Thermoregulation in African chameleons

Albert F. Bennett*

Department of Ecology and Evolutionary Biology, University of California, Irvine

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Abstract. Field active and laboratory preferred body temperatures and critical thermal limits were measured in six species of Kenyan chameleons: *Chamaeleo bitaeniatus, C. dilepis, C. elliotі, C. hohnelii, C. jacksonii,* and *C. schubotzi*. Given the opportunity, all six species are very competent heliothermic thermoregulators. Individuals typically spend the night low in shrubby vegetation with body temperatures equal to ambient air, and then climb to the top or edges of their bushes to bask when the sun shines. For most species, body temperatures quickly stabilize between 29 and 32°C, which they maintain while the sun shines (except *C. schubotzi* at 19°C). Preferred temperatures in the laboratory average 30 to 33°C, with voluntary minima of 27 to 29°C and voluntary maxima of 34 to 36°C. From the elaborate suite of behaviors undertaken and the distribution of environmental temperatures, it is clear that when solar radiation is available, these chameleon species do not passively accept environmental temperatures. Rather they regulate their body temperatures in the field, utilizing many of the behaviors that have become classically associated with heliothermic behavioral thermoregulation. All other chameleon species previously studied also have thermal preferenda around 30°C.

Keywords: Chamaeleo; chameleon; lizard; temperature; thermoregulation

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1. Introduction

Diurnal lizards of many different families have been shown to regulate body temperature behaviorally at high and stable levels by adjusting exposure to the sun [1,2]. In contrast, chameleons, members of the Old World family Chamaeleonidae, have previously been classified as having low activity temperatures [2], being thermoconformers [3] and thermally passive [4], and in fact preferring low body temperatures [5]. However, relatively few body temperature measurements have actually been reported for these lizards, and many of these are only anecdotal accounts [e.g., 3-8]. Here, measurements on field active and laboratory preferred temperatures and critical thermal limits are reported for six species of Kenyan chameleons. These previously unreported data were gathered as part of a series of studies on functional aspects of feeding, locomotion, and color change in these chameleons [9-13].

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* Department of Ecology and Evolutionary Biology, University of California, Irvine CA 92697-2525 USA, abennett@uci.edu, telephone 1-949-824-6930, fax 1-949-824-2181.

2. Material and methods

The following six species of chameleons (genus *Chamaeleo*) were collected in Kenya under Research Permit No. OP.13/001/18C94/19 from the Office of the President and Collection and Export Permits Nos. 1945, 5563, and 5564 from the Department of Wildlife Conservation and Management and University of California Irvine ARC permit 88-805: *C. bitaeniatus*, Rift Valley, vicinity Olepolos, approx. 2000 m above sea level; *C. dilepis*, coastal plains, vicinity Kibwezi, 800 m; *C. ellioti*, Western Highlands, Kapsabet, 1800 m; *C. hohnelii* and C. *jacksonii*, Nairobi, 1700 m; *C. schubotzi*, Mt. Kenya, 3300 m. Taxonomy and spelling conventions follow Welch [14]. Measurements of field body temperatures were made on collection or on the following day with thermocouple implants. Laboratory measurements were made at the University of Nairobi within three or four days of capture. Animals were watered frequently and subsequently either released or exported to the United States for further research.

A very fine (40 gauge), teflon-coated copper-constantan thermocouple wire was implanted about 1 cm intraperitoneally into the posterior abdomen of an animal on the day prior to measurements. The wire was secured with superglue, leaving an external lead approximately 1 m in length. Chameleons were then placed in bushes from which they were collected within their natural habitats. Body temperatures were measured every half hour by attaching a Tegam Model 821 thermocouple thermometer to the end of the thermocouple wire. Body temperatures were thus monitored on individual animals over the course on an entire day without touching or disturbing the lizards. The chameleons appeared unaffected by these implants or measurements: during these observations, they undertook a variety of different natural behaviors in addition to thermoregulation, including frequent feeding, defecation, copulation, and intraspecific aggression. Simultaneously with measurements of temperatures in these freely-moving lizards, temperatures of highly reflective and absorbtive painted copper models in full sun were determined, as well as that of a copper model in the shade.

Preferred body temperatures were measured in a linear thermal gradient created by suspending a 150 W photoflood lamp above one end of wooden dowel (8 - 10 mm in diameter, 2 m in length) upon which an animal was placed. Equilibrium temperature directly under the light was in excess of 50°C, above the critical thermal limit of all species. The cold end of the gradient was 17-23°C, temperatures below the voluntary minimum of all species. Bright illumination was maintained over the entire gradient. Lizards moved freely along the gradient, either choosing an intermediate position and establishing a very constant temperature or more usually shuttling back and forth between the heated and cooler areas of the gradient. In the latter case, the average temperatures at which an animal voluntarily left the heat or moved toward the heat were taken as the maximum and minimum voluntary temperatures, respectively. Animals were observed continuously from behind a cloth blind. A lizard was placed directly under the heat lamp at the beginning of an experiment, and observations were begun at the first sign of a movement of obvious thermoregulatory significance, usually retreat from the hottest portion of the gradient. Body temperatures were measured with an implanted intraperitoneal thermocouple (see *2.2*) connected to a Tegam thermocouple thermometer, and recorded every minute for one hour. The mean body temperature during this time was taken as the preferred body temperature.

Critical thermal limits and panting thresholds were determined by heating or cooling a lizard just until the righting response was abolished. A lizard was placed under a photoflood lamp or in a metal pan on ice water and rate of body temperature change was adjusted to approximately 1°C per min. Body temperature was monitored continuously with intraperitoneal thermocouples. When an animal approached critical temperatures, it was placed on its side and the first failure to right itself determined. It was then immediately removed and heated animals were placed in cool water. All animals recovered completely within a few minutes after termination of the experiment.

Mean values and standard errors are reported. Intergroup comparisons are done by *t*-tests or ANOVA with posthoc Tukey-Kramer Multiple Comparisons Tests.

3. Results

All six species of chameleons examined proved to be very competent heliothermic thermoregulators. Individuals typically spent the night low in shrubby vegetation, with body temperatures of the ambient air. As soon as the sun rose, they climbed to the top or edges of their bush. Body temperatures rose rapidly above those of the ambient air. For most species (except *C. schubotzi*), these quickly stabilized around 30°C, a value maintained as long as the sun shone. When the sun set or solid cloud cover and rain commenced, lizards moved to the bottom of the vegetation and body temperatures fell to ambient shade levels. Field body temperatures of each species during sunny periods and for the entire observation period are reported in Table 1. Figs. 1 and 2 show a typical pattern of body and environmental temperatures for an individual *C. jacksonii* and *C. ellioti*, respectively. For all species except *C. schubotzi* (which are exceptionally difficult to locate during the day), body temperatures of other, previously undisturbed individuals were measured with a rapid registering cloacal thermometer, according to more traditional methods [2,15]. These temperatures were statistically undistinguishable ($p > 0.1$) from the daily averages reported in Table 1. Mean field body temperatures vary significantly among species [$p < .0001$ by ANOVA for both average daily ($F_{5,28}$ = 128) and average sun temperatures ($F_{5,28}$ = 57)]: *C. schubotzi* had lower field temperatures than all other species ($p < .001$); none of others were consistently different from all the rest. Mean field body temperatures are positively correlated with mean annual minimum (p=.016) and maximum (p=.011) air temperatures measured at weather stations closest to collection localities [16] and estimated for Mt. Kenya [17,18].

Table 1
Field body temperatures (FBT) for six species of Kenyan chameleons (*Chamaeleo* spp.). FBT for both the entire measurement period (time of day) and for only those periods of intermittent or continuous sunshine are reported. All temperature measurements for an individual animal were averaged and the mean and standard error of these averages is reported along with number of animals observed (n). Measurements were begun 30 min after animals were placed in the vegetation and continued until sunset or rain commenced.

Species	n	Time of day	Mean Daily FBT (°C)	Mean Sun FBT (°C)
bitaeniatus	5	0945-1200	28.6 + 0.32	28.9 + 0.22
dilepis	6	0900-1730	31.7 + 0.34	32.0 + 0.36
ellioti	6	0930-1400	30.3 + 0.24	32.5 + 0.36
hohnelii	4	0930-1700	30.1 + 0.15	31.3 + 0.30
jacksonii	8	0930-1700	29.2 + 0.36	30.4 + 0.39
schubotzi	6	0800-1400	19.1 + 0.66	22.2 + 0.98

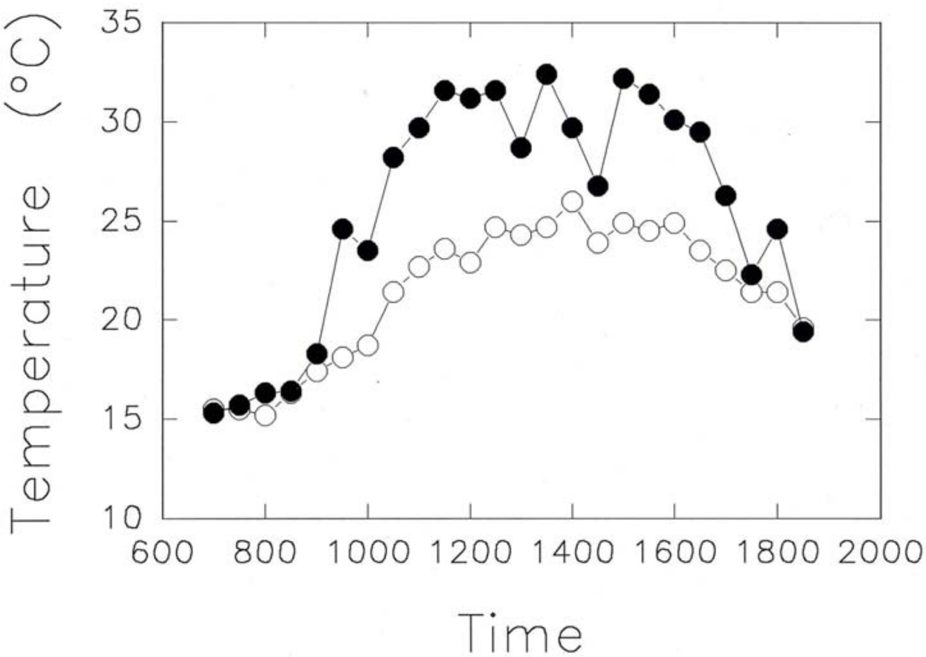

Fig. 1. Field body temperature of an individual *Chamaeleo jacksonii* (solid circles) and shade air temperature of a copper model (open circles). The day was cloudy and raining until 0845, when the first sun shone on the bush; sunshine was intermittent until sunset at 1820. The lizard illustrated had the median body temperature of all individuals measured.

A suite of characteristic body temperatures for each species is reported in Table 2. Statistically significant ($p < 0.001$) interspecific differences occur in critical thermal minima (F5,30 = 14) and maxima (F5,31 = 18) and in preferred body temperatures (F5,32 = 5.6), but not in voluntary minima or maxima or panting thresholds ($p > 0.05$).

Table 2
Laboratory-determined body temperatures for six species of Kenyan chameleons (*Chamaeleo* spp.). CTMin = critical thermal minimum, Vol Min = voluntary minimum, PBT = preferred body temperature, Vol Max = voluntary maximum, Pant Thresh = panting threshold, CTMax = critical thermal maximum. Data in degrees Celsius are reported as mean ± SE (number of individuals); except for CTMin and CTMax, mean values for each individual were first obtained by averaging all observations for that animal and reported statistics are based on those means. *C. dilepis* did not have well defined Vol Min or Vol Max.

Species	CTMin	Vol Min	PBT	Vol Max	Pant Thresh	CTMax
bitaeniatus	4.4+0.67(5)	26.7+2.05(2)	31.1+0.29(5)	35.5+0.52(3)	34.7+0.87(5)	42.1+0.21(5)
dilepis	7.6+0.22(5)	-	32.8+0.14(6)	-	38.1+0.50(5)	43.6+0.05(5)
ellioti	3.5+0.50(6)	26.6+0.60(2)	33.4+0.70(6)	35.0+0.47(4)	37.8+1.27(6)	41.8+0.38(6)
hohnelii	5.1+0.73(6)	26.8+0.60(5)	30.2+0.36(6)	34.3+0.42(5)	37.2+0.62(5)	40.8+0.20(7)
jacksonii	5.3+0.50(8)	29.1+0.32(7)	32.1+0.24(7)	34.2+0.31(7)	36.2+0.67(5)	41.0+0.15(8)
schubotzi	1.4+0.27(6)	29.1+1.95(4)	32.6+0.63(8)	35.5+0.34(6)	36.7+0.74(6)	41.6+0.21(6)

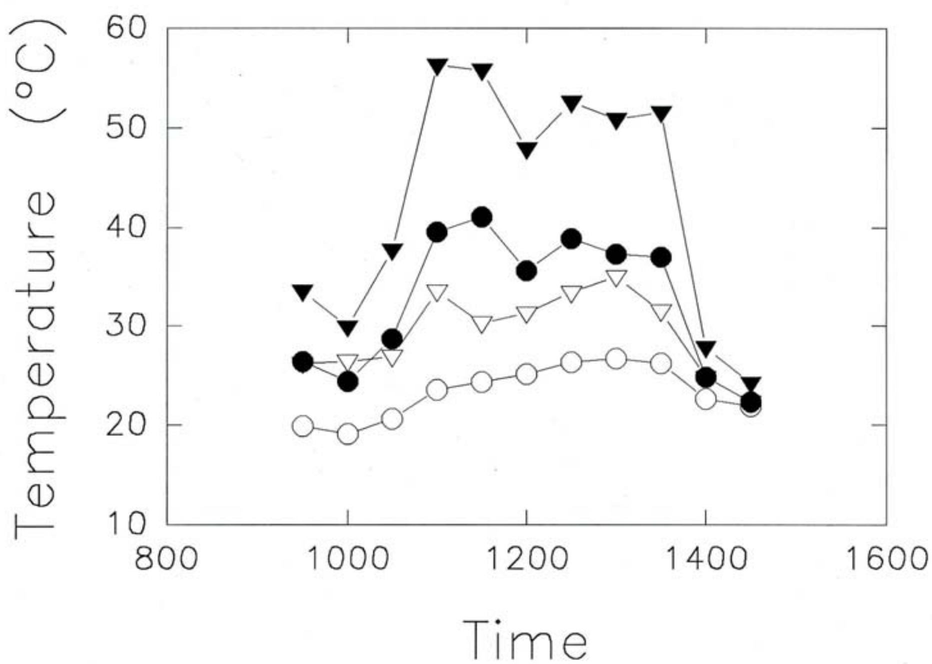

Fig. 2. Field body temperature of an individual *Chamaeleo ellioti* (open triangles) and associated environmental temperatures (copper model in shade: open circles; white painted copper model in sun: closed circles; black painted copper model in sun: closed triangles). Full sun shone on the site from 1035 to 1330, after which rain began at 1410 and the animal retreated to the base of the bush. Note that animal temperature is below the temperatures of both models in the sun. The lizard illustrated had the median body temperature of all individuals measured.

The critical thermal minimum of *C. dilepis* is greater than those of all other species and that of *C. schubotzi* is lower than those of all other species except *C. ellioti*. Critical thermal maximum of *C. dilepis* is greater than that of all other species. No species was consistently different from all the others in preferred temperature. Mean critical thermal minima are significantly correlated with mean annual minimum (p=.004) and mean annual maximum (p=.018) air temperatures. Other thermoregulatory temperatures measured in the laboratory are not significantly correlated with air temperature.

4. Discussion

From the elaborate suite of behaviors undertaken and the distribution of environmental temperatures, it is clear that these chameleon species are not indifferent to body temperature and do not passively accept environmental conditions. Rather, when solar radiation is available, they use it to regulate body temperature. They utilize most of the behaviors that have become classically associated with heliothermic behavioral thermoregulation [1]. As soon as the sun comes out, they climb to the exposed side or top of the vegetation and orient their bodies perpendicular to the rays of the sun. At this time, body color is uniformly dark, maximizing radiant heat absorption [12]. After reaching preferred thermal levels (Table 2), lighter and more cryptic coloration is assumed, and body temperatures are stabilized by moving back and forth between sunny and shady areas of the bush and by postural changes. Elevated basking posture [19], in which the body is oriented parallel to the sun's rays and the head points directly toward the sun and radiant heat gain is minimized, was very common in the middle of the day. With the exception of *C. schubotzi*, natural thermoregulation in these species is apparently not simply a matter of thermal maximization, that is, of getting as hot as the environment permits. Several observations support this conclusion: the shade-seeking behavior already discussed, and the temperatures of both animals and thermal models placed in full sun. Body temperatures of tethered lizards given no access to shade rapidly rose above those of freely thermoregulating animals (when panting was initiated, they were immediately moved into the shade). Copper models placed in the sun, the same size and shape of the lizards and painted either white, gray, or black, attained equilibrium temperatures far in excess of those observed for freely thermoregulating animals (e.g., Fig. 2). All these observations suggest that, given access to solar radiation, these chameleon species are competent behavioral thermoregulators and not thermal maximizers.

Field body temperature regulation in *C. schubotzi* requires further comment. The moorland slopes of Mt. Kenya, the endemic habitat of this species, are frequently covered by cloud and fog [17-19], limiting thermoregulatory opportunities. Body temperatures of animals in the field were monitored on two days, one that was cloudy and rainy and the other that dawned cloudless and sunny (Fig. 3) (data from only the latter are reported in Table 1). On the cloudy day, cloud cover ranged from 60 to 100%, shade and exposed black body temperatures peaked at 10.9 and 22.1°C, respectively. The four animals monitored reached a mean maximal body temperature of 20.4°C. A heavy rain began at 1330 and the lizards retreated into their bushes. On the sunny day, unobstructed sunlight shone on the study site from 0740 to 1100. The six chameleons monitored, which had a mean body temperature at 0730 of 3.5°C, climbed (slowly) to the topmost branches of their bushes and basked perpendicular to the sun's rays. Body temperatures rose to a mean maximum of 29.2°C at 1000-1030, when black body temperatures exceeded 50°C. Clouds began to move in at 1100 and a steady rain started at 1400, whereupon the lizards retreated into their bushes. Although sunny periods of intense insolation do occur on Mt. Kenya [19], they appear to be very restricted temporally and the weather may be cloudy for many days at a time [18]. Even on an exceptionally clear day, the resident chameleons were able to attain preferred temperatures for only about an hour. On many days, they never approach these levels, but are nevertheless field active. Given the opportunity, *C. schubotzi* will regulate higher body temperatures under field conditions. Six animals were placed in natural vegetation in the vicinity of Nairobi (the same location used to monitor field body temperatures of *C. hohnelii* and *jacksonii*), an area receiving considerably more insolation (black body temperature during trial = 55.9°C). They maintained an average temperature of 31.3°C (range of individual means = 30.4 to 34.0°C) throughout the sunny part of the day. These observations indicate that this species has low field body temperatures because of environmental temperature conditions, not an innately low behavioral preference for such temperatures.

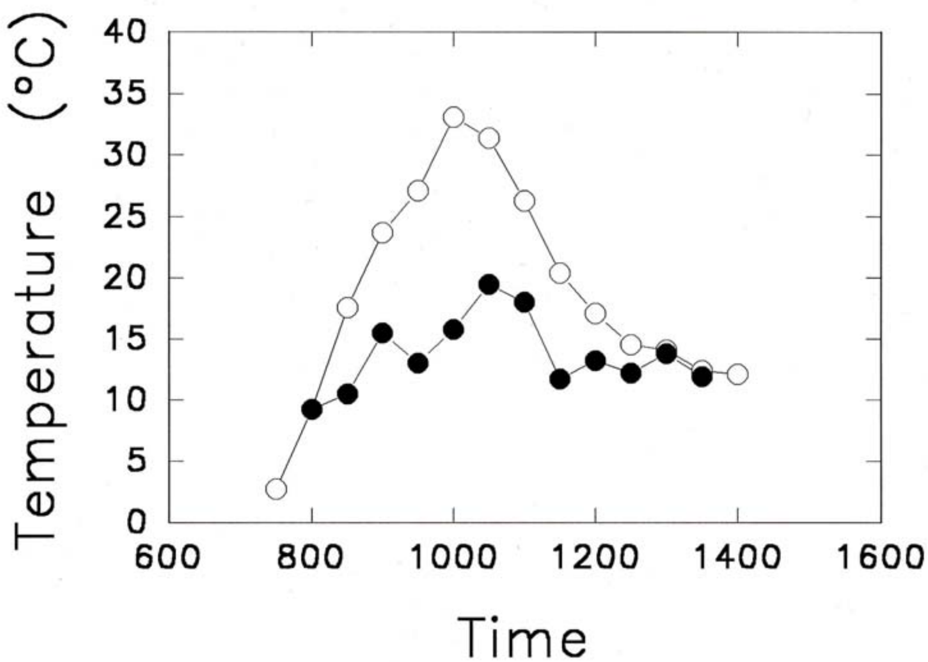

Fig. 3. Field body temperatures of two individual *Chamaeleo schubotzi* in the moorlands near the top of Mount Kenya, one on a cloudy day (22 Feb 1990, closed circles) and one on a sunny day (12 March 1990, open circles). Lizards illustrated had the median body temperature of individuals measured on each day.

The species investigated here and other previously examined chameleons have the ability to be active at low body temperatures. In the field, *C. schubotzi* climbed up into the sunlight with body temperatures of less than 5°C. Feeding was observed at 18.4°C in *C. jacksonii*, 24.2°C in *C. ellioti*, and 26.4°C in *C. schubotzi*. In the laboratory, *C. jacksonii* could feed, walk, and climb competently with a body temperature of 10°C. Other workers have reported feeding in *C. pumilus* at 3.5°C [8] and *C. hohnelii* at 7°C [4]. Most other lizards are not active at such temperatures, and these scattered anecdotal observations of chameleon activity in the field have given the erroneous impression that they are indifferent to temperature or actually prefer low temperatures [e.g., 4,5]. While chameleons do have the ability to maintain limited activity in the cold, they nevertheless seem to prefer to be warmer. Given access to heat, chameleons are effective and fairly careful thermoregulators. The six species studied here have preferred temperatures of 30-33°C, and other species of *Chamaeleo* studied similarly fall into this rather narrow range (*C. namaquensis*, 33°C, *C. dilepis*, 31°C [6]; *C. africanus*, 31°C, *C. chamaeleon*, 32°C [3]. Preferred temperatures of 25°C and 29°C have been reported for *C. pumilus* and *C. namquensis* [8], respectively, but these may be 24 h measurements and include inactive periods. Inclement weather, strong diurnal thermal fluctuations, and/or high altitude habitation may force them to spend part or even all of their day at low body temperatures, but given access to solar radiation, they seem little different than most other lizards in their preference for warm and constant body temperatures.

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