

Factors Affecting Body Temperatures of Toads

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Summary. Factors influencing levels and rates of variation of body temperature (T_b) in montane *Bufo boreas boreas* and in lowland *Bufo boreas halophilus* were investigated as an initial step toward understanding the role of natural thermal variation in the physiology and energetics of these ectothermic animals. Body temperatures of *boreas* can vary 25–30° C over 24-h periods. Such variation is primarily due to both nocturnal and diurnal activity and the physical characteristics of the montane environment. *Bufo boreas halophilus* are primarily nocturnal except during breeding and are voluntarily active at body temperatures ranging between 10 and 25° C. Despite variation in T_b encountered in the field, *boreas* select a narrow range of T_b in a thermal gradient, averaging 23.5 and 26.2° C for fasted individuals maintained under field conditions or acclimated to 20° C, respectively. In a thermal gradient the mean T_b of fasted *halophilus* acclimated to 20° C is 23.9° C. Skin color of *boreas* varies in the field from very dark to light. The dark skins absorb approximately 4% more radiation than the light ones. Light colored *boreas* should absorb approximately 5% more radiation than similarly colored *halophilus*. Evaporative water losses increase directly with skin temperatures and vapor pressure deficit in both subspecies. Larger individuals heat and cool more slowly than smaller ones. Calculation of an energy budget for boreal toads suggests that they could sit in direct sunlight for long periods without fatally overheating, providing the skin was continually moist.

Introduction

Variations in body temperature (T_b) are undoubtedly an important factor in the biology of ectothermic animals since T_b affects not only the kinetics of biochemical and physiological processes but also the rate at which energy and materials can be extracted from the environment and used for maintenance, growth, and reproduction. Under appropriate conditions many terrestrial

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ectotherms can stabilize T_b for certain periods by behavioral means (Cowles and Bogert, 1944; Brattstrom, 1963; Heath, 1965; Licht et al., 1966; DeWitt, 1967a, b; Bradshaw and Main, 1968; Lillywhite, 1971; Lillywhite et al., 1973; Gatten, 1974). However, most terrestrial ectotherms are exposed to some, if not substantial, daily and seasonal variation in T_b due to behavioral choice (Brett, 1971) or variation in ambient temperature (T_a). The precise effect of such variation on the physiology and energetics of an ectothermic species is currently difficult to define for two reasons. First, detailed information on the extent and rapidity of daily and seasonal variation of T_b is lacking for most species and second, the extent to which the physiological responses of laboratory acclimated animals to variation in T_b accurately reflect responses of similar individuals exposed to natural thermal variation is not clear.

Since T_b is a complex integration of behavior, physiology, morphology and characteristics of the physical environment of the animal (Bartlett and Gates, 1967; Norris, 1967; Porter and Gates, 1969; Tracy, 1972; Porter et al., 1973; Tracy, 1975; Bakken and Gates, 1975; Bakken, 1976b), an initial step in understanding the effect of thermal variation on the physiology and energetics of an ectothermic species is to document the fluctuations of the ambient environment and the particular properties of the group which might affect the range and rapidity of fluctuations of T_b . Since the implications of fluctuating T_b might be especially interesting in a species living in a habitat characterized by extensive daily and seasonal variations in ambient temperature, the particular group chosen for this study is the boreal toad, *Bufo boreas boreas*. It is a member of a widely distributed form with populations ranging from sea level to over 3550 m in western North America (Campbell, 1970). At the upper altitudinal reaches of its distribution, the high transparency and low density of mountain air provide little attenuation of solar insolation during the day and foster large radiational losses of heat at night. These factors combine to produce wide daily fluctuations in substrate and ambient temperature. *Bufo boreas halophilus*, a lowland relative occupying a thermally less variable habitat, is included for comparison. The physiological and energetic consequences of the variations in T_b encountered by these two groups will be addressed in subsequent papers.

Materials and Methods

Solar and Thermal Characteristics of the Montane Environment

Air temperatures and solar radiation were monitored at ground level (0.2 m) at the Rocky Mountain Biological Laboratory (RMBL), Gothic, Gunnison County, Colorado (elevation 2900 m), in June-August, 1973. Air temperatures were recorded by a hygrothermograph (Bendix Corp.) appropriately shielded from sunlight in a ventilated shelter. Intensity of solar radiation was registered by a recording pyranometer (Beaufort Instruments).

Body Temperatures of Active Toads

Bufo b. boreas were captured in the East River valley near RMBL between May and August, 1971-1975. They were collected in moist, grassy areas around beaver ponds or streams at altitudes

between 3000 and 3355 m. *Bufo boreas halophilus* were captured in March of 1972–1974 at the Devil's Gate Reservoir, La Canada, Los Angeles County, California. In the following discussion "boreas" will designate the nominate subspecies, *Bufo b. boreas*, and "halophilus" will designate the subspecies *Bufo boreas halophilus*.

The T_b of each toad was measured orally immediately after capture with a suitably calibrated small animal thermistor (time constant = 3.6 s) connected to a YSI telethermometer. The thermistor was inserted 2–4 cm into the esophagus, the exact distance depending on the size of the toad. The animal was grasped by the legs to minimize heat exchange with the fingers of the investigator. To determine whether grasping the animal in this manner affected the measurement, a thermocouple connected to a Honeywell-15 multipoint recording potentiometer was implanted near the heart in the body cavity of an anesthetized, 40-g toad. After the toad had come to thermal equilibrium in a refrigerator at 8° C and had recovered from the anesthetic, its T_b was taken orally with the thermistor by the same method used in the field. The time required for this measurement (5–10 s) left unchanged the deep T_b measured by the thermocouple. Therefore, this temperature was reflected adequately by the oral value.

Following determination of T_b , the air temperature (T_a) at the place where the toad was picked up was measured at ground level by a shaded YSI air probe. The temperature of the substrate (T_{sub}) was recorded with the small animal probe by inserting it 2–3 mm beneath the surface of the soil or water.

Telemetry of Body Temperatures of Bufo b. boreas

The T_b of six adult boreas, intensity of solar radiation, T_a , T_{sub} , and wind speed were measured for 24-h periods between late June and early August. The T_b was transmitted by a radiotransmitter (Mini-Mitter, Inc., Indianapolis, Indiana) which was 9 mm wide, 11 mm long, and weighed 2.4 g. It was calibrated in a water bath against a mercury thermometer which had been previously calibrated against a Bureau of Standards thermometer. To test whether the time constant of the telemetry device was sufficiently short to permit accurate tracking of T_b during heating and cooling, a copper-constantan thermocouple and the telemetry device were implanted in the abdomen of a 46-g anesthetized toad in such a manner that they registered T_b from the same region. The toad was transferred to a refrigerator following recovery from anesthesia. The rate of cooling recorded from the thermocouple with a Honeywell-16 recording potentiometer was similar to that indicated by the transmitter. The observed rate of cooling was faster than the rates noted in the field. The telemetry device was therefore judged to track changes in T_b accurately in the field. No hysteresis was noted when calibration curves for warming or cooling were compared. The transmitter, tested before and after each implantation in a toad, exhibited no drift in calibration. The transmitter was placed in the body cavity of a toad via a ventral incision after anesthesia with 2% tricaine methanesulfonate (1.0 ml/100 g body mass). Toads were not used for the telemetry study unless they were active and alert following surgery.

Approximately 48–72 h after implantation of the transmitter, the toad was placed in a 2.5 × 2.5 m enclosure of 0.5 m screen fence located near a beaver pond at 3050 m altitude. The toad had access within the enclosure to areas exposed to sunlight during the day, shade provided by willows (*Salix*) and a small spruce (*Picea*), and standing water from a small spring. The area in the enclosure resembled the moist substrate upon which the toads were typically captured. Measurements were recorded approximately 15 m from the enclosure so that the toad was not disturbed for the duration of the test. An antenna of copper wire was strung in parallel loops at 10 cm intervals on a wooden frame placed on the ground in the enclosures. Signals from the transmitter were picked up by the antenna and transferred by coaxial cable to the antenna of a battery powered AM radio. Substrate temperatures in an unshaded area of the enclosure were recorded by a small animal thermistor placed 1–2 mm beneath the surface of the soil and connected by a long lead to a YSI telethermometer. Wind speed measured by a microcup (2.5 cm) impulse anemometer (Rauchfuss Instruments) mounted 3–4 cm above the ground in the enclosure. Air temperatures at 1 cm were measured by a shaded YSI probe. Solar radiation was read directly from a pyranometer located in the sun 15 m from the enclosure.

Each toad was placed in the enclosure between 1800–2000 h. Recordings of T_b and environmental data began 0630 h the next morning and continued every 30 min until direct sunlight reached the enclosure at approximately 0800–0830 h (MTD). Between 0800 and 2000 h, readings were taken

every 5 min, between 2000 and 2200 every 30 min, and between 2200 and 0630 approximately every 2 h.

Two 24-h experiments tested the possibilities that confinement in the enclosure or implantation of the telemetry device altered the behavior of experimental toads. Two toads without implanted transmitters were released, one into a second enclosure similar to the one used for telemetry and the other into an adjacent marshy area. Body temperatures were taken orally approximately every 2 h. Temperatures recorded for these toads were compared with telemetered T_b of a third toad tested concurrently in the regular enclosure.

Thermal Preference

Selection of body temperatures by eight adult *boreas* in a thermal gradient was measured in June, 1973–74, at RMBL. The toads, with a mean body mass of 32.8 g (range 30.2–49.8 g), were captured near Gothic, Colorado, and housed under natural conditions of light and temperature. Additionally, temperature preferences of six *boreas* and eight *halophilus* acclimated to 20° C and a 12 h L/D photoperiod for at least one month were measured at The University of Michigan. The *boreas* were tested in August and September, 1973, and the *halophilus* in May 1972. Mean body masses of the acclimated animals were 34.5 and 41.2 g for *boreas* and *halophilus*, respectively. Male and female toads did not have significantly different T_b , so their values have been pooled for each subspecies.

A thermal gradient was constructed from a galvanized steel trough 2.8 m long, 0.4 m high, and 0.2 m wide. The apparatus was placed in a controlled temperature room at 10° C, which set the lower limit of the gradient. The upper temperature of the gradient, 43° C, was produced by a heat lamp positioned over the trough. A linear increase in temperature from the cold end was achieved by winding electrical heating tape from side to side in the trough in a zigzag pattern of increasing narrowness as the warm end under the heat lamp was approached. The floor of the trough was covered with 3 cm of peat moss saturated with water. The tape was completely covered by the peat moss, but toads often burrowed through the moss to sit directly on it. Water was added approximately every 12 h to keep the moss fully saturated. An overhead fluorescent lamp was turned on for 12 h each day. The heat lamp remained on at all times during the test.

About 24 h before a test, a toad which had been fasted for 6–8 days was anesthetized with 2% tricaine methanesulfonate. A previously calibrated 36-ga copper-constantan thermocouple was sewn into a dorsal incision in the back. The thermocouple was inserted about 2 cm into the body cavity between the lung and the viscera so that it registered T_b near the heart, with placement later confirmed by dissection. The fasted toad was placed in the trough at 0900 h and was undisturbed for the next 24 h except at 2100 h when water was added to the peat moss. At 0900 hr the next morning, the toad was force fed a meal of crickets equal to 1–2% of its body mass and replaced in the gradient for another 24 h. The meal size was selected because it equaled the mean mass of stomach contents of *boreas* in the field, corrected for the mass of digestive fluid (Carey, unpubl. data). Every 30 s body and substrate temperatures, measured by thermocouples placed in the peat moss every 0.4 m, were recorded to the nearest 0.1° C by a Honeywell-16 recording potentiometer. The toads usually wandered within the gradient for several hours following introduction into the trough and then settled in one location for the duration of the test. Body temperatures recorded during the initial period were omitted from consideration in determining the preferred T_b . Once the toad settled down, T_b recorded at 30- to 45-min intervals were taken from the potentiometer record. Ten to 30 records from each animal in both the fasted and fed condition were averaged to determine the preferred temperature of each subspecies and the effect of feeding on the preferences. Mean values were compared with a non-parametric Bayesian posterior probability test (Lindley, 1965), because assumptions of normality and equality of variances did not hold for these data. Statistical significance was assumed if $P < 0.01$.

To test whether implantation of the thermocouples altered the preferred temperatures, 10 unfed *boreas*, housed under natural conditions at RMBL, were placed individually in the trough for 24 h. Oral T_b were measured with a YSI telethermometer at 6-h intervals.

The possibility existed that the T_b selected by toads during the second 24-h period might reflect greater familiarity with the chamber containing the thermal gradient rather than the effect of feeding on preferred temperature (see Heath, 1965). To test this, two unfed toads were tested

in the gradient for 48 h each, with interruptions only every 12 h for addition of water to the peat moss.

Effects of Color Change on Absorption of Radiation

The skin color of *boreas* in the field varies from a dark brown to a light, creamy color. Dark colors are most often associated with toads at cooler T_b and light colors with toads at warmer T_b . Live toads were tested to determine if this variation in color could affect absorption of solar radiation.

Reflectance of wavelengths of 290–2600 nm by skins of live *boreas* was measured by a Beckman DK-2A dual beam, ratio-recording spectroreflectometer. Principles underlying the operation of the Beckman DK-2A for tests such as this are reviewed by Porter (1967).

Individual toads were immobilized by strapping them with electrical tape onto an aluminum block similar to that illustrated in Norris (1967). The T_b of the toad could be regulated by pumping water from thermostatically controlled water baths or ice baths through the block. Skin color of *boreas* was unaffected by short-term changes in T_b or electrical stimulation, methods which have been employed successfully to achieve color change and maximum blanching of reptiles (Norris, 1967; Porter, 1967). However, color change in these toads can be induced in the laboratory by maintaining them at cold or warm temperatures. Two dark toads, freshly captured in Colorado and held for 2 weeks at 10° C, were compared with two light toads acclimated to 30° C for 2 months. While the color of skins of these toads may not represent the absolute extremes of blanching or darkening possible for this species, the colors were quite distinct visually from each other and similar to observed differences in the field. After a toad was mounted on the aluminium block, a quartz disc, used to prevent light leaks and contamination of the integrating sphere, was tightly pressed on the back to one side of the spinal cord and fastened into place with black electrical tape. The block was mounted on the spectrophotometer in a way that the quartz disc fitted directly over the sample port. A similar quartz disc was placed over the reference slide covered with BaSO₄.

Ninety-seven reflectance values for each toad extracted from the spectroreflectometer record at prescribed intervals and were used in conjunction with the program devised by McCullough and Porter (1971) to calculate average absorption of solar radiation specific for the altitude and geographical location where the toads normally live.

Color change in *halophilus* is not as evident in the field as in *boreas* and cannot readily be induced by exposure to constant low or warm temperatures in the laboratory. One individual with a typical creamy, greenish skin was tested for comparison with the values for the montane species.

Relation of Evaporative Water Loss to Temperature

Evaporative water loss (EWL) of 40 to 60 g *boreas* and *halophilus* was measured in a system to be described in greater detail by Bakken (MS in prep.). Six animals of each subspecies were tested individually at The University of Michigan. Each was used only once at each test temperature. The toads were acclimated to 20° C for at least two weeks and starved for 4 days before testing.

The system consisted of a 20 × 10 × 13 cm chamber with two of the sidewalls and a detachable roof made of hollow Plexiglas. A metal pan covered with a wire screen and filled with mineral oil to catch urine served as a floor. The floor and wall temperatures were regulated near 10, 20, or 30° C by circulating water through the hollow Plexiglas from a temperature regulated water bath. The end walls of the chamber consisted of baffles constructed from horizontally placed plastic soda straws, 2 cm in length. All walls were painted non-reflective black. The sides and floor of the animal chamber and small fans for creating movement of air were enclosed in a temperature regulated, air-tight box. The roof of the chamber was flush with the top of the air-tight box. The fans recirculated the air, which was controlled at the same temperatures as the walls and roof of the chamber, into and out of the chamber through the baffles, producing essentially laminar flow (5% turbulence). The wind speed, 60.8 cm/s, was selected because it fell approximately in the middle of the range measured at ground level (3–4 cm) in the field. It was measured before and after each experiment with a temperature compensated anemometer (Thermo-Systems, Inc., model 1054A, probe 1330–18–20) connected to a TSI power supply, model 1051-2.

Dry air was introduced into the recirculating system from a compressed gas cylinder. The rate of flow of air was measured by a model 2232 TSI mass flowmeter. Most of the air was recirculated and the rest vented to the exterior. The system was maintained at a pressure slightly above that of the outside by bubbling the excurrent air through 2 cm of oil. The dew point was regulated in the chamber in part by the rate of inflow of dry air and in part by passing a portion of the recirculated air through a drying tube. A solenoid, controlled by a dew point hygrometer (EG & G Instruments, model 880), alternately routed the air leaving the animal through a Drierite (CaSO_4) filled drying tube, or a bypass which returned the air directly to the animal chamber. Water vapor pressure was accurately maintained at a relative humidity of 68–70% at the three temperatures tested. The water saturation deficit at this humidity varied from 3.68 mbar at 10°C to 12.72 mbar at 30°C. When the dew point was successfully regulated, input of water into the system by evaporation from the animal constituted its EWL at that temperature and wind speed.

A toad was weighed on a Mettler P160N top-loading balance after compressing the bladder to remove urine. Two copper-constantan thermocouples were inserted directly beneath the dorsal skin and glued into place with Permabond cement. One to 3 h were required for the water vapor pressure to reach the pre-set dew point and for the toad to become inactive. Then, drying tubes were weighed to the nearest 0.001 g on the Mettler balance and inserted into the recirculating air stream and at the excurrent air port. During each run of approximately 20–30 min, the dew point, flow rate of dry air, and temperatures of skin, air, roof, and walls were recorded every 2 min on a Kaye (Systems 8000) recorder. The amount of water collected in the drying tubes was determined gravimetrically and the lowest value for mass of water collected in the drying tubes during 3 runs was used as the EWL for each animal. The behavior of the toad was observed with a one-way mirror. Data for EWL were discarded if a toad moved in the chamber during the test. After each test was complete, the toad was quickly removed from the chamber and body temperature taken orally with a YSI thermistor and telethermometer. The toad was then reweighed. Decrease in body mass during the run cannot be used as an estimate of EWL due to the long equilibration period prior to the tests.

Relation of Rates of Heating and Cooling to Body Mass

The effect of body mass on the rate of heating and cooling was measured in the same apparatus used for measurement of EWL. Toads (15.3–60.7 g body mass) were anesthetized with 2% tricaine methanesulfonate. A thermocouple, sheathed with protective polyethylene surgical tubing, was implanted in the body cavity through the back. It was inserted 1 to 3 cm between the lung and spinal column into the viscera and glued into place with Permabond cement. An additional thermocouple was implanted directly beneath the dorsal skin. Each anesthetized toad was placed in the chamber in a posture similar to that used by toads basking in the field. The limbs were placed close to the body and the head lowered over the forelimbs. The toads remained anesthetized during the test, and the posture was not altered. Respiratory and heart rates were not observed due to the depth of the anesthesia. Air, wall, and roof temperatures were controlled at $9.4 \pm 0.2^\circ\text{C}$, $8.4 \pm 0.1^\circ\text{C}$ and $8.4 \pm 0.1^\circ\text{C}$, respectively. Dew point was regulated between 5 to 7.5°C . The rate of inflow of dry air was increased during heating and decreased during cooling to maintain dew point within those values. The effective wind speed, set at 30.4 cm/s, would have been slightly faster for larger toads, since they occupied more than 10% of the cross-sectional area of the chamber (W.P. Porter, pers. comm.). When the deep body T_b of the toad had approximately equilibrated with the surroundings, four Sylvania 500 Watt tungsten-halogen spotlights positioned 130 cm above the chamber were turned on. The radiation from these lamps passed through a 6 cm layer of water suspended in a Plexiglas box 1 m over the chamber and the Plexiglas roof of the chamber. The radiant heat load from the lamps was measured before and after each run with an Epply pyranometer, Model 8–48, connected to a Fluke 8000A digital multimeter. The radiation was constant for all runs at $1.15 \text{ cal (cm}^2 \cdot \text{min)}^{-1}$. Temperatures of the skin and core of the toad, air, wall, and roof and the dew point were recorded by the Kaye recorder. The lights were turned off when the T_b of the toad neared an equilibrium temperature. The T_b of the toad and environmental parameters were then recorded during cooling. Body temperatures extracted from the Kaye record for heating and cooling were analyzed using the program developed for this purpose by Bakken (1976a).

Results

Solar and Thermal Characteristics of the Montane Environment

Maximal values for solar radiation on clear, cloudless days reach 1.4–1.5 cal (cm²·min)⁻¹ (Fig. 1). Slightly higher values are recorded with scattered cloudiness due to reflection of solar radiation from the clouds. Periodic cloud cover results in highly variable levels of direct solar insolation reaching the ground on most days. Mountain peaks (3050–3680 m) on the eastern and western sides of the East River valley restrict the amount of direct solar insolation during the day. The intensity of solar insolation is already about 0.8–1.0 cal (cm²·min)⁻¹ by the time of morning the sunlight reaches the floor of the valley, and some parts of the valley are shaded from direct sunlight by a mountain as early as 1600 h in the afternoon.

Maximal daytime air temperatures reach 15–23° C on totally or mostly sunny days. Air temperatures on clear nights fall near or below 0° C. Cloud cover reduces daytime T_a to between 10–15° C, but accompanies higher nighttime temperatures ranging between 5 and 10° C. Late spring snowstorms occurring in late May to mid-June in 1973–75 produced daytime T_a near 0° C.

Body Temperatures and Behavior of Active Bufo boreas boreas

Activity of *boreas* in the fields is not confined to one phase of the daily period. After breeding in June, adults and juveniles (sexually immature, metamorphosed toads) are most often seen during the day in open, sunny, and moist areas near water. Orientation of the toads to the sun appears to be random. Toads sitting in the sun typically press the groin area onto moist substrate. Individuals rarely move more than a few meters during the day, long distance movements occurring primarily at night.

Body temperatures of toads are highly correlated with the extent of solar radiation. On clear days toads sitting in the sun have T_b ranging from 22–33° C, the exact temperature depending on the time of day. Temperatures of toads generally vary between 10 and 25° C on partly cloudy days, the exact values depending on the degree and frequency of cloud cover. At night the T_b of toads approximate T_a and T_{sub} , which are usually between 0 and 10° C. On nights when T_a drop below freezing, toads take cover under logs or submerge themselves under water. Several toads were caught between 0100 and 0200 h at night with frost on their backs and T_b of 0.2° C. The range of T_b recorded was 0.2 to 33.9° C with a mean \pm SE for 296 measurements of 20.7 \pm 0.4° C. Active males, females, and juveniles exhibited similar behavior and overlap in T_b .

Oral T_b of *boreas* are significantly ($P < 0.01$) correlated with both T_a and T_{sub} at the spot of capture (Fig. 2). Like T_b , levels of T_a and T_{sub} are highly correlated with the extent of solar radiation.

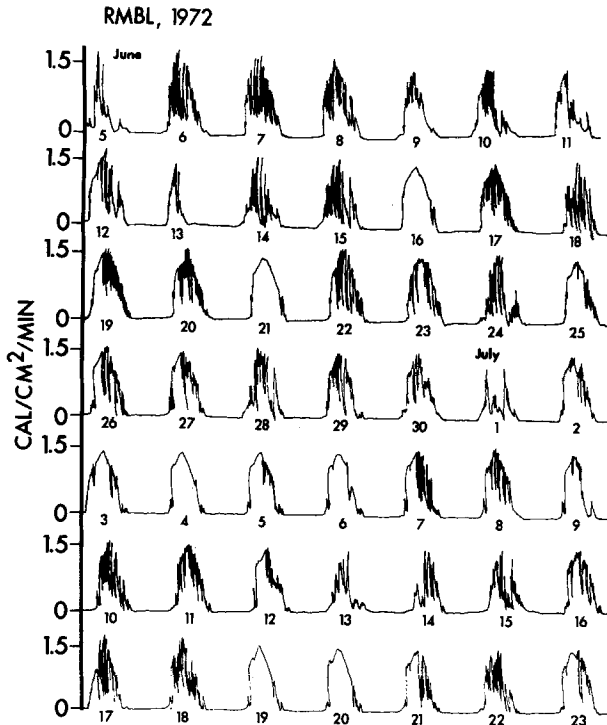


Fig. 1. Representative daily recordings of solar radiation for 5 June through 23 July 1972. Measurements were made at 2900 m near the Rocky Mountain Biological Laboratory, Gothic, Gunnison County, Colorado. Small numbers beneath each record denote day of month

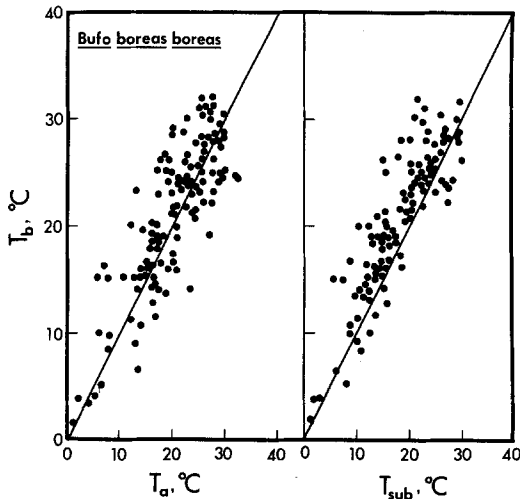


Fig. 2. The relations of oral body temperature (T_b) of *Bufo boreas boreas* to air temperature (T_a) measured at ground level and to substrate temperature (T_{sub}) at the point of capture of the toad. Measurements were made at 3050 m near Gothic, Gunnison County, Colorado. The data shown here represent only a portion of the total number of values collected, but the relation of T_b to T_a and T_{sub} shown by these data does not differ significantly from that of the total sample. The diagonal line in the middle of each graph marks equivalency between T_b and T_a or T_{sub} . Correlation coefficients for all data for T_b with T_a and T_{sub} equal 0.78 and 0.85, respectively. The linear relation between T_b and T_a for all data is best described by the least squares regression: $T_b = 4.5 + 0.825T_a$ ($n = 276$), and for the relation of T_b to T_{sub} : $T_b = 8.17 + 0.656T_{sub}$ ($n = 273$), where all temperatures are in degrees Celsius. The slope of both equations differs significantly from 1

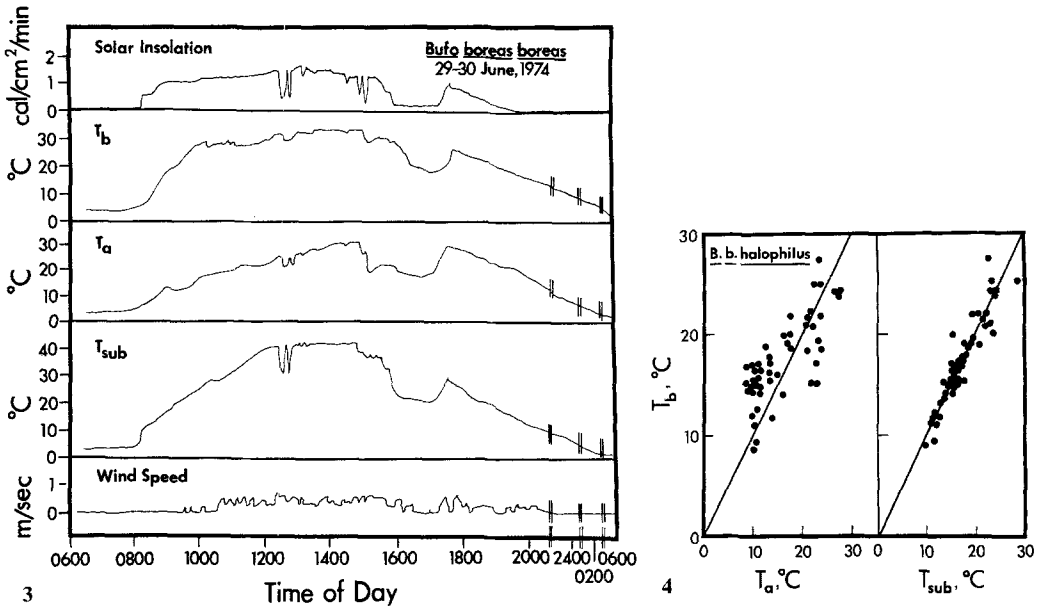


Fig. 3. Results of a typical 24-h measurement by telemetry of body temperature (T_b) of an adult, 52.1-g female *Bufo boreas boreas* in relation to solar insolation, ambient temperature (T_a), substrate temperature (T_{sub}), and wind speed. Dips in the record of solar insolation during daylight hours indicate periodic cloud cover. "Time of day" corresponds to Mountain Daylight Time. Initial values for T_b , T_a , and T_{sub} at 0630 on 29 June were 3.5, 4.0, and 2.9° C, respectively. Final values at the end of the test at 0630 on 30 June were 1.0° C (T_b), 0.5° C (T_a), and 1.5° C (T_{sub}). Measurements were made at an altitude of 3050 m near Gothic, Gunnison County, Colorado

Fig. 4. The relations of oral body temperatures (T_b) of *Bufo boreas halophilus* to air temperature (T_a) measured at ground level and to substrate temperature (T_{sub}) at the point of capture of the toad. Measurements were made at the Devil's Gate Reservoir, La Canada, Los Angeles County, California. The data presented here represent only a portion of the total number of values collected, but the relations of T_b to T_a and T_{sub} shown here do not differ significantly from that of the total sample. The diagonal line in the middle of each graph marks equivalency between T_b and T_a or T_{sub} . The least squares regression equation best describing the relation of T_b to T_a for all data is: $T_b = 8.37 + 0.519T_a$ ($n = 131$). The slope of that equation differs significantly from 1. The equation best describing the relation of T_b to T_{sub} is: $T_b = 0.12 + 1.00T_{sub}$ ($n = 131$)

Telemetry of Body Temperatures of Bufo b. boreas

Body temperatures of a 52.1-g adult female fluctuated between 1 and 32.1° C over a 24-h period (Fig. 3). Her T_b was 3.5° C at the start of the test at 0630 h on 29 June. When direct sunlight hit the enclosure, T_b increased at a rate averaging 0.19° C/min during the first hour. Body temperatures remained between 27 and 32.1° C from approximately 0945 to 1535 h. Short periods of cloud cover had a more dramatic effect on T_a and T_{sub} than on T_b . During prolonged periods of cloud cover, such as that commencing at 1535 h, T_b dropped from 31 to 21° C in 1 h. Body temperature decreased at an average rate of 0.12° C/min during the first hour after sundown.

Table 1. Twenty-four-h telemetry studies of body temperatures (T_b) of adult *Bufo boreas boreas*. Six values for rates of increase or decrease in T_b over 10-min periods were averaged to obtain the mean rate of warming (in the first hour after direct sunlight hit the enclosure after sunrise) and cooling (in the first hour following sunset) for each individual

Date ^a	Sex	Body mass (g)	Minimum T_b (°C)	Maximum T_b (°C)	Mean \pm SE rate of warming (°C/min)	Mean \pm SE rate of cooling (°C/min)
11–12 Aug.	♂	26.2	6.0	32.0	0.17 \pm 0.01	0.10 \pm 0.05
30 Jun.–1 Jul.	♂	32.5	0.5	31.5	0.23 \pm 0.04	0.06 \pm 0.02
2–3 Jul.	♂	34.2	3.2	30.0	0.18 \pm 0.02	0.09 \pm 0.04
29–30 Jun.	♀	52.1	1.0	32.1	0.19 \pm 0.03	0.12 \pm 0.02
1–2 Aug.	♀	63.7	5.2	30.5	0.15 \pm 0.01	0.10 \pm 0.04
10–11 Aug.	♀	82.7	7.0	27.5	0.16 \pm 0.01	0.11 \pm 0.03
2–3 Jul. ^b	♂	34.2	2.6	30.4	—	—
2–3 Jul. ^c	♂	31.4	2.8	27.7	—	—

^a All observations made in 1973 except 29–30 June and 30 June–1 July 1974

^b Oral T_b only, no telemetry device implanted. Toad restricted to enclosure similar to the ones used in all other tests

^c Oral T_b only, no telemetry device implanted. Toad not restricted to enclosure

Pertinent data for this toad are compared in Table 1 with those for 5 other toads obtained in similar 24-h tests. Body temperatures of these latter individuals fluctuated 20.5–30.0° C over the 24-h tests periods. The variation in T_b recorded for males and females is similar. Rates of heating and cooling were not significantly correlated with body mass because the data were collected under different weather conditions. Each toad heated faster than it cooled because solar radiation was intense in the early morning hours.

Implantation of the telemetry device appeared not to affect the range of T_b evident in toads. Telemetered T_b of a male toad recorded on July 2–3, 1974, closely approximated the oral T_b obtained concurrently from another male toad in a similar enclosure. However, containment in an enclosure might result in higher daytime T_b than those which the toads might attain if they were unconfined. Oral T_b of a free-ranging male were similar to telemetered T_b collected simultaneously at night. However, the daytime maximum was about 2.3° C lower than comparable telemetered daytime values.

Body Temperatures of Active Bufo boreas halophilus

Adult *halophilus* appear to be primarily nocturnal when not breeding, occupying burrows during the day. However, they are active both nocturnally and diurnally during the breeding season. Body temperatures of breeding adults range between 8.5 and 25.6° C with a mean \pm SE of 17.33 \pm 0.36° C for 131 measurements. The toads in this population are rarely active on nights when T_a fall below 10° C. On sunny and warm days the toads usually occupy their burrows or submerge themselves in deep water as T_b exceed approximately 25° C. Body

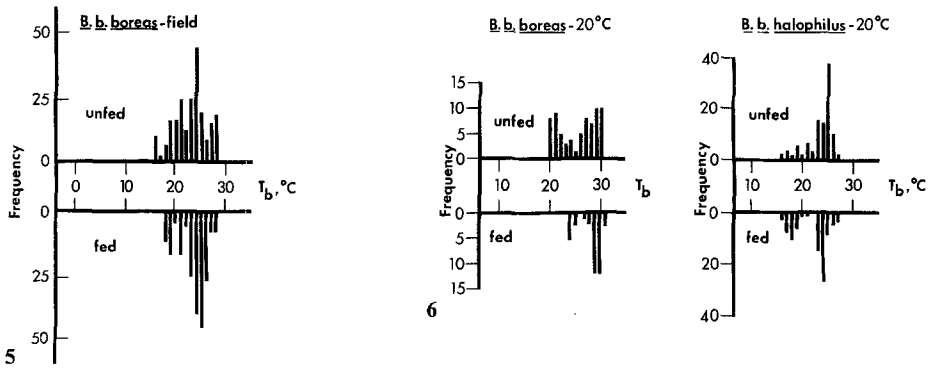


Fig. 5. Frequency distribution of body temperatures (T_b) of unfed (post-absorptive) and recently fed *Bufo boreas boreas* in a thermal gradient. Toads were maintained under natural conditions of photoperiod and temperature at the Rocky Mountain Biological Laboratory, Gothic, Gunnison County, Colorado

Fig. 6. Frequency distribution of body temperatures (T_b) of unfed (post-absorptive) and recently fed *Bufo boreas boreas* and *halophilus*. Animals had been acclimated to 20°C for at least one month before testing in a thermal gradient

temperatures of *halophilus* correlate significantly ($P < 0.01$) with air and substrate temperatures (Fig. 4). Since most of the toads were captured in the water, T_b is more highly correlated with T_{sub} ($r = 0.95$) than with T_a ($r = 0.73$).

Thermal Preference

Fasting *boreas* that had been maintained under natural conditions attained T_b averaging $23.5 \pm 0.23^\circ\text{C}$ ($\pm\text{SE}$) in a thermal gradient. After they were fed, their temperatures averaged $24.2 \pm 0.18^\circ\text{C}$ ($\pm\text{SE}$), a value slightly but significantly higher ($P < 0.01$) than that for unfed toads. The ranges of T_b for unfed and replete toads were 15.8 to 30.2°C and 18.0 to 29.2°C, respectively (Fig. 5). The variance of the preferred T_b for fed toads was significantly smaller ($P < 0.01$) than that for fasting toads, as judged by an F -test. Individual variation of T_b was small compared to the total variation for the group. For instance, two animals respectively selected mean ($\pm\text{SE}$) T_b of $24.4 \pm 0.18^\circ\text{C}$ (range 20.0 to 25.6°C) and $23.2 \pm 0.21^\circ\text{C}$ (range 21.0 to 24.9°C).

Implantation of the thermocouple had little influence on the level of thermal preference. The mean $\pm\text{SE}$ oral T_b of 10 fasted individuals placed in the thermal gradient without an implanted thermocouple was $23.7 \pm 0.30^\circ\text{C}$, a value not significantly different from that of toads with thermocouples. Significantly higher values for post-prandial toads appeared to be a response to feeding rather than the amount of time in the gradient. Two individuals placed in the gradient for 48 h without feeding selected mean $\pm\text{SE}$ T_b in the second 24 h ($22.4 \pm 0.42^\circ\text{C}$) which were not significantly different from the mean ($\pm\text{SE}$) values recorded during the first 24 h ($22.1 \pm 0.34^\circ\text{C}$).

Table 2. Mean \pm SE evaporative water loss (EWL), body and skin temperature, and experimental conditions of *Bufo boreas boreas* and *Bufo boreas halophilus* tested at wind speed of 0.60 m/s. Sample sizes are indicated by numbers in parentheses

	10° C	20° C	30° C
EWL mg (g·h) ⁻¹			
<i>B. b. boreas</i>	11.79 \pm 0.91(6)	21.74 \pm 1.30(6)	34.53 \pm 1.9(6)
<i>B. b. halophilus</i>	9.55 \pm 0.40(6)	27.20 \pm 1.70(6)	38.57 \pm 2.9(6)
Skin temp. (°C)			
<i>B. b. boreas</i>	7.45 \pm 0.14(30)	16.65 \pm 0.08(30)	25.11 \pm 0.09(30)
<i>B. b. halophilus</i>	7.34 \pm 0.08(30)	16.72 \pm 0.14(30)	25.09 \pm 0.09(30)
Oral T _b (°C)			
<i>B. b. boreas</i>	7.48 \pm 0.11(6)	17.21 \pm 0.27(6)	25.38 \pm 0.17(6)
<i>B. b. halophilus</i>	7.65 \pm 0.07(6)	17.58 \pm 0.11(6)	25.88 \pm 0.19(6)
T _a (°C)			
<i>B. b. boreas</i>	9.79 \pm 0.11(30)	19.97 \pm 0.19(30)	29.44 \pm 0.01(30)
<i>B. b. halophilus</i>	9.89 \pm 0.09(30)	20.40 \pm 0.08(30)	29.45 \pm 0.01(30)
Dew point (°C)			
<i>B. b. boreas</i>	4.0–4.8° C	13.6–14.2° C	23.0–23.6° C
<i>B. b. halophilus</i>	4.0–4.8° C	13.6–14.2° C	23.0–23.6° C

Fasted *boreas* acclimated to 20° C had T_b averaging 26.2 \pm 0.44° C (\pm SE), whereas the preference of fed individuals showed a significantly ($P < 0.01$) higher mean of 29.3 \pm 0.36° C. The range of temperatures selected decreased from 20.0–30.3° C for fasted individuals to 24.9–31.5° C for fed toads (Fig. 6). The variances of values for fed toads were significantly smaller ($P < 0.01$). The means for both fed and unfed *boreas* acclimated to 20° C are significantly ($P < 0.01$) higher than respective values for fed and fasted toads maintained under field conditions.

Unfed *halophilus*, acclimated to 20° C, selected temperatures averaging 23.9 \pm 0.26° C (\pm SE), a value not significantly different from the mean for fed toads, 23.2 \pm 0.38° C (Fig. 6). The variance for fed toads is significantly larger ($P < 0.01$) than for unfed toads. The mean of temperatures selected by fasted *halophilus* was not significantly different from that for unfed *boreas* maintained under field conditions, but the values for replete *boreas* are significantly higher ($P < 0.01$) than those for fed *halophilus*. Mean T_b for both fasted and replete *halophilus* are significantly lower than similar ones for *boreas* acclimated to 20° C.

Evaporative Water Loss

Evaporative water losses (EWL) of *boreas* and *halophilus* increase directly with skin temperature when measured under constant conditions of windspeed and relative humidity. The mean \pm SE EWL of *boreas* increased from 11.8 \pm 0.9 mg (g·h)⁻¹ at skin temperatures averaging 7.45° C to 34.5 \pm 1.9 mg (g·h)⁻¹ at a mean skin temperature of 25.11° C. Those of *halophilus* increased from 9.5 \pm 0.4

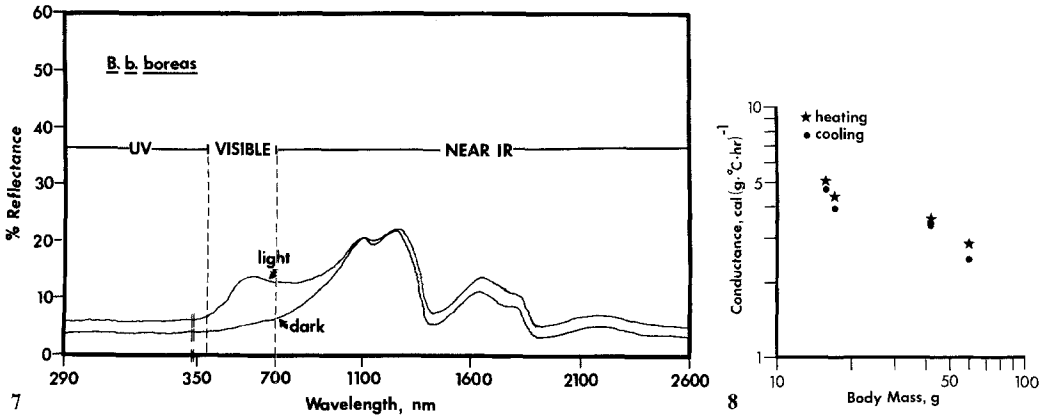


Fig. 7. Reflectance of various wavelengths by the light and dark colored skins of live *Bufo boreas boreas*. The values indicate the percent reflectance of monochromatic light of the same intensity at all wavelengths

Fig. 8. Relation of apparent conductance (k_a) to body mass in 4 *Bufo boreas boreas* under conditions of heating and cooling. The values are plotted on a double logarithmic grid

to $38.6 \pm 2.9 \text{ mg (g} \cdot \text{h)}^{-1}$ at similar temperatures (Table 2). Only at 20°C do the respective means for *boreas* and *halophilus* differ significantly ($P < 0.01$). Skin and deep body temperatures were consistently lower than air, wall, and roof temperatures.

Absorption of Solar Radiation

The reflectance curves for wavelengths of 290–2600 nm for a typically dark and a light-skinned *boreas* are shown in Figure 7. The principal differences between the curves are in the visible and near infrared wavelengths. The light skin reflects up to 12% of the radiation in the visible range, whereas the dark skin reflects from 4 to 6% in the same range (400–700 nm). The differences in the curves in the UV and near infrared are in part an artifact due to a greater amount of water on the surface of the light-skinned toad. The dips in the infrared at 1150, 1400, 1950, and 2400 nm are due to water absorption bands. Analysis of the entire reflectance curves by the program of McCullough and Porter (1971) reveals that the dark toad would absorb 92% and the light toad 88% of the total incident solar radiation on a clear, dustless day at 1200 MST on 21 June at 3000 m elevation and the geographical location of Gothic, Colorado.

A typically light colored skin of *halophilus* reflected between 6 and 21% of the radiation in the visible range. This skin would absorb 83% of the total incident solar radiation at the geographical location and altitude of Los Angeles, California on a clear, dustless day at 1200 PST on 31 March.

Table 3. Estimated (\pm SE) initial body temperatures (T_b^i), equilibrium body temperatures (T_b^{eq}), and time constants (τ) predicted by the program Newton II (Bakken, 1976) for *Bufo boreas boreas* of different body masses during heating and cooling

Body mass	Heating			Cooling			Cooling τ Heating τ
	T_b^i (°C)	T_b^{eq} (°C)	τ (s)	T_b^i (°C)	T_b^{eq} (°C)	τ (s)	
15.74	7.07 \pm 0.13	19.90 \pm 0.07	579.05 \pm 15.43	20.42 \pm 0.11	7.30 \pm 0.07	614.70 \pm 14.42	1.06
17.00	7.26 \pm 0.16	20.07 \pm 0.22	648.00 \pm 34.08	20.43 \pm 0.09	7.30 \pm 0.09	703.64 \pm 16.64	1.08
41.32	7.61 \pm 0.11	21.28 \pm 0.10	830.92 \pm 27.11	20.90 \pm 0.09	6.77 \pm 0.09	874.73 \pm 22.94	1.05
60.13	7.61 \pm 0.05	21.28 \pm 0.07	1034.37 \pm 15.94	20.90 \pm 0.20	6.77 \pm 0.55	1215.24 \pm 68.03	1.17

Relation of Rates of Heating and Cooling to Body Mass

The change in T_b of 4 toads measured under controlled conditions of radiant heat load, wind speed, dew point, and environmental temperatures were analyzed by the Newton II program (Bakken, 1976a). This program provided estimates of the initial T_b (T_b^i), the end point of the cooling curve (the final equilibrium temperature, T_b^{eq}) and τ , the constant defining the time for the T_b to reach 63% of the total response (T_b^{eq}) to thermal change for each toad (Table 3). As might be anticipated, toads with larger body masses heated and cooled more slowly than did smaller toads. Every animal heated more rapidly than it cooled. The ratios of the time constants for cooling to heating for each toad fell between 1.05 and 1.17. An approximation of the thermal conductance (K_o) can be obtained by dividing the specific heat [taken as 0.82 cal (g·°C)⁻¹ on the basis of the value for mice, Hart, 1951] by τ . These approximations, shown in Figure 8 for each animal, represent apparent K_o , as they have not been corrected for metabolic rate and EWL, both of which vary with T_b in toads (Table 2; Carey, unpubl. data). This variation results in a difference between measured and actual values of K_o (see Bakken and Gates, 1975; Bakken, 1976a). The dorsal skins of the anesthetized toads dried considerably during the course of the experiment, presumably due to the lack of adequate circulation. Calculation of the correction for EWL is thus hindered by the fact that the toads were not evaporating water from a totally saturated surface for the duration of the test. The absence of normal levels of respiratory and circulatory functions in the anesthetized animals undoubtedly minimized the contribution of metabolism to the rates of heating and cooling.

The relation of conductance, K_o in cal (g·°C·h)⁻¹ to body mass, W in g, for heating appears linear on a double log grid and is best described by the equation calculated by the method of least squares:

$$\log(K_o) = 1.11 - 0.36(\log W)$$

$$[n=4 \text{ SE of slope} = 0.06]$$

and for cooling:

$$\log(K_o) = 1.12 - 0.40 (\log W)$$

[$n=4$ SE of slope = 0.10].

As a result of the large error estimates and small sample sizes, analysis of covariance indicates that the slopes and the intercepts of these equations do not differ significantly. However, it should be noted that each animal served as its own control and heated faster than it cooled.

Skin temperatures at the beginning of the heating test were 0.15–0.25° C lower than deep body temperatures. With application of radiant heat load, skin temperatures rapidly exceeded T_b . Skin temperatures fell below T_b within 10 min in the smaller toads (15.7 and 17.5 g) but remained 1–2° C higher than T_b for the duration of the test in the larger toads (41.3 and 61.2 g).

Discussion

Range and Level of T_b in Nature

Body temperatures of boreal toads (*Bufo b. boreas*) can fluctuate 20–30° C over 24-h periods in the field (Table 1) and T_b can drop 10° C in 1 h (Fig. 3) when weather conditions change. These data are consistent with observations on other montane *Bufo*. *Bufo boreas halophilus* are active at T_b as low as 3.0° C near the upper altitudinal limit of their distribution (Mullally, 1952). Temperatures of active *Bufo canorus* in the Sierras have been recorded from 2.2° C (Karlstrom, 1962) to 30.6° C (Mullally and Cunningham, 1956). *Bufo spinulosus* at 4300 m in Peru show diurnal fluctuations in T_b from 2 to approximately 25° C (Pearson and Bradford, 1976).

Although lowland *Bufo* may experience this range in T_b on a yearly basis, the daily range of T_b of montane toads appears substantially greater than that of lowland toads. Behavior of montane toads appears to differ in two major respects from that of lowland toads. First, they appear to be voluntarily active over a wider range of T_b than lowland toads. During breeding, *Bufo boreas halophilus* sought deep water or the protection of their burrows if T_b fell much below 10° C or rose above 25° C. When they become primarily nocturnal after breeding, they are probably exposed to a narrower daily range of T_b than during breeding since their burrows would protect them from high daytime temperatures. A northern population of *Bufo woodhousei fowleri* was active between 13 and 32° C (Hadfield, 1966) and breeding choruses were not noted below 19° C in a southern population of *Bufo fowleri* (Martof, 1962). Individuals of *Bufo americanus* were active from 17.5 to 32.3° C (Fitch, 1956). "Maximum" and "minimum voluntary" T_b of individuals of several other lowland *Bufo* fell between 11.2 and 33.7° C (Brattstrom, 1963).

Secondly, diurnal activity, including sitting in direct sunlight, is a typical feature of the behavior of montane toads. Although extensive diurnal activity has been documented for post-metamorphic juveniles of *Bufo debilis* (Seymour, 1972), *Bufo b. boreas* (Black and Black, 1969; Lillywhite, 1974), *Bufo boreas halophilus* (Lillywhite et al., 1973) and *Bufo americanus* (Fitch, 1956), only occa-

sional diurnal activity has been noted for adult *Bufo* of certain lowland populations (Stebbins, 1951; Fitch, 1956; Karlstrom, 1962; Hadfield, 1966). As noted above, individuals of the lowland population of *Bufo boreas halophilus* used in this study were diurnally active only during breeding.

Diurnality enables montane toads to attain a higher level of T_b than if they were strictly nocturnal. However, such behavior also exposes them to a number of hazards, such as diurnal predators, relatively intense UV radiation, and the danger of desiccation on hot, dry substrates. Daily activity over such a broad range of temperatures may also require the development of extensive capacities for metabolic regulation. Such regulation could well be important to maintenance of the functional integrity of the organism at all T_b , particularly during sudden decreases or increases in T_b . Finally, the capacity for activity over a very broad range of temperatures may have obviated establishing optimal function over a narrow range of T_b . If any of these hazards posed substantial problems for toads invading montane areas, compelling benefits must have existed favoring selection for diurnal behavior.

The simplest explanation for extensive diurnality in montane toads could be that their food may be active primarily at warm, daytime temperatures. Most of the principal food sources of *boreas* are diurnally active, especially during warm, sunny periods (Carey, unpubl. data). In addition, the action of the tongue in feeding is very slow at low T_b (Carey, unpubl. data). Cold and the availability of prey do not completely exclude nocturnal feeding by toads, but they seem to favor these animals' seeking warm places, especially those in the sun. Therefore, the high daytime T_b of montane toads may simply be a by-product of food-seeking. Another explanation for diurnal behavior is that optimal function of some physiological processes may require high T_b , as in reptiles (see reviews by Dawson, 1975; Bennett and Dawson, 1976). Warm T_b may be necessary to obtain and digest enough food for growth and reproduction in the short period of activity each year. The requirements of high T_b for rapid growth and digestion have been suggested in juvenile *Bufo boreas halophilus* (Lillywhite et al., 1973), *Bufo debilis* (Seymour, 1972), and adult *Bufo woodhousei fowleri* (Hadfield, 1966).

Behavioral Thermal Preferences

Both food-seeking at warm temperatures and basking behaviors require the ability to measure thermal parameters. Studies of behavior of amphibians in thermal gradients have demonstrated that this group clearly has the capacity to discriminate among a variety of substrate or water temperatures. Larvae (Brattstrom, 1962; Lucas and Reynolds, 1967; Herreid and Kinney, 1967; Licht and Brown, 1967) and post-metamorphic individuals (Rosenthal, 1957; Lillywhite, 1971; Cabanac and Jeddi, 1971; Lillywhite et al., 1973; Duclaux et al., 1973) can confine T_b to a narrow range in thermal gradients. The mechanism underlying this capacity to detect environmental temperatures and to select not only a characteristic level but also a narrow range of T_b are poorly understood. Although some peripheral receptors may be involved (Cabanac and Jeddi,

1971), the central nervous system appears to be the primary site of thermal measurement and direction of behavioral temperature selection (Lillywhite, 1971; Duclaux et al., 1973).

Bufo b. boreas held under field conditions select body temperatures in a thermal gradient that lie near the warmer levels of T_b at which they are active in the field. Unlike certain reptiles (Regal, 1967), *boreas* and *halophilus* do not preferentially select cooler T_b in a thermal gradient during the dark portion of the photoperiod. Therefore, the cooler T_b at which these toads are active at night are an exclusive function of the cold T_a of their environment.

The level of preferred temperature of *boreas* can be altered by several factors. The mean preferred T_b of recently fed boreal toads maintained under field conditions was significantly higher than that for unfed toads. However, the difference in the means (0.7° C) appears of minimal biological importance, especially considering the wide range of T_b within which the toads normally operate. Recent feeding increases the amount of time spent basking in the field (Regal, 1966; Moll and Legler, 1971) and the level of preferred T_b in thermal gradients in certain reptiles (Gatten, 1974) and juvenal anurans (Lillywhite et al., 1973). However, it appears to have little effect on preferred T_b in other reptiles (Gatten, 1974; Diefenbach, 1975) and adult anurans (Lillywhite, 1971). The fact that neither *boreas* under field conditions nor *halophilus* acclimated to 20° C selected distinctly higher T_b following feeding suggests that basking or seeking warm T_b may have little functional significance for digestion. Since adult *halophilus* are principally nocturnal, it is unlikely that strong selection for thermophilic behavior following feeding has occurred. Indeed, one disadvantage of higher T_b to *boreas* following feeding is the reduction of absorptive efficiency, which declines with relatively rapid passage of food through the digestive tract at higher T_b (Carey, unpubl. data). It should be noted that none of the field-collected boreal toads dissected during the course of the study had an empty stomach or intestine (Carey, unpubl. data). Therefore, the toads are operating in the field almost exclusively in the "fed" condition.

Acclimation to 20° C has a pronounced effect on the thermal preference of boreal toads. This is not without precedent, acclimation having been shown to alter the level of preferred T_b in some other anurans (Lucas and Reynolds, 1967; Lillywhite, 1971), fishes (Norris, 1963), and lizards (Wilhoft and Anderson, 1960). However, such effects are not universal, judging by results obtained from certain salamanders (Licht and Brown, 1967) and lizards (Licht, 1968). Further data on preferred T_b of boreal toads acclimated to a variety of constant and fluctuating temperature regimes are needed to determine the reason for the difference in the response between the acclimated toads and individuals held under field conditions. The data do suggest that caution should be applied in the extrapolation of preferred levels of acclimated toads to preferred levels for activity in the field.

Although the physiological significance of preferred levels of T_b in reptiles is becoming well characterized (see review by Dawson, 1975), insufficient correlations between preferred level and physiological performance are available to permit satisfactory analysis of the functional importance of such preference for amphibians. The importance is particularly obscure for *boreas* where the

attainment of preferred levels each day may be restricted by environmental circumstances. Although many of the T_b taken orally in free-ranging boreal toads in the field fall close to the preferred level of T_b , telemetric data (Fig. 3) indicate that under some conditions T_b may exceed preferred levels by as much as 7 to 8° C for 5 to 7 h. Activity of reptiles at T_b above preferred levels has been attributed to the lack of a suitable heat sink or to the exchange of thermal "comfort" for additional time above the surface to defend territories (Licht et al., 1966; DeWitt, 1967a, b; Bradshaw and Main, 1968). These explanations may not apply adequately to the activity of *boreas* above preferred levels of T_b . First, these toads wander widely and do not appear to defend feeding territories. Second, boreal toads do have suitable heat sinks available in the shade, where temperatures rarely reach 25° C. Although toads are often found in the shade, most individuals (with the exception of females living on dry hillsides) do not use burrows or cavities beneath rocks or logs except during hail and snow storms, and nights with subfreezing temperatures. Similarly, the behavior of these toads differs from that of certain reptiles in that they are active at night and on cloudy days much below their preferred levels of T_b . Therefore, the capacity of this group for selecting temperatures in a thermal gradient may relate more to their capacity to note variability in environmental temperatures, to avoid lethal temperatures, and to select appropriate temperatures at which prey are likely to be active, rather than to direct behavior for activity over a narrow range.

Evaporative Water Loss

Certain desert reptiles can maintain fairly constant T_b during portions of the day by shuttling between heat sources, such as direct sunlight, and heat sinks, such as shade or burrows (DeWitt, 1967a, b). When sunlight is continuously available during midday, telemetered T_b of boreal toads vary only 4–6° C for several hours (Fig. 3). Since the toads were not observed during the telemetry

Table 4. Determination of a thermal budget of a toad (Part A) and estimation of parameters used in the budget (Part B). Toad, weighing 40 g, is sitting in the sun with $T_b=28^\circ\text{C}$, $T_a=25^\circ\text{C}$, wind speed=60 cm/s, relative humidity=80%, on June 22 at noon at the altitude and geographical location of Gothic, Colorado

Part A. Total steady-state thermal budget

$$\dot{Q}_{abs} = q_{rad} + q_{conv} + q_{evap} + q_{cond} + \text{work}$$

Total heat gain

$$\dot{Q}_{abs} = SA_{sit}(1.53)(0.88)(39) = 52.5 \text{ cal/min}$$

Heat loss by radiation

$$q_{rad} = FA_s \epsilon \sigma (T_a^4 - T_{skin}^4) = (0.9)(87.6)(8.13 \times 10^{-11})(0.97)[(298)^4 - (301)^4] = -2.00 \text{ cal/min}$$

Heat loss by convection

$$q_{conv} = A_s h_c (T_a - T_s) = (87.64)(0.025)(297 - 301) = -8.76 \text{ cal/min}$$

Heat loss by evaporation

$$q_{evap} = LA_s h_p (\rho_a - \rho_s) = (0.582)(87.64)(89.61)[(0.8)(0.02305) - (0.02724)] = -40.22 \text{ cal/min}$$

Table 4 (continued)

Part B. Estimation of parameters

Parameter	Value	Method of estimation
S (total incident radiation)	1.53 cal ($\text{cm}^2 \cdot \text{min}$) ⁻¹	Program of McCullough and Porter (1971)
a (absorptivity of light skinned toad)	88%	Program of McCullough and Porter (1971)
A_{sil} (silhouette area)	39 cm^2	$A_{sil} = 0.40A_{total}$ (Tracy, 1972)
A_{total} (total surface area of toad)	97.4 cm^2	$A_{total} = 12.39W^{0.559}$ (Tracy, 1972)
W (body mass)	40 g	given
F (view factor)	90%	(Tracy, 1972)
A_s (area for heat exchange by all routes other than conduction)	87.64 cm^2	$A_s = A_{total} - A_{ventral}$ (Tracy, 1972)
$A_{ventral}$ (ventral surface area)	9.97 cm^2	$A_{ventral} = 0.425W^{0.85}$ (Tracy, 1972)
σ (Stefan-Boltzmann constant)	8.13×10^{-11} ($\text{cm}^2 \cdot \text{min} \cdot \text{T}^4$) ⁻¹	
ϵ (emmissivity)	0.97	(Tracy, 1972)
T_a (ambient temperature)	298°K	given
T_{skin} (skin temperature)	301°K	assumed to = T_b
h_c (convective heat transfer coefficient)	0.025 cal ($\text{cm}^2 \cdot \text{min} \cdot ^\circ\text{K}$) ⁻¹	$h_c = \frac{Nu \cdot k_a}{L_{sv}}$
Nu (Nusselt Number)	53.81	$Nu = 0.258 Re^{0.667}$ (Tracy, 1972)
Re (Reynolds Number)	3000	$Re = \frac{L_{sv} \cdot v}{\nu}$
L_{sv} (snout-vent length)	7.75 cm	$L_{sv} = 2.68W^{0.288}$ (Tracy, 1972)
k_a (thermal conductivity of air)	3.68×10^{-3} cal ($\text{cm} \cdot \text{min} \cdot ^\circ\text{K}$) ⁻¹	(Monteith, 1973)
v (wind velocity)	60 cm/s	given
ν (kinematic viscosity of air)	$0.155 \text{ cm}^2(\text{s})^{-1}$	(Monteith, 1973)
L (latent heat of evaporation)	$0.582 \text{ cal}(\text{mg})^{-1}$	(Monteith, 1973)
h_D (mass transfer coefficient)	$89.61 \text{ cm}(\text{min})^{-1}$	$h_D = \frac{Sh \cdot D}{L_{sv}}$
Sh (Sherwood Number)	45.04	$0.216 Re^{0.667}$ (Tracy, 1972)
D (diffusion coefficient of water vapor in air)	15.42 cm^2 (min) ⁻¹	(Monteith, 1973)
ρ_a (vapor density in air at 25° C)	0.02305 mg (cm^3) ⁻¹	(Monteith, 1973)
ρ_s (vapor density of water at skin surface temperature at 28° C)	0.02724 mg (cm^3) ⁻¹	(Monteith, 1973)

test, it is not possible to determine whether the relatively constant T_b were due to behavioral shuttling between sunlight and shade or by balancing heat gain from direct sunlight with heat loss by evaporation, convection, and conduction. The ability to remain motionless in the sun for long periods would have obvious benefits for sit-and-wait predators such as toads whose movement would alert prey. Much of the detailed data required for a full calculation of a thermal budget for a toad sitting in the sun are not available, but an extremely simplified budget may be constructed as shown in Table 4. It is assumed for the purpose

of these calculations that parameters used for the estimation of convection coefficients and anatomical dimensions of *Rana pipiens* (Tracy, 1972) would be applicable to toads. The standard metabolism of a resting toad at 28° C, calculated to be 0.016 cal/min (Carey, unpubl. data) is ignored. These calculations predict that evaporation, radiation, and convection could account for 50.98 cal/min, or 97% of the total absorbed radiation, leaving 1.52 cal/min, or 3%, to be lost by conduction, assuming that a sitting toad is performing no external work (defined in cal/min). Under these specified conditions, this hypothetical toad could sit in the sun for long periods without overheating, provided that the surface of the skin remains fully saturated. Although much attention has previously focused on the physiological abilities of amphibians for limiting water loss (see reviews of literature by Bentley, 1966; Shoemaker, 1975), none has dealt with abilities for maximizing water loss under conditions of high heat loading. The skin of *Bufo* poses some resistance to water loss (Machin, 1969). Toads are able to supplement or supplant water loss through the skin by moving water contacted from moist substrate by the ventral surface to the lateral and dorsal areas (Lillywhite and Licht, 1974). Under conditions of rapid evaporation at high skin temperatures and wind speed, such a mechanism might ensure complete saturation of the skin. In addition, evaporation of ground water would reduce the loss of body solute which accompanies evaporation of body water (Campbell et al., 1967).

The high substrate temperatures (up to 42° C), low relative humidity in areas without standing water, and intense solar radiation at high elevations produce conditions which make it unfavorable for montane toads to move away from water or moist substrates for long periods during the day. Some females live some distance from water on dry hillsides. They appear to restrict their activity, remaining near or within a burrow, and rehydrate by traveling to water at night. Most long distance movements by male *boreas* and montane *Bufo spinulosus* of both sexes (Pearson and Bradford, 1976) also occur at night. Cold nocturnal temperatures not only eliminate the dangers of overheating, but also reduce EWL at the low skin temperatures and high relative humidities. Therefore, the retention of nocturnal behavior by montane toads allows them to live for extended periods farther away from water than if they were strictly diurnal.

Modification of Rates of Heating and Cooling

Mechanisms for rapid heating following sunrise or cloud cover and for retarding cooling when solar radiation becomes unavailable might be beneficial if a physiological premium is attached to warm T_b for montane toads. One possible mechanism for maximizing the rate of warming is modification of skin color in a manner increasing absorption of solar radiation. *Boreas* exhibit a wide variety of skin tones, the darker ones more usually associated with colder animals. *Bufo spinulosus* are also darkly pigmented (Pearson and Bradford, 1976). Analysis of the effect of skin color on rates of heating suggests that a darker toad would not heat appreciably faster than a light toad. The difference in absorbed radiation

between dark and light skin would be about 2.4 cal/min. Considering the resultant difference in vapor pressure at the surface of the skin, the difference in skin temperature would be approximately 0.34° C. Even if the darker toad could warm to its equilibrium temperature faster than a light toad, the difference of a few additional minutes at the warm T_b may have limited biological importance. The short time at a warm T_b would not noticeably benefit the rate of digestion, as it takes 3–4 days for *boreas* to pass a prey item through its digestive tract at body temperatures fluctuating between 5 and 30° C (Carey, unpubl. data). The thermal importance of skin color would be that a lighter toad would reach a lower equilibrium temperature (about 0.5° C) than a darker toad. This may contribute to prevention of overheating.

Large body mass may benefit animals such as Galapagos marine iguanas, *Amblyrhynchus cristatus*, which bask on land in the sun and then feed in the cold sea. Most terrestrial ectotherms, however, do not experience rapid changes in thermal environment such as they are exposed to in laboratory tests of heating and cooling rates, but rather would track equilibrium T_b as their thermal environment heats or cools following sunrise, sunset, etc. In these instances, differences in rates of heating and cooling attributable to body mass observed in the laboratory may have limited importance in the field.

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