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Thermal Relations of the Neotropical Frog
Hyla labialis (Anura: Hylidae)by Dario Valdivieso¹ and J.R. Tamsitt²

Abstract—The heliothermic frog, *Hyla labialis*, in Bogotá, Colombia, was found to have daily activity patterns primarily controlled by temperature; overcast skies reduced activities. Ambient temperatures affected body temperatures, which were maintained within broad limits. Activity range for body temperatures of *H. labialis* varied from 11 to 28°C with a mean of 18°C. Body temperatures of most frogs, however, ranged from 13 to 22°C. Mean body temperatures were lowest at night (14.5°C) and highest when basking (22.9°C). [Anura; Hylidae; *Hyla labialis*; thermal relations.]

Introduction—Temperature relations of most tropical anuran amphibians are not well documented (Brattstrom, 1970), but information on frogs that live at high elevations in the neotropics is particularly limited. Brattstrom (1963) gave body temperatures of some montane anurans from North and Central America and later (1968) presented data on thermal acclimation for a few frogs that occur at higher elevations in Costa Rica. Because of this paucity of information on temperature requirements of neotropical

frogs that live at high altitudes near the equator, we describe thermal relations *in situ* of *Hyla labialis* Peters, a species locally abundant in the Bogotá Savanna (2,650–3,150 m; 04°40'N, 74°06'W).

Methods—We recorded body temperatures (T_b) of 196 *H. labialis* in the field from 0700 to 0100 hr under a variety of ambient conditions in July 1967 and June and July 1969. Frogs were captured by hand, and heat conduction was minimized by holding the frog by the hind foot. T_b s were recorded with a 0–50°C Schultheis rapid equilibrium thermometer (E.W. Schultheis Corp., Brooklyn, N.Y.) inserted cloacally (ca 1 cm) immediately after capture. T_b s were not taken of frogs that had exhibited prior locomotory activity. Air temperatures (T_a) were measured in the shade about 5 mm from the substrate where the frog was taken. Snout-vent length (SVL) was measured in mm as the straight-line distance between the snout and the anus. Other data recorded for each capture included sex (except that of juveniles), colour phase (green or brown), per cent cloud cover, amount of light (bright sunshine, shade, dim), moisture (drizzle,

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rain), and behaviour of frog at time of capture, e.g., basking, exposed on vegetation in shade or at night, concealed in vegetation. Soil temperatures were not taken because we never saw frogs in direct contact with the ground. Frogs were not weighed because metabolic studies were not undertaken.

Terms employed here are modified from those defined by Cowles and Bogert (1944) and summarized by Brattstrom (1965). Although common in the literature, we consider traditional definitions, i.e., voluntary minimum and maximum, optimum, normal activity range, to be inappropriate for field studies, in that such biological factors as predator avoidance and water requirements may alter temperatures of environments into which an animal will venture beyond values that are physiologically optimum. Practical definitions are: *minimum*, lowest body temperature recorded; *maximum*, highest body temperature recorded; *activity range*, range of body temperatures between minimum and maximum; *basking range*, range of body temperatures within the activity range for basking frogs; and *mean*, the average of all body temperatures recorded within the activity range.

All $T_{b,s}$ are given to the nearest 0.1°C . A Model II regression of $T_{b,s}$ on $T_{a,s}$ was computed by the method devised by Bartlett (1949). The programme was adapted from that in Davies (1971) to calculate the slope and to compute three significant tests, each with $(n - 3)$ degrees of freedom: (1) to test the significance of the regression; (2) to test whether there is significant departure from isometry; and (3) to test whether the relationship between x and y is linear. These three statistics are designated T_0 , T_1 , and T_L , respectively. Computations were performed on an IBM 370 computer at the University of Toronto Computer Centre. Other regressions were calculated by the least-squares method (Sokal and Rohlf, 1969). The method of multiple comparisons of Duncan (1955) as modified by Kramer (1956) for unequal sample sizes and programmed for the computer by Vanzolini

(1969) was used to compare means. Asterisks denote probability values as follows: *** = $P \leq 0.001$; ** = $P \leq 0.01$; * = $P \leq 0.05$; and the notation ns = $P > 0.05$. Specimens collected were deposited in the Royal Ontario Museum, Toronto, and identifications were made by the authors.

Species Studied—*Hyla labialis*, a semi-arboreal frog, occurs in moist situations in the highlands (2,000–3,500 m) of the eastern Andean Cordillera of Colombia from the southern part of the Departamento de Cundinamarca northward into the Departamento de Norte de Santander (Cochran and Goins, 1970). This species, although strongly heliotropic, is active during day and night. Frogs frequently rest in the open and bask on vegetation near pools of still water in gardens, grassy margins of spring basins, in flat pastures of dense, matted grasses and sedges, and on plants in paramos (Stebbins and Hendrickson, 1959). Reproduction is acyclic, and oögenesis occurs throughout the year (Hunter and M. de Valdivieso, 1962). The call, a low croak, is given occasionally during the day but is more commonly heard during the early hours of darkness. *H. labialis* has several colour phases (Dunn, 1944), but the most frequent colouration is a uniform, bright green dorsum, with a paler venter and blue in areas of concealed surfaces. Some frogs lack any shade of green and are golden brown. Between these extremes occur all combinations of dorsal colouration, with various shades of green or golden brown forming irregular spots on the background. This frog has some ability to change the tone of colour but not the pattern.

Adult males, distinguished by a vocal sac and the swollen base of the thumb, reach 43 mm in SVL whereas larger adult females may measure 60 mm. Most frogs studied (150) were juveniles that measured 20–34 mm in SVL. Twenty-eight were adult males (SVL 35–39 mm), and nine were adult females (SVL 42–60 mm). Nine frogs with SVLs between 39 and 42 mm were classi-

fied as young adult females (ova ≤ 1.2 mm; see Hunter and M. de Valdivieso, 1962). As juveniles represented 76.5 per cent of the sample, we tested mean SVLs of five groups from different thermal environments and found them not to differ statistically (F -ratio = 1.523 ns; $df = 4, 125$). Therefore we concluded that all juveniles came from the same population, and SVLs were pooled for statistical analyses.

Study Area—Observations were made in a garden of a country home in a northern suburb of Bogotá. Although several ornamental plants grew in the garden, frogs seldom frequented them but were abundant on the leaves and stems of the amaranth (*Eresine linden*) and the California privet (*Ligustrum ovalifolium*). Leaf litter and debris several centimetres deep at the base of the stems of these shrubs were often used by frogs as cover at night. In the garden, where more juveniles than adults were encountered, free water was not available except for an unused, covered well that was rarely inhabited by frogs. Adjoining the garden to the east was a shallow, water-filled drainage ditch in which tadpoles of *H. labialis* were numerous.

Climate—The Bogotá region is situated in the lower montane dry forest formation (Espinal and Montenegro, 1963). Rain falls in every month, but generally two dry and two wet seasons with poorly defined limits alternate. At Bogotá the number of extreme days of rainfall varies annually from 152 to 264, with an average maximum rainfall of 1,083 mm (Pérez Arbeláez, 1954). In 1967 most rain (>60 mm) fell in February, April through June, and September through November, and in 1969 in April through June and October through December. In July 1967 precipitation measured 84.6 mm and was recorded on 21 days; in June and July 1969 precipitation was 69.2 mm for 17 days in June and 14.1 mm for 14 days in July. Normal, daily temperature fluctuation is from 4.4°C at night to 17.2°C in midafter-

noon (U.S. Army, 1961). The yearly mean temperature at Bogotá is 14.5°C and nearly constant from warmest to coldest months (Pérez Arbeláez, 1954). In July 1967 and in June and July 1969 the minimum recorded air temperatures, respectively, were 3.5° , 6.2° , and 0.9°C , and maximum temperatures were 19.6° , 22.2° , and 20.8°C , respectively. The annual mean relative humidity at Bogotá is 69 per cent (Pérez Arbeláez, 1954), and mean relative humidities for July 1967 and June and July 1969 were 73, 78, and 79 per cent, respectively. For these months relative humidities were higher in the morning (46–100 per cent) and in the evening (60–94 per cent) and lower in the early afternoon (41–79 per cent). Mean and extreme dew point values for July 1967 and June and July 1969 were, respectively, 7.9 (7.0–8.7), 11.1 (9.3–12.1), and 11.7 (10.6–12.8). Winds were never strong, and mean velocities (m/sec) averaged 6.1 in July 1967 and 5.2 and 6.9, respectively, in June and July 1969. The total annual variation in day length at latitude 4°N in Colombia is approximately 24 minutes (Miller, 1959).

Results

Body Temperatures—The activity range of *H. labialis* was 11 – 28°C (Table 1). The minimum (11.4°C) was recorded from an adult female exposed on vegetation at night (1935 hr) when $T_a = T_b$. The maximum (28.0°C) was that of an adult, basking male at 1406 hr when T_a was 16.0°C . The mean T_b of all frogs was $18.2^{\circ}\text{C} \pm 0.29$. Activity ranges of age groups were 11.8 – 27.6°C for juveniles, 16.2 – 26.4°C for young adults, and 11.4 – 28.0°C for adults. The basking range of all frogs was 18.0 – 28.0°C (although only one T_b was 28.0°C , and most were less than 25.0°C). T_b s among age groups, however, did not differ from each other (F -ratio = 0.731 ns; $df = 2, 193$).

T_b s of frogs taken in the morning (mean, $19.8^{\circ}\text{C} \pm 0.51$) were not statistically different (F -ratio = 1.851 ns; $df = 1, 130$) from those taken in the afternoon (mean,

Table 1. Ambient (T_a) and body (T_b) temperatures ($^{\circ}\text{C}$) of the frog *Hyla labialis* from Bogotá, Colombia

	n	Mean $\pm$ S.E.	Activity range	CV
DAY				
Basking				
T _b	26	22.9 $\pm$ 0.58	18.0–28.0	12.8
T _a		17.2 $\pm$ 0.43	13.4–20.8	12.8
Shade, exposed on plants				
T _b	68	20.5 $\pm$ 0.43	15.4–27.6	17.3
T _a		15.2 $\pm$ 0.20	12.2–19.8	11.0
Shade, concealed in plants				
T _b	37	16.9 $\pm$ 0.24	14.6–21.2	8.7
T _a		15.6 $\pm$ 0.20	13.6–18.8	8.0
All frogs				
T _b	131	20.0 $\pm$ 0.32	14.6–28.0	18.3
T _a		15.7 $\pm$ 0.16	12.2–20.8	11.8
NIGHT				
Exposed on plants				
T _b	47	14.2 $\pm$ 0.24	11.4–19.0	11.6
T _a		11.6 $\pm$ 0.14	9.6–13.4	8.5
Concealed in plants				
T _b	18	15.5 $\pm$ 0.51	12.4–20.8	14.1
T _a		13.3 $\pm$ 0.25	10.8–15.0	7.8
All frogs				
T _b	65	14.5 $\pm$ 0.24	11.4–20.8	13.1
T _a		20.1 $\pm$ 0.15	9.6–15.0	10.3

$19.5^{\circ}\text{C} \pm 0.43$). The lowest T_b taken in the morning was 14.8°C ($T_a = 15.4^{\circ}\text{C}$) at 1140 hr from an adult male concealed in vegetation on a cloudy morning, and the highest morning T_b (27.6°C) was recorded from a basking juvenile at 1112 hr when $T_a = 15.2^{\circ}\text{C}$. The lowest afternoon T_b (14.6°C) was that of an adult female concealed in vegetation at 1515 hr when the sky was overcast and T_a was 14.2°C .

T_b s of frogs taken in the morning and afternoon were significantly higher (F -ratio = 124.537^{***} ; $df = 1, 194$) than those taken at night. At night the highest T_b (20.8°C) was that of a juvenile concealed in vegetation (1612 hr; $T_a = 16.0^{\circ}$). The mean T_b for frogs taken at night was $14.7^{\circ}\text{C} \pm 0.25$.

Response to Environmental Temperatures—
SVLs of all frogs on body and air tempera-

tures were tested by the least-squares method of regression. SVLs and T_b s were not statistically related ($t = 0.669$ ns; $df = 172$), nor were SVLs and T_a s ($t = 0.034$ ns; $df = 174$). Body temperatures generally exceeded air temperatures (Fig. 1), and a line was fitted to these data by the method of Bartlett. The regression of T_b s and T_a s was statistically significant ($T_0 = 12.848^{***}$; $df = 193$), but there was no statistically significant departure from isometry ($T_1 = 0.134$ ns; $df = 193$) or from linearity ($T_L = 0.388$ ns; $df = 193$). Moreover, all correlations of T_a s and T_b s were statistically significant (all temperatures: $r = 0.674^{***}$, $df = 194$; diurnal temperatures: $r = 0.437^{***}$, $df = 129$; nocturnal temperatures: $r = 0.311^{**}$, $df = 63$). Although the regression and correlations are significant, this merely indicates a causal relationship between T_a s and T_b s,

but the closeness of such a relationship may not be biologically important and could be due to a common relation to other variables such as metabolic, bioclimatic, and even geographic conditions.

Only 30 frogs possessed T_{bs} within 1°C of the air temperature. Nine individuals were recorded with T_{bs} $0.2^{\circ}\text{--}1.2^{\circ}\text{C}$ less than ambient temperatures, and six frogs maintained T_{bs} greater than 10°C above ambient

temperatures. Only five frogs had T_{bs} that were isothermic with ambient temperatures. Body temperatures of frogs in deep shade deviated the least ($1.6^{\circ}\text{C} \pm 0.23$) from ambient temperatures, and those with the greatest deviations of T_{bs} from T_{as} were basking frogs ($5.8^{\circ}\text{C} \pm 0.68$) and frogs in exposed, resting positions under overcast skies ($5.3^{\circ}\text{C} \pm 0.35$). The maximum positive deviation of T_b from T_a (12.0°C) was that of one basking frog.

Coefficients of variation (CV) of T_{bs} of frogs in different environmental situations ranged from 8.7 to 17.3 (Table 1). The least variable T_{bs} were those of frogs concealed in vegetation on cloudy days, those of frogs exposed on vegetation at night, and those of frogs that were basking. The largest CVs were those of temperatures of frogs concealed in vegetation at night and of those exposed on vegetation in the day during cloudy periods. T_{as} s, however, were generally less variable than T_{bs} (Table 1), and the lowest CVs were those of T_{as} taken at night and in vegetation on cloudy days.

Heterogeneity among T_{bs} of frog samples was pronounced (F -ratio = 17.792***; $df = 4, 191$), more so during the day than at night (Fig. 1). Results of Duncan's multiple range test (Table 2) demonstrated that of the five means tested, only two subsets were significantly different, and the non-significant subsets were sharply demarked into those

frogs with higher T_{bs} and those with lower T_{bs} .

Daily Activity Cycle—Adults and subadults of *Hyla labialis* were active in the morning and early afternoon but were seldom out at night. Juveniles, on the other hand, were active at all hours but most active at night. At T_{as} s of 16°C or greater and T_{bs} more than 18 – 20°C , frogs began to jump and were difficult to approach. If T_{as} were less than 16°C and T_{bs} less than 18 – 20°C , frogs did not jump but walked slowly when disturbed. Lethargy induced by cold did not immobilize them, however, as frogs could easily be prodded to move when T_{bs} were as low as 12°C . Although calls were heard occasionally during the day, most frogs began to call at dusk and then intermittently throughout the night.

Daily cycle of activity was influenced by fluctuating meteorological conditions. Heavy rain (8.5 mm) inhibited activity, but light continuous rain (0.5 mm) increased activity. Usually a continuous drizzle throughout the night and dew in the early morning also increased activity. Frogs tended to remain concealed in vegetation during days with periods of light cloudiness and occasional sprinkles. Winds were usually light in the early morning (ca 0.96 m/sec at 0700 hr) and early evening (ca 2.12 m/sec at 1900 hr) but stronger toward mid-day (ca 5.23 m/sec at 1300 hr) and did not seem to affect

Table 2. Results from Duncan's multiple range test for body temperatures ($^{\circ}\text{C}$) of the frog *Hyla labialis* from Bogotá, Colombia. Horizontal lines connect maximally non-significant subsets of means.

	Basking		Other positions		
		Exposed (shade) on plants	Concealed (day) in plants	Concealed (night) in plants	Exposed (night) on plants
Mean $\pm$ S.E.	22.9 ± 0.58	20.5 ± 0.43	16.9 ± 0.24	15.5 ± 0.51	14.5 ± 0.24
n	26	68	37	18	47

noticeably activities of frogs. Maximum wind velocities, e.g., 10.3 m/sec on 4 days in July 1969, similarly did not affect behaviour.

H. labialis did not orient themselves to receive maximal, incident insolation but maintained a fixed position for several hours when basking. Positions appeared to be random or disoriented to the direction of the sun. The shape of the plant or object on which they rested appeared to determine their orientation. Moreover, they usually did not move if shade or partial shade resulted from a change in the position of the sun. They normally rested on leaves of plants in a semihorizontal, prostrate position with the posterior part of the body toward the petiole. They were rarely seen in vertical positions or on broad-leaved plants. Once a resting or basking site was occupied, a frog rarely moved from it during the day. The diurnal site was usually abandoned at dusk or after sunset. Often a frog would bask or rest at the same site for several consecutive days, e.g., an adult female basked in the centre of a rose flower for 4 consecutive days in July 1969.

Casual observations indicated that frogs of both colour phases basked equally on plants with green or dark-red leaves, but when exposed at night, more appeared to occupy leaves of dark-red plants rather than those of green plants, possibly to minimize heat loss.

Discussion—In thermoregulatory behaviour, *H. labialis* is a thermophilic heliotherm whose body temperatures are usually higher than ambient temperatures owing to basking or by absorbing solar radiation that filters through light cloud cover. Although the activity range of body temperatures of *H. labialis* was previously reported to be only a few degrees (Brattstrom, 1970), we found this frog to have an activity range of almost 17°C.

Although data are meagre for high-altitude, neotropical anura, T_b s of *H. labialis* are not unlike other eurythermic, montane

species of the genus; e.g., *H. regilla* from Oregon has an activity range of 8–22°C but a lower mean T_b (15°C as opposed to 18.2°C in *H. labialis*), and *H. californiae* has an activity range of 13–26°C and a mean T_b of 19.5°C (Brattstrom, 1963). Data presented here for *H. labialis* support the conclusion of Brattstrom (1968) that neotropical, montane frogs, in terms of ability to adjust physiologically to temperature changes, react similarly to temperate species from equivalent thermal latitudes. Moreover, *H. labialis*, which has a relatively narrow altitudinal distribution and a wide geographic distribution, differs from many lowland-derived montane hylids with restricted geographic ranges (Brattstrom, 1970) by having a wide temperature tolerance but little ability for short-term physiological adjustment (Hutchison, 1971).

In the Andes, ambient temperatures are modified by long-distance ocean effects, whereas insolation, on the other hand, is correlated with latitude (Schwabe, 1968). The discordance between insolation and ambient temperatures results in pronounced, daily climatic fluctuations, and at high altitudes differences between microclimates are exaggerated. Consequently, a wide selection of temperatures is encountered. In air, amphibians may have temperatures well above ambient when exposed to radiant heat, but, in shade, their body temperatures tend to fall toward the dew point, as the skin presents a moist surface (Lillywhite, 1971). Dew point fluctuates less than dry bulb temperatures, and terrestrial amphibia therefore have a more constant thermal environment than would be otherwise expected (Fry, 1967). In the Bogotá Savanna, frost, except at ground level, is rare, although night-time temperatures lower than 10°C (e.g., 8.2°C on 15 July 1967) are not uncommon. That low temperatures *per se* are ever a serious problem is unlikely for *H. labialis*, which spends considerable time in sheltered locations. Moreover, these frogs apparently do not exhibit heat stress, for they were never seen to retreat from exposure to continuous

sunlight to microhabitats that had lower ambient temperatures.

Resumen—Estudiamos las relaciones termal de la rana heliotérmica *Hyla labialis* en Bogotá, Colombia, a una altura de 2.650 m en julio de 1967 y en junio y julio de 1969. Los modelos de actividad diarios son controlados principalmente por la temperatura. Cielos nublados, lo mismo que temperaturas bajas, reducen los movimientos de este anfibio. *H. labialis* mantiene temperaturas corporales entre límites bastante amplios. Dichas temperaturas son afectadas notablemente por las temperaturas ambientales. Límites de actividad normal de las temperaturas del cuerpo varían de 11°C a 28°C, siendo la temperatura media 18.2°C. Las temperaturas corporales de la mayoría de las ranas estudiadas (76 por ciento), sin embargo, se extienden entre 13°C y 22°C. El promedio de las temperaturas del cuerpo es inferior durante la noche (14.5°C) y superior cuando se exponen al sol (22.9°C).

El comportamiento termorregulatorio de esta rana se debe a la insolación o a la absorción de radiación solar que penetra a través de ligeras capas de nubes uniformes. Por esta razón las temperaturas del cuerpo son usualmente mayores que las temperaturas ambientales. *H. labialis* permanece

considerable tiempo en lugares resguardados, aparentemente no exhiben tensión termal alguna debido a los rayos solares, ya que estas ranas no se retiran de sus moradas de exposición continua al sol a otros lugares de temperaturas ambientales inferiores.

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