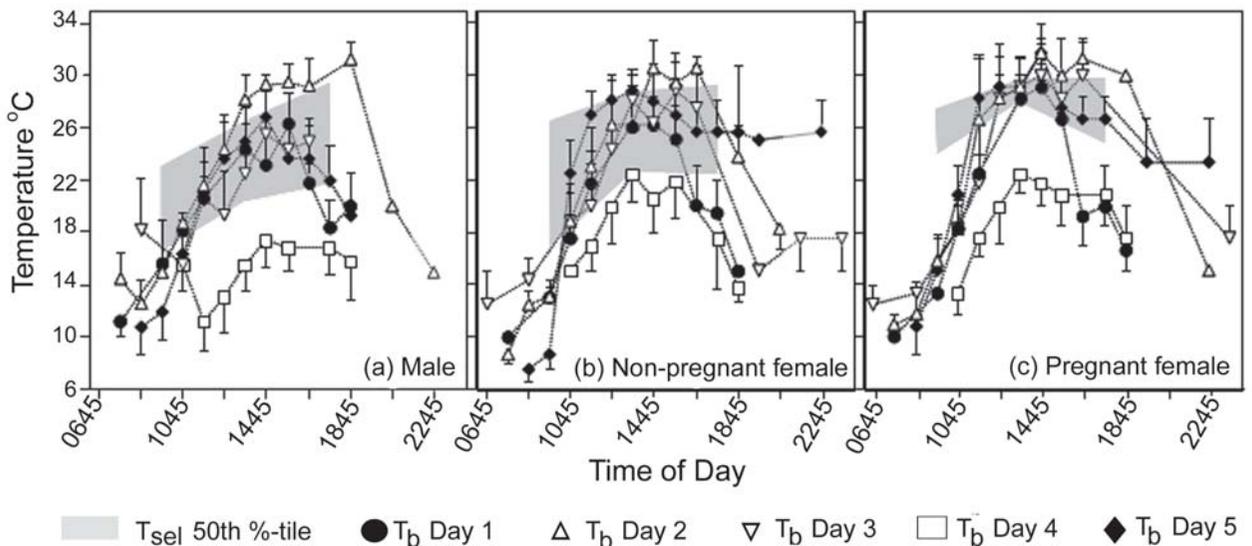


Fig. 3. Comparison of body temperatures monitored across multiple times of day on several different days (symbols represent means for times when data for at least two individuals per reproductive group were collected) with selected temperatures (T_{sel} , shaded area) respective for each reproductive group. For clarity of interpretation, one way-error bars are shown (as per Fig. 2) and aberrant data points for 0845 on Day 1 are excluded (see Results). T_{sel} values were measured prior to surgical implantation procedures; represented is the central 50% of values around the median (i.e. from the 25th to 75th percentile).

22.6±0.7 °C to 26.2±1.1 °C after surgery (Fig. 1; $P>0.05$). Pre-implantation values for T_{sel} were similar in males and non-pregnant females (16.7–29.3 °C and 17.0–29.1 °C, respectively) but were generally higher (with a narrower range) in pregnant females (24.3–29.6 °C).

Variation in field T_b with time of day, reproductive condition and relative to T_{top}

Body temperature was recorded on nine days, for a varying number of hours per individual, and revealed extreme variation (up to 30 °C) both within and between days. Means calculated for each hour in which at least two individuals per reproductive group had T_b recorded were 19.9±1.2 °C (range of 5–32 °C) for males, 21.0±0.8 °C (5–35 °C) for non-pregnant females and 22.2±0.9 °C (7.5–35 °C) for pregnant females. On five days, data were available for all 11 individuals at the same time of day: on all five days time of day was found to have a highly significant effect on T_b ($P\leq 0.0001$ for all days: 5 March (9 h data), $F_{8,56}=18.15$; 8 March (9 h data), $F_{8,48}=16.39$; 9 March (8 h data), $F_{7,56}=17.94$; 12 March (8 h data), $F_{7,42}=7.22$; 13 March (11 h data), $F_{8,56}=18.15$; Fig. 2). All geckos exhibited a triphasic diel pattern: T_b increased quickly after sunrise (0630), maintained a relatively stable midday–afternoon plateau (the magnitude of which varied greatly among days) and then began a slow decrease prior to sunset (1930), reaching values below 14 °C during the night that deviated little from microhabitat temperatures (T_{top}).

There was considerable overlap in T_b among reproductive conditions, and the interaction between time and reproductive condition was not significant for any day ($P>0.05$). However, when T_b values at the warmest time of day (approximately 1445) were compared by ANOVA, using a nested design to include individual identification

(ID), reproductive condition had a significant effect on T_b ($F_{2,44}=3.62$, $P\leq 0.05$; with a significant effect of ID, $F_{8,44}=3.44$, $P\leq 0.05$). Pregnant females in particular had higher T_b values than males (Bonferroni post-hoc test $P\leq 0.05$ with no other significant differences between reproductive groups, $P>0.05$). The pattern of diurnal variation in T_b for pregnant females was also notable in its steep rate of increase between 0900 and 1200 (on both warm and cool days) and relatively slow rate of decrease late in the day.

Considerable variation was observed in the range of T_{top} both within the five-day sampling period (8.9–27.6 °C) and within a single day (e.g. from 10.6 to 27.6 °C). Despite this climatic variability, geckos in all reproductive groups were capable of thermoregulation, achieving T_b values that were often higher than T_{top} at the warmest times of day (Fig. 2). Indeed, on all five days, maximum T_b frequently exceeded T_{top} by approximately 4 °C and sometimes by as much as 8 °C on the warmest days. Mean differentials measured across all times of day between T_b and T_{top} were +0.7±0.9 °C for males, +1.3±0.9 °C for non-pregnant females and +3.3±0.4 °C for pregnant females. Though daily increases in T_b roughly mirrored diurnal increases in T_{top} , the rise in T_b generally preceded the rise in T_{top} , especially for females. On days when T_{top} profiles were similar (e.g. Fig. 2c and 2e) there was remarkable similarity in the rates of increase in T_b , which generally preceded the T_{top} warming curve. An extreme rise in T_b was recorded in advance of T_{top} at 0845 on Day 1 for all reproductive conditions (Fig. 2a); whilst these observations could reflect a sudden event of extreme thermoregulation such as direct solar basking, the fact that it occurred for geckos in all reproductive conditions, lasted only briefly and was not observed on any other

days suggests alternatively that it may be an aberration in recording telemetry data.

Field T_b and T_{sel}

Body temperatures for all reproductive groups were frequently within the central 50% of values for each groups' respective T_{sel} at the warmest times of day (Fig. 3). On average, throughout the day, mean differentials between T_b and the lower bounds of T_{sel} were -1.0 ± 1.2 °C for males, -0.2 ± 1.0 °C for non-pregnant females and -2.0 ± 1.6 °C for pregnant females. However, on Day 4, which was especially cool, mean T_b values fell below the lower limits of the respective T_{sel} ranges by up to 7 °C for males, 2 °C for non-pregnant females and 5 °C for pregnant females (Fig. 3).

DISCUSSION

The use of temperature telemetry as a powerful and efficient method for characterizing the variable properties of thermoregulation in reptiles is well established (Taylor et al., 2004). However, its application is still technologically limited by variation in body size and microhabitat. In this study, the small body size of *Hoplodactylus maculatus* limited battery size of the transmitter, constraining the time available both for geckos to recover from surgery and for logging of T_b in the field. Although we used the smallest transmitters then available, body size also necessitated surgical modification of females to accommodate the implants. However, our results indicate that implantation of transmitters did not affect thermoregulation or, in most cases, the progression of female reproduction in *H. maculatus*. We found that mean T_{sel} values did not differ before and after surgical implantation of transmitters and T_{sel} values were similar to the average range recorded previously for wild-caught animals in late summer (Rock et al., 2002). Although one female aborted an embryo following implantation, presumably as a stress response to the research procedures including capture, anaesthesia and transmitter implantation, reproductive condition in other recaptured females appeared to be unaffected by the research procedures.

Telemetry revealed that daytime T_b values for *H. maculatus* were highly variable, and extend the previously characterized extreme range of field body temperatures for the Macraes population to 7.5–31.7 °C. Previous measurements of spot T_b ranged from 8 to 29 °C, with averages of approximately 14–20 °C for different reproductive groups in the same season (Rock et al., 2002). Clear diurnal cycles were observed, with maximum T_b usually coinciding with the maximal microhabitat temperature (T_{top}). Coolest T_b values (5–14 °C) were recorded shortly before dawn, with the effects of thermal inertia of both gecko bodies and tors contributing to the slow cooling of T_b after sunset; body temperatures lower than T_{top} at night probably indicate surface foraging activity in the cooler open air. Considerable variation in diurnal T_b values was also revealed between days; on some days the majority of T_b values only reached 10–15 °C, with 30 °C recorded on the subsequent day. The marked elevation of T_b above T_{top} and the accelerated rates of increase in T_b relative to

T_{top} indicate that geckos were employing highly selective microhabitat choice. Temperature differences between the underside of surface rocks versus substrate rocks in microhabitats for other thigmothermic species have been shown to be about 5–8 °C, with differentials even approaching 20 °C (Kearney, 2001; Webb & Shine, 1998), and geckos make postural adjustments capitalizing on these warm microhabitat temperatures (Kearney, 2001; Rock et al., 2002). Further, at the pinnacle of the tor used in this study there were several thin rock slabs that may have had the potential to reach higher temperatures than T_{top} measured on the adjacent tor. Additional evidence for diurnal movements of *H. maculatus* within the tor system can be inferred from changes in radio signal strength during the day; we hypothesize that weakened or distorted transmitter signals were probably associated with movements of geckos deep under multiple layers of rock.

Temperature differentials between field T_b , T_{sel} and T_{top} indicate that all geckos were able to thermoregulate effectively, where weather conditions allowed. Indeed, this study provides evidence that *H. maculatus* is an efficient thermoregulator, employing “shuttling thigmothermy” to capitalise on a thermal environment that is highly stratified. Occasionally, common geckos at Macraes have been observed to bask at the mouths of crevices, absorbing direct solar radiation (G. Loh, pers. comm.; A. Cree, pers. obs.); our data support such a strategy. Previously assumed, as most geckos, to be an obligate nocturnal thigmotherm, *H. maculatus* may be better described as diurno-nocturnal, rather than fully nocturnal, and not exclusively thigmothermic. This study provides additional support for the view that reptiles are capable of significant thermoregulation even in environments of apparently poor thermal quality (e.g. Herczeg et al., 2003; Row & Blouin-Demers, 2006).

Sex and reproductive condition have been found to strongly influence field T_b and T_{sel} in *H. maculatus* (Rock et al., 2000, 2002). Although we were unable to detect a significant effect of reproductive condition on variation in T_b over time in this study, this may reflect the small sample sizes used (exacerbated by loss of data for one pregnant female that aborted). The data certainly suggested a trend for pregnant females in particular to maintain higher plateau (midday) T_b values with the highest positive differentials between T_b and T_{top} . Pregnant females (and their embryos) clearly experience and tolerate substantial variation in T_b that must have consequences for the speed of embryonic development (Cree et al., 2003; Rock & Cree, 2003). Even on cool days, relative differences in differentials between T_b and T_{top} suggested that pregnant females thermoregulate more carefully than males, which adopted a more passive thermoconforming approach. These results demonstrate that remote telemetry measurement of T_b remains a highly desirable method for investigating the effect of reproductive physiology on thermoregulation in *H. maculatus*. It would be particularly informative to investigate how the high index of thermoregulatory effectiveness seen in pregnant females in certain seasons (Rock et al., 2002) correlates with thermoregulatory movements within their microhabitat at variable times of day and in different

weather conditions. For example, determining if thermoregulatory strategy differs in late-pregnant females just before winter versus just after winter (i.e. immediately before parturition), or in early summer when pregnant females have the biggest differential in T_{sel} compared with other groups, would be particularly important for clarifying the influence of environmental temperature on the evolution of extended gestation (Rock, 2006). Answers to these questions, however, await further advances in temperature telemetry that minimize battery size and increase signal strength.

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