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Field Thermoregulatory Behavior in the Western Canarian Lizard *Gallotia galloti*

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ABSTRACT.— I studied the thermoregulatory behavior of a field population of the Canarian lizard *Gallotia galloti*, using null hypotheses based on (1) the measurement of operative temperatures available in full sun and in the shade (T_e), and (2) the distribution of randomly positioned models with respect to sun and shade. The activity curve of the lizard population was unimodal, with a pronounced peak in the morning and lower (though roughly constant) levels at later times of day. Activity levels were positively correlated with the difference between T_e in the sun and T_e in the shade, but negatively correlated with T_e in the shade. The distribution of lizards into sun-shade categories was highly selective relative to paper models, with an overall daily selectivity pattern that was symmetrical around midday (selection of sunlit perches early and late in the day, shade seeking at midday, and random distribution at intermediate hours). The low dispersion of hourly mean operative temperatures at lizard perching sites relative to random locations of models (average values calculated weighting mean T_e s with frequencies of sun-shade use and sun-shade availability) suggested a high degree of thermoregulatory precision. Dark, adult males basked for longer periods than juveniles, whereas subadults/females showed intermediate basking times, which suggests that body size and color differences may play a role in behavioral thermoregulation by these lizards.

RESUMEN.— Se ha estudiado el comportamiento termorregulador de una población de Lagarto Tizón *Gallotia galloti galloti* en el sur de Tenerife, Islas Canarias, a partir de hipótesis nulas basadas en: 1) las temperaturas disponibles para los lagartos al sol y a la sombra (temperaturas operativas) medidas utilizando modelos de cobre; y 2) la distribución (al sol, a la sombra, o al sol filtrado por la vegetación) de modelos de cartón distribuidos al azar. La curva circadiana de actividad resultó monomodal, con un máximo por la mañana y niveles más bajos aunque constantes durante el resto del día. La actividad se correlacionó positivamente con la diferencia de temperaturas operativas entre el sol y la sombra (rango de temperaturas al alcance de los lagartos). La distribución de los lagartos en áreas de sol y sombra fue claramente selectiva en comparación con los modelos distribuidos al azar, con un patrón global simétrico en torno al mediodía (selección positiva de las áreas al sol por la mañana y por la tarde, búsqueda de refugios a la sombra en las horas centrales del día, y distribución al azar en las horas intermedias). La baja dispersión a lo largo del tiempo de las temperaturas operativas en los microclimas seleccionados por los lagartos, respecto a las temperaturas correspondientes a las posiciones al azar de los modelos (medias de las temperaturas al sol y a la sombra ponderadas con la distribución de frecuencias de animales o modelos en esas mismas categorías), sugieren un alto grado de precisión termorreguladora. La duración media de los periodos de exposición al sol, en individuos cuyo comportamiento pudo cronometrarse, fue superior en los machos adultos, de coloración más oscura, que en los juveniles, mientras que hembras y subadultos mostraron valores intermedios, lo que sugiere que tanto el tamaño corporal como el colorido desempeñan algún papel en la termorregulación comportamental de estos lagartos.

The physiological consequences of habitat selection are crucial for ectotherms because microclimates vary spatially over time, and this variation translates into body temperatures that affect short-term physiological performance and hence organismal fitness (Huey, 1991). However, the very concept of thermal dependent habitat selection implies a previous knowledge of the distribution in space and time of the environmental temperatures available (Huey et al., 1977; Huey, 1982; Hertz, 1992a, b). Otherwise,

a constant body temperature, or even changes in the proportion of individuals apparently basking in the sun, can merely reflect changes in the thermal environment. An inanimate object, for instance, can show a U-shaped daily pattern of time spent in the sun, and fairly constant temperatures, if placed on a tree trunk that receives full sun in the early morning and late afternoon but is in the shade during the heat of midday (Heath, 1964; Huey et al., 1977). Therefore, the design of field studies of ther-

moregulation requires information about available temperatures. Such operative environmental temperatures (T_e), that represent the sum of factors conditioning heat exchange between the organism and its environment, can be measured using metal or plastic models whose physical properties mimic the thermal responses of non-thermoregulating animals at any given microsite and time (Bakken and Gates, 1975; Bakken, 1992).

Active (i.e., non random) temperature regulation by microhabitat selection is affected behaviorally, as first demonstrated by Cowles and Bogert (1944). Shuttling between sun and shade, retreating into the deep shade of crevices, or basking for periods of variable duration, are obviously behavioral decisions. Lizards from hot, arid regions offer a unique combination of behavioral and ecological features for studying the evolution of behavioral and physiological performance (e.g., Huey and Bennett, 1987), because their relatively narrow preferred temperature range is usually combined with remarkably heterogeneous environmental thermal regimes (Bradshaw, 1986; Pianka, 1986; Heatwole and Taylor, 1987).

In this paper I present the results of a short-term field study of thermoregulatory behavior in the Canarian lizard *Gallotia galloti*, with an emphasis on the use of null hypotheses for evaluating the extent of temperature regulation (Hertz, 1992a, b) and on the behavioral mechanisms implied. *Gallotia galloti* is a species whose ecology is little known (though see Molina, 1985). It was chosen because of the potential interest of extreme climatic differentiation within the island of Tenerife (Fernandopulle, 1976). My specific goals were: (1) to describe the patterns of daily activity and daily selection of sunlit/shaded perches in a lizard population from the hot, arid coastal region of southern Tenerife, (2) to explain these patterns in terms of the T_e s available, and (3) to explore the variation of thermoregulatory behavior (duration of basking events) among time periods and sex/age classes.

MATERIALS AND METHODS

Study Area.—Field observations were carried out between 21 and 29 August 1992 in a coastal gorge located 2 km east of El Medano, southern Tenerife, Canary Islands (28°N, 16°50'W). Environmental conditions in the south of the island are those of a semi-desert, with a hot (mean monthly air temperature of 20–25°C at altitudes of 0–250 m), arid, high insolation climate (Fernandopulle, 1976). The vegetation of the study plot consisted mainly of cactus-like plants such as the Canarian forb *Euphorbia canariensis* or the introduced, widespread weed *Opuntia dillenii*,

together with the endemic forbs *Euphorbia balsamifera* and *E. obtusifolia*, the fleshy fruit bearing Rubiaceae *Plocama pendula*, the shrubs *Launaea arborescens* and *Schizogyne cericea*, and sparsely distributed patches of grass. This plant community was established on young, basaltic substrates produced by volcanic activity. The study area was crossed by a number of basalt walls. Rocks in these walls were irregular in size and shape, forming numerous crevices that served as lizard refuges together with some of the above plants.

Study Animal.—*Gallotia galloti* is a medium-sized (snout-vent length = 130–145 mm), omnivorous lacertid lizard. Its diet consists of plant material, including flowers, buds, twigs, leaves, and fruits, but arthropods are also eaten occasionally (Barbadillo, 1987). The population reported here is assigned to *G. g. galloti* (Bischoff, 1982).

Field Sampling.—Lizards were censused at hourly intervals by walking 300 × 5 m transects along the west facing slope of the gorge and counting all animals detected. Daily activity was estimated as the mean numbers of lizards per transect corresponding to one hour periods between 0600 and 1800 h EST (European Standard Time). This was an adequate procedure because lizards sought burrows and crevices when inactive, thus becoming invisible during the transects. I walked five transects per hourly interval, always on at least two different sampling days.

In order to evaluate the extent of thermal related microhabitat selection and its variation throughout the day, when a lizard was first observed, its location was noted as follows: full sun, partial sun (sun filtered by vegetation), full shade, or undetermined (the lizard was moving when first sighted and I could not state precisely what perch category it had departed from; this later category was excluded from the analyses). In addition, I quantified the temporal variation of sunlit perch availability with the help of 50 pieces of white paper, sized as an average lizard, that had been fixed to the ground, inside the vegetation or on basalt surfaces, just after sunset of the first sampling day. These simulated, non-thermoregulating lizard models were thus placed at spots that were randomly positioned with respect to the distribution of sun and shade. However, they were all left within a distance of less than 2 m from the nearest basalt wall or commonly used perch species (*Opuntia dillenii* or *Plocama pendula*). Previous observations of lizard behavior showed that this was the largest distance from refuge-providing habitat features at which perching lizards could be found. Pieces of paper were thus scattered randomly through the habitat actually used by the lizards. The availability of

sunlit perches was estimated by counting the number of papers in each of the above categories (full sun, partial sun, or full shade) at hourly intervals between 0600 and 1800 h. The selectivity of lizards for sunlit or shaded perches was tested for significance using χ^2 tests applied on contingency tables comparing the distributions among sun, shade, and partial sun, of lizards and pieces of paper.

I also measured the maximum and minimum T_e values a lizard could attain at any time of day in full sun and full shade locations, respectively. For this purpose, I used two hollow copper models approximately the size of a lizard, one placed in full sun and the other in full shade, and read their inner temperature with an electronic digital thermometer (± 0.1 C precision). Models were copper cylinders with a small hole allowing insertion of the sensing tip of the thermometer (Van Berkum et al., 1986). Though I did not measure the absorptance of models or lizards to solar radiation, I checked that copper models provided reasonably close approximations of actual lizard temperatures by comparing, under the same environmental conditions, their temperature readings with the "cloacal" temperatures of three dried carcasses of lizards, one adult male and two subadults (Bakken, 1992). The mean values for the three lizards and the two copper models were highly correlated ($r^2 = 0.99$), satisfying the criterion for T_e determinations in Bakken et al. (1985). The resulting regression equation ($T_e = 6.78 + 0.81 \times \text{measured copper temperature}$), whose slope had a standard error < 0.02 ($N = 20$), was used to hold for the effect of differences in solar radiation absorptance or other thermal properties. The T_e values presented hereafter were thus computed by entering field measurements into the above equation.

Temperatures were recorded in blocks of one reading every 5 min at each sunlit or shaded site, after having checked that thermal equilibrium with the environment was reached in about three minutes. Sites were chosen trying to reflect the actual sunlit or shaded perches more frequently used by lizards, according to observations made during my activity transects. Overall, I sampled twenty different sites (ten in full sun and ten in the shade) in six different sampling dates, obtaining sample sizes of 14–26 temperature readings per hour and type of perch (sunlit-shaded).

Behavioral thermoregulation by means of basking implies controlling either the duration or frequency of individual basking events (Avery, 1976; Diaz, 1991). I investigated the first of these possibilities by monitoring the behavior of a number of lizards that were classified as males (large size and uniform color pattern),

females/subadults (medium to large size and striped pattern) or juveniles (small size and striped pattern) according to size and coloration differences. These focal lizards were spotted emerging from refuges in the shade (where their movements could not be followed), so that I could measure the duration of basking events (± 1 sec) with a stop watch. Only lizards remaining stationary for more than 30 sec in the sun were considered to be basking, in order to exclude exposure to sun during the course of other, non thermoregulatory activities. Basking durations were normalized by log-transformation before being employed in parametric tests.

RESULTS

The pattern of daily activity revealed in this study was clearly unimodal (Fig. 1), with a pronounced peak in the morning (0800–1100 h) and lower though roughly constant levels at later times of day. Differences among hourly periods in the numbers of lizards seen were highly significant (Kruskal-Wallis test: $H = 49.9$, $P < 0.001$). There were also marked differences over the course of the day in the distribution of lizards into sunlit and shaded perches (Fig. 2a). Most lizards perched in full sun in the early morning (0700–0800 h) and late afternoon (1600–1700 h), while at midday (1000–1400 h) only about 20% of the lizards were in full sun at first sighting. These temporal trends were the opposite of what would be expected considering the availability of sunlit perches, as reflected in the distribution of paper models (Fig. 2b). As a consequence, the selectivity of lizards for potential basking sites (Table 1 and Fig. 2) was positive in the early morning, then null (random distribution), negative at midday (rejection of sunlit perches by shade seeking lizards), null, and again positive before activity ceased. The resulting overall pattern was symmetrical around midday (Table 1 and Fig. 2).

Changes in microhabitat selection were paralleled by changes in the behavior of focal lizards. The hourly mean durations of individual basking events were correlated negatively with the corresponding mean values of T_e in the sun (Fig. 3). Though the effects of both time of day (central hours, 1000–1400, vs. morning and evening, 0600–1000 and 1400–1800) and sex/age class on the duration of basking events (Table 2) were only close to statistical significance (Table 3), adult males basked for longer periods than juveniles (Table 2: a posteriori multiple range test based on 95 percent LSD intervals), whereas subadults/females showed intermediate basking durations. The difference between males and juveniles was not due to a divergence in activity times (for instance later emergence times of juveniles), since the distri-

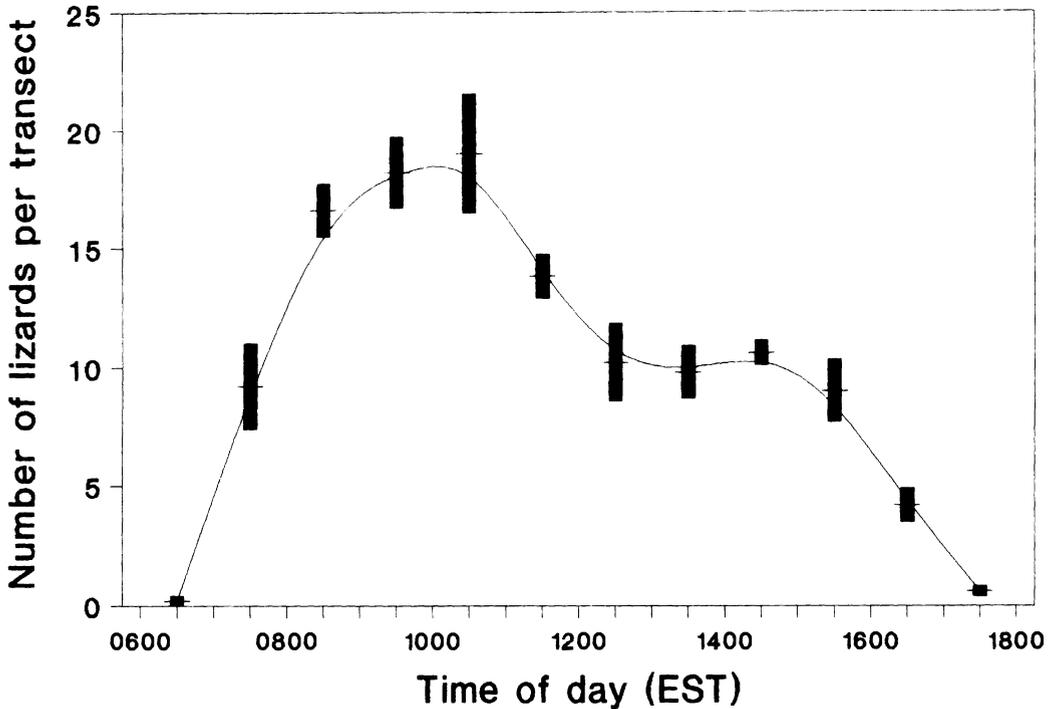


FIG. 1. Curve of daily activity (European Standard Time) in the lizard population studied: hourly means (± 1 SE) of the number of lizards seen per 300 m transect ($N = 5$ in all cases).

bution of observations into time periods was similar for all lizard classes ($\chi^2 = 1.23$, $df = 1$, $P > 0.5$).

Operative environmental temperatures varied significantly with time of day (Fig. 4), the variation being larger in maximum (sun) T_e than in minimum (shade) T_e (one-way ANOVAs; sun: $F_{11,266} = 104.1$; shade: $F_{11,266} = 59.5$; $P < 0.001$ in both cases). More important, the variation in T_e proved to be a powerful predictor of lizard ac-

tivity and microdistribution (i.e., selection of sunlit/shaded perches). Thus, activity (measured as mean number of lizards per transect) was strongly correlated with the difference between T_e in the sun and in the shade ($r = 0.903$, $N = 12$, $P < 0.001$), so that the number of lizards seen increased with the range of body temper-

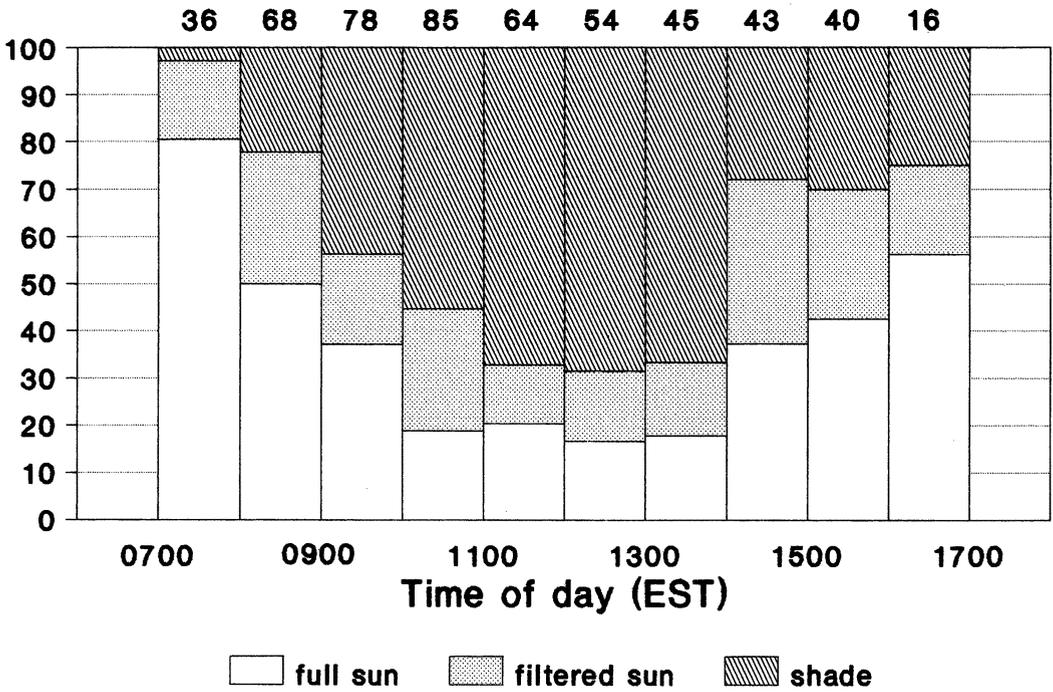
TABLE 1. Selectivity of lizards with respect to sunlit and shaded perches: results of χ^2 tests comparing the frequency distributions of lizards and randomly positioned paper models into sun-shade categories (Fig. 2). $df = 2$ in all cases.

Time of day (h)	χ^2	P	Type of perch selected
0700-0800	17.69	<0.001	Sunlit
0800-0900	3.31	0.191	—
0900-1000	5.14	0.077	—
1000-1100	16.20	<0.001	Shaded
1100-1200	21.79	<0.001	Shaded
1200-1300	19.72	<0.001	Shaded
1300-1400	12.18	0.002	Shaded
1400-1500	3.67	0.160	—
1500-1600	5.65	0.059	—
1600-1700	12.37	0.002	Sunlit

TABLE 2. Average duration of individual basking events (in minutes, back-transformed from logarithms) according to time of day (0700-1000/1400-1700 vs. 1000-1400) and sex/age categories: mean, interval within ± 1 SE around the mean, range, and sample size. Common superscripts indicate homogeneous groups according to multiple range tests based on 95 percent LSD intervals. See Table 3 for results of ANOVA.

Time of day (h)	Bask duration (min)			
	\bar{x}	± 1 SE	Range	N
Morning + evening	2.9 ^a	2.4-3.4	0.7-18.0	28
Midday	1.9 ^a	1.7-2.3	0.6-11.0	22
Sex/age class				
Juveniles	1.9 ^b	1.6-2.2	0.6-4.6	15
Subadults/females	2.2 ^{b,c}	1.7-2.7	0.6-18.0	20
Males	3.6 ^c	2.9-4.4	0.9-11.0	15

a. Use of sunlit/shaded perches



b. Availability of sunlit/shaded perches

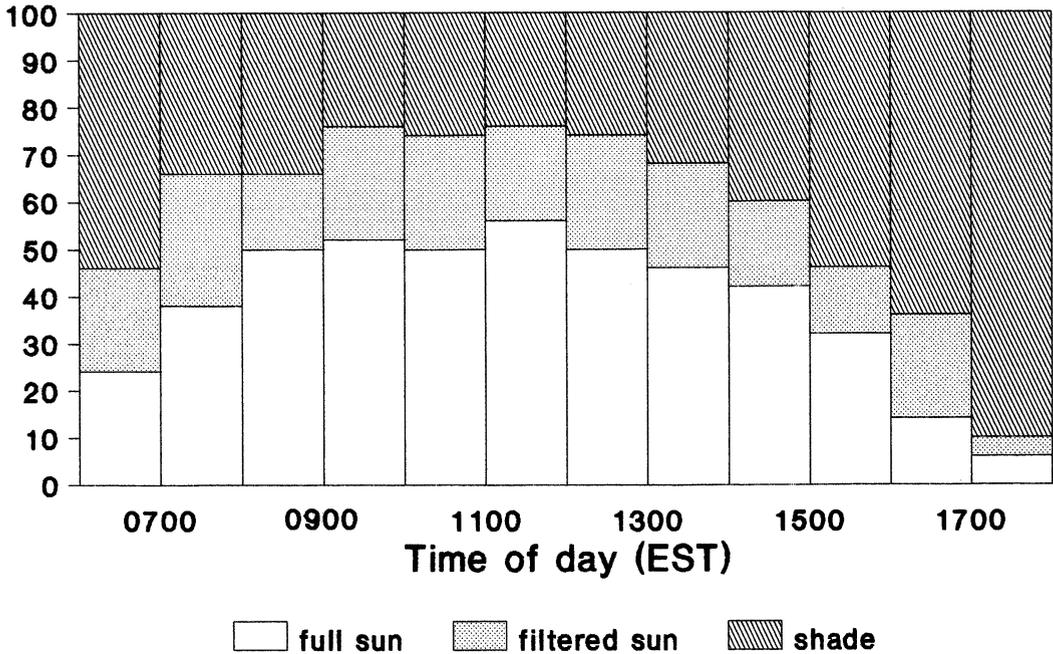


FIG. 2. Frequency of use and relative availability of sunlit and shaded perches. (a) Percentage of lizards in each sun-shade category at hourly intervals; sample sizes are shown on top of each column. (b) Distribution of non thermoregulating paper models into the same sun-shade categories at hourly intervals; N = 50 in all cases.

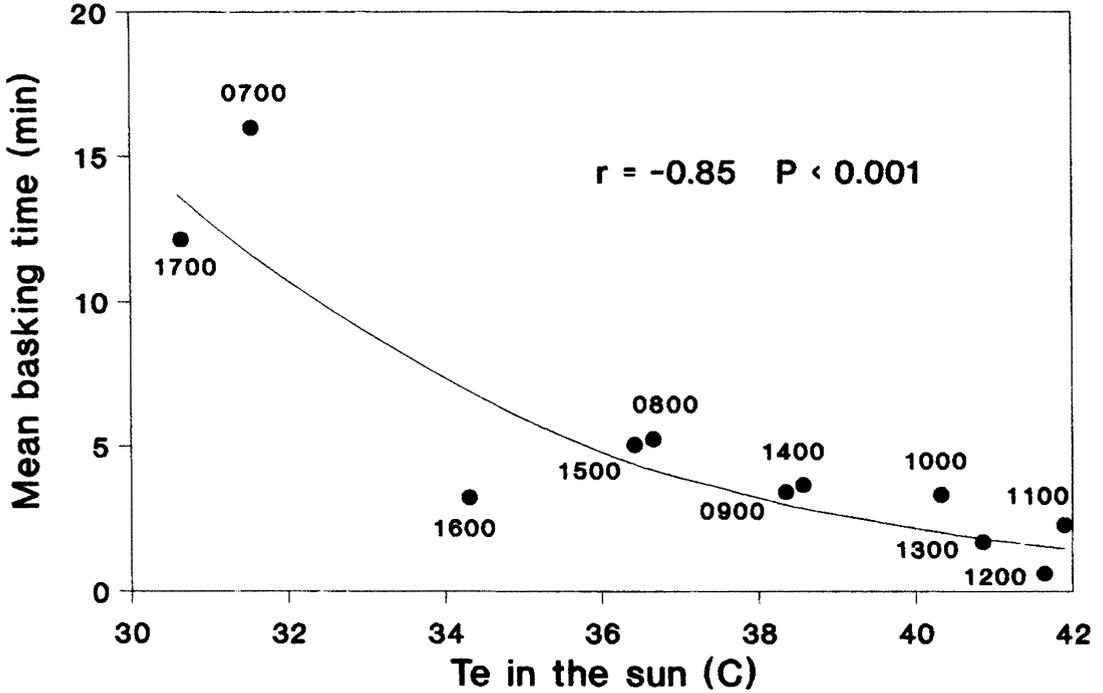


FIG. 3. Mean hourly durations of individual basking events as a function of operative temperature (T_e) in the sun. $N = 11$ due to the lack of behavioral observations between 0600 and 0700 h.

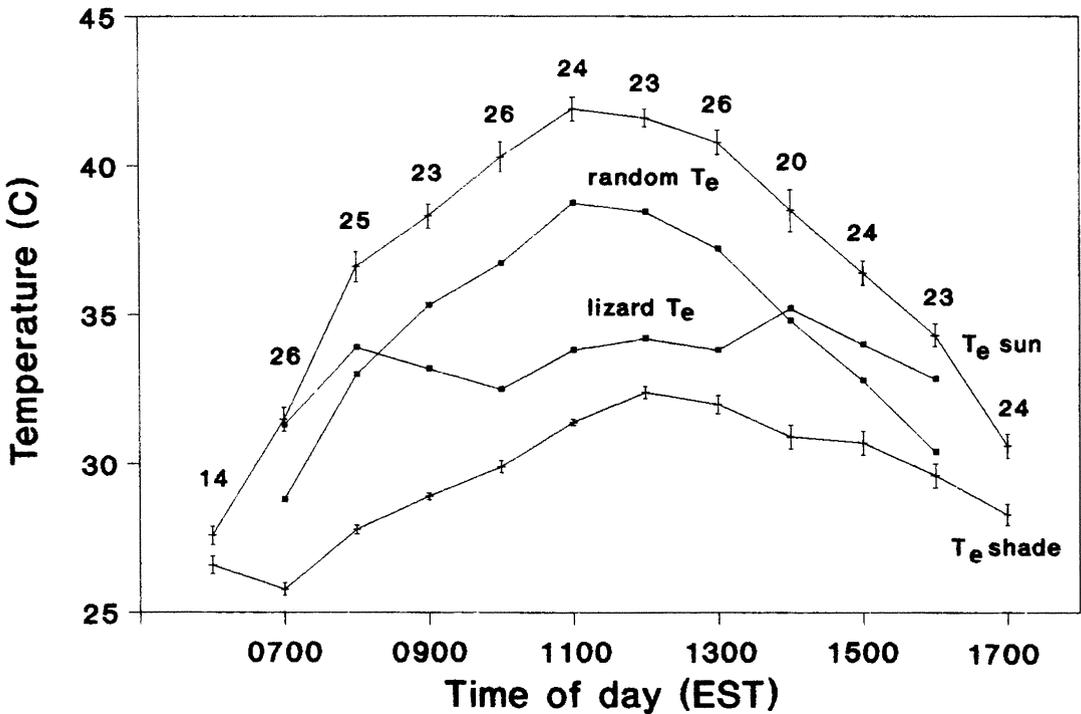


FIG. 4. Daily variation (mean ± 1 SE) of operative environmental temperatures measured with hollow copper models in full sun (T_e sun) and in the shade (T_e shade), with sample sizes shown above each pair of error bars, and mean temperatures obtained weighting T_e values with the frequency distributions into sunlit/shaded areas of lizard perching sites (lizard T_e) and randomly positioned models (random T_e).

atures they could attain. The residuals of this later model were, in turn, negatively correlated with T_e in the shade ($r = -0.625$, $N = 12$, $P < 0.05$).

Concerning microhabitat selection, I used T_e values, together with the frequency of use of sunlit and shaded perches (Fig. 2a), to calculate an average of sun and shade values weighted by observed usage (lizard T_e in Fig. 4, which is equivalent to the effective operative temperature in Vispo and Bakken, 1993). By the same procedure, i.e., weighting sun and shade values with the observed distribution of paper models (Fig. 2b), I also calculated the daily variation of the temperatures available if the distribution of lizards had been random with respect to sun and shade (random T_e in Fig. 4). Although the means of both series of estimates (lizard: $\bar{x} = 33.5$, $SD = 1.16$; random: $\bar{x} = 34.4$, $SD = 3.34$; $N = 10$ in both cases) did not differ significantly one from each other ($t = 1.02$, $P > 0.3$), the variance was much larger in the case of randomly positioned models ($F_{9,9} = 9.62$, $P < 0.005$), showing that the distribution of lizards was not only selective but also highly efficient in buffering variations of the thermal environment.

DISCUSSION

Perhaps the main finding of this study is that the spatiotemporal distribution of *G. galloti* (selection of sunlit perches and circadian activity curve) could be explained to a large extent invoking thermoregulatory behavior (Grant and Dunham, 1988; Carrascal and Díaz, 1989; Adolph, 1990; Grant, 1990; Díaz, 1992). Though I could not measure lizard body temperatures because of the difficulty of catching (or noosing) even small numbers of unrestrained animals (Avery, 1982), average T_e estimates at lizard perching sites can be regarded as reasonable simulations of lizard thermal responses under comparable microclimatic conditions (Grant and Dunham, 1988; Hertz, 1992a). Thus, mean body temperatures of *G. galloti* in the field can be predicted to oscillate around 33.5 C, a value that is remarkably close to the mean body temperature (33.2 C) of field active *G. simonyi* (Barbadillo, 1987) in the neighboring island of El Hierro. However, more important than the value of field body temperatures is the fact that lizards in this study chose to be active in the microhabitats and at times of day that allowed them to minimize variations in the surrounding thermal environment. This behavioral choice of nearly constant microclimates seemed to be responsible for a high degree of thermoregulatory precision, as suggested by the low dispersion of hourly mean operative temperatures at lizard perching sites (interquartile range = 1.2) relative to random locations of paper models

TABLE 3. Two-way ANOVA for the effects of time of day and sex/age categories on the log-transformed average duration of individual basking events.

Source of variation	SS	df	MS	F	P
Main effects	5.857	3	1.952	2.767	0.053
Sex/age	4.033	2	2.016	2.857	0.068
Time of day	2.423	1	2.427	3.440	0.070
Interaction	2.532	2	1.266	1.794	0.178
Error	31.053	44	0.706		

(interquartile range = 4.4). In addition, the fact that active thermoregulation did actually take place was made clear by the highly selective distribution of lizards relative to paper models (Table 1 and Fig. 2).

The digestive efficiency of herbivorous lizards (Harlow et al., 1976) and the gut-passage time of insectivorous ones (Waldschmidt et al., 1986; Van Damme et al., 1991) have been shown to exhibit a strong thermal dependence. The gut-passage time of *Lacerta vivipara*, for instance, increased rapidly within the range 20–30 C, and then decreased at 35 C during the course of long-term exposure experiments (Van Damme et al., 1991), though the thermal performance breadth of this function (Huey, 1982) was relatively wide. For the medium-sized, primarily herbivorous lizards reported here, and under circumstances of no apparent restriction in food supply (edible plants were abundant in the study plot), it may be important to minimize temperature shifts in order to process as much food as possible in the shortest possible time. Vegetarian Galapagos land iguanas have been shown to select microhabitats within their home ranges in order to maintain a constant body temperature for the longest possible portion of the day (Christian et al., 1983).

The circadian activity of the population studied was clearly unimodal (Fig. 1). This is in contrast with the pattern found in most lizards from hot, arid, desertic or semi-desertic regions, that (at least in the warmer season) restrict their activity to relatively short time periods in the early morning and late afternoon, and retreat to their burrows at midday (Pianka, 1986; Grant and Dunham, 1988; Grant, 1990; Hertz, 1992b). In the system studied, however, T_e s measured were cooler than in most deserts, and temperatures in the shade were lower than the mean temperatures of the sites selected by perching lizards in all times of day, including the heat of midday. The significant correlations between numbers of lizards per transect and T_e values (see Results) show that activity decreased at midday, despite the relatively wide range of operative temperatures available, because even

shaded perches were probably warm enough for most lizards. Nevertheless, activity could be maintained, though at lower levels, also at midday, when lizards shortened the duration of basking periods and restricted their movements to the scarce shaded perches available. Another interesting possibility that deserves further investigation is that lizards could select basalt walls in which crevices—i.e., retreat sites in the sense of Huey et al. (1989)—allowed the maintenance of body temperatures enabling them to undertake short, but not rare, bursts of surface activity.

Apparently, lizards controlled heat gains behaviorally by regulating the duration of basking events throughout their whole time of surface activity, as shown by the highly significant negative correlation between hourly means of basking duration and mean values of T_b in the sun (Fig. 3). This is in contrast with the data available for other lacertids of smaller body size that basked for long periods after morning emergence but subsequently shifted to regulate basking rate (number of basking events per unit time) rather than basking duration (see e.g., Diaz, 1991, for *Psammodromus algirus*; or Carrascal et al., 1992, for *Lacerta monticola*). In fact, body size, and associated differences in surface-to-volume ratio, proved to have a significant effect on basking behavior. Thus, juveniles basked for shorter periods than adult males despite their strongly overlapped temporal distributions (see Schwarzkopf and Brooks, 1985, and Carrascal et al., 1992, for similar results). Differences in coloration, however, also seemed to play a role (Norris, 1967; Pearson, 1977), since basking times of females and subadults were not significantly shorter than those for darker but larger adult males.

Finally, it should be noted that my study was restricted to a single season and, probably more important, to just one locality in the arid, low altitude southern area of Tenerife. With respect to seasonal changes in thermoregulatory behavior, which have been reported in other lizards (Huey et al., 1977; Christian et al., 1983; Van Damme et al., 1987), they are unlikely to be pronounced, since seasonal rhythms in temperature are low at the lower altitudes of the island. Geographic variation within Tenerife, however, affects seasonality, extent of diurnal rhythms, temperature, and insolation levels (Fernandopulle, 1976). This variation is both altitudinal (from the sea level up to the 3718 m tip of Teide, which is the highest Spanish peak) and longitudinal (the northern coast is cooler and more humid), and it is congruent with the microevolutionary differentiation of *G. galloti* according to scale counts (Thorpe and Baez, 1987). The extent to which the different sub-

species have different thermal physiologies is, however, completely unknown. The results presented here provide information on thermoregulatory behavior at a typical southern locality with which future data from other latitudes and/or altitudes can be compared. Such comparison could shed light on the mechanisms underlying variable patterns of correlation between behavior, physiology, and environment (Feder, 1987) in a species that has offered good opportunities for evolutionary studies on morphological variation at a microgeographic, within-island scale (Thorpe, 1985; Thorpe and Baez, 1987; Thorpe and Brown, 1989).

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