

SEASONAL VARIATION IN THERMOREGULATORY BEHAVIOR AND BODY TEMPERATURE OF DIURNAL KALAHARI LIZARDS¹

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Abstract. We discuss seasonal variation in thermoregulatory behavior and its consequences on body temperature for 12 species of diurnal lizards in the southern Kalahari semidesert of Africa and also evaluate several methods of attempting to document thermoregulatory behavior using a descriptive data base.

Lizards vary time of activity among seasons, which limits the variation in ambient conditions actually experienced. Ground-dwelling lizards and probably arboreal lizards move nonrandomly with respect to sun and shade; thus the percentage of lizards in sun is inversely proportional to air temperature. Arboreal lizards shift to higher perches at midday in summer and to logs or ground in winter thus decreasing and increasing incident heat loads, respectively. Both juveniles and adults of 3 species, only juveniles of 2 species, and only adults in 1 species are active in winter: both adults and juveniles of 6 species brumate [= hibernate].

Mean body temperature (T_b) varies within days and among months and is positively correlated with corresponding mean air temperature (T_a) in almost all species. Nonetheless, correlation and regression analysis suggests that thermoregulatory behaviors reduce the impact of variations in ambient conditions on Kalahari lizards.

The mean T_b of different species reflect evolutionary relationships. In summer, mean T_b is proportional to the percentage of lizards in sun and with the tendency of lizards to be active only in summer. Thus, lizards with inferred low optimal temperatures are active during more months of the year.

Key words: Activity cycles; body temperature; Kalahari; lizards; microhabitat shifts; Reptilia; thermoregulation.

INTRODUCTION

In the 30 or more yr since the discovery that diurnal desert lizards behaviorally regulate body temperatures (Cowles and Bogert 1944), biologists have gathered voluminous data on thermoregulation both in the field and the laboratory (Brattstrom 1965, Cloudsley-Thompson 1971, Dawson 1975, Huey and Slatkin 1976). Unfortunately, most studies have been restricted to summer months, giving a limited and biased view of the scope, nature, and flexibility of lizard thermoregulatory responses. A few studies are exceptions (e.g., Norris 1953, Fitch 1956, Mayhew 1964, Heath 1965*b*, Heatwole 1970, Case 1976) but are scattered among divergent faunas or are incomplete. Thus general patterns of thermoregulation remain to be described for the lizard fauna of any arid region.

Here we discuss seasonal patterns in body tempera-

ture, time of activity, basking incidence, microhabitat utilization, and adult-juvenile activity cycles for most of the 14 species of diurnal lizards in the southern Kalahari semidesert of southern Africa (*Chamaeleo dilepis* and *Lygodactylus capensis* were rarely encountered or too small for accurate determination of body temperature). Also, we analyze species-specific activity temperatures in terms of evolutionary affinities and ecological correlations.

Our data base is descriptive and indirect. Attempts to establish thermoregulatory behavior from similar data are hazardous (Heath 1964), and we therefore are particularly concerned with developing analytical techniques that reduce these risks (see Assumptions).

We gathered most of these data between late November 1969 and mid-October 1970 on 10 study sites (all data lumped here to minimize problems of sample size) during an investigation of lizard species density in the Kalahari (Pianka 1971); a few additional records from these sites were obtained between December 1975 and March 1976. Various data and statistics on location, vegetation, topography, climate,

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saurofauna, and avifauna of these areas are given in Pianka (1971), Pianka and Huey (1971), Huey et al. (1974), Huey and Pianka (1974, 1977), and Pianka et al. (1977). General aspects of the vegetation in the Kalahari are described by Leistner (1967).

METHODS

We spotted lizards by random walks through our study areas and recorded microhabitat and time of activity for each undisturbed lizard sighted (observations on a few lizards that escaped are included) and measured cloacal and air (shaded bulb, chest height) temperatures at capture with Schultheis thin-bulb thermometers. Temperatures were not recorded if lizards were chased or handled excessively.

To quantify seasonal activity niche breadth, we use the diversity index of Simpson (1949), $1 / \sum_i p_i^2$, where p_i is the proportion of individuals of a given species observed during the i th season (spring plus fall combined). Because these values are not corrected for seasonal differences in intensity of collecting, seasonal activity niche breadths are only relative among species.

We use (unless noted) Spearman rank tests (r_s) for correlations among means, parametric tests for other correlations, G -tests with STP analysis for frequency data, and analysis of variance with Student-Newman-Keuls tests for differences among means (Sokal and Rohlf 1969).

ASSUMPTIONS

To establish thermoregulatory behavior from descriptive field data, we must assume that the behavior of a thermoregulating lizard will be adjusted to reduce heat loads and thus prevent overheating when ambient temperatures are high but to increase heat loads and thus raise body temperatures when ambient temperatures are cool. Patterns of behavior achieving these results can be predicted from biophysical models (e.g., Porter et al. 1973) and then compared with actual observed behavior.

Such comparisons can, however, be misleading. As we will demonstrate (**Discussion** and **Appendix**), a lizard moving randomly with respect to incident heat loads can, in certain microhabitats, appear to be thermoregulating. Also, any behavior that matches deductions from a thermoregulatory hypothesis can be matched to deductions from alternative hypotheses. For example, lizards might not be thermoregulating *per se* but rather following prey items that are thermoregulating. Herbivorous lizards and lizards in laboratory thermal gradients, however, exhibit many of the behaviors described below; and, whatever the cause of the behaviors, they inevitably have thermoregulatory effects. Finally, after demonstrating that temperatures of inanimate objects (water-filled beer cans) are similar to those of lizards in the field, Heath (1964) persua-

sively argued against inferring thermoregulatory behavior in the absence of controls or of observations on regulation itself.

Heat exchange between the environment and a lizard or a beer can represents complex interactions, but the close similarity of temperatures and of thermal relations of beer cans with heliothermal lizards (Heath 1964) is partially a result of the moderate weather conditions during the demonstration (J. E. Heath, *personal communication*), the use of can temperatures only from a restricted time of day, the analysis of temperatures only of cans in full sun (Heath 1965a), and the passive orientation of cans to the sun. Because cans were vertical rather than horizontal, maximum surface areas were exposed to the sun early and late in the day; this may help explain why beer cans were relatively hot at low air temperatures. W. P. Porter (*personal communication*) notes that the colored sides and reflective tops of beer cans may have also increased can temperatures at low sun angles. These comments reinforce Heath's (1964) still timely message: inferring thermoregulation in the absence of controls or direct observation is risky.

To attempt to circumvent some of these problems, we first determine not only whether observed and predicted behavior correspond, but also whether the observed behavior is nonrandom (see **Discussion**). Second, we note that if ground-dwelling lizards are thermoregulating, then body temperatures of lizards will generally be warmer relative to ambient temperatures during cool periods than during warm periods. Statistically, this is detectable by showing (1) that the difference between body and air temperature is inversely proportional to air temperature, or (2) that the slope of the body temperature vs. air temperature regression is ≈ 0 (0 = perfect thermoregulation, 1 = thermoconformity, Huey and Slatkin 1976). As noted in the **Discussion** section, however, these statistical indices are unreliable for arboreal lizards. Given these comparisons and types of circumstantial evidence, we believe that descriptive field data can be used to infer with reasonable certainty whether lizards are thermoregulating.

RESULTS

Average cloacal (T_b) and air (T_a) temperatures for diurnal Kalahari lizards are presented in Table 1. There is a significant correlation between T_b and T_a in all species (Table 1, all $P < .01$). The range of mean T_b values of the lacertids (36.3°C to 39.3°C) is higher than the mean T_b of *Agama* (36.2°C) or than the range of the skinks (33.6°C to 36.0°C). Within the lacertids (Pianka et al. 1977) and within the skink genus *Mabuya* (Huey and Pianka 1977), mean T_b values differ significantly.

Monthly variation in mean body temperature

Monthly mean body temperatures (T_b) of common species, plotted in Fig. 1, vary considerably for all

TABLE 1. Thermal statistics of diurnal Kalahari lizards. Microhabitat categories: SA = semiarid, T = terrestrial, SNB = seasonal activity niche breadth. In brumate categories, "Ad" indicates only adults brumate. Correlations: A = T_b vs. T_a , B = monthly mean T_b vs. monthly mean T_a , C = monthly mean T_b - mean T_a vs. monthly mean T_b - mean T_a , D = hourly mean T_b - mean T_a vs. hourly mean T_b - mean T_a . * = $P < .05$, ** = $P < .01$, *** = $P < .001$

Species	Mi-cro-habi-tat	Bru-mate	T_b		T_a		Mean T_b (Summer)			Correlations				Slope T_b , T_a
			$\bar{X} \pm SE$	(N)	$\bar{X} \pm SE$	(N)	$\bar{X} \pm SE$	(N)	SNB	A	B	C	D	
Scincidae														
<i>Mabuya variegata</i>	T	No	33.6 ± .56	(20)	28.2 ± .81	(71)	34.6 ± 1.65	(4)	2.6	.69***26
<i>Mabuya striata</i>	SA	No	34.1 ± .18	(281)	28.1 ± .24	(369)	34.9 ± .21	(75)	2.5	.46***	.81***	-.74**	-.97***	.29
<i>Mabuya spilogaster</i>	SA	No	34.5 ± .17	(271)	28.8 ± .27	(309)	35.6 ± .17	(111)	2.6	.46***	.85***	-.96***	-.97***	.28
<i>Mabuya occidentalis</i>	T	Yes	36.0 ± .23	(136)	30.0 ± .29	(164)	36.2 ± .22	(103)	1.8	.54***	.80***	-.82**43
Agamidae														
<i>Agama hispida</i>	SA	Ad	36.2 ± .14	(215)	28.6 ± .29	(264)	36.9 ± .26	(79)	2.3	.44***	.82***	-.98***	-.93***	.28
Lacertidae														
<i>Merolex</i>														
<i>suborbitalis</i>	T	No	35.5 ± .10	(480)	26.5 ± .22	(663)	36.8 ± .18	(124)	2.6	.55***	.96***	-.92***	-.95***	.22
<i>Ichnatropis</i>														
<i>squamulosa</i>	T	Yes	36.3 ± .18	(92)	31.3 ± .23	(110)	36.3 ± .17	(85)	1.1	.31***21
<i>Eremias</i>														
<i>lineo-ocellata</i>	T	Ad	36.9 ± .11	(649)	28.9 ± .17	(886)	37.7 ± .13	(290)	2.5	.58***	.95***	-.93***	-.98***	.27
<i>Eremias lugubris</i>	T	Yes	37.7 ± .19	(176)	29.1 ± .22	(221)	38.2 ± .20	(112)	1.9	.45***	.85**	-.84***37
<i>Eremias</i>														
<i>namaquensis</i>	T	Yes	37.8 ± .16	(151)	30.1 ± .25	(195)	37.4 ± .23	(70)	2.1	.33***	.54*	-.93***19
<i>Nucras tessellata</i>	T	Yes	39.3 ± .42	(43)	31.6 ± .39	(84)	39.5 ± .39	(39)	1.4	.67***49
<i>Nucras intertexta</i>	T	Yes	38.9 ± .88	(3)	34.0 ± .27	(4)	38.9 ± .88	(3)	1.0	.86***

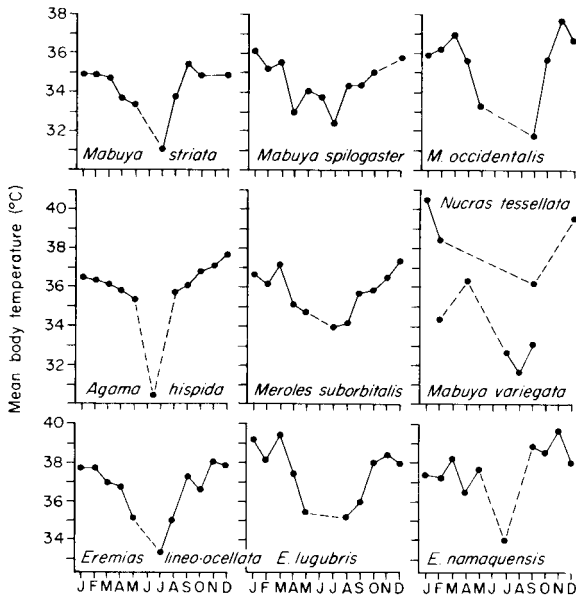


FIG. 1. Monthly mean body temperature (T_b) of Kalahari diurnal lizards sampled while active. Minimum sample size equals 2, but is generally much larger.

species except for those with short seasonal activity patterns (*Nucras tessellata* and *Ichnotropis*). Whether seasonal variation in mean T_b reflects a change in the operating temperature range of these lizards is unknown (Porter et al. 1973:24).

Monthly mean T_b is positively correlated (all $P < .01$) with monthly mean T_a for all species except *Eremias namaquensis* (Table 1). The difference between mean T_b and mean T_a in a given month is negatively correlated (all $P < .01$, Table 1) with monthly mean T_a for all species: thus, mean T_b values are high relative to mean T_a values during cool winter months. This is circumstantial evidence that the lizards are thermoregulating (see Assumptions).

Within-day variation in body temperature at different seasons

The mean T_b values of lizards captured at hourly intervals in different seasons for the lacertid *Eremias lineo-ocellata* (the species for which we have most complete data) is plotted in Fig. 2. Hourly mean T_b is strongly correlated with hourly mean T_a ($r = .932$, $P < .001$). The relatively flat slope of this relation (0.315) suggests that these lizards are thermoregulating (see Assumptions). However, if significant, positive seasonal acclimatization of physiological optimal temperatures occurs (e.g., Mayhew and Weintraub 1971), this analytical technique underestimates the precision of thermoregulation. A crude check compares slopes of the mean T_b vs. mean T_a among seasons: values considerably less than the yearly slope would suggest acclimatization. These slopes for *E. lineo-ocellata* (0.353 for summer, 0.187 for spring plus fall, and 0.337 for winter) are, however, generally similar to the slope

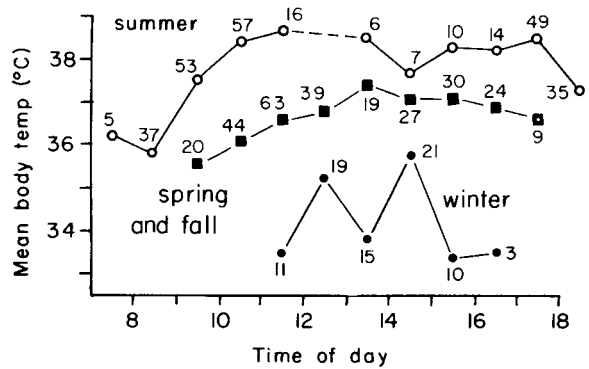


FIG. 2. Mean body temperature (T_b) vs. time of day of *Eremias lineo-ocellata* sampled while active during different seasons. Sample sizes indicated.

for the entire year. We also computed correlation coefficients of hourly mean T_b vs. mean T_a and of mean T_b - mean T_a vs. mean T_a for other common species that are active all year (Table 1). These species also appear to be careful thermoregulators by these criteria.

Seasonal variation in time of activity

We determined the percentage of lizards observed during hourly intervals at different seasons (data uncorrected for variation in time of sunrise or intensity of collecting). We have already published these data for the lacertids (Pianka et al. 1977) and *Mabuya* (Huey and Pianka 1977). Data for *Agama hispida*, the remaining common species, exemplify trends (Fig. 3). In summer, *Agama* has a bimodal activity pattern and is thus relatively inactive at midday (only *Nucras tessellata* has a unimodal activity pattern during summer; see Pianka et al. 1977). During spring and fall, *Agama* delays onset of activity much beyond what would be expected from changes in time of sunrise, is active primarily at midday, and ceases activity early. During winter, these lizards are active only at midday. Indeed, during the entire Kalahari winter, we saw only 3 lizards of all species before 1100 h and only 2 after 1700 h, despite intensive search.

Seasonal variation in basking incidence

The percentage of all lizards, observed at various times, that were perched in sun when first sighted in-

TABLE 2. Percentage of lizards perched in full sun by season (semiarboreal species only). Lizards in partial sun counted as half in sun, half in shade. The 2 *Mabuya* show very significant ($P < .001$) seasonal differences, as does *Agama* ($P < .025$)

Season	<i>Agama</i>		<i>Mabuya spilogaster</i>		<i>Mabuya striata</i>	
	%	N	%	N	%	N
Summer	66.3	101	37.9	137	30.3	132
Spring + fall	79.0	158	76.4	129	65.3	206
Winter	93.3	30	93.5	52	83.8	68

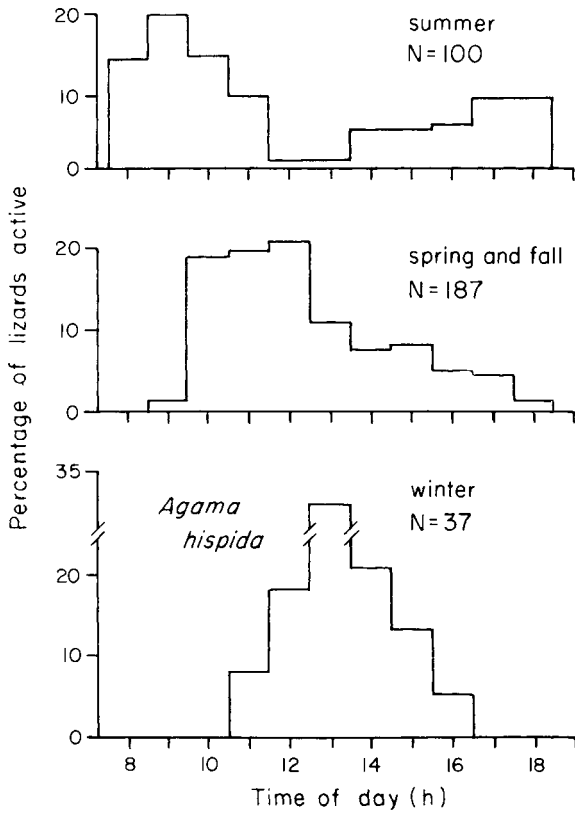


FIG. 3. Percentage of total *Agama hispida* observed (*N*) during each season (summer, spring + fall, or winter) that were observed at different times of day.

dexes relative basking intensity (but see **Discussion**). Semiarboreal species (*Agama*, *Mabuya striata*, and *Mabuya spilogaster*) show significant seasonal differences in percentage of lizards in sun (Table 2, all $P < .025$): more individuals of these species are perched in sun during winter. Among ground-dwelling species, however, only *E. lineo-ocellata* shows significant seasonal variation (Table 3, $P < .001$), again with more lizards in sun during winter (*Meroles* has a similar, but insignificant, trend, $P < .1$). The remaining species brumate (= hibernate, see Mayhew 1968) during winter.

The diel pattern of basking intensity also changes seasonally (Fig. 4). For example, *E. lineo-ocellata* primarily basks early and late in the day during sum-

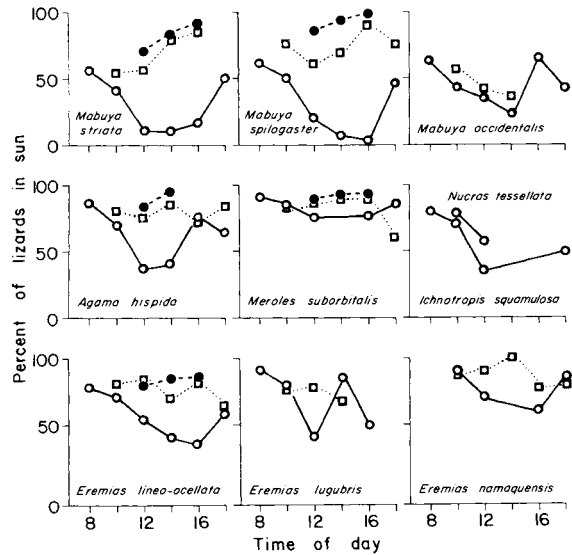


FIG. 4. Percentage of all lizards observed that were perched in sun when first sighted at various times of day. Circles = summer, squares = fall + spring, dots = winter. Minimum sample size equals 5.

mer (open circles); at midday they are more frequently seen in shade. This bimodal or U-shaped basking pattern characterizes all species during summer (except *N. tessellata*, which are seemingly inactive in the afternoon, and possibly *Eremias lugubris*). During spring and fall, the midday decline in basking is generally not evident; and, in winter, lizards tend to be in the sun whenever active. The percentage of lizards in sun during 2-h intervals at different seasons is inversely correlated (all $P < .01$) with mean T_a in the common species (*E. lineo-ocellata* [Fig. 5] $r_s = -.903$, *Meroles* = $-.775$, *Agama* = $-.742$, *Mabuya striata* = $-.853$, and *M. spilogaster* = $-.895$).

Seasonal variation in microhabitat associations

Microhabitat associations of the semiarboreal species change seasonally (all $P < .001$, Table 4). During summer, *M. striata* and *M. spilogaster* generally perch on trees or shrubs, but rarely on logs. During winter, however, both perch more frequently on logs (and therefore closer to the ground). *Agama hispida* also tends to become more ground dwelling in winter (Table 4).

TABLE 3. Percentage of lizards during each season that were first spotted in full sun (ground-dwelling species only). Only *E. lineo-ocellata* shows significant seasonal heterogeneity ($P < .001$)

Season	<i>Meroles</i>		<i>E. lineo-ocellata</i>		<i>E. lugubris</i>		<i>E. namaquensis</i>		<i>N. tessellata</i>		<i>Ichnotropsis</i>		<i>Mabuya occidentalis</i>	
	%	N	%	N	%	N	%	N	%	N	%	N	%	N
Summer	84.3	198	62.6	346	76.4	146	81.3	80	78.2	78	64.4	90	45.0	141
Spring + fall	86.0	306	76.0	321	77.0	71	78.5	88	63.0	8	68.7	8	45.0	56
Winter	90.5	95	83.5	85	87.4	8	87.5	4

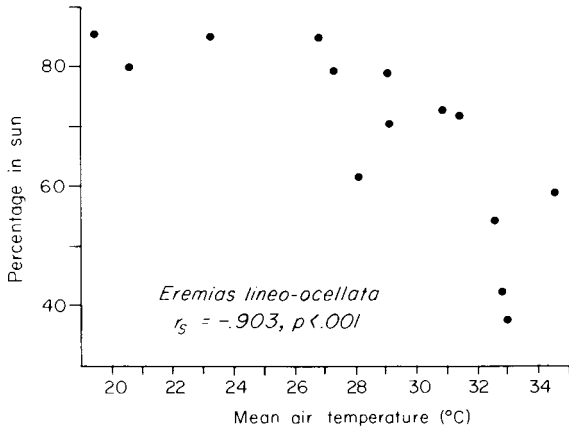


FIG. 5. Percentage of *Eremias lineo-ocellata* in sun during 2-h intervals in each season vs. mean air temperature (T_a). Minimum sample size equals 5.

We have sufficient data to examine diel shifts in perch height during summer of *M. striata* and *M. spilogaster*. These lizards perch higher (all $P < .01$, Table 5) at midday (1101 to 1500 h) than at other times of day.

Correlates of mean body temperature

Lizard species' mean T_b for the summer is correlated ($r_s = .673, P < .05$) with percent of lizards in sun during summer (Tables 1 to 3). Thus lizards that are frequently in the sun tend to have high body temperatures. Also, mean T_b during summer is negatively correlated with seasonal activity niche breadth (Table 1) such that lizards having high body temperatures in summer tend to be active primarily during summer months ($r_s = -.629, P < .05$). Percent of lizards in sun during summer is not, however, correlated with the seasonal activity niche breadth ($r_s = -.236, P > .05$). Summer mean T_b is not significantly correlated with mean time of activity ($P > .5$) during the early part of the day (before 1300 h) or with standard deviation in T_b during summer (Table 1, $P > .5$). Average mean T_b of ground-dwelling species in summer ($37.3 \pm .59^\circ\text{C}$) is slightly but not significantly higher ($P > .1$) than those of semi-arboreal species ($35.8^\circ \pm .59^\circ\text{C}$). Finally, standard deviation in body temperature of semiarboreal species ($\bar{X} = 2.0 \pm .18$) is slightly but not significantly smaller than that of

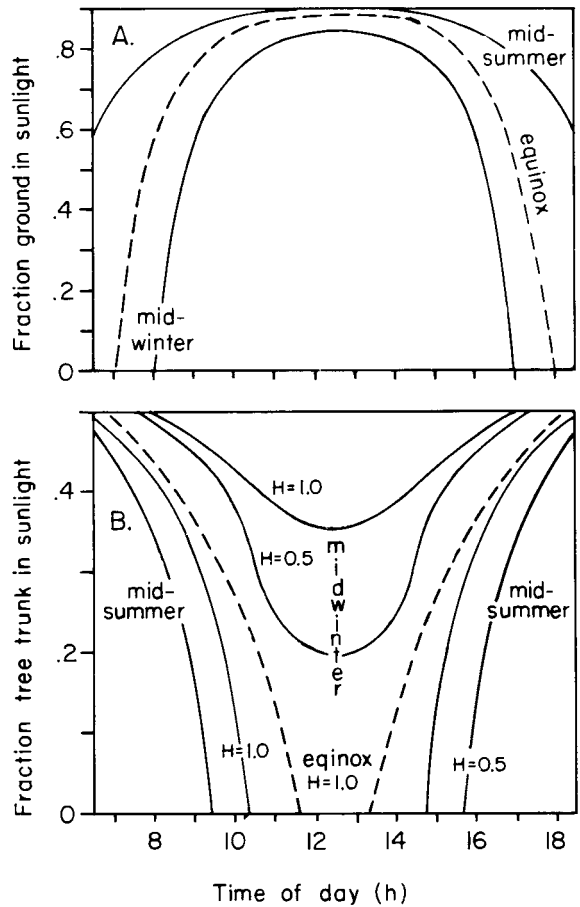


FIG. 6. (A) Fractional sunlit area of ground surface in Kalahari as a function of clock time and season, assuming 10% plant coverage. (B) Fractional sunlit area of surface of tree trunk at 2 values of H (trunk height/crown radius), assuming a solid crown.

ground-dwelling species ($\bar{X} = 2.1 \pm .17$) (see Parker and Pianka 1973).

Activity of adults in winter

As in many lizard faunas (Huey and Slatkin 1976), only juveniles of *Eremias lineo-ocellata* and *Agama hispida* are commonly active during winter months. Adults and juveniles of the three nonbrumating *Mabuya* are, however, commonly active. The remaining lizards either brumate almost entirely (Table 1) or,

TABLE 4. Percentage of lizards at different seasons that were first spotted on ground, logs, or shrubs and trees (N = sample size). All species show significant seasonal heterogeneity ($P < .001$)

Season	<i>M. spilogaster</i>				<i>M. striata</i>				<i>A. hispida</i>			
	Ground	Logs	Arbo-real	N	Ground	Logs	Arbo-real	N	Ground	Logs	Arbo-real	N
Summer	28.3	4.1	67.7	145	20.9	4.3	74.8	115	81.8	0.9	17.3	110
Spring + fall	29.1	24.4	46.5	127	26.2	20.1	53.7	214	93.8	1.5	4.6	194
Winter	34.4	34.4	31.1	61	25.5	36.2	38.3	94	97.0	3.0	...	33

TABLE 5. Percentage of all lizards observed that were perched at various heights at different times of day during summer. Perch heights vary significantly within the 2 *Mabuya* species ($P < .01$)

Time of day	<i>M. spilogaster</i>				<i>M. striata</i>			
	Ground	<1.3 m	>1.3 m	N	Ground	<1.3 m	>1.3 m	N
Early + late	36.6	41.1	22.3	112	29.3	37.3	33.3	75
Midday	8.3	47.2	44.4	36	5.7	42.9	51.4	35

as in *Meroles*, have no juveniles in the population during winter (Pianka et al. 1977).

DISCUSSION

Lizards typically thermoregulate behaviorally by shuttling between sun and shade or other hot and cold microenvironments (which alters heat flux), by regulating times of activity (which alters heat loads), and by modifying posture (which alters surface areas exposed to heat sources or sinks). We have data on only the first 2 types of behaviors; also, we ignore physiological mechanisms (Templeton 1970).

Time of activity varies seasonally. During summer, Kalahari lizards are typically active early and late in the day (except *Nucras tessellata*); in contrast, all nonbrumating species during winter are active only at midday; in spring and fall, lizards are active at intermediate times. This pattern, well known in individual species (Mayhew 1968, Porter et al. 1973, Huey and Slatkin 1976), effectively limits the seasonal variation in ambient conditions to which lizards are actually exposed: by avoiding activity at midday in summer, the lizards avoid the hottest time of year; and by being active only at midday in winter, the lizards avoid the coldest time of year. These changes in activity probably result in lowered costs of thermoregulation (Huey and Slatkin 1976) or lowered variance in body temperatures during activity or both. Nonetheless, the total hours of activity must be much less during winter than during summer.

The percentage of lizards in sun at particular times of day, an index of basking intensity, varies among seasons and with mean T_a . In general, lizards are in sun when the environment is cool but are in shade when the environment is warm (Fig. 5). However, because the proportions of a substrate which is sunlit changes with solar altitude (Appendix, Fig. 6), a change in percentage of lizards in sun with time doesn't necessarily imply thermoregulation, though many workers have implicitly made this assumption (e.g., Huey 1974). Therefore, to assert that thermoregulation is involved, we must show that lizards are actually moving nonrandomly with respect to sunlit and shaded substrates.

Initially we separate arboreal and ground substrates for which patterns of shading are very different (Fig. 6, Appendix). Consider a tree trunk in summer. Early and late in the day, up to 0.5 of its surface is in direct sun; but at midday, most or all of the surface area will

probably be shaded (Fig. 6B). Alternatively, consider an open spot on the ground in summer (Fig. 6A). Early and late in the day, most of the ground is shaded by shadows from shrubs and trees, but at midday most of the ground surface will be in sun. The proportion of substrate in sun at a given time of day varies seasonally (Fig. 6). A higher percentage of a tree trunk will probably be in sun at midday in winter than at midday in summer (solar altitude is lower in winter), and a lower percentage of ground surface will then be in sun.

If lizards move randomly with respect to patches of sun and shade, the percentage of lizards in sun at various times will be proportional to the relative surface areas of substrates that are in sun at those times. Thus, the U-shaped pattern of basking incidence of arboreal species in summer (e.g., *Mabuya striata*, Fig. 4), while appearing to index thermoregulatory movements, would occur even if these lizards moved randomly (only if percentage of lizards in sun exceeds 50% can one assert nonrandom movements). Similarly, an inverse correlation between percentage of lizards in sun and mean T_a would occur in randomly moving "trunk" species. In winter, however, the very high percentage of lizards in sun (Fig. 4, Table 2) strongly suggests that the arboreal species are moving nonrandomly and apparently thermoregulating. Nevertheless, for arboreal species, U-shaped patterns and increases in percentage of lizards in sun during winter must be interpreted with caution. We also note that the slope of the T_b vs. T_a regression, which has been used as an index of the extent of thermoregulation (Huey and Slatkin 1976), of a randomly moving arboreal lizard will tend toward zero simply because of changes in the fractional sunlit area during the day. Thus, slopes of this regression must also be interpreted cautiously.

In contrast, if ground-dwelling lizards moved randomly, the percentage in sun would be inversely U-shaped in summer, fewer lizards would be in sun in winter than in summer, and the percentage in sun would be positively correlated with air temperature. The observed U-shaped distribution of ground-dwelling species (Fig. 4) and the inverse percentage in sun vs. mean T_a correlation (Fig. 5, Table 1) strongly support the hypothesis of active site selection. The significant increase in basking intensity of *Eremias lineo-ocellata* (Table 3) during winter also supports this hypothesis. The similar trend in behavior of *Meroles suborbitalis* (Table 3), while not statistically significant, is probably biologically significant because the available surface

area in sun during winter is relatively low. Overall, our data suggest, most clearly for ground-dwelling species, that lizards move nonrandomly with respect to sun and shade, both on daily and seasonal levels: this behavior should effectively reduce within-day and within-season variance in body temperatures experienced by active lizards relative to those of randomly moving lizards.

Types of perches utilized at different seasons and perch heights utilized at different times of day appear to reflect thermoregulatory movements; these shifts are nonrandom. The change from perches on tree trunks or shrubs to relatively unshaded logs or to the open ground in winter (Table 4) increases radiant heat loads and convective heat transfer at midday (Bartlett and Gates 1967, Fig. 6), and the movement to higher perches at midday (Table 5) reduces heat loads in summer (Gates 1962, Porter et al. 1973). (We note, however, the *Agama* may be arboreal during summer for social reasons. These movements will, nonetheless, have thermoregulatory effects.)

The activity of juvenile lizards only in many faunas during winter is generally thought to reflect surface-to-volume considerations (Cowles 1941, Fitch 1956) or relatively low fat reserves of juveniles necessitating greater activity in winter (anonymous reviewer, *personal communication*). Of the 5 nonbrumating Kalahari lizards that have adults and juveniles active during winter, only *Eremias lineo-ocellata* and *Agama hispida* definitely show this pattern. Adults and juveniles of the remaining three species are all typically active at low body temperatures, even in summer (all *Mabuya* except *M. occidentalis*, Table 1), suggesting that low "optimal" body temperatures may be correlated with the ability of adults to be active year around (below).

Despite the use of these thermoregulatory behaviors, mean T_b values of Kalahari lizards vary somewhat both within a day (Fig. 2) and among months (Fig. 1). Seasonal variation in mean T_b could, however, reflect seasonal acclimatization (Mayhew and Weintraub 1971). Information on seasonal variation in preferred body temperatures (mean body temperature selected in a laboratory thermal gradient, Licht et al. 1966) would be of definite use in helping to determine whether monthly variation in mean T_b is a function of acclimatization or of behavior maximizing net energy gains (Huey and Slatkin 1976).

Mean body temperatures of lizards are generally thought to reflect primarily evolutionary relationships rather than ecological associations (Bogert 1949; Brattstrom 1965; Licht et al. 1966; Huey and Slatkin 1976). For Kalahari lizards, the average difference between mean T_b values of species in summer is significantly lower ($P < .05$) for within-family comparisons (Scincidae, $N = 6$, $\bar{X} = 0.92 \pm .20^\circ\text{C}$; Lacertidae, $N = 10$, $\bar{X} = 1.44 \pm .29^\circ\text{C}$) than for comparisons between these families ($N = 20$, $\bar{X} = 2.61 \pm .28^\circ\text{C}$). Mean body temperatures thus appear to reflect, in part, evolutionary affinities.

Nonetheless, mean body temperatures of Kalahari lizards also correlate with certain ecological associations. Ground-dwelling lizards may have slightly higher summer mean T_b values than do seimarboreal lizards. In summer, species with a high T_b perch more frequently in the sun and also tend to be active primarily in summer months; conversely, lizards with a low summer T_b tend to be active all year. (The latter correlation might be due to an inverse relationship between thermal niche breadth and mean T_b [see Licht 1964]; however, the standard deviation in T_b during summer is not significantly related to mean T_b during summer for these species [$P > .5$].) These correlations are partially dependent on previously discussed evolutionary relationships: for example, 3 or 4 skinks (low-temperature family, Table 1) are active all year, compared with only 2 of 7 lacertids (high-temperature family, Table 1). However, these frequencies do not differ significantly (Fisher exact test, $P > .05$).

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LITERATURE CITED

- Bartlett, P. N., and D. M. Gates. 1967. The energy budget of a lizard on a tree trunk. *Ecology* **48**:315-322.
- Bogert, C. M. 1949. Thermoregulation and ecritic body temperatures in Mexican lizards of the genus *Sceloporus*. *Ann. Inst. Biol. Mexico* **20**:415-426.
- Brattstrom, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.* **73**:376-422.
- Case, T. J. 1976. Seasonal aspects of thermoregulatory behavior in the chuckawalla, *Sauromalus obesus* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **10**:85-95.
- Cloudsley-Thompson, J. L. 1971. The temperature and water relations of reptiles. *Marrow Publ. Co., Watford*. 159 p.
- Cowles, R. B. 1941. Observations on the winter activities of desert reptiles. *Ecology* **22**:125-140.
- Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**:261-296.
- Dawson, W. R. 1975. On the physiological significance of the preferred body temperatures of reptiles, p. 443-473. *In* D. M. Gates and R. B. Schmerl [eds.] *Perspectives of biophysical ecology, ecological studies Vol. 12*. Springer-Verlag, New York.
- Fitch, H. S. 1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. *Univ. Kansas Publ. Mus. Nat. Hist.* **8**:417-476.
- Gates, D. M. 1962. Energy exchange in the biosphere. Harper and Row, New York. 151 p.
- Heath, J. E. 1964. Reptilian thermoregulation: evaluation of field studies. *Science* **146**:784-785.

- . 1965a. Reply to M. Soulé. *Science* **148**:1251.
- . 1965b. Temperature regulation and diurnal activity in horned lizards. *Univ. California Publ. Zool.* **64**:97–136.
- Heatwole, H. 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. *Ecol. Monogr.* **40**:425–457.
- Huey, R. B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* **184**:1001–1003.
- Huey, R. B., and E. R. Pianka. 1974. Ecological character displacement in a lizard. *Am. Zool.* **14**:1127–1136.
- . 1977. Patterns of niche overlap among broadly sympatric versus narrowly sympatric Kalahari lizards (Scincidae: *Mabuya*). *Ecology* **58**:119–128.
- Huey, R. B., and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**:363–384.
- Huey, R. B., E. R. Pianka, M. E. Egan, and L. W. Coons. 1974. Ecological shifts in sympatry: Kalahari fossorial lizards (*Typhlosaurus*). *Ecology* **55**:304–316.
- Leistner, O. A. 1967. The plant ecology of the southern Kalahari. *Bot. Surv. South African Mem.* **38**:1–172.
- Licht, P. 1964. The temperature dependence of myosin-adenosinetriphosphatase and alkaline phosphatase in lizards. *Comp. Biochem. Physiol.* **12**:331–340.
- Licht, P., W. R. Dawson, V. H. Shoemaker, and A. R. Main. 1966. Observations on the thermal relations of Western Australian lizards. *Copeia* **1966**:97–110.
- Mayhew, W. W. 1964. Taxonomic status of California populations of the lizard genus *Uma*. *Herpetologica* **20**:170–183.
- . 1968. Biology of desert amphibians and reptiles, p. 195–356. *In* G. W. Brown, Jr. [ed.] *Desert biology* Vol. 1. Academic Press, New York.
- Mayhew, W. W., and J. D. Weintraub. 1971. Possible acclimatization in the lizard *Sceloporus orcutti*. *J. Physiol. (Paris)* **63**:336–340.
- Norris, K. S. 1953. The ecology of the desert iguana, *Dipsosaurus dorsalis*. *Ecology* **34**:265–287.
- Parker, W. S., and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. *Herpetologica* **29**:143–152.
- Pianka, E. R. 1971. Lizard species density in the Kalahari Desert. *Ecology* **52**:1024–1029.
- Pianka, E. R., and R. B. Huey. 1971. Bird species density in the Kalahari and the Australian deserts. *Koedoe* **14**:123–130.
- Pianka, E. R., R. B. Huey, and L. R. Lawlor. 1977. Niche segregation in desert lizards. *In* D. J. Horn, R. Mitchell, and G. R. Stairs [eds.] *Analysis of ecological systems*. Ohio State Univ. Press, Columbus. (*In press.*)
- Porter, W. P., J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology—thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* **13**:1–54.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**:688.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman and Co., San Francisco. 776 p.
- Templeton, J. R. 1970. Reptiles, p. 167–221. *In* G. C. Whitton [ed.] *Comparative physiology of thermoregulation* Vol. 1. Academic Press, New York.

Appendix

CALCULATING THE FRACTIONAL SUNLIT AREAS OF TREES AND GROUND SURFACES

The fractional sunlit areas of environmental surfaces at various times and seasons should ideally be determined in the field by routine sampling procedures. This is, however, generally impractical; but one can use geometric methods to approximate basic temporal patterns of shading.

In calculating the fractional sunlit areas, the calculations are for a standard tree with a single, straight trunk of known height and diameter D and with a crown that is represented as a solid oblate spheroid of ellipticity e whose major (unit) radius is used as the scaling factor. The final term H is the ratio of the height of the trunk to the radius of the crown.

The first part of the calculations requires determining the fractional sunlit areas of a tree trunk f as a function of the elevation angle of the sun α . The derivation is simple geometry and will not be given here. The resulting fraction f in terms of the parameters is:

$$f = \frac{1}{2H} \left\{ \sqrt{1 - e^2} + H - \sqrt{1 - e^2} \left(\frac{\tan^2 \alpha}{1 - e^2} + 1 \right)^{-1/2} - \tan \alpha \left[\left(\frac{1 - e^2}{\tan^2 \alpha} + 1 \right)^{-1/2} - \frac{D}{4} \right] \right\}. \quad (1)$$

This complete formula can be applied to any field situation. To simplify the equation, the trunks were considered sufficiently narrow ($D \ll 1$) to allow the approximation $D = 0$. At the two extremes of ellipticity, Eq. 1

reduces for $e = 1$ ("pancake" crown) to

$$f = \frac{1}{2} (1 - \tan \alpha / H) \quad (2)$$

and for $e = 0$ (spherical crown) to

$$f = \frac{1}{2} \left[1 - \frac{1}{H} (\sec \alpha - 1) \right]. \quad (3)$$

The results given below are for $e = 0$ but are not sensitive to the ellipticity parameter.

The fractional area of the ground in sun depends in part on the density and shape of trees and shrubs (assumed solid). The area of the shadow cast by a tree on the ground (for $D \ll 1$, the crown area is effectively the total area) is insensitive to ellipticity near noon but becomes more sensitive when the sun is near the horizon. For $e = 0$ (spherical crown) the area of the unit radius crown is π (scales as radius squared). With the sun at elevation α , the ground area is $\pi / \sin \alpha$.

Shadowing of one tree by another need be considered only when the sun is low in the sky and when the trees are densely packed. If the average separation of tree trunks is S (scaled to crown radius), then the sun elevation below which shadowing must be considered is:

$$\alpha \leq \arctan[(2 + H)/S], \quad (4)$$

(e.g. for a separation $10 \times$ the crown diameter [$S = 20$] and a trunk height equal to the crown diameter [$H = 2$], then $\alpha = 11.3^\circ$, which is near sunrise or sunset at the latitude of the Kalahari [$27^\circ S$]).

Next for both ground and trunk, it is necessary to calculate the sun's altitude as a function of time of day (t.o.d.), because the observations will be plotted with t.o.d. as the abscissa to permit comparison with lizard data. If H_s is the hour angle of the sun (related to t.o.d. as described below), ϕ is the latitude and δ is the celestial declination of the sun (varying from -23.5° in December to $+23.5^\circ$ in June), then the elevation α is given by:

$$\sin \alpha = \sin \phi \sin \delta + \cos \phi \cos \delta \cos H_s. \quad (5)$$

The relation of clock time to hour angle (actual position of the sun in the sky) is determined by two factors: the observer's position within the standard time zone and the astronomical equations of time that reflect the nonuniformity of motion of the actual sun through the sky. The former effect can be up to 30 min and is constant throughout the year (for the Kalahari clock time is ≈ 30 min ahead of sun time). The latter effect is at most 18 min and varies during the year both in sign and in

magnitude. Because of the coarse time scale on which the observations are plotted, corrections for this latter effect are ignored.

Figure 6A shows the computed fractional area of the ground in sunlight as a function of clock time and season assuming 10% ground coverage by plants; Fig. 6B showed the fractional

area of a tree trunk in sunlight for 2 representative trunk height/crown size ratios. For rough monthly interpolation, the months on either side of midwinter or midsummer can be read off the same curves while the months on either side of the equinoxes would fall about halfway between the equinoctial and solstice curves.