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THERMAL ECOLOGY OF DESERT TORTOISES IN THE EASTERN MOJAVE DESERT: SEASONAL PATTERNS OF OPERATIVE AND BODY TEMPERATURES, AND MICROHABITAT UTILIZATION

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ABSTRACT: We monitored meteorological variables, daily and seasonal patterns of body temperature, corresponding operative temperatures, and microhabitat utilization by desert tortoises (*Gopherus agassizii*) during the 1991 and 1992 activity seasons of tortoises in the eastern Mojave desert. We studied tortoises in enclosures of natural habitat at the Desert Tortoise Conservation Center (DTCC) near Las Vegas, Nevada and a population of free-ranging tortoises in a field site adjacent to the DTCC. Air, ground and operative temperatures coincided with daily and monthly patterns of incident solar radiation. Variation in body temperature was primarily a consequence of microhabitat selection, principally use of burrows. During July–October, in the morning, body temperatures of tortoises in burrows were cooler than those of individuals on the surface. During midday, tortoises remained in burrows where body temperatures were cooler than extreme surface operative temperatures. While tortoises remained in burrows during much of the day, tortoises typically did not sleep in burrows at night. Microhabitat utilization was dictated by avoidance of extreme temperatures during midday, and microhabitat selection corresponded qualitatively to maintenance of energy and water balances. Effective conservation efforts to preserve habitat of desert tortoises will focus upon managing variables associated with integrity of burrows.

Key words: Desert tortoise; Mojave desert; Operative temperature; Testudinidae; Thermoregulation

BODY temperature of ectothermic animals is a consequence of, and is consequential to, their physiological and behavioral ecology (Bennett, 1980; Huey, 1982). Body temperature of ectotherms influences many physiological variables including metabolic rate (Bennett and Dawson, 1976; Stevenson et al., 1985), cardiovascular function (Baker and White, 1970; Baker et al., 1972; Gatten, 1974; Voigt, 1975), skeletal muscle contractility (Licht et al., 1969), sprint speed (Crowley, 1985; Hertz et al., 1983; Stevenson et al., 1985), digestion (Harlow et al., 1976; Parmenter, 1981; Stevenson et al., 1986; Troyer, 1987; Waldschmidt et al., 1985; Zimmerman and Tracy, 1989), reproduction (Licht, 1966; Noeske and Meier, 1977), water balance (Cloudsley-Thompson, 1965; Foley and Spotila, 1978), immune response (Gorden et al., 1977; Hazen et al., 1978) and sensory

perception (Werner, 1972). Additionally, body temperature of ectotherms influences behavior (Bennett, 1980; Crawford et al., 1983; Hertz et al., 1982; Rand, 1964; Waldschmidt et al., 1986), and daily and seasonal timing of activity (Grant and Dunham, 1988; Porter et al., 1973). As a result, body temperature of ectotherms influences such ecological variables as natural selection (Fox, 1978; Huey and Bennett, 1987), energy balance (Bennett, 1982; Pough, 1980; Zimmerman and Tracy, 1989), foraging efficiency (Avery et al., 1982), susceptibility to predation (Christian and Tracy, 1981), habitat utilization (Christian et al., 1983a,b; Dunham et al., 1989; Grant and Dunham, 1988), and patterns of regional and geographic distribution and abundance (Porter and Tracy, 1983; Riechert and Tracy, 1975; Zimmerman and Tracy, 1989). Accordingly, knowledge of thermal ecology is fundamental to our understanding of the biology and natural history of animals, and is crit-

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ical to the effective management of threatened species and their habitat.

Desert tortoises (*Gopherus agassizii*) are herbivorous, diurnal reptiles which were formerly more common in southwestern deserts (Berry, 1984). Declining population sizes have been principally associated with habitat destruction and disease (Berry and Nicholson, 1984). Desert tortoises spend much of their lives in burrows to avoid daily and annual thermal extremes (McGinnis and Voigt, 1971; Woodbury and Hardy, 1948). During the summer, burrows have the coolest of all available environmental temperatures during the day and the warmest temperatures at night (McGinnis and Voigt, 1971). Accordingly, variation in body temperatures of desert tortoises can be related to daily and seasonal patterns of microhabitat selection (principally use of burrows).

Daily and seasonal variation in body temperature profoundly affects the energetics of ectotherms through thermal influences on rates of energy assimilation and expenditure (Karasov and Diamond, 1985; Zimmerman and Tracy, 1989). Energy and water balance of herbivorous ectotherms living in north temperate regions may be particularly constrained by availability of environmental temperatures optimal for assimilation of refractory plant material coincident with availability of seasonally and annually variable food resources (Zimmerman and Tracy, 1989). Hydroregulation in deserts is constrained by low annual precipitation, and a high gradient for evaporative water loss due to hot temperatures seasonally and low humidity annually. Moreover, water balance is additionally constrained in herbivorous ectotherms because of the comparatively low water and high electrolyte content of plant material eaten during summer months (Nagy, 1972, 1973; Zimmerman, 1989).

One of the most important regulatory processes of desert-dwelling organisms is thermoregulation, i.e., maintenance of body temperature within physiological limits (defined by lethal extremes) or ecological boundaries (e.g., temperatures augmenting energy balance). Accordingly,

studies of thermoregulation indicate mechanistic bases for thermal effects on habitat utilization and observed patterns of growth and reproduction in populations of desert-dwelling ectotherms (Case, 1976*a,b,* 1982; Christian et al., 1983*a;* Dunham et al., 1989; Snell and Snell, 1987) including desert tortoises (Nagy and Medica, 1986). To ensure that adequate thermal features are available for desert tortoises in any managed, disturbed or marginal area, studies of thermal consequences of microhabitat utilization throughout the range of desert tortoises are essential.

During 1991 and 1992, we studied three aspects of the thermal ecology of desert tortoises in the eastern Mojave desert. Our objectives were: (1) to quantify meteorological variables influencing the thermal environment of desert tortoises in Las Vegas valley; (2) to measure operative temperatures (Bakken and Gates, 1975) to consider resource availability (i.e., spatial distribution of thermal microclimates within the environment) and resource utilization (i.e., microhabitat selection by desert tortoises); and (3) to monitor daily and seasonal patterns of body temperature and microhabitat utilization. Here we describe meteorology during the activity season (April–November) of tortoises and compare daily body temperature profiles with operative temperatures during the hottest part of the activity season (principally July–September). These results illustrate the relationship between thermal lability in and microhabitat utilization by desert tortoises.

MATERIALS AND METHODS

Gopherus agassizii ranges from the southwestern corner of Utah southwest through the Mojave and Sonoran deserts into west central Mexico. The Desert Tortoise Conservation Center (DTCC) is located in the eastern Mojave desert southwest of Las Vegas, Clark county, in southern Nevada. Altitude is approximately 800 m.

In 1991, we studied four adult tortoises (Table 1) within a 4 ha enclosure of natural habitat at the DTCC. In 1992, we studied a population of tortoises in a 7.7 km² field site adjacent to the DTCC. Periodically,

we monitored five–six individuals for approximately 30 consecutive h (30 h track) during each of six observation periods from mid-July to mid-October. We studied a total of 16 adults (eight females and eight males) (Table 1).

We established an automated meteorology station in a 4 ha enclosure at the DTCC. Total incident solar radiation was measured with a radiometer (Eppley model 8-48). Wind speed was measured with a cup anemometer (Cassella model 3044) positioned at a height of 75 cm above the ground. Air and ground temperatures were measured with white-painted thermocouples (24 ga Cu-Cn) affixed to a wooden dowel at heights from the ground of 0, 0.5, 1, 2, 5, 10, 20 and 50 cm. The radiometer, anemometer and thermocouples were connected to a data logger (Campbell Scientific 21X) that recorded ambient values at 15-min intervals 24 h/d.

Operative temperatures were measured with aluminum casts of desert tortoises (Zimmerman et al., 1992). We used two sizes of models (maximum carapace length, MCL = 200 and 260 mm). These lengths bracketed the mean length (MCL = 240 mm) of tortoises in this study (Table 1). Smaller models were solid. Larger models were solid but had a fist-sized (approximately 10 × 8 × 5 cm) hollow space in the midthoracic-abdominal area. Because of the large mass and thermal inertia of these tortoise replicas compared to hollow operative temperature models typically used to represent smaller animals (Bakken and Gates, 1975), we were concerned that the models might respond to changes in the thermal environment more slowly than tortoises. Modeled time constants for heating and cooling of 2 kg ectotherms with wind speeds of 1 m/s ranged from 75 min with lower than expected blood flow rates to 60 min with expected blood flows, to 44 min for tortoises with 10 times the expected blood flow rate. Modelled time constants for a larger (size of a 3 kg animal) aluminum model was 50 min with the same wind speed. Comparisons of predicted responses to sudden changes in environmental temperature showed much faster predicted responses in aluminum models than

TABLE 1.—Sex and dimensions of desert tortoises (*Gopherus agassizii*) studied in a 4 ha enclosure (during 1991) at the Desert Tortoise Conservation Center (DTCC) near Las Vegas, Nevada, and in a field site (during 1992) adjacent to the DTCC.

Tortoise number	Sex[a]	Body mass (kg)	MCL (mm)[b]
		1991	
781	F	1.6	217
824	M	2.4	230
873	F	2.9	246
975	F	2.3	226
		1992	
996	M	4.0	276
1049	M	2.2	228
1053	F	2.6	238
1054	F	2.1	223
1058	F	2.2	228
1060	F	2.8	243
1070	M	4.0	282
1077	M	3.4	266
1080	M	3.2	263
1090	F	2.3	232
1092	M	2.3	231
1094	M	2.1	225
1097	M	3.1	257
1098	F	2.1	229
1099	F	2.0	220

[a] F = female, M = male.
[b] MCL = midcarapace length.

in tortoises (O'Connor, unpublished). Thus, we concluded that aluminum models of tortoises were able to respond thermally more than rapidly enough to describe operative temperatures of living tortoises. Accordingly, we considered body temperatures relative to operative temperatures measured by these aluminum models to discern the range of body temperatures potentially attainable by desert tortoises.

We painted operative temperature models teal blue (Krylon enamel 1904) to match the integrated spectral absorptivity of tortoises (68.0–73.2% measured by K. Hatch with a DK-2 spectroreflectometer in the laboratory of W. Porter, Univ. of Wisconsin, Madison). Thermocouples (24 ga, Cu-Cn), implanted in the models, were connected to a data logger (Campbell Scientific 21X) that recorded operative temperatures at 15 min intervals 24 h/d. We distributed 50 models to two (25 models each) arrays in a 4 ha enclosure at the DTCC. Models were placed in subjectively typical tortoise microhabitats within <1 m

of the vertices of a square grid, 25 m on a side, with 5 m between vertices. As a result, operative temperature models were positioned in a wide variety of potential microclimates including open areas exposed to full sun during the day, partially protected areas such as under a bush or in a pallet (a shallow depression in the ground made by a tortoise, typically at the base of a shrub), and on various slopes offering different angles of exposure to the sky. Moreover, we positioned three additional models in sheltered areas. Two models were placed at the base of artificial burrows (bisected PVC pipe, 1.7–2.0 m long, diameter = 30 cm, buried at an angle of ~20° to the surface), one of which was oriented generally north and the other generally south. The third model was positioned 2 m into a caliche den. We did not measure operative temperatures in burrows or caliche dens until August 1992.

To measure body temperature of living tortoises, we affixed to tortoises single-channel radio transmitters (AVM Instrument Co., SB2 M-Module) with a frequency range of 150–151 MHz, an external temperature-sensitive sensor, and a whip antenna. Four tortoises within a 4 ha enclosure at the DTCC were equipped with two transmitters to measure both internal (T_{bi}) and external (T_{be}) body temperatures. Tortoises at the field site carried one transmitter to measure external body temperature.

Each transmitter was affixed to a thin metal plate that was glued with epoxy to the anterior marginal scutes lateral to the midline. This unit was covered with silicone sealant. The entire package with potting weighed approximately 110 g. External probes (T_{be}) were affixed with Super Glue (Duro) in the scapular area, i.e., the skin posteriolateral to the neck. In four individuals, internal probes (T_{bi}) were inserted into the coelomic cavity through a hole drilled in the upper medial corner of an abdominal scute. During this procedure, tortoises were anesthetized systemically with Ketamine HCl (Aveco Co., Inc.) and infiltrated locally with Lidocaine HCl (Elkins-Sinn, Inc.). The internal thermal sensor was held in place with dental resin

(The Hygenic Corporation, Type II Class I) applied to the plastron around the point of insertion.

Body temperatures were detected remotely using a hand-held directional antenna and a scanner/receiver (Telonics TS-1/TR2) connected to a digital data processor (Telonics TDP2). In addition, we noted time of day, location of each tortoise and its behavior.

During each 30 h track, two field observers monitored two–three tortoises each. As a result, individual tortoises were not monitored continuously because field observers made rounds of their subjects. Tortoises were monitored as intensively as possible during morning and afternoon activity periods. When tortoises were in burrows or sleeping, body temperatures were measured approximately every 2 h during the day and every 3 h at night. Dates of the six 30 h tracks conducted in 1992 were 15–16 July ($n = 5$ tortoises), 27–28 July ($n = 6$), 12–13 August ($n = 6$), 27–28 August ($n = 6$), 23–24 September ($n = 5$) and 14–15 October ($n = 5$).

One-way analyses of variance (ANOVA) were used to test for differences in body temperature related to month, time of day or microhabitat. Untransformed data were analyzed with the Statview 512+ statistical software package for the Macintosh computer. Chi-squared analyses were used to test for differences in sleeping-site selection. Expected frequencies were determined by assuming tortoises had equal preference for both burrow and surface sleeping sites, or shaded and open epigeal sleeping sites. The significance level for all analyses was chosen to be $P \leq 0.05$.

RESULTS

Meteorology

During the activity season of tortoises (April–November) in 1992, peak solar irradiance was highest (1000–1200 W/m²) during June and July (Fig. 1a). In April, peak solar irradiance was 800–1000 W/m², and by November, peak values had declined to 200–400 W/m² (Fig. 1a). Daily and seasonal air (Fig. 1b) and ground (Fig. 1c) temperatures followed the same general
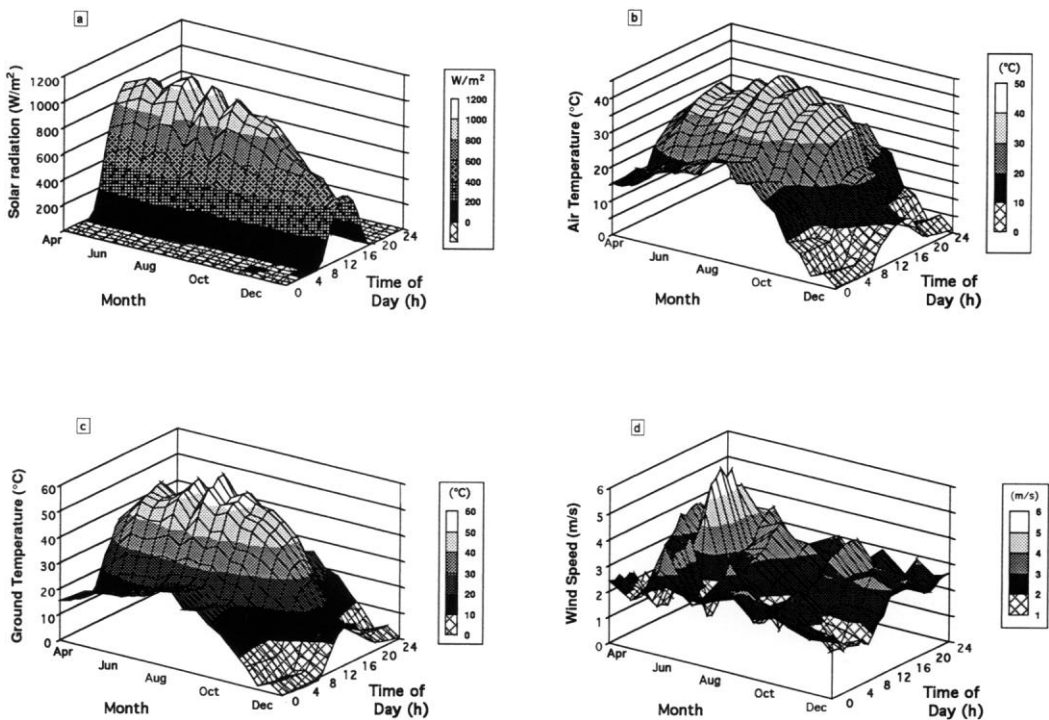
FIG. 1.—Daily and monthly patterns of meteorological variables at the Desert Tortoise Conservation Center near Las Vegas, Nevada during April–November 1992. Solar radiation (a) was measured with an Eppley radiometer. Air temperature at a height of 50 cm from the ground surface (b) was measured with a thermocouple (24 ga Cu-Cn) coated with white enamel paint. Ground temperature (c) was measured with a thermocouple positioned just below the ground surface. Wind speed (d) was measured with a cup anemometer at a height of 75 cm above the ground.

pattern, with maximum values centered around mid-July and extending from mid-June through late August. Ground temperatures varied by approximately 40 C daily through October (Fig. 1c). Daily and seasonal air temperatures at a height of 50 cm were generally cooler and less variable than ground temperatures. Peak air temperatures were 25–30 C in April, 30–35 C in July and 20–25 C in October (Fig. 1b). Wind speed was variable throughout the activity season and was highest in July (Fig. 1d).

Operative Temperature

Mean daily and seasonal surface operative temperatures (Fig. 2A) followed a pattern similar to that described for solar radiation, and air and ground temperatures. Highest operative temperatures occurred in July and generally peaked ca.

1330 h daily. During midday, mean surface operative temperatures exceeded 40 C from late April to October. Putatively lethal mean surface operative temperatures (≥ 50 C) occurred from approximately 1300–1600 h in June, 1100–1700 h in July, 1200–1600 h in August and 1300–1500 h in September (Fig. 2A). At night, surface operative temperatures were substantially lower and less variable than daytime operative temperatures.

In contrast to daily fluctuations in mean surface operative temperatures, mean operative temperatures in burrows typically varied less than 1 C per day, averaging 29 C in late August and steadily declining to 7 C in December (Fig. 2B).

Superimposition of potential activity times of tortoises, determined both by activity surveys and focal observations of surface-active individuals (Ruby et al., 1994),
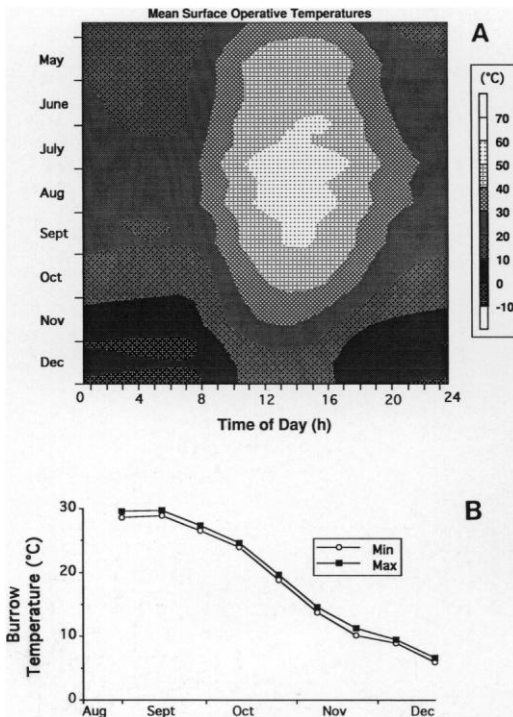
FIG. 2.—Daily and monthly patterns of operative temperatures at the Desert Tortoise Conservation Center near Las Vegas, Nevada. Mean surface operative temperatures (A) and mean maximum and minimum operative temperatures in burrows (B) were measured with aluminum models of tortoises. Models were painted to match the integrated spectral absorptivity of tortoise shells.
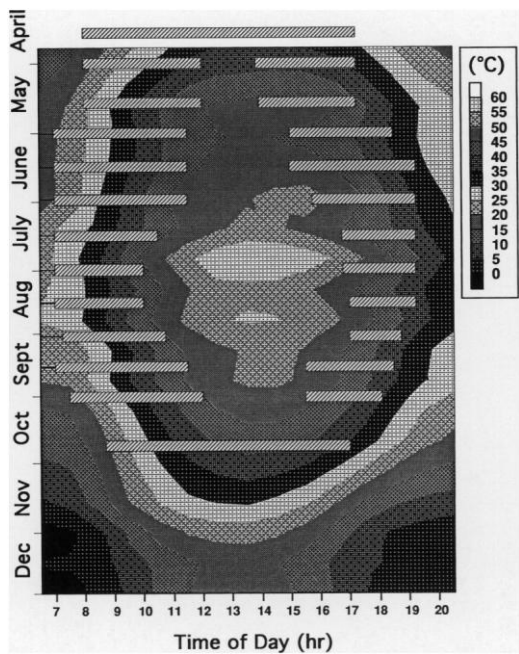
FIG. 3.—Daily and monthly potential activity times (horizontal bars) of desert tortoises superimposed on mean surface operative temperatures at the Desert Tortoise Conservation Center near Las Vegas, Nevada. Potential activity times were determined by conducting censuses of and focal observations on individuals active on the surface in four 4-ha enclosures at the DTCC beginning before tortoises emerged from burrows and continuing until individuals ceased surface activity. Beginning times of morning activity ca. 0700 h are artifacts of scheduling constraints. Operative temperatures were measured with thermal replicas of desert tortoises described in the legend for Fig. 2.

on mean surface operative temperatures (Fig. 3) suggests that time spent by tortoises on the surface was constrained by high temperatures during midday. Note that potential activity times in Fig. 3 represent the end of morning activity and the duration of afternoon activity of tortoises. Morning start times ca. 0700 h were artifacts of scheduling constraints. Daily patterns of potential surface activity were distinctly bimodal during May–September. Periods of surface inactivity generally coincided with operative temperatures greater than 45 C. Tortoises entered burrows in the morning when operative temperatures reached 40–45 C and emerged in the afternoon when operative temperatures fell to 45–50 C. Daily potential activity time of tortoises became unimodal

towards the end of the activity season when operative temperatures did not exceed 30 C (Fig. 3).

Body Temperature

We quantified the relationship between internal (T_{bi}) and external (T_{be}) body temperatures of four adults as $T_{bi} = 3.08 + 0.91 \cdot T_{be}$; $R^2 = 0.85$, $n = 822$. (T_{bi} was measured in the coelomic cavity and T_{be} was measured on the skin in the scapular area.) Within the typical range of external body temperatures of tortoises measured during the activity season (25–35 C), internal body temperatures differed from external body temperatures by <1 C. T_{be} predicted T_{bi} less reliably when tortoises experienced
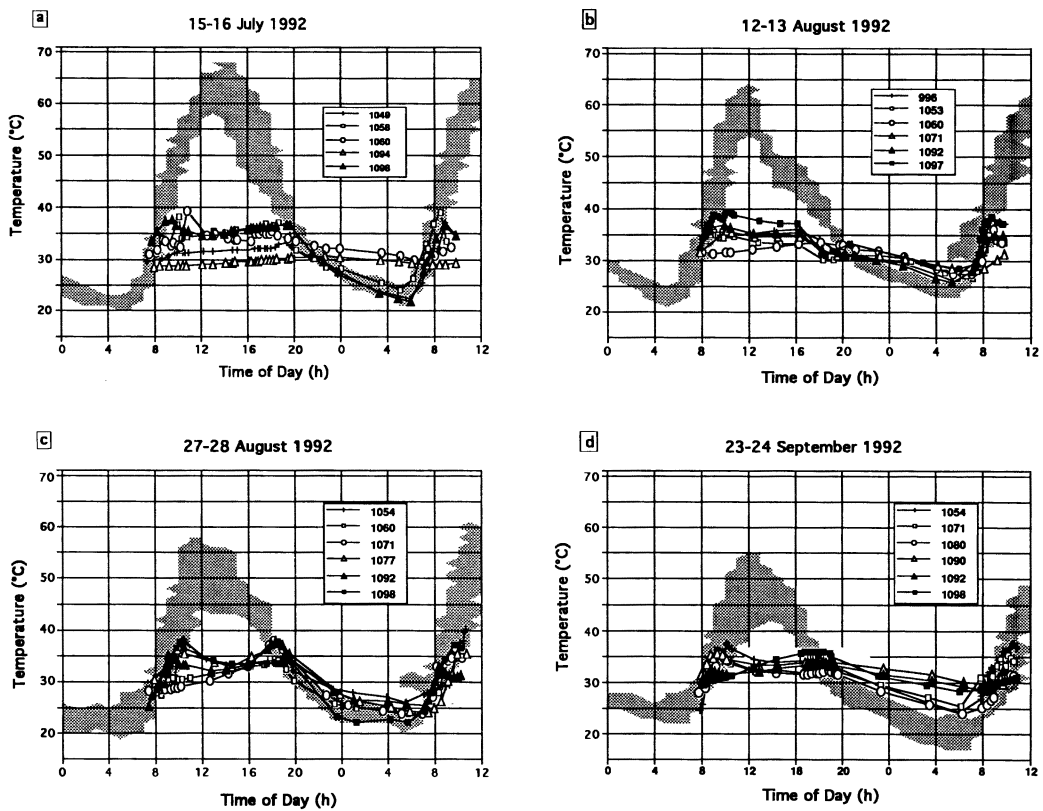
FIG. 4.—Daily patterns of body and operative temperatures of desert tortoises free-ranging in a 7.7 km² field site adjacent to the Desert Tortoise Conservation Center near Las Vegas, Nevada. Body temperatures were measured with temperature-sensitive radio transmitters affixed to each individual. Each symbol represents the body temperatures of a different tortoise identified by the tortoise numbers in the legends. Ranges of operative temperatures, indicated by shading, were measured with thermal replicas of desert tortoises described in the legend for Fig. 2. Individuals were monitored for approximately 30-h periods. Dimensions and sexes of individuals are described in Table 1. (a) 15–16 July, (b) 12–13 August, (c) 27–28 August, (d) 23–24 September.

marked thermal flux such as when entering or leaving a burrow.

Body temperatures of desert tortoises varied widely depending upon time of day, microhabitat selection (principally use of burrows) and time of the activity season. Operative temperatures in Fig. 4 were measured in epigeal microclimates and accurately predicted body temperatures of tortoises on the surface. Body temperatures below minimum operative temperatures during the day or above maximum operative temperatures at night indicate that those individuals were in burrows, pallets or caliche dens.

Superimposition of body temperatures on corresponding operative temperatures

(Fig. 4) revealed that body temperatures were within the range of epigeal operative temperatures during activity on the surface. As epigeal operative temperatures increased, body temperatures fell below minimum surface operative temperatures as tortoises invariably sought thermal refuge in burrows following morning activity during July–September. Tortoises typically retreated to burrows when mean operative temperatures reached approximately 40 C in the morning (Fig. 4). Mean body temperature before entering a burrow following morning activity was 34.9 C (SD = 2.5 C, n = 35).

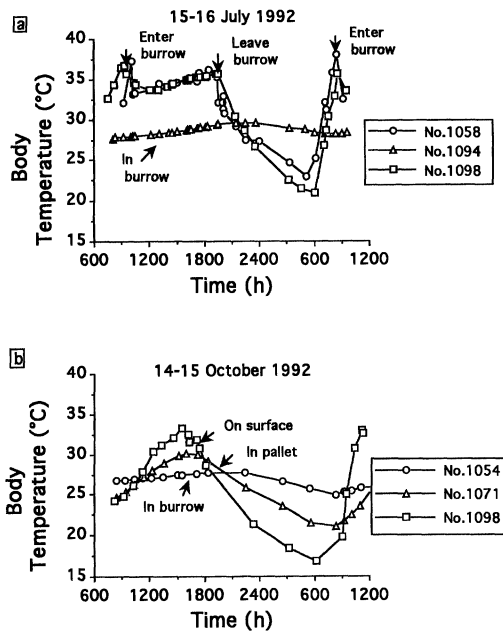After entering burrows following morning activity, body temperatures of tortoises

FIG. 5.—Examples of thermal consequences of microhabitat utilization by tortoises free-ranging in a 7.7 km² field site adjacent to the Desert Tortoise Conservation Center near Las Vegas, Nevada. Body temperatures were measured with temperature-sensitive radio transmitters affixed to each individual and were recorded while monitoring individuals for approximately 30-h periods. Each symbol represents the body temperatures of a different tortoise identified by the tortoise numbers in the legends. Dimensions and sexes of individuals are described in Table 1. (a) Thermal consequences of moving between burrows and the surface compared with remaining in a burrow during 15–16 July. (b) Thermal consequences of occupying a burrow, a pallet, or being on the surface during 14–15 October.
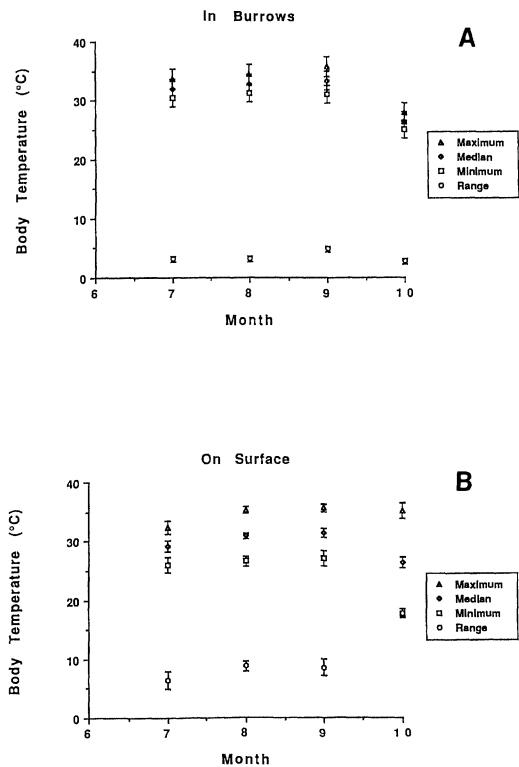

FIG. 6.—Mean monthly body temperatures (A) in burrows and (B) on the surface. Body temperatures were measured with temperature-sensitive radio transmitters affixed to tortoises free-ranging in a 7.7 km² field site adjacent to the Desert Tortoise Conservation Center near Las Vegas, Nevada. Body temperatures were recorded while monitoring individuals for six approximately 30-h periods in 1992.

generally decreased and stabilized (Figs. 4, 5). After equilibrating to ambient burrow temperature, body temperatures remained fairly stable until tortoises emerged during late afternoon or evening for a bout of activity. Tortoises were typically visible

TABLE 2.—Thermal consequences of microhabitat selection: Comparison of body temperature metrics of desert tortoises in burrows and on the surface. Values are means calculated for all of times of day during a 24 h period of each 30-h observation. Standard error is in parentheses.

Micro-habitat	Body temperature (°C)			
	Maximum	Median	Minimum	Range
Burrow	34.1 (0.45)	32.4 (0.41)	30.0 (0.45)	3.4 (0.39)
Surface	34.6 (0.46)	30.2 (0.44)	25.8 (0.68)	8.8 (0.76)

near the mouth of burrows before emerging. Correspondingly, body temperatures often increased 3–4 C before tortoises emerged from burrows. Tortoises emerged from burrows for afternoon activity after epigeal operative temperatures cooled to approximately 50 C (Fig. 4). Mean body temperature before emergence for afternoon activity was 32.6 C (SD = 1.4 C, n = 12). When tortoises emerged in the afternoon, body temperatures for all individuals monitored within 30 min of emergence rose toward ambient surface operative temperatures and then fell as operative temperatures continued to fall (Fig. 4). Mean maximum afternoon activity body temperature was 34.5 C (SD = 2.0 C, n = 8).

TABLE 3.—Mean monthly body temperatures of desert tortoises in burrows and on the surface during the morning and at night. Temperatures are averaged single values for each individual measured within 0.5 h of each other. Standard error is in parentheses.

| | Body temperature (°C) | | | |
| | Morning activity | | Sleeping site | |
Month	Burrow	Surface	Burrow	Surface
July	30.5 (0.53)	35.8 (0.55)	30.5 (0.63)	25.5 (1.10)
August	30.4 (1.26)	34.7 (0.41)	27.3 (1.25)	25.3 (0.64)
September	31.2 (0.85)	34.0 (0.34)	30.9 (0.60)	27.2 (0.83)
October	27.3 (0.24)	35.6 (1.95)	26.7[a]	19.2 (0.89)

[a] Only one individual was observed to sleep in a burrow during the October observation period.

We calculated rate of heating for surface-active tortoises as the change in body temperature through time. Rates of heating after emergence in the morning (0.10 C/min, SD = 0.04 C/min, n = 15) were faster than following emergence in the afternoon (0.03 C/min, SD = 0.02 C/min, n = 3, One-way ANOVA $F_{1,17}$ = 10.03, P = 0.006).

Thermal Consequences of Microhabitat Selection

Variability in body temperatures was principally related to microhabitat selection (Fig. 5). Tortoises that shuttled between the surface and burrows during the middle of the activity season (Fig. 5a) or who remained on the surface throughout the day and night towards the end of the activity season (Fig. 5b) had more variable body temperatures than individuals who remained in burrows or pallets.

Regardless of time of day or season, tortoises in epigeal sites experienced a broader range of body temperatures than tortoises in burrows ($F_{1,70}$ = 36.70, P = 0.0001) (Table 2, Fig. 6). Body temperature metrics in Table 2 were determined by pooling all body temperatures of tortoises in burrows and on the surface for all times of day during all six 30-h tracks. During July–October, mean maximum body temperature did not differ between surface and burrow microhabitats ($F_{1,70}$ = 0.63, P = 0.43); mean median ($F_{1,70}$ = 12.81, P = 0.0006) and mean minimum ($F_{1,70}$ = 33.20, P = 0.0001) body temperatures were cooler on the surface than in burrows (Table 2).

During the morning activity period,

body temperatures of individuals on the surface were higher than body temperatures of individuals in burrows ($F_{1,31}$ = 55.17, P = 0.0001) (Table 3). At night, body temperatures of individuals sleeping in epigeal sites were lower than body temperatures of tortoises sleeping in burrows ($F_{1,32}$ = 16.56, P = 0.0003) (Table 3).

Tortoises typically did not sleep in burrows throughout July–October. During this time, 70% (n = 44) of observed sleeping sites were epigeal (χ^2 = 6.57, P = 0.01). When on the surface at night, tortoises typically slept under bushes instead of in open areas (χ^2 = 7.68, P = 0.01). Approximately 86% (19 of 22) of individuals who slept in epigeal sites remained on the surface during the ensuing morning activity period and 75% (6 of 8) of individuals who slept in burrows did not emerge during the ensuing morning activity period.

Discussion

Constraints on Activity

Operative temperature modelling quantifies the range of potential body temperatures imposed by abiotic conditions of the thermal environment, and illustrates thermal constraints on microhabitat selection and potential daily and seasonal activity times of animals (Grant and Dunham, 1988; Zimmerman and Tracy, 1989). The critical thermal maximum (CTM; body temperature at which animals become incapacitated) of desert tortoises and other testudinids ranges from 38.6–45.1 C (Naegle, 1976). Hence, during much of the activity season of tortoises, operative temperatures on the surface were lethal for

several hours during midday (Figs. 2A, 4). Accordingly, tortoises had no behavioral or physiological recourse but to eliminate surface activity and retreat to burrows where operative temperatures were more moderate (Figs. 2B, 4). Burrows provided the only ambient temperatures below the lethal range of this species during midday. These results indicate that tortoises will not be found on the surface when epigeal operative temperatures exceed approximately 40 C in the morning. Tortoises may be found active on the surface in the afternoon or evening when operative temperatures fall below approximately 50 C. (While 50 C exceeds the maximum CTM reported for testudinids, tortoises emerging from burrows after midday had transiently cooler body temperatures than operative temperatures of models that had remained on the surface during the hottest part of the day.)

Activity times of tortoises may be severely constrained by temperature both daily and seasonally as observed in other desert dwelling ectotherms (Grant and Dunham, 1988; Porter et al., 1973). Tortoises typically were inactive when it was dark. (They may become active at night during rainfall.) Accordingly, the beginning of morning activity and end of afternoon activity were dictated by photoperiod. During the day, the end of morning activity and beginning of afternoon activity were regulated by surface temperatures (Fig. 3). As a result, during warm months (viz., June–September), surface operative temperatures may limit potential activity time of tortoises to only a few hours per day. We are analyzing operative temperature data further to (1) quantify spatial distribution of thermal microclimates within the habitat of desert tortoises and (2) quantify potential activity times based upon empirical and simulated operative temperatures during comparatively wet and dry years (O'Connor and Zimmerman, in prep.).

Even when thermal conditions are amenable to surface activity, tortoises may remain inactive. Annual time budget estimates for desert tortoise populations indicate that tortoises spent >98% of time per year inactive in burrows or pallets and <2% of time active on the surface (Marlow, 1979; Nagy and Medica, 1986). Calculated feeding time comprised 0.3%, or 29 h, of the annual time budget (Nagy and Medica, 1986). Activity of desert tortoises coincided with maintenance of energy, water and salt balance, and tortoises were particularly active following sporadic summer rains (Nagy and Medica, 1986). Accordingly, environmental thermal and hydric constraints on energy and water balance strongly influence activity time of desert tortoises annually.

Thermoregulation

During surface activity, body temperatures of desert tortoises were more variable than has been observed in other reptiles. For example, Galapagos land iguanas (*Conolophus pallidus*) and chuckwallas (*Sauromalus obesus*), both xeric-adapted, large, herbivorous species, maintained a relatively constant body temperature for as long as possible during the day, through postural and microhabitat shifts (Christian et al., 1983a; Zimmerman and Tracy, 1989). Desert tortoises did not demonstrate the thermoregulatory shuttling behavior characteristic of many lizards (Cowles and Bogert, 1944). However, we observed other thermoregulatory behaviors including postural adjustments, limiting daily activity time, seasonal shifts in activity times and microclimate selection. While these behaviors are not necessarily solely thermoregulatory, they are important to the thermal ecology of desert tortoises.

Anolis cristatellus thermoregulates less precisely in habitats where thermoregulatory costs seem high (Huey, 1974). Eurythermy in desert tortoises may be similarly related to high costs of thermoregulation. Possible costs include the energetic expense of shuttling a large mass. Whereas in eurythermic forest-dwelling lizards, areas exposed to the sun are at a premium (Huey, 1974; Huey and Webster, 1975), in the desert, shade patches are rare. Accordingly, shuttling may not only be energetically costly, but temporally disadvantageous as well. Thus, for heavy-bodied

adults, it may be energetically more efficient to rely upon inertially damped heating rate and the thermal buffering capacity of the shell in thermoregulation (McGinnis and Voigt, 1971). In this sense, desert tortoises thermoregulate more like alligators (Spotila, 1974, 1980; Spotila et al., 1972, 1977; Terpin et al., 1979), which also take advantage of large body size, than like lizards, which must rely on shuttling. An interesting question regarding the ontogeny of thermoregulation is whether younger/smaller desert tortoises thermoregulate more by shuttling like lizards than do the thermally buffered adult tortoises.

Body temperatures generally decreased after individuals entered burrows in the morning and increased after individuals emerged from burrows later in the day. The difference between body and surface operative temperatures after tortoises emerge from burrows likely is a function of the greater thermal inertia (i.e., slow change in body temperature through time owing to low thermal conductance and high thermal capacitance due to large mass) of living tortoises compared to aluminum models. Tortoises retreated from the surface to burrows in the morning at higher body temperatures and lower operative temperatures than when tortoises emerged from burrows later in the day (Fig. 4).

These patterns suggest that tortoises may extend surface activity time by remaining on the surface for as long as possible while operative temperatures increased in the morning. Then they utilized burrows as a heat sink in which to dissipate body heat following morning activity. Later in the day, when operative temperatures were still extreme but declining, inertially damped heating rates may have allowed tortoises (then cooled to more moderate burrow temperatures) to emerge while operative temperatures were still near lethal levels. Tortoises did not overheat because, by the time their body temperatures had increased, operative temperatures had fallen to more moderate levels (Fig. 4). As a result, tortoises may have extended surface activity time by anticipating retreat to cooler microclimates in the morning and

by exploiting their thermal inertia to dampen heating rate in the afternoon.

Body and surface operative temperatures coincided more closely at night than during the day (Fig. 4). This is attributable to environmental temperatures being more homogeneous at any given time, and less variable temporally, at night (Fig. 2A). Additionally, because tortoises were stationary at night, they were more likely to be in equilibrium with their thermal microclimate thus reducing any transient difference between body and surface operative temperatures.

In general, heating rates (indicated by the slope of increase in body temperature per unit time) following emergence from burrows in the morning were faster than heating rates following emergence from burrows in the afternoon even though the environmental thermal gradient was steeper in the afternoon because of higher operative temperatures (Fig. 4). This suggests that tortoises behaviorally and/or physiologically enhanced heating rate in the morning. We have often observed tortoises basking in the sun in the morning with forelimbs and hindlimbs extended distally. This may be a behavioral adaptation to increase surface area exposed to solar radiation for rapid heating as seen in other heliothermic ectotherms (Hammond et al., 1988). Moreover, desert tortoises have been observed to heat more rapidly than they cool in an environment with a radiative source of heat (Naegle, 1976; Voigt, 1975). Differential heating and cooling rates suggest that desert tortoises have some physiological capacity to augment heating. Increased blood flow to the limbs, with a greater ratio between surface area and volume, would further enhance heat transfer from the environment (Turner and Tracy, 1983) provided that operative temperature exceeds body temperature and that thermal influx exceeds convective efflux across limbs.

Microhabitat Selection

Microhabitat selection imposes energetic and hydric tradeoffs on maintenance of energy and water balance by desert tortoises. These tradeoffs are related to the

presence of higher operative temperatures and lower humidities on the surface than in burrows (Kay, 1977; Minnich and Ziegler, 1977). Thermal effects on assimilation are likely to be particularly pronounced in these herbivorous ectotherms if plant cell wall, a refractory dietary component, is digested in desert tortoises as it is in other tortoise species (Bjorndal, 1987, 1989). On the surface during the day, tortoises have opportunities to elevate body temperature above cooler burrow temperatures (Fig. 5, Table 3), to forage and to interact socially (Woodbury and Hardy, 1948). Energetic and hydric costs incurred by surface activity include thermally and activity-induced higher rates of metabolism and evaporative water loss (Naegle, 1976). In burrows during potential activity time, body temperatures are cooler than on the surface (Fig. 5, Table 3), metabolism is lower because of lower body temperature and reduced activity, and rate of water loss is lower because of cooler temperatures (Naegle, 1976) and higher humidity (Gates, 1980; Geiger, 1965). However, no foraging is possible while in the burrow. Social interactions may occur if tortoises co-occupy a burrow (Bulova, 1994).

According to estimated annual time budgets (Marlow, 1979; Nagy and Medica, 1986) discussed previously, desert tortoises spend much time in burrows even when surface operative temperatures are amenable for activity. As a result, while energy intake is not possible and rate of digestion may be reduced by cooler temperatures, energy and water losses are minimized when tortoises remain in burrows during potential activity times. Desert tortoises may often be in negative energy and/or water balance, particularly during drought years (Nagy and Medica, 1986). Minimizing energy expenditures and water loss through reduced activity and by selecting cooler microclimates may be essential for desert tortoises to maintain energy and water balance annually.

Conservation Implications

Burrows are a habitat requirement of singular importance to the thermal ecology of desert tortoises. Accordingly, it is essential to manage environmental variables influencing the integrity of burrows. Such variables include soil compaction and particle size, and vegetative cover (as both a convective and thermal shield). Controlled studies of thermal consequences of disruption of soil and vegetation variables are needed. Limiting off-road vehicle use in desert tortoise habitat is clearly warranted. In addition, mortality or injury of desert tortoises will be reduced if human activity in tortoise habitat is restricted during the activity season to times (temperatures) of day when tortoises will not be active (i.e., operative temperatures $\geq \sim 45$ C).

Thermal constraints on activity and microhabitat utilization in desert tortoises are fundamental pieces of a larger puzzle describing our understanding of mechanistic bases for observed patterns of growth, reproduction and health of individuals, and patterns of distribution and abundance of desert tortoise populations. Environmental temperatures influence energy and water balance of individuals through thermal effects on foraging time, and on rates of assimilation, metabolism and evaporation. In addition, reproductive success of individuals will depend upon thermal constraints on time for courtship and mating, and temperatures optimal for egg production and incubation, including sex determination of hatchlings (Spotila et al., 1994). Combining a better understanding of characteristics of the thermal environment, the thermal dependence of time, energy and water budgets of desert tortoises (Nagy and Medica, 1986), and estimates of seasonal and annual variation in availability of food and water, are fundamental to our understanding of the life history of desert tortoises. The thermal ecology of desert tortoises is an essential consideration in habitat assessment and in predictions about population dynamics of this threatened species.

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