

Thermal constraints and the influence of reproduction on thermoregulation in a high-altitude gecko (*Quedenfeldtia trachyblepharus*)

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Abstract

Temperature plays a crucial role for ectotherm performance and thus for fitness. Terrestrial ectotherms, including reptiles, regulate their body temperature mainly by behavioural means. At high altitude, however, thermal constraints make precise thermoregulation costly. The cost–benefit model of lizard thermoregulation predicts that thermally challenging environments should favour the evolution of thermoconformity. Yet, several species maintain high and stable body temperatures even in cool environments. We studied the Atlas Day Gecko, *Quedenfeldtia trachyblepharus*, a cold-adapted lizard endemic to the High Atlas Mountains of Morocco. We quantified thermoregulation in gravid females, non-gravid adult females, and adult males during the active season. Geckos thermoregulated during their active season, and thermoregulated with more effectiveness early in the season than late in the season. In the laboratory, the preferred body temperature ranges of gravid females, non-gravid females, and males were not significantly different. In the field, however, gravid females had smaller deviations from the preferred body temperature and maintained higher body temperatures than males and non-gravid females. Our study suggests that cold-adapted reptiles adjust their thermoregulatory behaviour in response to thermal constraints and reproductive status.

Introduction

Terrestrial ectotherms typically use behavioural means to regulate their body temperature and thereby optimize performance (Huey & Kingsolver, 1989; Blouin-Demers, Weatherhead & McCracken, 2003). The ability to thermoregulate depends on ambient environmental conditions that fluctuate in time and space. Thus, environmental conditions have a strong impact on ectotherm life-history by influencing crucial behavioural and physiological processes such as energy acquisition and reproduction (Lourdais *et al.*, 2004; Blouin-Demers & Weatherhead, 2008; Angilletta, 2009). Adaptations to cold climates are especially important to consider because thermal constraints are supposedly very high at high latitude and at high altitude (Addo-Bediako, Chown & Gaston, 2002). Only a few terrestrial ectothermic vertebrates are capable of exploiting cold environments with low thermal quality (Blouin-Demers & Weatherhead, 2001; Herczeg *et al.*, 2003; Besson & Cree, 2010; Lourdais *et al.*, 2013).

Important variation exists in the thermoregulatory strategies of ectotherms, ranging from active and nearly perfect thermoregulation to thermoconformity. According to the cost–

benefit model of lizard thermoregulation (Huey & Slatkin, 1976), the extent of thermoregulation should depend on habitat thermal quality. Thermal quality is usually indexed by the mean deviations of operative environmental temperatures (T_e) from the preferred temperature range (T_{set}) of the species (d_e index; Hertz, Huey & Stevenson, 1993) while the extent of thermoregulation is usually indexed by comparing the deviations of the field body temperatures from T_{set} to the d_e (E index; Hertz *et al.*, 1993; d_e-d_b index; Blouin-Demers & Weatherhead, 2001). Intuitively, the cost–benefit model of thermoregulation predicts that ectotherms should actively thermoregulate when the associated fitness costs (e.g. loss of energy or time, exposure to predators, etc.) do not outweigh the fitness benefits (i.e. increased performance). Thermal conformity is thus expected in habitats with low thermal quality (Huey & Slatkin, 1976).

A growing body of evidence indicates that behavioural investment in thermoregulation can be more important in thermally challenging climates than in favourable climates (Blouin-Demers & Weatherhead, 2001; Blouin-Demers & Nadeau, 2005; Picard, Carrière & Blouin-Demers, 2011; Vickers, Manicom & Schwarzkopf, 2011; Lourdais *et al.*, 2013). The fitness

loss associated with thermoconformity may have been underestimated under challenging thermal conditions, and a rigorous evaluation of the costs and benefits of thermoregulation is necessary to further our understanding of the conditions that favour the evolution of careful thermoregulation in ectotherms. Reproduction, for instance, is highly sensitive to temperature. For reproductive females, accessing preferred body temperatures, even for a brief period, may be associated with significant fitness benefits, notably in terms of phenology (date of birth) which can be critical for offspring survival in cold climates, or in terms of reproductive output (Le Hénanff, Meylan & Lourdaï, 2013; Lourdaï *et al.*, 2013).

Lizards provide an opportunity to study thermoregulation in cold climates because several species have adapted to either high latitude or high altitude. The common lizard *Zootoca vivipara*, Lacertidae has an Euro Siberian distribution that reaches the polar circle (Gasc *et al.*, 1997). The cold adaptations of this viviparous species have attracted considerable interest (Gvozdík, 2002; Herczeg *et al.*, 2003). *Zootoca vivipara* continues to thermoregulate actively at high latitude because thermal conditions under cover are too cold and would not permit persistence (Herczeg *et al.*, 2003). Other examples of cold-adapted species exist in the lacertid genus *Iberolacerta* in the Pyrénées Mountains (Arribas & Galan, 2005; Aguado & Braña, 2014). Among Iguanidae, *Liolaemus* reaches the southernmost latitudes in Patagonia and up to 3000 m in the Andes of Northern Chile (Marquet *et al.*, 1989). Finally, the agamid *Phrynocephalus vlangalii* can reach 4500 m in the Qinghai Tibet Plateau (Wang *et al.*, 2014). Reproductive mode (i.e. the evolution of viviparity) and maternal basking strategies play a key role in the adaptation to cold climates (Shine, 1995; Lourdaï *et al.*, 2013; Wang *et al.*, 2014). Extended embryonic retention and improved maternal control of developmental temperature likely provide significant advantages over oviparity in cold climates (Arribas & Galan, 2005; Rodríguez-Díaz & Brana, 2012).

Geckos (infra order Gekkota) are a successful group of lizards (>1450 species) that occupy a diversity of habitats. While most geckos occupy tropical regions (Pianka & Pianka, 1976; Bauer, 2013), a few species are adapted to cold climates. This is the case of the Common Gecko *Hoplodactylus maculatus* in New Zealand and of the Bent-toed Geckos (genus *Cyrtodactylus*) from the Himalayas of Tibet. The genus *Quedenfeldtia* (Atlas Day Gecko) is endemic to the Atlas Mountains of Morocco. *Quedenfeldtia trachyblepharus* is a strictly diurnal species found above 1400 m in the High Atlas Mountains and reaching 4000 m in the Jbel bou Imbraz, the highest altitude of any reptile in Morocco (Bons & Geniez, 1996). While nocturnality is an ancestral and predominant trait in geckos (Vitt *et al.*, 2003; Gamble *et al.*, 2015), repeated transitions to diurnality have occurred (Gamble *et al.*, 2015) as in the genus *Quedenfeldtia*. *Quedenfeldtia trachyblepharus* therefore offers an opportunity to examine the impacts of thermal constraints associated with high altitude on thermoregulation.

We investigated patterns of thermoregulation in *Q. trachyblepharus* in a thermally challenging environment and we focused on the effects of seasonality and of reproduction. First, we determined thermal preference in a laboratory thermal

gradient. Then, we collected data on body temperatures of field active geckos while simultaneously recording environmental operative temperatures.

We used these data to address the following two hypotheses: (1) Because thermal constraints vary seasonally, the extent of thermoregulation should also vary. Specifically, we predicted that *Q. trachyblepharus* should thermoregulate more precisely in spring than in summer to minimize reduced performance associated with low body temperatures (Blouin-Demers & Nadeau, 2005). (2) Because the benefits associated with thermoregulation vary between gravid females, non-gravid females and males, the extent of thermoregulation should also vary by reproductive state. Specifically, we predicted that gravid females should prefer higher body temperatures and thermoregulate more precisely compared to males and non-gravid females (Blouin-Demers & Weatherhead, 2001).

Materials and methods

Study species and study site

The Atlas Day Gecko, *Q. trachyblepharus* (Boettger, 1874), is a small (approximately 4.4 cm snout–vent length, 3 g) high-altitude gecko endemic to the High Atlas Mountains of Morocco. Generally, it lives in open, rocky habitats, aggregating in rock crevices for shelter and nesting. *Quedenfeldtia trachyblepharus* is oviparous and females typically lay calcified eggs in rock crevices (Schleich, Kästle & Kabisch, 1996; A. Bouazza, pers. obs.). The Atlas Day Gecko is the dominant species in the alpine lizard assemblage above 2500 m (Bons & Geniez, 1996; Schleich *et al.*, 1996; Comas, Escoriza & Moreno-Rueda, 2014). The species is regularly observed basking close to rock crevices, often communally. A clear dimorphism in dorsal coloration and in head size exists (Blouin-Demers *et al.*, 2013), and it is therefore possible to identify gender by sight. Gravid females show an enlargement of the abdomen and of the calcium storing endolymphatic glands located at the base of the throat as described in other geckos (Bauer, 1989; Ineich & Gardner, 1989; Brown & O'Brien, 1993; Brown *et al.*, 1996).

We conducted this study from March to July 2012 and 2013 at Oukaïmeden (7°52'52"W, 31°12'32"N, altitude 2700 m). The study site (10 ha) is covered in fractured sandstone rocks. It is characterized by mountainous vegetation with plants of alpine and boreal origin (Alaoui Haroni, Alifriqui & Simonneaux, 2008). The climate is cold temperate, with precipitation around 500–600 mm per year. Mean temperatures range from 22°C in the warmest month to –4°C in the coldest month, with 82–139 days of frost per year (Alaoui Haroni *et al.*, 2008). Snowfall occurs mainly between November and March, and sometimes snow cover remains until the end of May.

Validation of body temperature measurements

Skin surface temperature (T_{sk}) gives an accurate estimate of cloacal temperature (T_b) in small lizards (Herczeg *et al.*, 2006; Hare, Whitworth & Cree, 2007; Carretero, 2012). This

non-invasive technique minimizes disturbance to animals and avoids handling stress. The use of T_{sk} is particularly suited to the Atlas Day Gecko which is an inquisitive species, allowing researchers to get very close (<50 cm) without inducing a flight response. We validated the use of T_{sk} in the field on 50 individuals in spring 2011 by comparing measurements of cloacal temperature made with a rapid-reading mercury thermometer (Schulteis T6100, Schulteis, NY, USA) to those of skin temperature (T_{sk}) made with a high-resolution infrared thermometer (Fluke 572, Raytek Corporation, Santa Cruz, CA, USA, accuracy $\pm 0.75^\circ\text{C}$). To measure T_{sk} , we used the procedure described in Andrews (2008) and followed the recommendations from Hare *et al.* (2007): emissivity set at 0.95 and the thermometer was oriented in-line with the body axis. When an individual was located, T_{sk} was measured from approximately 30–50 cm aiming at the abdomen or dorsum. The individual was then immediately captured by noosing and cloacal temperature was measured within 15 s after capture by inserting the thermocouple 5 mm in the cloaca. Skin and cloacal temperatures were highly correlated ($r^2 = 0.92$, $P < 0.001$, $T_{sk} = -0.22 + 1.08 \times T_b$).

Thermal preference

We measured T_{set} in adult males ($n = 13$, mass = 2.2–3.1 g), non-gravid adult females ($n = 13$, mass = 1.8–2.2 g), and gravid females ($n = 13$, mass = 2.1–2.6 g) during May and June 2013. Individuals were captured in the field and brought to a nearby indoor location (Chalet du Club Alpin Français à l'Oukaïmeden). T_{set} was measured in a thermal gradient (100 × 30 × 30 cm, length × width × height) made with opaque PVC to avoid any visual disturbance. The gradient was placed in a controlled temperature room at 17–20°C. A light bulb (60 W) at one end of the thermal gradient generated a smooth temperature gradient ranging from 20 to 45°C. The substrate in the gradient was sand, rocks were provided as shelter, and metal mesh allowed geckos to bask under the light bulb. Geckos were placed individually in the gradient one hour before the first measurement to minimize possible stress from handling and to allow exploration of the new environment. Hourly measurements of T_{sk} were made between 08:00 and 18:00 h reflecting the daily activity period of the species in the field. Geckos were returned to their sites of capture after the experiment. For each individual, we calculated the mean T_b in the gradient and T_{set} as the 75 and 25% quartiles of the T_b distribution (Hertz *et al.*, 1993).

Skin temperature sampling in the field

We collected T_{sk} during 15 days in 2012 and during 17 days in 2013, spread over the activity period between March and July. T_{sk} was collected under diverse weather conditions between 08:00 and 17:00 h. Each day of T_{sk} data collection, the study site was patrolled for 6 to 9 h by the same person (AB). Air temperature (T_{air}) and wind speed (maximum and minimum) at the beginning and at the end of the session were measured using a thermometer-anemometer (LM-8000, Reed, Toronto, Canada). When an adult gecko was located, it was

approached within 30–50 cm and T_{sk} was measured, on the abdomen or dorsum, as indicated above. We also noted the sex of the individual, and if female its reproductive status. We recorded three values of substrate temperatures (T_{rock}) randomly chosen around the animal (<50 cm), the time of day, and cloud cover at the time of measurement (cloudy vs. sunny). In total, we recorded 1338 T_{sk} from lizards (588 from males, 429 from gravid females, and 321 from non-gravid females).

Operative environmental temperatures

We used 16 iButton dataloggers (DS1922L, Maxim Integrated, San José, CA, USA) to describe the thermal environment available to geckos. Each iButton was covered with epoxy resin, attached to a rock, and painted to approximate the colour and reflectance of *Quedenfeldtia* (Tracy, 1982; Bakken, 1992; Walsberg & Wolf, 1996). iButtons did not reproduce the exact size and shape of Atlas Day Geckos, but studies have demonstrated that model shape, size, and colour have minor effects on T_e (<1°C on mean T_e ; Vitt & Sartorius, 1999; Shine & Kearney, 2001). We deployed the 16 iButtons from March to August 2012 and 2013 in various microhabitats with different sun and wind exposures to capture the spatial heterogeneity in T_e and programmed them to collect T_e every 20 min. To assess thermal constraints, we calculated for each day the time (in minutes) during which it was possible to have a T_{sk} above the lower bound of T_{set} based on our T_e measurements.

Indices of thermoregulation

We used skin temperature (T_{sk}) as a proxy for T_b . We used the indices proposed by Hertz *et al.* (1993) and calculated the accuracy of body temperature (d_b ; mean absolute deviation of T_b from T_{set}) and the thermal quality of the environment (d_e ; mean absolute deviation of T_e from T_{set}). Because our T_{sk} sampling was sporadic, we calculated our indices by matching each of the 1338 T_{sk} collected with the T_e values for the closest time point (at most 10 min apart). Finally, the effectiveness of thermoregulation was calculated as $d_e - d_b$ (Blouin-Demers & Weatherhead, 2001).

Statistical analyses

All statistical analyses were performed in R (R Development Core Team, 2013). First, we compared thermal preferences between groups using a one-way ANOVA. We examined variation in monthly T_e and time available above T_{set} using a mixed model (lme models, nlme package) treating month and time of day as fixed factors and day as a random factor. We also examined variation in hourly body temperature considering month and time of day as fixed factors. We examined the determinants of T_b variation using regression between T_b and several predictors (T_{air} , T_e and T_{rock}). Finally, we examined the influence of reproductive status and month (fixed factors) on daily mean T_b , d_b and $d_e - d_b$ using a GLM treating month as a fixed factor and day as a random factor. We report all means \pm SE and we considered tests significant at $\alpha < 0.05$.

Results

Thermal preference

Thermal preference did not vary between reproductive groups. We found no significant differences between males, non-gravid females, and gravid females for all variables tested (mean T_b , $F_{2,36} = 0.46$, $P = 0.63$; 75% quartile, $F_{2,36} = 1.99$, $P = 0.15$; 25% quartile, $F_{2,36} = 0.29$, $P = 0.74$). Mean T_b selected in the thermal gradient, across all individuals, was $30.7 \pm 0.6^\circ\text{C}$ and the mean 75 and 25% quartiles were $31.7 \pm 0.9^\circ\text{C}$ and $29.8 \pm 0.7^\circ\text{C}$, respectively.

Operative environmental temperatures and thermal quality

When considering only data collected during the activity hours (8:00 to 18:00 h), we found variation in T_e between months ($F_{15,17743} = 706.11$, $P < 0.0001$, Fig. 1a). Importantly, mean T_e never reached the lower bound of T_{set} in any month. When considering the daily amount of time during which it was possible to reach the lower bound of T_{set} , we also found important variation between months ($F_{5,145} = 21.72$, $P < 0.0001$) with

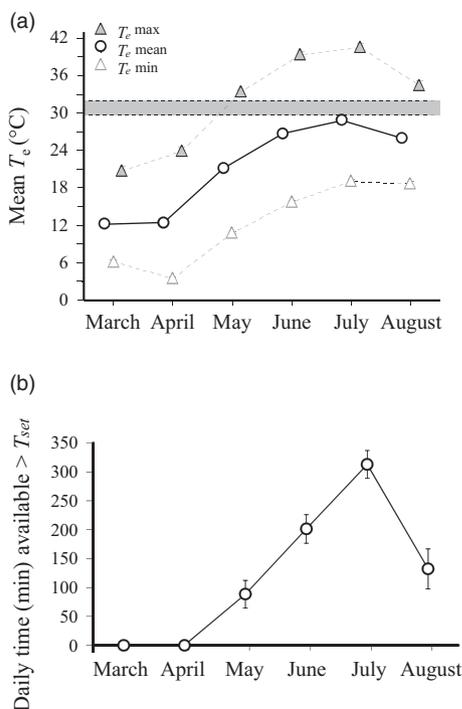


Figure 1 (a) Monthly variation in daily (08:00–18:00 h) mean operative environmental temperatures (T_e) recorded at Oukaimeden, High Atlas Mountains of Morocco and (b) monthly variation in the mean amount of daily time (min \pm SE) when it is possible for *Quedenfeldtia trachyblepharus* to reach the lower bound of its preferred body temperature range. The horizontal grey band represents the range of preferred body temperatures in a laboratory thermal gradient.

very limited time to reach T_{set} in March and in April (Fig. 1b).

Variation in body temperature

Body temperature was strongly influenced by month ($F_{4,1327} = 96.92$, $P < 0.0001$) and by time of day ($F_{8,1323} = 12.18$, $P < 0.0001$) with a significant interaction between the two terms ($F_{28,1291} = 4.96$, $P < 0.0001$) reflecting the variable effect of time of day on T_b between months (Fig. 2). T_b values were significantly higher in June and July ($31.3 \pm 0.2^\circ\text{C}$, $31.4 \pm 0.2^\circ\text{C}$ respectively) than in March, April and May ($28.1 \pm 0.2^\circ\text{C}$, $26.7 \pm 0.2^\circ\text{C}$, $28.3 \pm 0.1^\circ\text{C}$ respectively).

Hourly patterns of T_b revealed that geckos rarely reached T_{set} from March to May. In contrast, geckos spent most of the day with T_b within T_{set} in June and July (Fig. 2). Body temperatures were correlated with mean T_e ($r = 0.50$, $P < 0.0001$) and with T_{air} ($r = 0.52$, $P < 0.0001$), but most correlated with T_{rock} ($r = 0.79$, $P < 0.0001$).

Gravid females were detected only between March and June. When restricting the analysis to this period, we found a significant influence of reproductive status on mean T_b ($F_{2,1145} = 12.37$, $P < 0.0001$) as well as a significant effect of month and of their interaction ($F_{6,1145} = 2.23$, $P = 0.038$). Gravid females maintained higher T_b ($29.2 \pm 0.2^\circ\text{C}$) than males ($28.4 \pm 0.2^\circ\text{C}$) and non-gravid females ($27.8 \pm 0.3^\circ\text{C}$), but the difference between the reproductive classes was most marked in April and May ($F_{2,900} = 14.20$, $P < 0.0001$; Fig. 3a) when the thermal quality of the habitat was lower (mean $d_e = 12.6 \pm 0.2^\circ\text{C}$). No significant difference in T_b was detected between males and non-gravid females throughout the season ($F_{4,901} = 2.29$, $P = 0.06$).

We found that mean d_b varied significantly between months ($F_{3,1145} = 41.38$, $P < 0.0001$) and with reproductive status ($F_{2,1145} = 8.42$, $P < 0.001$, Fig. 3b). The interaction between the two terms was not significant ($F_{6,1145} = 1.79$, $P = 0.09$). Mean d_b was high in March ($3.3 \pm 0.2^\circ\text{C}$), April ($3.0 \pm 0.1^\circ\text{C}$) and May ($2.3 \pm 0.1^\circ\text{C}$), but decreased markedly in June ($0.8 \pm 0.2^\circ\text{C}$) and in July ($0.7 \pm 0.2^\circ\text{C}$). Reproductive females had lower mean d_b than males and non-gravid females in April ($F_{2,298} = 8.24$, $P = 0.0003$) and in May ($F_{2,373} = 6.71$, $P = 0.001$). No difference in d_b was detected between males and non-gravid females throughout the season ($F_{4,901} = 0.68$, $P = 0.60$).

We obtained similar results when considering the effectiveness of thermoregulation ($d_e - d_b$). Thermoregulatory effectiveness peaked early in the activity season and decreased progressively ($F_{4,1333} = 285.83$, $P < 0.0001$, Table 1). Gravid females tended to have higher thermoregulation effectiveness than males and non-gravid females in April and in May (Table 1).

Discussion

Cold climates are particularly challenging for ectothermic animals because thermal conditions constrain physiological performance and activity (Gvozdík, 2002; Lourdais *et al.*, 2013). Only a few specialized species can exploit high latitude or

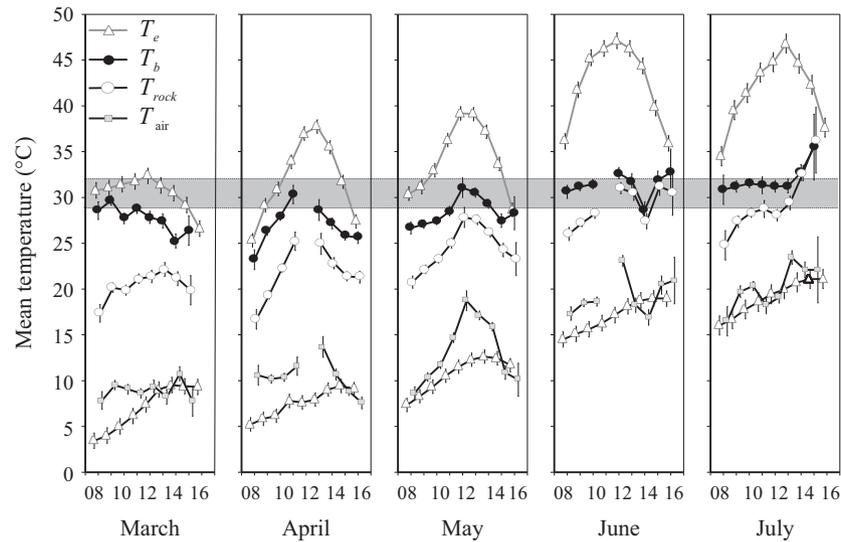


Figure 2 Monthly variation in hourly mean environmental temperatures (T_e , minimum and maximum), rock temperature (T_{rock}), air temperature (T_{air}), and body temperature (T_b) of *Quedenfeldtia trachyblepharus* at Oukaïmeden, High Atlas Mountains of Morocco. The horizontal grey band represents the range of preferred body temperatures in a laboratory thermal gradient.

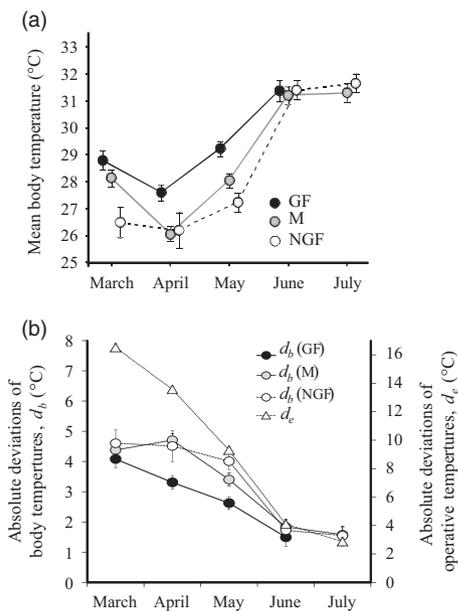


Figure 3 (a) Monthly variation in daily (08:00–18:00 h) mean body temperature ($T_b \pm 1$ se) of gravid females (GF, black circle), non-gravid females (NGF, grey circle), and males (M, open circle) and (b) monthly variation in daily (08:00–18:00 h) mean d_e (triangle) and mean d_b of gravid female (GF, black circle), non-gravid female (NGF, open circle) and male (M, grey circle) *Quedenfeldtia trachyblepharus* at Oukaïmeden, High Atlas Mountains of Morocco.

high altitude habitats. The Atlas Day Gecko, *Q. trachyblepharus*, is the only Mediterranean gecko specialized in high mountain habitats and is the dominant species above 2500 m in the High Atlas (Bons & Geniez, 1996; Schleich *et al.*,

1996; Comas *et al.*, 2014). In this study, we demonstrated that *Q. trachyblepharus* has narrow thermal preferences similar to those found in other geckos from warmer climates (Huey & Kingsolver, 1989; Angilletta, Montgomery & Werner, 1999). Therefore, living at high altitude does not seem associated with a lowered thermal preference.

Our data on operative environmental temperature demonstrated that access to T_{set} is constrained, notably early in the activity season (March–April). Thermal conditions improved during late spring and summer when solar radiation was more intense. Accordingly, our data on body temperature indicated that time spent within T_{set} was limited early in the activity season and that more time was spent within T_{set} as the season progressed. The field body temperatures of geckos were usually below T_{set} , reflecting thermal constraints. In agreement with our first prediction, thermoregulatory effectiveness ($d_e - d_b$) was higher early in the season. We found a close correlation between ambient thermal conditions and body temperature. Notably, T_b was more closely related to the temperature of the substrate (i.e. rocks) than to operative temperature or to air temperature. Well exposed rocks accumulate heat quickly and therefore provide a major thermal advantage (mean difference with air temperature = 10.6°C; mean difference with T_e = 2.8°C). Our field observations indicated that geckos engage in prolonged periods of thermoregulation, even under cool conditions (T_{air} = 4°C), by maintaining a close ventral contact with the rock surface.

No differences in thermal preference were detected between reproductive groups in the thermal gradient. In the field, however, gravid females minimized deviations from T_{set} and maintained higher body temperatures than males and non-gravid females, in agreement with our second prediction. Several proximate mechanisms could be invoked to explain more effective thermoregulation in gravid females. First, gravid

Table 1 Effectiveness of thermoregulation (calculated as $d_e - d_b$) in gravid female, non-gravid female and male *Quequenfeldtia trachyblepharus* at Oukaïmeden, High Atlas Mountains of Morocco. Different letters represent significant differences between groups

Month	Effectiveness			Post hoc tests				
	Mean effectiveness	Males	Non-gravid females	Gravid females	Statistical test: effect of status	Males	Non-gravid females	Gravid females
March	12.5 ± 0.3	12.2 ± 0.4	13.4 ± 1	11.8 ± 0.5	$F_{2,229} = 0.92, P = 0.39$	a	a	a
April	9.4 ± 0.3	9.2 ± 0.3	9.0 ± 0.8	10.3 ± 0.3	$F_{2,298} = 2.75, P = 0.06$	ab	b	a
May	6.0 ± 0.2	6.8 ± 0.3	5.9 ± 0.4	7.8 ± 0.3	$F_{2,373} = 2.49, P = 0.08$	a	b	a
June	2.4 ± 0.3	2.3 ± 0.4	2.4 ± 0.5	2.3 ± 0.5	$F_{2,245} = 0.08, P = 0.91$	a	a	a
July	2.1 ± 0.3	2.1 ± 0.5	2.2 ± 0.5	–	$t_{179} = 0.24, P = 0.80$	a	a	–

females appear to bask longer and seem less responsive to disturbance (A. Bouazza & O. Lourdais, pers. obs.). Gravid female vipers also spend more time basking and spend less time under shelter after a simulated attack (Lorioux, Lisse & Lourdais, 2013). Second, many lizards modify their skin colour while basking to increase absorption of short wave radiation (Pearson, 1977; Sherbrooke, Castrucci & Hadley, 1994). Marked colour changes occur in *Q. trachyblepharus* with darker coloration often observed when air temperature is cold. It is possible that gravid females experience more marked colour changes than males and non-gravid females, and this aspect deserves further inquiry. Higher investment in thermoregulation during reproduction is a widespread phenomenon in ectotherms, notably to optimize embryonic developmental conditions (Shine, 1995; Lourdais *et al.*, 2013). However, maternal control on embryonic life is limited in oviparous geckos because egg laying occurs shortly after ovulation (Bauer, 2013). Nevertheless, oviparous geckos accumulate massive amounts of calcium in specialized endolymphatic glands to produce thick shelled eggs (Bauer, 1989). Calcium metabolism involves vitamin D production and is known to influence thermoregulation and basking time (Ferguson *et al.*, 2003; Kroenlein *et al.*, 2011). This process may explain the modified thermoregulatory behaviour of gravid females; gravid females could be attempting to optimize calcium mobilization required for egg shelling and thereby accelerate egg formation. Our criteria for identifying gravid females were enlarged calcium glands or enlarged abdomen. Therefore, we cannot distinguish between the effects of more calcium mobilization and of vitellogenesis, two processes that may influence thermal physiology and increase thermoregulatory effort. Males also exhibited high body temperatures in March, which is possibly linked to the thermal requirements of spermatogenesis (Joly & Saint-Girons, 1975; Joly & Saint-Girons, 1981).

Under cold climates, reproductive success is strongly dependent upon the date of birth because of a short activity season and, consequently, a reduced temporal window for reproduction. Maternal effects on phenology are thus critical (Wapstra *et al.*, 2010; Le Hénanff *et al.*, 2013) because early oviposition improves offspring survival and growth before the first winter (Olsson & Shine, 1997). Early oviposition can also be beneficial to the mother by enhancing her ability to recoup energy or to lay additional clutches (Le Hénanff, 2011). Gravid females maintained higher body temperatures and minimized deviation from T_{set} in the field. More efficient thermoregulation by gravid females may allow their offspring to hatch early. More generally, modified thermoregulation, particularly during reproduction, may be a key aspect allowing terrestrial ectotherms to exploit cold climates (Lourdais *et al.*, 2013; Wang *et al.*, 2014). Empirical evidence supports the notion that active thermoregulation is prevalent in habitats with low thermal quality (Blouin-Demers & Nadeau, 2005). For example, in the common lizard *Z. vivipara*, a boreal species, active thermoregulation is the only available option to achieve T_{set} (Gvozdík, 2002). Importantly, the actual 'costs' of thermoregulation (e.g. in terms of energy or of survival) depend on multiple components including the spatial and temporal heterogeneity in thermal conditions. That is, even if thermal quality is on average

low, specific microhabitats such as those with high exposure to solar radiation may still provide significant thermal benefits and allow thermoregulation.

Geckos constitute a very successful group of lizards that has attracted considerable scientific attention (Bauer, 2013; Gamble *et al.*, 2015). While most geckos are nocturnal and occupy warm climates, adaptation to low temperature seems important, for example to allow foraging at night (Huey *et al.*, 1989; Gamble *et al.*, 2015). Only a few diurnal gecko species living under cold climates have been studied (Hare *et al.*, 2010). Our study on the Atlas Day Gecko clearly indicates that active thermoregulation is required to maintain T_b close to T_{set} . Interesting behaviours potentially linked to cold-climate living, such as aggregation at basking sites and communal nesting, have been reported in this species (Schleich *et al.*, 1996) and await further investigation.

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