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Lizards in the slow lane: Thermal biology of chameleons

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Abstract

1. Field body temperatures (T_b's) of *Chamaeleo chamaeleon* in southwestern Spain averaged 28 °C in October and 30 °C in June. Slopes of regressions of T_b on T_a (ambient temperature at perch height) indicated that individuals were able to maintain a preferred body temperature of about 30 °C in June but not in October.
2. Review of data from the literature indicated that chameleons in general have field body temperatures and selected body temperatures (means 30 and 31 °C, respectively) that are low relative to those of most other diurnal lizards.

Keywords: *Chamaeleo chamaeleon*; Chamaeleonidae; Field body temperature; Selected body temperature; Thermal biology; Thermoregulation

1. Introduction

Body temperatures of lizards measured during normal activity in the field (T_b) exhibit a strong phylogenetic signal at the generic level, and even at higher taxonomic levels (Avery, 1982; van Berkum, 1988; Huey et al., 1989; Andrews, 1998). These patterns emerge despite variation in T_b that results from the constraints and opportunities provided by particular habitats, weather patterns, interspecific interactions, etc. (Huey and Slatkin, 1976; Downes and Shine, 1998; Rock et al., 2002). Nonetheless, phylogenetic patterns can be sharpened with a metric that disentangles body temperature from environmental influences. T_{sel}, the body temperature selected by lizards on laboratory thermal gradients, provides information on actual thermal 'preference' (Huey et al., 1989; Andrews, 1998; Hertz et al., 1993).

The above characterization of the thermal biology of lizards is based largely on data from a subset of lizard diversity, re *Anolis*, *Sceloporus*, macroteiids, skinks, and geckos. Are these characterizations applicable to other lizard groups? Chameleons comprise a relatively large (about 130 species) group of highly specialized arboreal predators (Necas, 1999; Pough et al., 2004). The family is characterized by prey capture by ballistic tongue projection, zygodactylus grasping feet, prehensile tails, slow deliberate movements, and reliance on crypsis for predator avoidance (Wainwright and Bennett, 1992; Cuadrado et al., 2001; Butler, 2005). An *a priori* expectation from their homogeneous 'slow-lane' lifestyle and energy-conservative behavior is that the family would be characterized by relatively low T_b's.

This study had two major objectives. The first was to add to the very limited set of information available on the thermal biology of chameleons. In accord, I measured T_b's of *Chamaeleo chamaeleon* in Spain. *C. chamaeleon* is widely distributed in northern Africa with isolated populations in Spain and Portugal and on a number of Mediterranean islands (Pleguezuelos et al., 1999). In Spain, the species is restricted to small patches of native Mediterranean scrub along the southwestern coast (Mellado et al., 2001). The second objective was to summarize available information on the thermal biology of the Chamaeleonidae and to compare this information with that of other diurnal lizards.

2. Materials and methods

I made observations on the thermal biology of *C. chamaeleon* in and around the Jardin Botánico at Rota and at the Centro Recuperación Especies Amenazadas facility at El Puerto de Santa María, Cádiz Province,

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Spain, during 25–27 October 2005 and on 14 June 2006. Measurements of T_b were made between 1000 and 1400 h. The weather was sunny with scattered clouds (2 days in October and in June) or hazy (1 day in October). In general, October is relatively cool and June is relatively warm; mean maximum temperatures at El Puerto de Santa María for these months for 2001–2006 were 24.7 and 29.3 °C, respectively. Individuals ranged in size from 50 to 123 mm snout–vent length (4–37 g), although most individuals were adults (SVLs >85 mm).

Body temperatures of chameleons were measured within a few seconds of capture. In June, T_b's ($n = 16$) were measured with an Omega thermocouple thermometer (Model HH21) inserted 1–2 cm into the cloaca. In October, temperatures of 22 individuals were measured using an infrared (IR) thermometer (Raytek Raynger ST60). Readings were taken at the center of the trunk region on the right and left flanks (Hare et al., 2007). Cloacal temperatures of seven of these individuals were also measured using a Schultheis quick-reading thermometer immediately after recording IR temperatures. To determine the association between cloacal temperature and IR temperature, T_b (cloacal) was used as the dependent variable and the lower, higher, and mean of the two IR temperatures were used as independent variables in regression analyses. The higher of the two IR temperatures provided the best predictor of T_b ($T_b = 0.44 + 0.96$ IR, $F_{1,5} = 40.0$, $P = 0.0015$, $R^2 = 0.89$). Equations for all three IR temperatures predicted T_b's accurately at the high end of the observed T_b range. At an IR value of 31 °C, for example, the models predicted T_b's of 30.5–31.5 °C. At the low end of the observed T_b range, however, the model using the higher of the two IR temperatures performed far better than the other models. At an IR value of 25 °C, for example, the former model predicted a T_b of 25.4 °C and the mean IR and the lower of the two IR temperature models underestimated T_b by 1.1 and 2.9 °C, respectively. The higher of the IR values was accordingly used as a surrogate for T_b for the 15 individuals for whom T_b was not measured directly. Shaded air temperatures (T_a) at 1 cm above the perch site were measured with the Omega thermocouple thermometer. The Omega and Schultheis thermometers were calibrated against a NIST-certified thermometer in the laboratory. Data on long-term (2001–2006) ambient temperatures were obtained for the Estación Meteorológica de Puerto de Santa María posted on the web site of the Instituto Andaluz de Investigación y Formación Agraria y Pesquera.

Additional observations on the thermal biology of chameleons were found from web-based and standard literature searches. The data were screened for quality and consistency (e.g. presentation of original data, adequate sample size, data presented for adults, or at least, relatively large individuals in a population, observations of T_b made during the normal daytime activity period). When observations of T_b's were reported for different seasons, I used data for the season when the opportunities for thermoregulation were the greatest. Coastal locations were arbitrarily assigned an elevation of 20 m if elevation was not given in the paper. T_{sel}'s were from studies on individuals in laboratory thermal gradients or in outdoor cages provided with areas of full sun and heavy shade. Ambient temperature gradients in both situations provided chameleons the potential to achieve T_b's well above and below actual selected body temperatures.

Parametric analyses were conducted using SAS software (SAS Institute, 1996). Probability values of less than 0.05 were considered significant. The assumption of homogeneity of slopes for ANCOVAs was satisfied by testing for significance of the interaction of the covariate with treatment variables.

3. Results and discussion

3.1. Observations on C. chamaeleon

Chameleons were typically perched in the sun or in partial shade at 30–50 cm (range 0–200 cm) above the ground. *Retama monosperma* was the most commonly used perch site; this was the most common shrub on the study areas, although chameleons were occasionally found on other shrubby vegetation. Thermoregulatory behavior of chameleons consisted of movements between the exposed branches on the sides and tops of shrubs and their relatively shaded centers. Thirty-five of the 38 chameleons observed were females.

Overall, T_b's of chameleons averaged 28.8 °C ($n = 38$, range 24.0–32.3 °C). T_b was related to T_a (Fig. 1) as $T_b = 13.0 + 0.62T_a$ ($F_{1,36} = 30.5$, $P < 0.0001$, $R^2 = 0.46$). The slope ($b = 0.62$) differed from 1.0 ($t = 3.3$, $p < 0.01$, Sokal and Rohlf, 1981).

Seasonal differences were pronounced. T_b's were lower during October than during June ($F_{1,36} = 9.7$, $P = 0.004$, one-factor ANOVA) in accord with lower T_a's. Respective

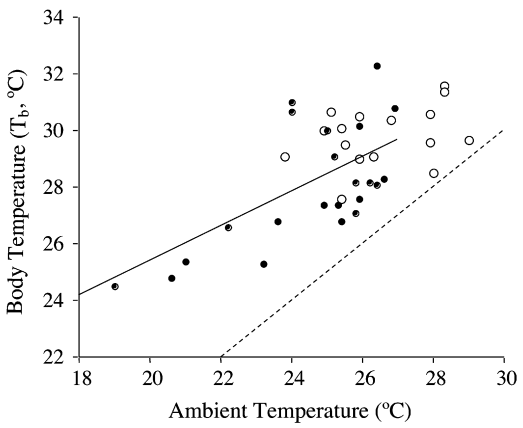

Fig. 1. Body temperature (T_b) as a function of ambient temperature (T_a) for *Chamaeleon chamaeleon* ($n = 38$). Data collected in October are indicated by solid circles and data collected in June by open circles. The dashed line represents isothermy and the solid line is the overall regression between T_b and T_a.

mean T_b's for October and June were 28.0 °C (range 24.5–32.3 °C) and 29.8 °C (range 27.6–31.6 °C) and respective mean T_a's were 24.5 and 26.5 °C. During October when T_a was relatively low, T_b was positively correlated with T_a ($r = 0.66$, $P = 0.001$, $n = 22$). In contrast, during June when T_a was relatively high, T_b was independent of T_a ($r = 0.33$, $P = 0.22$, $n = 16$). Nonetheless, after accounting for T_a, T_b's in October and June did not differ ($F_{1,35} = 1.7$, $P = 0.19$, one-factor ANCOVA with T_a as the covariate).

Individual *C. chamaeleon* were active thermoregulators. Overall, the slope of the regression between T_b and T_a was less than 1; T_b's were relatively high when T_a was the lowest and relatively low when T_a was the highest. Moreover, the lower, higher, and mean of the two IR temperatures were very similar to observed T_b's when T_b's were relatively high (31 °C), but only the higher of the IR temperatures was similar to T_b when T_b was low (25 °C). These observations suggest that at low ambient temperatures chameleons were oriented perpendicular to the sun such that the shaded flank would have a lower IR than the insolated flank, but that when ambient temperature was high, chameleons were not directly exposed to the sun and as a consequence their IR and (cloacal) T_b's were similar.

The 'preferred' T_b of *C. chamaeleon* was about 30 °C, the mean T_b observed in June. This conclusion is based on the observations that: (1) maximum observed T_b's were the same in October and June, that is, 32 °C, (2) T_b was not correlated with T_a in June; the independence of T_b relative to T_a indicates active thermoregulation, and (3) T_b's observed in June were exhibited during the time of year with the greatest potential for raising T_b's to preferred levels; long-term maximum ambient temperatures for June, July, and August averaged 29.3, 30.5, and 30.0 °C, respectively.

3.2. Selected and field body temperatures of chameleons

I found information on T_{sel} or T_b or both for 17 populations and 12 species of chameleons (Table 1). With the exception of *Furcifer pardalis* from Madagascar, all species were African. The overall mean T_{sel} was 30.9 °C with a range of 25.0–33.4 °C. Mean T_b was 29.7 °C with a range of 22.2–32.5 °C. While mean T_{sel} and T_b were similar, the range of T_{sel}'s was less than the range of T_b's. T_{sel} and T_b were not correlated ($r = 0.04$, $P = 0.91$, $n = 10$). T_b was not related to latitude ($r = 0.19$, $P = 0.54$, $n = 13$) but was negatively correlated with elevation ($r = -0.58$, $P = 0.04$, $n = 13$). Inspection of the data (Fig. 2) indicated that individuals were able to maintain T_b's of about 31 °C up to about 2000 m; at higher elevations T_b's declined below preferred levels.

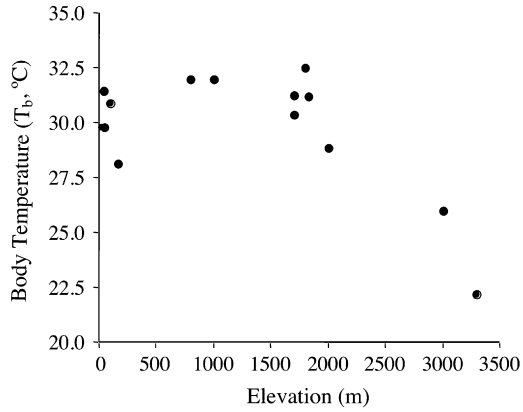

Fig. 2. Field body temperatures (T_b) of chameleons as a function of elevation. Data are from Table 1.

Table 1
Mean field and selected body temperatures (°C) of chameleons

Species	Selected T_{sel}'s	Field T_b's	Elevation (m)	Latitude	Source
BRpu	25.0	28.1	140	34°S	Burrage (1973)
CHaf	31.0	–	20	37°N	Dimaki et al. (2000)
CHbi	31.1	28.9	2000	2°S	Bennett (2004)
CHca	32.9	–	40	17°N	Zari (1993)
CHca	30.4	–	–	–	Andrews, unpublished
CHch	–	29.8	20	37°N	This study
CHch	31.6	–	20	38°N	Dimaki et al. (2000)
CHdi	–	31.2	1830	26°S	Stebbins (1961)
CHdi	32.8	32.0	800	2°S	Bennett (2004)
CHel	33.4	32.5	1800	0°N	Bennett (2004)
CHho	–	26.0	>3000	1°S	Hebrard et al. (1982)
CHho	30.2	31.3	1700	2°S	Bennett (2004)
CHja	32.1	30.4	1700	2°S	Bennett (2004)
CHna	29.3	32.0	1000	23°S	Burrage (1973) (inland)
CHna	29.3	30.9	100	23°S	Burrage (1973) (coastal)
CHsc	32.6	22.2	3300	0°S	Bennett (2004)
FUpa	31.0	31.3	20	15°S	Ferguson et al. (2004)

BRpu: *Bradypodion pumilum*; CHaf: *Chamaeleo africanus*; CHbi: *Chamaeleo bitaeniatus*; CHca: *Chamaeleo calyptratus*; CHch: *Chamaeleo chamaeleon*; CHdi: *Chamaeleo dilepis*; CHel: *Chamaeleo ellioti*; CHho: *Chamaeleo hohnelii*; CHja: *Chamaeleo jacksonii*; CHna: *Chamaeleo namaquensis*; CHsc: *Chamaeleo schubotzi*; FUpa: *Furcifer pardalis*.

Chameleons exhibit relatively low T_b's for diurnal lizards. For example, T_b's of species from low to moderate elevations (<1700 m) averaged 31 °C with a range of only 28.1–32.0 °C (Table 1). In contrast, diurnal lizard species of open-habitats at low to moderate elevations exhibit mean T_b's of 34–40 °C (Huey et al., 1989; Andrews, 1998; Belliure et al., 1996). This difference does not reflect habitat *per se* because chameleons also exhibt low T_b's relative to sympatric diurnal lizards (*Psammodromus*: Belliure et al., 1996; *Mabuya*: Hebrard et al., 1982). Despite relatively low T_b's, however, chameleons are not thermoconformers or thermally passive (Bennett, 2004). The similarity of T_b and T_{sel} indicates that chameleons actively maintain body temperatures about 30 °C when ambient conditions permit. At very high elevations, chameleons and other lizards are seldom able to achieve 'preferred' temperatures because of low ambient temperature and pervasive cloud cover (Hebrard et al., 1982; Andrews, 1998; Bennett, 2004). Nonetheless, a T_{sel} of about 30 °C is typical. For example, when *Chamaeleo schubotzi* individuals were transplanted from 3300 to 1700 m, T_b's increased from 22 °C (Bennett, 2004) to over 30 °C (Angilletta et al., 2006).

Relatively low body temperatures thus appear to be part of a suite of coadapted characters of chameleons. Chameleons rely on camouflage for predator avoidance (Cuadrado et al., 2001). They are 'cruising' predators that move slowly, but relatively frequently (Butler, 2005). Locomotion speed is limited by the physiology, biochemistry, and morphology of muscles (Guppy and Davison, 1982; Abu-Ghalyun et al., 1988). Prey capture occurs at a distance by tongue projection once cautious movement has brought the chameleon within striking distance. Chameleons feed frequently and most prey items, including spiders, heteroptera, and flying insects such as diptera and hymenoptera, are small (Pleguezuelos et al., 1999; Hofer et al., 2003). Chameleons, however, do not share the reduced standard metabolism that characterizes reclusive predators such as gekkonids and xantusiids (Andrews and Pough, 1985). Standard (fasting, during normal period of inactivity) metabolic rates of *Chamaeleo calyptratus* are similar to those of other day-active lizards (data in Zari (1993) were compared with predictive equations of Andrews and Pough, 1985). Nonetheless, field metabolic rates of chameleons are likely to be lower than those of other day-active lizards because of the combination of slow locomotion and relatively low T_b's. T_b's are often substantially lower than T_{sel} because individuals are active at times of day and seasons when they are unable to thermoregulate carefully. A *Chamaeleo hohnelii*, for example, projected its tongue and captured a prey item when its T_b was 7 °C (Hebrard et al., 1982) and *Chamaeleo jacksonii* individuals fed and moved about at T_b's of 10 °C (Bennett, 2004). *C. chamaeleon* individuals are active year round despite low winter temperatures (Mellado et al., 2001); the lowest temperatures at my study sites are in January and February, with mean monthly minimum and maximum ambient temperatures of 5 and 16 °C. Similarly, *Bradypodion pumilum* are active at a wide range of T_b's as a result of diel and seasonal changes in weather (Burrage, 1973).

While members of the family Chamaeleonidae may share most, if not all, features of a slow-lane lifestyle, information on their thermal biology is limited to the genera *Chamaeleo*, Furcifer, and *Bradypodion*. Because their geographic ranges include the diversity of habitats occupied by the entire family, it is unlikely that the thermal biology of these genera reflects thermal specialization based on habitat. Nonetheless, generalizations provided here should only tentatively be extended to the family as a whole.

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