Thermal Biology of Nocturnal Ectotherms: Is Sprint Performance of Geckos Maximal at Low Body Temperatures?

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Abstract

*Nocturnal geckos are active with body temperatures (T_b) that are low and variable relative to those of diurnal lizards. If the physiology of geckos is evolutionarily adapted to these low and variable T_b's, then the physiology of geckos should function best at relatively low and variable temperatures. We tested a specific prediction of this hypothesis by comparing the thermal dependence of sprint speed of nocturnal geckos versus diurnal lizards. In fact, optimal temperatures and performance breadths for sprinting of several geckos (*Coleonyx brevis, C. variegatus, Hemidactylus frenatus, H. turcicus, Lepidodactylus lugubris*) do not differ substantially from those of diurnal lizards from other families. As a result geckos normally forage at night at T_b's that should be suboptimal for sprinting. Potential evolutionary explanations (e.g., evolutionary inertia of thermal physiology, possible selection pressures favoring high optimal temperatures) for the similarity of the thermal dependence of sprinting of geckos and diurnal lizards are evaluated.*

Introduction

Several lineages of terrestrial ectotherms (e.g., lepidoptera, reptiles) have undergone evolutionary radiations in time of activity and often include both nocturnal and diurnal forms. Because time of activity sometimes influences potential body temperatures ectotherms can achieve, lineages evolving new

Table 1

Body temperature (° C) statistics for geckos versus diurnal lizards

Desert	T_b	SD T_b
Australia:		
Diurnal species (33)	35.0 ± .37	2.94 ± .136
Nocturnal species (12)	26.4 ± .49	4.15 ± .313
P	<.001	<.001
Kalahari:		
Diurnal species (13)	36.4 ± .48	2.48 ± .102
Nocturnal species (6)	26.1 ± .51	3.48 ± .127
P	<.001	<.001
North America:		
Diurnal species (9)	37.1 ± 1.12	2.27 ± .154
Nocturnal species (1)	28.4	3.4
P	=.039	=.048

Note. Means are reported ± SE. Data summarized from app. D in Pianka (1986), excluding fossorial or secretive taxa (*Delma, Eremiascincus, Lerista, Pygopus, Typhlosaurus, Xantusia* and *Varanus*). T_b = unweighted mean body temperature of active lizards; SD T_b = unweighted mean SD in body temperatures. *N* in parentheses.

activity times may experience body temperatures that diverge from ancestral ones. If those new body temperatures reduce physiological performance, then compensatory (or coadaptational) evolution in thermal physiology might be favored (Huey and Bennett 1987).

Many lizard lineages show evolutionary divergence in time of activity and thus are suitable subjects for studies of compensatory evolution of thermal physiology. A conspicuous example involves gekkonoid lizards (geckos and their allies; Kluge 1987). Although most lizard species forage by day, most geckos forage by night (however, some nocturnally foraging geckos bask within protected sites by day and hence are called "diurno-nocturnal"; Werner and Whitaker 1978), and geckos almost certainly evolved nocturnality early in their history (Underwood 1970).

Nocturnal geckos are active with lower and more variable activity temperatures than are sympatric diurnal lizards (table 1 summarized from Pianka 1986; see also data in Stebbins 1961; Licht et al. 1966*b;* Heatwole 1976; Werner 1976; Werner and Whitaker 1978; Pianka and Huey 1978; Avery 1982), presumably reflecting the low ambient temperatures and limited opportuni-

ties for behavioral thermoregulation at night (Porter and Gates 1969). If the physiology of geckos is evolutionarily adapted to these low and variable activity temperatures (Cowles and Bogert 1944), then gecko physiological capacities should function well across a broader range of temperatures and reach peak performances at lower temperatures than do those of diurnal lizards (Bustard 1967; Werner 1976; but see Discussion and van Berkum 1986, 1988; Huey and Bennett 1987).

The thermal physiology of geckos has received little attention. Moreover, the few available data are intriguingly contradictory. For example, optimal temperatures for auditory sensitivity of some species of geckos are low and broad relative to diurnal lizards (Werner 1972, 1976). In contrast, the critical thermal maxima and thermal preferences of some other species of geckos can be high. In fact, these temperatures may approach or even exceed those of many diurnal lizards (Brain 1962; Licht, Dawson, and Shoemaker 1966a, 1969; Spellerberg 1972; Dial 1978).

These contradictory patterns lead to the question, To what extent does the thermal sensitivity of performance match activity temperatures of nocturnal geckos? Here we address this question by determining the thermal sensitivity of maximum sprint speed of several geckos. Sprint speed is only one component of physiological performance (see Discussion). Nevertheless, it is an ecologically relevant and temporally repeatable trait that may influence predator avoidance, predation success, social dominance, and survivorship (Greenwald 1976; Bennett 1980; Christian and Tracy 1981; Avery, Bedford, and Newcombe 1982; Huey and Dunham 1987; A. F. Bennett and B. C. Jayne, personal communication; see also John-Alder, Morin, and Lawlor 1988). By making comparisons with similar data on diurnal lizards, we sought to determine whether the sprint speeds of nocturnal geckos are maximal at relatively low and variable body temperatures (Bustard 1967; Werner 1972, 1976; Huey and Bennett 1987), or at high body temperatures, as might be expected because of high tolerance limits and thermal preferences (Licht et al. 1966a, 1966b; Dawson 1975; Dial 1978). If the former expectation is correct, then nocturnal geckos forage at body temperatures optimal for sprint locomotion; but if the alternative expectation is correct (see van Berkum 1986; Huey and Bennett 1987), then nocturnal geckos forage at body temperatures suboptimal for sprinting.

We examined the thermal dependence of sprint speed in five nocturnal geckos (*Hemidactylus turcicus, H. frenatus, Coleonyx variegatus, C. brevis,* and *Lepidodactylus lugubris*). Using field or literature data, we also determined their field activity temperatures and their laboratory thermal

preferences. Finally, we compared these data with parallel data on diurnal lizards (Huey et al., in preparation).

The geckos studied here represent two of the three families of gekkonoid lizards (Kluge 1987). *Hemidactylus turcicus* (Gekkonidae) are scansorial geckos. Their native range extends from the Mediterranean region east to India (Arnold and Burton 1980), but they have been introduced in the southern United States where they are commonly collected on the walls of buildings (Selcer 1987). *Hemidactylus frenatus,* which also commonly inhabit walls, occur in many tropical and subtropical regions (McCoy 1980). The Hawaiian population was probably introduced during or shortly after World War II (McKoewn 1978). *Lepidodactylus lugubris* (Gekkonidae) are parthenogenetic and arboreal, with a broad distribution similar to that of *H. frenatus* (McKoewn 1978). The Hawaiian population is thought to have reached the Hawaiian Islands as stowaways aboard Polynesian canoes (McKoewn 1978). *Coleonyx brevis* (Eublepharidae) are terrestrial and are sympatric with *H. turcicus* in xeric regions of Texas and northern Mexico (Dial 1978). *Coleonyx variegatus* are terrestrial and are distributed in the southwestern United States and adjacent parts of Mexico (Stebbins 1966).

Material and Methods

Field Body Temperatures

Field T_b's for geckos studied herein are summarized with measures of location (median, Q_1 and Q_3 [the lower and upper interquartile T_b, respectively], see DeWitt 1967; Werner and Whitaker 1978; van Berkum 1986), but mean field T_b's are also presented for comparative purposes. We measured field T_b (with a Bailey BAT-12 thermocouple thermometer) of *Hemidactylus turcicus* that were active at night on the walls of the general store at Rio Grande Village, Big Bend National Park, Texas, (altitude 500 m) in early August 1986. We attempted to sample temperatures evenly between 2229 and 0315 hours. Additional samples of field body temperatures were obtained by A. E. Dunham and S. Beaupre (personal communication) in late June 1987.

We used a quick-reading Schultheis thermometer to measure cloacal T_b for *H. frenatus.* We sampled animals between 1946 and 2307 hours (September 8, 1987) on the walls of the United Methodist Church and its parish house in Kekaha, island of Kauai, Hawaii (sea level). Because the resulting data were obtained only on a single night, they are at best tentative index of the typical activity T_b of this species.

We made no field observations of T_b of *Coleonyx variegatus* or of *C. bre-*

vis. However, data from the literature (below) are available for these species. We have no data on field T_b for *L. lugubris* as these geckos were too small for a Schultheis thermometer.

For the thermal-preference and sprint-speed experiments, we collected *H. turcicus* ($N = 8$, mass = 2.8 ± 0.16 g, mean ± SE) and *C. brevis* ($N = 2$, mass = 1.8 g) near Rio Grande Village, Texas, in early August 1986. *Coleonyx variegatus* ($N = 8$, 4.4 ± 0.20 g) were collected from several localities in southern California by J.K. (fall 1986) and in Baja California by L. J. Vitt (spring 1986). *Hemidactylus frenatus* ($N = 14$, 3.3 ± 0.21 g) and *Lepidodactylus lugubris* ($N = 15$, 1.1 ± 0.06 g) were collected in Hawaii in September 1987 (as above). All lizards were subadults or adults.

Geckos from Texas and Hawaii were maintained in an environmental chamber (13L:11D, 30°C:28°C) for at least 4 d with food (crickets, vitamin supplements) and water (ad lib.) before testing. *Coleonyx variegatus* were maintained under similar conditions, but a few individuals had been in captivity up to 3 mo before testing.

Preferred Body Temperatures

To determine preferred body temperatures (T_p, Licht et al. 1966*b*) of *H. frenatus* and *L. lugubris* in laboratory thermal gradients, we placed single geckos at night in darkened 10-gal terraria with an overhead IR-heat source at one end. Operative environmental temperatures (Bakken 1976), which represent the potential body temperatures of geckos at the extremes of the gradient and were measured using model lizards, ranged from 26.5 to 38.0°C (*H. frenatus*) or 26.2 to 36.8°C (*L. lugubris*). After 1 h we took cloacal temperatures (thermocouple thermometer) of each gecko and then took additional temperatures each h for the next 4 h. The T_p reported for these species is the grand mean of the averages of individual T_p's.

The T_p's of *C. variegatus* were taken at night in a darkened 150 × 8-cm thermal gradient (5–50°C). The gradient was maintained along the copper plate surface using an ice bath and a hot plate at opposite ends. Only one temperature was taken of individual *C. variegatus*.

Measurements of Speed

Sprint speeds of each gecko at night were obtained at several T_b's. We attempted to use the same temperatures for all species, but this was complicated by differences among species in their ability to cool by panting at high T_b. The sequences we used were as follows: *H. turcicus* and *C. brevis*: 30,

20, 25, 34, 30, 37.5, 40°C; *C. variegatus:* 30, 20, 25, 15, 34, 30, 37.5, 40°C; *H. frenatus:* 30, 20, 25, 15, 34, 30, 37, 20, 39.5°C; *L. lugubris:* 30, 20, 25, 15, 34, 30, 36.5, 20°C. The two trials at 20 or 30°C enable us to detect changes in health or motivation of the geckos during the experiment. Following Hertz, Huey, and Nevo (1983), we excluded from the analyses any gecko that lost more than 15% in speed between the two trials, or that lost more than 15% of body mass by the end of the trials, or that broke a tail.

Protocols for racing followed Hertz et al. (1983). We gave the lizards at least 1 h to equilibrate to the test temperature and then chased them by hand along a 2-m racetrack (1-m for *H. frenatus* and *L. lugubris*) that was equipped with photocells at set intervals. The photocells were connected to a microprocessor, which calculated speeds ($m \cdot s^{-1}$) over each interval between adjacent photocells. We raced each gecko four times per temperature and selected the gecko's single fastest speed as the estimate of its maximal sprint speed at that temperature. We gave the geckos an hour rest between runs at each temperature and a day rest between temperatures. Speeds of $0 \, m \cdot s^{-1}$ were arbitrarily assigned to the critical thermal minimum (CTMin, loss of righting response) and critical thermal maximum (CTMax) using methods in Hertz et al. (1983). Most lizards ran on the horizontal bed of the track. However, one *H. turcicus* typically ran down the vertical walls. This individual was excluded from the analysis as it usually missed the photocells.

For *H. turcicus, C. variegatus,* and *C. brevis,* we placed the photocells at 0.25-m intervals and analyzed the fastest time from among all 0.25-m distances. For *H. frenatus* and *L. lugubris,* we placed photocells at 0.10-m intervals and recorded fastest times over 0.2-m and 0.1-m intervals, respectively.

Analyses

To describe the thermal dependence of sprint speed, we used a modified minimum-polygon algorithm (van Berkum 1986) and then estimated several descriptive measures (Huey and Stevenson 1979; Hertz et al. 1983; see fig. 1 in van Berkum 1986). For each lizard we calculated two measures of "thermal performance breadth" (B_{95}, B_{80}—the ranges of temperatures over which the gecko ran no slower than 95% or 80% of maximal speed, respectively), the "optimal" temperature for sprinting (T_o, the midpoint of the 95% performance range), and the relative performance at several important body temperatures (maximum and minimum field T_b, mean field T_b, mean preferred T_p). (Because of the shape of the performance curve, the T_o calculated by the minimum-polygon algorithm is usually slightly lower than the

actual T_b at which speed was fastest.) We also calculated Q_{10}'s of speed for the 10°C-range below T_o (Huey and Bennett 1987). By comparing CTMin, T_o, and CTMax of geckos with those of diurnal lizards, we can determine whether the locomotor performance curves of geckos are shifted to low temperatures relative to the performance curves of diurnal lizards. By making similar comparisons for performance breadths and Q_{10}'s, we can also determine whether geckos run well over broad ranges of temperatures relative to diurnal lizards. Because of the small number of species of geckos (and also because of the lack of statistical independence between the two species of *Coleonyx* and of *Hemidactylus;* see Felsenstein 1985; Huey 1987), we do not use formal hypothesis testing in comparisons of geckos with diurnal lizards and instead rely on qualitative comparisons.

The diurnal lizards used in our comparisons include *Agama, Ameiva, Cnemidophorus, Ctenotus, Dipsosaurus, Egernia, Gambelia, Sceloporus, Stellio, Uma,* and *Uta.* All data were analyzed as above and are summarized from an unpublished review (Huey et al., in preparation). For comparative purposes we have arbitrarily included only open-habitat lizards and have thus excluded secretive, montane, or interior-forest species such as *Anolis, Eremiascincus, Hemiergis, Lepidophyma,* certain *Sceloporus* (e.g., *S. malachiticus*), and *Xantusia.*

Results

Body Temperatures, Thermal Preferences

Median and mean activity temperatures (at night) of *Coleonyx* spp. and of *Hemidactylus* spp. average 7–8°C below those activity temperatures (by day) for the sample of diurnal lizards (table 2). Field temperatures of *Lepidodactylus lugubris* were not taken but are probably low. We caution that the median T_b for *H. turcicus,* though low compared with that for the diurnal species (table 2), may be unrepresentatively warm for this gecko. Rio Grande Village is much hotter than other localities in Texas where we have seen this lizard (nighttime air temperature [2-m height] at capture averages 30.0 ± 0.56°C), and the walls of the village store are sheltered from the cold night sky by a projecting roof.

The interquartile ranges of body temperatures (the range including the central 50% of T_b, a measure of T_b variability) of geckos are all larger than the average for diurnal lizards (table 1). Because T_b's of geckos change markedly with season (see Mayhew 1968; Pianka and Huey 1978; Pianka 1986), the greater T_b variability of geckos relative to diurnal lizards (table

TABLE 2

Body temperature (° C) statistics for geckos and averages for geckos and for diurnal lizards

Taxon (N)	$T_b \pm SE$	Median T_b	Q_1	Q_3	Q_{3-1}	T_p
Coleonyx brevis	28.6[a]	28.7	26.8	31.8	5.0	31.8[a]
C. variegatus	26.8[b]	29.7[b]	23.3[b]	30.7[b]	7.4[b]	31.1[c]
Hemidactylus						
frenatus (8)	27.4 ± .60[c]	27.9[c]	25.8[c]	28.9[c]	3.2[c]	31.8[c]
H. turcicus (34)	31.3 ± .40[c]	31.4[c]	29.0[c]	33.4[c]	4.4[c]	...
Lepidodactylus						
lugubris (8)	...	...	...	...	...	29.2[c]
Geckos (5 species)	28.5	29.4	26.2	31.2	5.0	31.0
Diurnal lizards						
(13 species)	36.5[d]	37.1[d]	35.4[d]	38.1[d]	2.8[d]	36.2[d]

Sources. [a]Dial (1979, personal communication); [b][Brattstrom (1965), Cunningham (1966), Mayhew (1968, personal communication), Vance (1973), Parker and Pianka (1974), Pianka (1986)]; [c]Herein; [d]Huey et al., in preparation.
Note. T_b = mean body temperature of active lizards; Q_1 and Q_3 are the upper and lower interquartile T_b; Q_{3-1} is the interquartile range of T_b; and T_p is the laboratory thermal preference. Taxa constituting the "diurnal lizard" category are listed in Material and Methods.

1) would certainly be magnified if we had sampled geckos for more than a few days (see Material and Methods).

Thermal preferences of geckos in the laboratory are 3–4°C warmer than their normal field temperatures (table 2), a pattern consistent with those of many geckos (Brain 1962; Licht et al. 1966b; Dial 1978). (Our estimate of T_p for *H. frenatus* [31.8°C, table 2] compares closely with an estimate for a Philippine population of this species [32.1°C, Feder and Feder 1981].) Even so, thermal preferences of geckos are 4–7°C lower than those diurnal lizards (table 2, see also Licht et al. 1966b; Avery 1982; Bennett and John-Alder 1986).

Critical Thermal Limits

Critical thermal minima of geckos are not consistently different from those of diurnal lizards (table 3). The two Hawaiian geckos (*H. frenatus* and *L. lugubris*) had slightly higher CTMin's than did the temperate-zone geckos. Critical thermal maxima of all geckos are, however, lower than the average

TABLE 3

Thermal dependence of sprint speed in geckos versus diurnal lizards

Taxon (N)	CTMin (°C)	CTMax (°C)	T_o (°C)	B_{95} (°C)	B_{80} (°C)	Q_{10}	V_{max} (m·s^{-1})
Coleonyx brevis (2)	8.5	41.6	35.6	7.4	13.1	1.3	1.3
C. variegatus (8)	7.6	43.0	35.8	4.3	12.5	1.5	1.7
Hemidactylus							
frenatus (14)	11.9	42.4	34.1	6.2	13.3	1.4	2.2
H. turcicus (9)	10.5	41.1	36.8	5.6	13.1	1.3	1.7
Lepidodactylus							
lugubris (15)	11.5	40.2	33.7	4.8	11.1	1.4	1.6
Geckos (5 species)	10.0	41.7	35.2	5.7	12.6	1.4	1.7
Diurnal lizards							
(13 species)	10.1	44.7	36.0	5.2	12.3	1.5	...

Note. Symbols defined in Material and Methods.

for diurnal lizards (table 3). Even so, the magnitude of the differences between these geckos and the average for diurnal lizards are minor (all <4.5°C) relative to the differences between these groups in activity temperatures (5–10°C).

Thermal Dependence of Sprinting

Sprint speeds of geckos increased with body temperature, usually leveled at around 35°C, and then usually dropped sharply near 40°C (table 4). Optimal temperatures (see Material and Methods, Analyses) for sprinting of our geckos averaged 35.2°C, which is very similar to the average for diurnal lizards (36.0°C, table 3). The Q_{10}'s, B_{95}'s, and B_{80}'s of geckos are also very similar to those of diurnal lizards (table 3). Therefore, geckos and diurnal lizards appear to have similar thermal dependencies for sprinting.

To estimate how much sprint speed of geckos is depressed by activity at low T_b, we calculated relative sprint speeds of the geckos at ecologically relevant T_b (table 5). Low activity T_b clearly reduce sprint speeds of geckos. For example, geckos at their mean activity T_b's should be able to run only 78%–91% as fast as the speeds they can achieve at their optimal temperatures. In contrast, diurnal lizards are typically active at body temperatures that enable them to run closer to maximal speeds (94%, table 5). Were

TABLE 4

Sprints speeds $(m \cdot s^{-1})$ *[$\bar{X} \pm SE$ (N)] of geckos at various body temperatures*

Taxon	Body Temperature (°C)						
	15	20	25	30	34	37.5	40
Coleonyx brevis:							
Complete	...	.73 (2)	.98 (2)	1.25 (2)	1.13 (2)	1.30 (2)	1.26 (2)
Selected	...	.73 (2)	.98 (2)	1.25 (2)	1.39 (1)	1.49 (1)	1.26 (2)
C. variegatus:							
Complete	.53 ± .039 (8)	.86 ± .110 (8)	1.18 ± .107 (8)	1.31 ± .110 (8)	1.42 ± .108 (8)	1.31 ± .094 (8)	1.49 ± .119 (8)
Selected	.53 ± .039 (8)	1.00 ± .174 (4)	1.19 ± .123 (7)	1.48 ± .051 (5)	1.53 ± .138 (5)	...	1.49 ± .119 (8)
Hemidactylus frenatus:							
Complete	.65 ± .029 (14)	1.21 ± .035 (14)	1.67 ± .031 (14)	2.05 ± .071 (14)	2.09 ± .084 (14)	1.99 ± .086 (14)[a]	1.88 ± .097 (14)[b]
Selected	.65 ± .029 (14)	1.26 ± .025 (11)	1.66 ± .038 (8)	2.12 ± .056 (12)	2.21 ± .098 (9)	2.03 ± .099 (7)[a]	1.88 ± .097 (14)[b]
H. turcicus:							
Complete	...	.93 ± .062 (8)	1.19 ± .040 (8)	1.50 ± .044 (8)	1.51 ± .030 (8)	1.63 ± .038 (8)	1.63 ± .041 (8)
Selected	...	.93 ± .062 (8)	1.24 ± .046 (5)	1.49 ± .021 (6)	1.50 ± .029 (5)	1.64 ± .044 (7)	1.63 ± .041 (8)
Lepidodactylus lugubris:							
Complete	.56 ± .023 (15)	.97 ± .025 (15)	1.15 ± .048 (15)	1.43 ± .054 (15)	1.43 ± .059 (15)	1.54 ± .052 (15)[c]	...
Selected	.56 ± .023 (15)	.97 ± .027 (14)	1.19 ± .066 (10)	1.49 ± .059 (11)	1.51 ± .080 (8)	1.54 ± .052 (15)[c]	...

Note. Both complete and selected values are tabulated. Selected values represent averages of data used in the minimum polygon analysis, which deletes certain values (see van Berkum [1986] for culling criteria).

[a] Actual T_b was 37° C.
[b] Actual T_b was 39.5° C.
[c] Actual T_b was 36.5° C.

TABLE 5

Speed of geckos versus diurnal lizards at various body temperatures relative to speeds at their optimal temperatures

Taxon	T_b	T_p	Q_1	Q_3
Coleonyx brevis	.87	.94	.79	.94
C. variegatus	.78	.88	.67	.87
Hemidactylus frenatus	.85	.95	.80	.90
H. turcicus	.91	. . .	.86	.93
Lepidodactylus lugubris	. . .	.89	. . .	. . .
Geckos	.85	.91	.78	.91
Diurnal lizards	.94	.94	.94	.95

Note. Sample sizes as in table 3. Symbols explained in Material and Methods.

geckos to forage instead at their preferred T_b's they would be able to run somewhat faster (88%–95% of maximal speed, table 5).

Discussion

In nature nocturnal geckos often forage at body temperatures that are low and variable relative to those of diurnal lizards (tables 1 and 2, and references above). Low and variable body temperatures are a consequence of activity at night when the absence of shortwave radiation restricts opportunities for behavioral thermoregulation (Porter and Gates 1969).

Given the low and variable body temperatures of active geckos, one might anticipate that the optimal temperature range for sprinting geckos would be lower and broader than that for diurnal lizards (Cowles and Bogert 1944; Bustard 1967; Werner 1976; see also Huey and Slatkin 1976; van Berkum 1986; Huey and Bennett 1987). Our results strongly contradict this expectation. The average optimal temperature, performance breadths, and Q_{10}'s for sprinting are very similar for geckos and diurnal lizards (table 3). Our findings appear consistent with earlier studies showing that some geckos have high optimal temperatures for maximal twitch tension (Licht et al. 1969) and possibly for hearing sensitivity (Werner 1976).

The discrepancy between activity and optimal temperatures for sprinting

(table 5) may have significant ecological implications because geckos should therefore forage at temperatures suboptimal for speed and probably for acceleration (Huey and Hertz 1984). Indeed, the predicted speed of geckos at their average nighttime temperature is only 85% of their maximum possible speed at any temperature, whereas that of diurnal lizards at their daytime T_b is 94% of their maximum (table 5). This reduction in speed of geckos might potentially limit their feeding success, escape from predators, or social dominance (references above) in comparison to their hypothetical activity at higher body temperatures.

Evolution of Gekkonoid Thermal Physiology

Our primary finding—that geckos have low and variable activity temperatures (relative to diurnal lizards) but have similar optimal temperatures and performance breadths for sprinting—raises issues concerning the physiological adjustments that follow the evolution of nocturnality (Huey and Pianka 1983). The simple hypothesis that optimal temperatures should be evolutionarily coadapted with activity temperatures holds for many lizards (Huey et al., unpublished data) but clearly does not apply to geckos. Moreover, it may not apply to amphibians and reptiles that are sometimes active at low T_b's (tuatara: Werner and Whitaker 1978, Saint Girons 1980; marine iguana: Bartholomew, Bennett, and Dawson 1976; *Anolis*: van Berkum 1986; nocturnal skinks: Huey and Bennett 1987; nocturnal or aquatic snakes: Hailey and Davies 1988; tree frogs: John-Alder et al. 1988) or to some fishes (Fry and Hart 1948). We cannot at present determine the evolutionary reason for this discrepancy in geckos, but we can offer several possible explanations that are potentially subject to comparative testing.

1. The discordance between activity and optimal temperatures might reflect either the recent evolution by geckos of nocturnal activity or the general evolutionary inertia of thermal physiology. For geckos either explanation may be unlikely. Geckos are an ancient group of lizards and are primitively nocturnal (Underwood 1970; A. G. Kluge, personal communication). Therefore, evolution has had considerable time in which to operate. Moreover, even though thermal physiology is usually evolutionarily conservative in lizards (Bogert 1949; Huey 1982; Hertz et al. 1983; Crowley 1985), it is not inert (van Berkum 1986; Huey and Bennett 1987). Nevertheless, the issue of evolutionary inertia in geckos will be resolved only by comparing the thermal physiology of a variety of geckos (see Huey and Bennett 1986).

2. Perhaps the optimal temperatures of other physiological functions (e.g., digestion) more closely match the low nighttime activity temperatures

of geckos, such that the thermal sensitivity of sprinting is a misleading predictor of the thermal sensitivity of most physiological systems. Data on geckos are unavailable to test this hypothesis, but optimal temperatures for sprinting of other reptiles are in fact similar to those of other physiological systems (fig. 6 in Huey 1982; Stevenson, Peterson, and Tsuji 1985; Hailey and Davies 1988). This hypothesis is currently unsupported.

3. Perhaps the thermal physiology of nocturnal geckos is coadapted, not to low body temperatures experienced by geckos foraging at night, but rather to the high body temperatures geckos may experience during the day (see below). Such high T_b's can result from "protected basking" by geckos within their diurnal retreats: protected basking might promote digestion (Bustard 1967; Werner and Whitaker 1978), foster escape from diurnal predators (Huey and Bennett 1987), or enhance social dominance within retreats (Frankenberg 1982; but see Cooper, Caffrey, and Vitt 1985). Alternatively, if cool diurnal retreats are unavailable (Heatwole 1976; Dial 1978; Huey 1982; Huey et al. 1989), geckos would require high critical thermal maxima simply to survive the high T_b's forced on them during the day (Huey and Bennett 1987). (Many geckos do have high critical thermal maxima [Brain 1962; Licht et al. 1966a, 1966b; 1969; Spellerberg 1972; table 3].) In this case, a high optimal temperature would probably evolve as a correlated response because of the apparent difficulty of evolving a high critical thermal maximum but a low optimal T_b (see Huey and Bennett 1987, p. 1112). By this general hypothesis, the high optimal temperatures for sprinting and the high critical thermal maxima of many geckos might be the result of selection pressures (van Berkum 1986; Huey and Bennett 1987) favoring survival at high temperatures by day (or possibly performance by day) even though this results in reduced sprint performance at low temperatures by night. If this hypothesis is correct, we should reconsider the assumption (see Introduction) that the ability to run quickly at night is important to geckos (Huey and Bennett 1987).

This hypothesis can be tested indirectly because it requires that body temperatures of geckos in their diurnal retreats are sometimes high. Unfortunately, relevant data are absent for the species studied here, but T_b's of other geckos in their diurnal retreats are always higher than those of geckos foraging at night (Licht et al. 1966b; Dial 1978; Werner and Whitaker 1978; Y. L. Werner, personal communication). Because shallow-soil and under-rock temperatures are often extremely warm by day (Dial 1978; Huey 1982, p. 64; Huey et al. 1989), many geckos in hot environments will necessarily experience high T_b's during the day, even if they select diurnal retreats carefully.

Our findings for geckos parallel those for some Australian skinks (Huey and Bennett 1987). Nocturnality is evolutionarily derived in a few lineages of skinks, and it results in their activity at low T_b's (Bennett and John-Alder 1986). Even so, the optimal temperature for sprinting and the CTMax of a nocturnal skink (*Eremiascincus fasciolatus*) from the hot Australian interior are equivalent or perhaps slightly higher than those of its closest diurnal relatives (*Sphenomorphus*) from the cooler periphery of Australia. This pattern might also reflect the selective importance of being able to survive high daytime temperatures, especially in hot environments, even though this reduces potential sprint performance while foraging at night.

Resolution of these issues will obviously require additional study. We encourage parallel studies of other taxa, especially studies involving close relatives (Huey and Bennett 1986; Huey 1987) that differ in times of activity. Parallel studies of the thermal dependence of other physiological functions (especially of digestion) are clearly relevant, as are studies that examine the linkage between physiological performance and fitness (Arnold 1983). Finally, we encourage comprehensive studies of the body temperatures of geckos during diverse seasons and especially while in their diurnal retreats (Dial 1978; Werner and Whitaker 1978; see also Huey et al. 1989). Such natural history data are often a key to physiological and evolutionary understanding (Greene 1986).

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