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COVARIATION OF THERMAL BIOLOGY AND FORAGING MODE IN TWO MEDITERRANEAN LACERTID LIZARDS[1]

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Abstract. Body temperatures, heat exchange rates, behavioral thermoregulation, and movement behavior (as an index of foraging mode) were studied in two widely distributed, medium-sized lacertid lizards (*Acanthodactylus erythrurus* and *Psammodromus algirus*). *P. algirus* mainly inhabits broad-leaved forests, whereas *A. erythrurus* prefers open, sandy areas with sparsely distributed vegetation. These habitat preferences parallel differences between the areas in which both genera presumably originated: Eurosaharian xeric steppes with high operative temperatures (T_e) for *Acanthodactylus,* and Mediterranean open forests with lower T_e for *Psammodromus.*

Field observations showed that percentage of time spent basking and basking rate (number of basks per minute) were negatively related to T_e, although average bask duration was not. Percentage of time spent moving, moving rate (number of moves per minute), and the average duration of individual moves were inversely related to T_e and were higher in *P. algirus.* The percentage of total locomotion time that was spent moving in the shade was also higher in *P. algirus.* Behavioral thermoregulation strategies differed in a laboratory thermogradient, where *P. algirus* basked more often and for shorter periods and selected warmer patches than did *A. erythrurus.* Selected body temperatures (T_b) in a laboratory thermogradient were significantly higher in *A. erythrurus* than in *P. algirus.* Shade Seeking T_b was higher in *A. erythrurus,* but Resume Basking T_b did not differ significantly between the two species. Heating and cooling rates also differed in the two species: *A. erythrurus* warmed more slowly and cooled faster than did *P. algirus.*

Our data support the existence of a complex syndrome that combines aspects of the behavior, physiology, and ecology of both species. The thermal consequences of inhabiting a certain type of habitat can be counterbalanced by behavioral and physiological means that, in turn, affect movement and, hence, foraging behavior. Thus, the more active species (*P. algirus*) heated faster, cooled more slowly, and basked more often but for shorter periods and at warmer patches than the less active species (*A. erythrurus*).

Key words: Acanthodactylus erythrurus; *basking behavior; foraging mode; heat exchange rates; lacertids;* Psammodromus algirus; *selected body temperature; thermoregulation; western Mediterranean.*

INTRODUCTION

Foraging modes, usually classified as sit-and-wait vs. widely foraging (Pianka 1966, Huey and Pianka 1981), according to the mobility of predators, are correlated with major differences in ecological (Eckhardt 1979, Huey and Pianka 1981), physiological (Anderson and Karasov 1981, Huey et al. 1984), life history (Vitt and Congdon 1978), and morphological (Webb 1984) characters. Foraging modes of lizards fit well into this dichotomous view of foraging strategies (Pietruszka 1986, McLaughlin 1989). Widely foraging lizards have higher rates of energy expenditure and higher rates of food intake than do sit-and-wait species (Anderson and Karasov 1981); they show greater endurance but lower burst speed (Huey et al. 1984); their relative clutch mass is often lower (Vitt and Congdon 1978, Magnusson et al. 1985); and they eat more prey that are sedentary and clumped (e.g., termites) and fewer prey that are active (Huey and Pianka 1981, Magnusson et al. 1985).

Since the pioneer demonstration by Cowles and Bogert (1944) that desert lizards behaviorally regulate their body temperature (T_b), thermoregulation has come to be seen as a major aspect of reptilian ecology (Huey and Stevenson 1979, Huey 1982), with crucial effects on locomotion and foraging performance (Bennett 1980, Avery et al. 1982). However, there is no agreement in the literature about the ways in which movement behaviors influence, and are restricted by, thermoregulatory behavior (but see Hillman 1969, Anderson and Karasov 1988). Whereas some authors have

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suggested that thermoregulation would require complex behaviors (e.g., postural adjustments) incompatible with continuous movements and, hence, with active foraging (Regal 1983), others have argued that active foragers would be more able to exploit the thermal patchiness of their environment (Magnusson et al. 1985), thus achieving body temperatures that would enhance locomotor performance (Bennett 1980, Hertz et al. 1983, van Berkum 1986, Van Damme et al. 1989). Such disagreement reflects a surprising lack of data, in that thermoregulatory behavior determines the efficiency of locomotor and foraging performance (Bennett 1980, Avery et al. 1982, van Berkum 1986, Van Damme et al. 1991), and movement patterns, together with available microclimates, determine the duration of exposures to different thermal conditions and, hence, the rates of heat exchange with the environment. In other words, movement patterns translate into body temperatures through species-specific heat exchange rates that are modulated behaviorally by the selection of, and time of residence in, thermally different patches (Díaz 1991, Carrascal et al. 1992). Thus, neither the behavioral mechanisms of thermoregulation (e.g., shuttling heliothermy) nor the alternative locomotion patterns suggested by the dichotomous view of predator search modes (MacArthur and Pianka 1966, Pianka 1966, Schoener 1969, McLaughlin 1989) can be properly understood without considering the effects they have on each other.

In this paper, we study two widely distributed Mediterranean lacertid lizards that differ both in their habitat selection patterns and in thermal conditions within their habitats: *Psammodromus algirus* and *Acanthodactylus erythrurus* (see Salvador 1985, Arnold 1989). Lacertids are usually viewed as active foragers, although there is some evidence of interspecific variation in movement rates (Huey and Pianka 1981, Huey et al. 1984). Subtle differences in movement behavior between species with similar foraging modes may actually provide a conservative, fine-grained test of the interaction between their thermal biology and their position along the continuum of foraging modes. This test would cast light on the behavioral and ecophysiological effects of movement intensity (i.e., foraging mode), without following the usual procedure of comparing extreme sit-and-wait and continuous searchers.

Our main objective is to analyze the integration of different behavioral and ecophysiological traits in these lacertid lizards that exploit different habitats. As an example, frequent shuttles between sun and shade, which require continuous movements, are likely to be a more feasible strategy in forest thermal mosaics than in xeric shrubsteppes with a scarcity of shade. Rather than testing whether or not the combinations of traits that we study represent adaptive syndromes (requiring a much larger scale study with more emphasis on evolutionary mechanisms), our goal is to understand how these traits interact in a comprehensive and structured way, defining patterns of covariation that represent equally efficient thermoregulatory strategies. We specifically address the following questions:

1) To what extent are behavioral thermoregulation and movement behavior (i.e., foraging mode) dependent one on each other?

2) How does the interaction between movement and basking behavior relate to interspecific differences in thermal preferences and heat exchange rates?

3) Are these associations consistent with interspecific differences in habitat selection patterns?

MATERIAL AND METHODS

Organisms

Although the phylogenetic relationships of lacertids have not been resolved, the available data (see Bauwens et al. 1995 and references therein) indicate that the related genera *Psammodromus* and *Gallotia* diverged from other clades within the family (including *Acanthodactylus*) very early in the history of the Lacertidae (33–35 × 10^6 yr BP). *Psammodromus algirus* is a medium-sized lacertid lizard (adult snout–vent length up to 82 mm) that inhabits a great variety of habitats in the western Mediterranean, being commonest in broadleaved (both deciduous and perennial) degraded forests with a well-developed undergrowth of shrubs (Arnold 1987, Díaz and Carrascal 1991). It is a ground-dwelling, shuttling heliotherm with a bimodal pattern of daily activity in the summer months (Carrascal and Díaz 1989). Its foraging mode is somewhat displaced toward the active-searching side of the continuum (McLaughlin 1989), as judged by our data on percentage of time spent moving and movement rate (see Table 3 and *Results*). In fact, many food items are searched for and captured in the leaf litter beneath shrubs or trees, although short foraging incursions into open areas, usually triggered by the detection of large and/or fast moving prey (Díaz and Carrascal 1993), are not infrequent.

Acanthodactylus erythrurus is also a medium-sized lacertid (adult snout–vent length up to 82 mm) that prefers open, sandy areas with sparsely distributed vegetation (Arnold 1987). It belongs to an advanced clade of Eurosaharian species from xeric climatic zones (Arnold 1989), and it is the only species within its genus that is present in western Europe. Other species of *Acanthodactylus* are found in North Africa and the Middle East. Its distribution range in the Iberian Peninsula is contained within that of *P. algirus* (Salvador 1985). However, both species show differences in microhabitat selection patterns, with *Psammodromus algirus* more dependent on dense vegetation cover (Mellado 1980). *A. erythrurus* adults show a unimodal circadian rhythm during all months in which they are active (Pollo and Pérez-Mellado 1989). Both species are active at the same times of year (Barbadillo 1987), but *A. erythrurus* is clearly a less active forager than *P. algirus*, based on its considerably lower percentage of time moving and movement rate (see Table 3 and *Results*). Casual observations, both in the field and in captivity, and dietary data (Pérez-Mellado 1992) suggest that *A. erythrurus* feeds mainly on ants (probably a widespread prey type in shrubsteppe habitats) and on fast-moving prey that it captures in the open after short, rapid attacks launched from ambushing sites.

Study areas

Field observations of behavior were obtained in two different areas representative of the habitats typical of each species. The behavior of *P. algirus* was recorded in Soto de Viñuelas, Madrid, central Spain (40°35′ N, 03°34′ W). The study plot ($\approx$10 ha) is located within a protected, large Mediterranean evergreen forest in which holm oaks (*Quercus rotundifolia*) are the dominant species in the tree and shrub layers. Canopy height averages 1.3 m, with a mean cover of 54.5% (estimates obtained using a scored stick held vertically at a number of random spots; details in Díaz 1993). Behavioral data for *A. erythrurus* were collected in a plot of $\approx$25 ha at La Punta (Devesa del Saler, Valencia, southeastern Spain, 37°40′ N, 0°30′ E). The study plot is a well-preserved dune field sparsely covered with several species of small shrubs and grasses (*Ononix natrix, Helichrysum stoechas, Halimium halimifolium, Ammophila arenaria*). Vegetation cover is 40%, with a mean vegetation height of 50 cm.

Field observations of behavioral thermoregulation

Field observations were conducted on *P. algirus* in June–July 1990 and on *A. erythrurus* in June–July 1992. In both cases, samples were taken between 0700 GMT (onset of the activity period; Carrascal and Díaz 1989, Pollo and Pérez-Mellado 1989) and 1200 (sun zenith). Activity of focal individuals was observed with binoculars from a distance of 3–6 m, dictating continuous behavioral observations to a portable tape recorder. When transcribing the tapes, we took time measurements with a precision of ±1 s. No sequence of $<$5 min was included in the analyses. Only lizards not reacting to observer presence were monitored. For each observed individual, we noted time of day, sex, and an estimate of its snout–vent length. At the end of each observation period, we recorded the environmental operative temperatures (T_e), both in full sun and in deep shade, with the aid of an electronic digital thermometer (precision of 0.1°C). Measurements were taken at the exact place where the lizards were initially observed and at the nearest available sunlit or shaded patch (for lizards in the shade or in full sun when first sighted, respectively). For this purpose, we used hollow copper cylinders, approximately the size of a lizard, that were closed at both ends, except for a small fissure allowing introduction of the thermometer's probe. The cylinders were sufficiently sealed so that no air transfer occurred through the fissure.

In a pilot study, we analyzed the variation of T_e in the field. We sampled the temperature of 30 copper models disposed on a linear transect in the Soto de Viñuelas area. Distance between consecutive models was 6 m, a greater distance than that moved across by focal individuals whose behavior was sampled for 5–20 min in the field (an area rarely exceeding the surface of a 5-m radius circle). Every 60 min, from 0600 to 1100 GMT, we recorded the T_e of models and noted if they were in full sun or deep shade. By means of a two-way ANOVA with time of day and sun exposure as factors, we partitioned the variation observed in T_e. The percentage of variance explained by time of day was 54.6% ($F_{5,\,121} = 60.69$, $P \ll 0.001$; degrees of freedom were reduced because we used only the models fully exposed to sun or shade, eliminating the ones corresponding to sun-filtered patches, as in our field study). Differences between sun and shade accounted for 29.9% of the variance observed ($F_{1,\,121} = 103.04$, $P \ll 0.001$). The error component (random differences between sampling points) accounted for 15.1% of the variance observed. Thus, T_e varied much more among times of day and sun–shade patches (84.9% of variance for both components together) than among temperature readings at different spots within the same time of day and sun–shade category. This empirical result demonstrates that operative temperatures within a given habitat (holm oakwood) varied quite little among microsites that were fully illuminated or fully shaded. Therefore, our unreplicated T_e measurements associated with focal animals provided a useful indication of the thermal state of their environment.

We checked that the copper models provided reasonably close approximations of actual lizard temperatures by comparing, under the same conditions of radiant heat loads (100-W bulb at different heights), their temperature readings with the cloacal temperatures of two freshly dead lizards of each species. At equilibrium, the mean values of lizard T_b and model T_e were highly correlated ($R^2 > 0.99$ for both species), satisfying the criterion for T_e determinations in Bakken et al. (1985). The resulting regression equations had slopes and intercepts that did not differ from one and zero, respectively. There were seven replicates for each dead lizard; *P. algirus*: $T_b = -1.04 + 0.99\ (T_e)$; *A. erythrurus*: $T_b = -0.71 + 1.01(T_e)$. Thus, this procedure allowed us to measure the approximate temperatures attained by lizards at the pertaining microsites and times (availability of T_b data; Bakken and Gates 1975, Grant and Dunham 1988, Bakken 1992, Hertz 1992).

As behavioral variables, we selected: (1) the duration of each basking event (where basking is defined as a period of $>$10 s motionless in full sun); (2) the number of basking events per minute (basking rate); (3) the duration of movements and pauses, recording shuttles between sun and shade; (4) the number of movement periods per minute (movement rate); and (5) the distance covered in each movement period. We also recorded the total time employed in each behavioral sequence. Combining these original variables, we calculated the percentage of time spent basking, the average moving speed (including stops <1 s), and the amount of time spent moving in the sun and in the shade.

The availability of ground surface exposed to sun in each study area was estimated from the line transects done while searching for lizards to monitor their behavior. The percentage of ground not covered by vegetation that was in full sun was estimated visually at 100-m intervals.

Rates of heat exchange

All heating and cooling rates were experimentally determined at the Estación Biogeológica El Ventorrillo, using 15 individuals of *P. algirus* in July 1990 and 11 individuals of *A. erythrurus* in July 1992. The animals, captured at the sites where behavioral sequences were obtained, were introduced into a portable refrigerated box until their body (cloacal) temperatures (T_b) fell to ≈20°C (approximately the temperature of a lizard retreated into the deep shade of its refuge; L. M. Carrascal and J. A. Díaz, *personal observation*). Each animal was measured (snout–vent length) and weighed before being employed in a trial. For *A erythrurus* (n = 11), snout–vent length was 58.9 ± 2.7 mm ($\bar{X}$ ± 1 SD) and body mass was 5.5 ± 0.9 g; for *P. algirus* (n = 15), snout–vent length was 69.4 ± 5.6 mm and body mass was 8.3 ± 1.9 g. Thus, lizards were significantly larger in our sample of *P. algirus* than in that of *A. erythrurus* ($P < 0.001$ in both t tests).

The experimental subject was fixed with two bands of transparent masking tape, around the base of the tail and on top of the forelimbs, to a 12 × 25 cm wooden table, and was exposed to direct solar radiation. To standardize conditions of radiant heating, we oriented the body axis of lizards toward the sun, although heating rates in the similarly-sized *Lacerta monticola* are unrelated to the lizard's body orientation toward the sun (Martín et al. 1995). The slope of the body axis in the horizontal plane was always 0°, as *P. algirus* and *A. erythrurus* bask and forage on nearly flat ground. A Miller-Weber quick-reading mercury thermometer (±0.1°C) was inserted into the lizard's cloaca and continuous readings of T_b were obtained at 20-s intervals (Avery and MacArdle 1973). Heating experiments finished when the cloacal temperature reached 36–37°. This procedure did not allow animals to use postural adjustments during heating because we were interested in measuring physiological, not behavioral, interspecific differences. After animals were warmed, they were moved to a full-shade position for measurement of cooling rates. Body temperature readings were again registered every 20 s from the moment T_b began to fall.

For each heating or cooling trial, we measured the operative temperature in the immediate surroundings of the experimental lizard, using a thermocouple inserted into a copper model placed on the wooden table.

Both heating and cooling rates (in degrees per minute) were determined as the slopes of the linear regressions relating T_b to time elapsed. This was a better procedure than the use of time constants (Spotila et al. 1973) because the T_b values of these small species perching in the sun did not attain or even approach an equilibrium temperature, at least within the lizard's tolerance range. In fact, the MS errors were extremely low for the linear regression models, and the coefficients of determination for heating and cooling trials were all >0.95.

Selected body temperatures

In September 1992, 13 individuals of each species (all adults with a snout–vent length >50 mm) were captured at the study areas and were transported to the Estación Biogeológica El Ventorrillo (Navacerrada, Madrid; 40°40′ N, 3°50′ W), where they were allowed to acclimatize for 1 wk in 100 × 50 × 40 cm terraria subject to a light : dark cycle of 12:12 h. Food (crickets and mealworms) and water were supplied ad libitum. Duration of captivity was <25 d and, by the end of the study, the animals were released at the areas where they had been collected.

A 150-W light bulb suspended 11 cm above one end of a terrarium created a thermal gradient with operative temperatures ranging from 18° to 58°C. A second 60-W bulb outside the cage illuminated the cool end of the gradient. This thermal gradient covered the range of temperatures available during the annual activity period in the study areas of both species (L. M. Carrascal and J. A. Díaz, *personal observation*). Food and water were provided ad libitum in the experimental terrarium during the trials.

A Miller-Weber quick-reading mercury thermometer was used to measure T_b of active lizards after 1 h in the thermogradient. These temperature readings were considered to be estimates of Selected T_b values, that is, temperatures lizards would attempt to achieve in the field, in the absence of physical and biotic restrictions (Licht et al. 1966). All measurements were taken using single animals instead of pairs or groups. We obtained two estimates per individual, always on different days, and used the mean of the two replicates for subsequent analyses.

We also used the thermogradient to record two other T_b measurements that provide an approach to the threshold T_b levels controlling basking behavior (Heatwole and Taylor 1987). We defined the Shade Seeking temperature as the cloacal temperature at the moment when a lizard stopped basking and began moving to cooler places. After spending some time in the shady end of the gradient, lizards began to move back to the hot end, presumably to bask again; we measured their T_b at that time as an estimate of the Resume Basking temperature. Measurement of these temperatures began after animals were left undisturbed for ≥15 min. We obtained two replicates for each individual on different days, and averaged them for subsequent statistical analyses. To test whether or not two temperature readings per individual were enough data to describe interspecific differences in T_b, we performed repeated-measures ANOVAs with the body temperature data obtained in the thermogradient, estimating the effect size (variance partitioning) of the between-factor term (species) and the within[repeated]-factor term (first and second measurements per individual). The results of these analyses for Selected, Resume Basking, and Shade Seeking T_b showed that the repeated-measures factor (within-individual variation) was not significant in any case ($P > 0.3$, df = 1, 24 in the three ANOVAs). Moreover, its contribution was always <5% of the total variance. The percentage of variance explained by the between-species term was 4.2 times higher than the percentage explained by the between-measurements term for Selected T_b, 498 times higher for Shade Seeking T_b, and 30 times higher for Resume Basking T_b. Therefore, the average of two readings per individual was a proper sample to test interspecific differences in T_b.

All measurements of Selected T_b values were taken during the time of day when both species are active in the field, and we interspersed measurements of the two species to control for possible differences linked to time of day.

Analysis of behavior in a thermogradient

The same thermogradient described in the previous section was used to study the selection of basking sites differing in mean T_e values, and the patterns of basking behavior in the two species, controlling for the effects of the thermal and physical (e.g., vegetation structure) environment. Lizards used in this procedure were the same animals employed in the study of selected T_b values. Subjects were placed in the experimental terrarium 5 min before the behavioral observations began. This time was considered to be long enough for the animal to recover an undisturbed pattern of behavior. During the following 25 min, the same variables of thermoregulatory behavior measured in the field were precisely recorded in a quantitative way, using a computer behavioral observation program (The Observer, NOLDUS) run out in a notebook computer. We obtained two samples per individual on different days, so that overall behavioral sequences totalled 50 min/individual. Again, we interspersed trials for both species to control for differences linked to time of day.

For the behavioral sequences, we divided the terrarium into five zones differing in the amount of radiation received and, hence, in T_e (estimates obtained from the extreme with the 150-W bulb onwards: 58°, 34.5°, 22.1°, 18°, 17.3°, and 17°C). We defined basking events as stays of >10 s immobile in the two zones closest to the bulb end, and we measured the duration and rate of basking events in each of the two basking zones.

Data analyses

We used analyses of covariance (ANCOVA) to compare field observations of behavior between both species, taking the operative temperature in full sun as the covariate. This statistical procedure was used to remove the effect of differences in thermal environment (T_e) between the two study areas. However, other important ecological features (number of predators, distance to the nearest refuge, food availability, et cetera) may differ between habitats to an unknown extent. Thus, we assumed that the main habitat differences that influence the behaviors studied are correlated with the thermal environment. Rates of heat exchange were also compared using ANCOVAs, with operative temperature as the covariate. To assess interspecific differences in selected temperatures, we employed *t* tests. For behavioral observations in the thermogradient, we used Mann-Whitney *U* tests. All statistical analyses were carried out using SPSS for Windows 5.0 (Norusis 1992).

RESULTS

Field observations of behavior

Operative temperatures were higher in the study area of *A. erythrurus* than in that of *P. algirus,* both in full sun (*A. erythrurus*: 41.9 ± 1.04°C, $\bar{X} \pm 1$ SE, $n = 29$; *P. algirus*: 39.0 ± 0.72°, $n = 43$; $t = 2.40$, $P = 0.019$) and in full shade locations (*A. erythrurus*: 32.6 ± 1.21°, $n = 29$; *P. algirus*: 25.3 ± 0.66°, $n = 43$; $t = 5.71$, $P < 0.001$).

Percentage of time spent basking and basking rate (number of basks per minute) were negatively related to T_e, although average bask duration was not. The pattern of covariation between these behavioral variables and T_e was similar for both species (test for homogeneity of regression slopes: $P > 0.1$). Basking behavior in the field did not differ significantly between the two species after we corrected for the effects of differences in thermal environment between study areas (see observed and adjusted values in Table 1 and results of ANCOVAs in Table 2). Thus, percentage of time spent basking, bask duration, and number of basks per unit time were similar in both species.

With respect to locomotion (Tables 3 and 4), T_e was inversely related to the percentage of time spent moving, the movement rate (number of moves per minute), the average duration of individual moves, and the percentage of total time moving that was spent in full sun. Average speed did not covary with operative temperature in the pooled sample of the two species, although there was a significant interaction between species and covariate. A reanalysis of the relationship between speed and T_e, using simple correlations within each species, showed that average speed was positively cor-

TABLE 1. Mean, standard error, and sample size for the variables describing thermoregulatory behavior of two lacertid lizards in the field. The table shows both observed values and those adjusted for the effects of operative temperature (T_e).

		Observed values		Adjusted values	
	n	$\bar{X}$	1 SE	$\bar{X}$	1 SE
% time spent basking					
A. erythrurus	29	40.6	6.6	48.6	4.4
P. algirus	43	47.3	4.6	42.0	3.6
Basking rate (no./min)					
A. erythrurus	29	0.38	0.08	0.44	0.05
P. algirus	43	0.37	0.04	0.33	0.04
Bask duration (s)					
A. erythrurus	23	133.0	34.5	142.1	25.3
P. algirus	38	94.4	12.9	88.9	19.4

TABLE 2. ANCOVA with variables describing thermoregulatory behavior of *A. erythrurus* and *P. algirus* in the field. Interspecific differences are tested in the Treatment (species) rows. The sign of covariation with T_e is shown in brackets, except for bask duration, which is not correlated with temperature.

	df	F	P
% time spent basking			
Covariate (T_e [−])	1, 69	70.41	<0.001
Treatment (species)	1, 69	1.32	0.254
Interaction	1, 68	0.72	0.400
Basking rate (no./min)			
Covariate (T_e [−])	1, 69	31.81	<0.001
Treatment (species)	1, 69	2.82	0.098
Interaction	1, 68	2.83	0.097
Bask duration (s)			
Covariate (T_e)	1, 58	2.32	0.134
Treatment (species)	1, 58	2.68	0.107
Interaction	1, 57	0.32	0.572

TABLE 3. Mean, standard error, and sample size for the variables describing locomotor performance of lizards in the field. The table shows both observed means and means based on values adjusted for the effects of T_e, except for those variables showing a significant effect of the interaction between Treatment (species) and Covariate (T_e). Speed refers to mean moving speed, including short stops.

		Observed values		Adjusted values	
	n	$\bar{X}$	1 SE	$\bar{X}$	1 SE
% time spent moving					
A. erythrurus	29	8.3	2.0	9.6	2.4
P. algirus	43	19.5	2.2	18.6	1.9
Movement rate (no./min)					
A. erythrurus	29	0.64	0.1	···	···
P. algirus	43	1.11	0.1	···	···
Move duration (s)					
A. erythrurus	23	7.2	1.0	7.8	1.0
P. algirus	39	10.8	0.7	10.5	0.7
Speed (cm/s)					
A. erythrurus	14	10.5	1.3	···	···
P. algirus	38	6.8	0.6	···	···
% moving time in full sun					
A. erythrurus	29	99.1	0.5	98.5	4.4
P. algirus	43	31.7	3.7	36.4	3.6

TABLE 4. ANCOVA with variables describing locomotor performance in the field of *A. erythrurus* and *P. algirus*. Interspecific differences are tested in the Treatment (species) rows. The sign of covariation with T_e is shown in brackets, except for speed, which is not correlated with temperature.

	df	F	P
% time spent moving			
Covariate (T_e [−])	1, 69	6.92	0.010
Treatment (species)	1, 69	8.32	0.005
Interaction	1, 68	1.16	0.286
Movement rate (no./min)			
Covariate (T_e [−])	1, 69	4.55	0.037
Treatment (species)	1, 69	4.42	0.039
Interaction	1, 68	7.10	0.010
Move duration (s)			
Covariate (T_e [−])	1, 59	6.19	0.016
Treatment (species)	1, 59	4.59	0.036
Interaction	1, 58	0.21	0.650
Speed (cm/s)			
Covariate (T_e)	1, 49	0.65	0.425
Treatment (species)	1, 49	7.87	0.007
Interaction	1, 48	10.24	0.002
% moving time in full sun			
Covariate (T_e)	1, 59	0.30	0.588
Treatment (species)	1, 59	129.73	<0.001
Interaction	1, 58	0.51	0.479

related with T_e in *A. erythrurus* ($r = 0.67$, $n = 14$, $P = 0.008$) but not in *P. algirus* ($r = -0.21$, $n = 41$, $P = 0.194$).

P. algirus and *A. erythrurus* differed significantly in all behavioral traits associated with locomotor performance (see observed and adjusted values in Table 3 and results of ANCOVAs in Table 4). Percentage of time spent moving and duration of individual moves were higher in *P. algirus,* whereas *A. erythrurus* spent a higher proportion of its total locomotion time moving in full sun (see treatment effects in Table 3). For these variables, the pattern of covariation with T_e was similar in both species (see nonsignificant interaction terms in Table 4). For the movement rate, the effects of the interaction between species and T_e were significant (Table 4). The movement rate decreased significantly with operative temperature in *A. erythrurus,* but it remained constant throughout the observed range of operative temperatures in *P. algirus* (Fig. 1). The variance of moving rates was significantly higher in *A. erythrurus* ($s^2 = 3.33$) than in *P. algirus* ($s^2 = 0.46$; $F_{12,12} = 7.309$; $P = 0.002$).

In *A. erythrurus,* locomotion took place in full sun (Table 3) in a significantly larger proportion than expected by chance (t test against the null hypothesis that

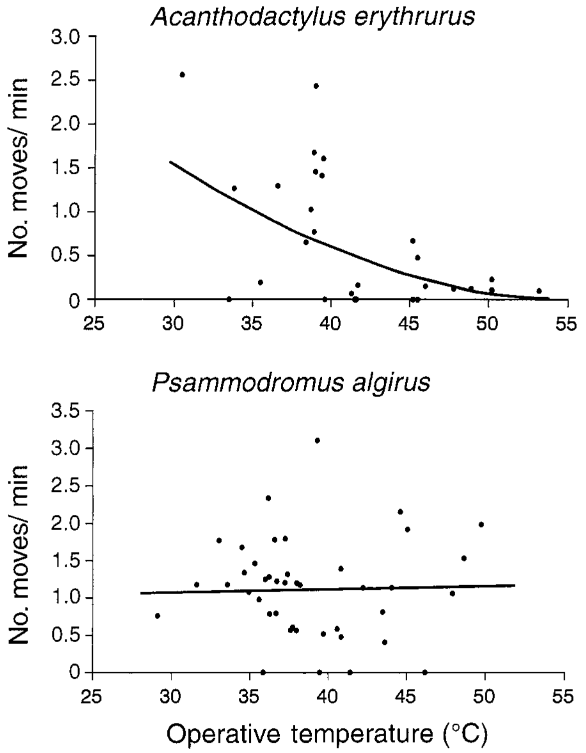

FIG. 1. Relationship between environmental operative temperature (T_e) and field movement rate (number of moves per minute) in two lacertid lizards, *A. erythrurus* and *P. algirus*.

the mean proportion of locomotion time spent in full sun equals the 44.5% availability of ground surface exposed to sun: $t = 118.6$, $P \ll 0.001$). *P. algirus,* however, crossed sunny areas while moving (Table 3) in a proportion almost coincident with the availability of ground surface exposed to sun (35.6%; $t = 0.079$, $P = 0.937$).

Selected body temperatures and thermoregulatory set points

Selected T_b was significantly higher in *A. erythrurus* than in *P. algirus* ($P = 0.033$; Table 5). Similarly, mean Shade Seeking temperature was also higher in *A. erythrurus* ($P < 0.001$; Table 5). Resume Basking temperature, however, did not differ significantly between the two species ($P = 0.097$; Table 5).

Heating and cooling rates

Table 6 summarizes the heating and cooling rates of *P. algirus* and *A. erythrurus,* adjusted for body mass and T_e. The rate of heat gain increased significantly with T_e ($F_{1,41} = 326.39$, $P < 0.001$; covariate effect in the corresponding ANCOVA) and decreased with body mass ($F_{1,41} = 4.86$, $P = 0.033$) in the pooled sample of the two species. Although the heating rate was significantly higher in *P. algirus* ($F_{1,41} = 11.50$, $P = 0.002$), the regression slope of heating rate vs. T_e differed significantly between species (interaction term: $F_{1,41} = 11.82$, $P = 0.001$). Regression slope was lower in *A. erythrurus* (standardized regression coefficients: 0.109 for *A. erythrurus* and 0.161 for *P. algirus*). Thus, heating rates increased more rapidly with T_e in *P. algirus* than in *A. erythrurus.*

The cooling rate was significantly higher in *A. erythrurus* ($F_{1,40} = 13.67$, $P = 0.001$), and it decreased with T_e (measured in the shade; $F_{1,40} = 7.52$, $P = 0.009$) but not with body mass ($F_{1,40} = 0.14$, $P = 0.714$) in the pooled sample of both species. Regression slopes of cooling rates vs. T_e did not differ significantly between the two species (interaction term: $F_{1,40} = 0.06$, $P = 0.810$).

These results demonstrate the existence of physiological differences in the heat exchange mechanisms of these two species. *A. erythrurus* warmed more slowly and cooled faster than *P. algirus.*

Behavior in a thermogradient

Observations of field thermoregulatory behavior were complemented with data collected under controlled and perfectly comparable laboratory conditions to detect subtle interspecific differences in (1) the selection of thermal properties of basking sites, and (2) the trade-off between bask duration and basking rate. Although the percentage of time spent basking did not differ significantly, the two species showed different ways of attaining a given basking time. Mean duration of basking periods was higher in *A. erythrurus* than in *P. algirus,* whereas the number of basks per unit time was higher in *P. algirus* (Table 7). These results modulate the nonsignificant pattern obtained using field data. Within the two zones of the thermogradient available for basking, the percentage of time spent basking in the warmest zone ($T_e = 58$°C) was higher in *P. algirus,* whereas *A. erythrurus* basked mainly in the

TABLE 5. Body temperatures (T_b, in °C) and t-test comparisons between *A. erythrurus* and *P. algirus* for Selected, Shade Seeking, and Resume Basking T_b values.

	Selected T_b		Shade Seeking T_b		Resume Basking T_b		
	$\bar{X}$	1 SE	$\bar{X}$	1 SE	$\bar{X}$	1 SE	n
A. erythrurus	36.3	1.07	37.6	0.63	33.3	1.55	13
P. algirus	35.2	1.38	36.2	0.82	34.1	0.70	13
t	2.25		5.16		1.72		
P	0.033		<0.001		0.097		

TABLE 6. Heating and cooling rates of two lacertid lizards. The table shows both observed means and means based on values adjusted for the effects of T_e and body mass. Mean T_e was 32.2°C (range 21.8–43.7°) in heating trials and 27.4° (range 18.2–38.7°) in cooling trials.

			Observed values		Adjusted values	
Variable	Species	*n*	$\bar{X}$	1 SE	$\bar{X}$	1 SE
Heating rate (°C/min)	*A. erythrurus*	22	1.59	0.19	1.51	0.17
	P. algirus	24	1.76	0.21	1.84	0.20
Cooling rate (°C/min)	*A. erythrurus*	22	0.86	0.06	0.82	0.06
	P. algirus	23	0.41	0.05	0.44	0.04

not-so-warm patch (T_e = 34.5°). *P. algirus* spent a higher proportion of time in the deep shade areas (the three zones farthest from the light bulb; Table 7).

Thus, behavioral thermoregulation strategies differed between the species. *P. algirus* basked more often and for shorter periods, but at warmer patches than did *A. erythrurus*. Alternatively, cooler patches (i.e., areas in deep shade) were visited more often by *P. algirus* in between-basking activity bouts.

DISCUSSION

Our results suggest that the observed differences between *P. algirus* and *A. erythrurus* reflect a functional interaction between thermoregulatory and movement (foraging) behavior. We will first evaluate such differences and then argue how they combine into strategies that are consistent with the habitat preferences and probable evolutionary history (Arnold 1987, 1989) of these species.

Our analysis of the T_b values measured in a thermogradient revealed that *A. erythrurus* preferred higher temperatures than did *P. algirus*, since both Selected T_b and Shade Seeking T_b were higher in the former species. A relatively higher Selected T_b in *A. erythrurus* was also found by Bauwens et al. (1995), using samples from other populations of these species. Moreover, field T_b values are higher in *A. erythrurus* than in *P. algirus* (Pollo and Pérez-Mellado 1989), and information on the thermal sensitivity of sprint speed in these two species shows that both the optimal temperature for sprinting and the critical thermal maximum are higher in *A. erythrurus* than in *P. algirus* (Bauwens et al. 1995). Thus, *A. erythrurus* runs fastest at higher temperatures and tolerates higher temperatures than does *P. algirus*. These differences are consistent with the kind of areas in which both genera presumably have evolved: hot, xeric steppes for *Acanthodactylus*, and Mediterranean open forests with lower T_e values for *Psammodromus* (Arnold 1973, 1983, 1989, Salvador 1982, Pérez-Mellado 1992).

Nevertheless, Resume Basking T_b was statistically indistinguishable between the two species. This could be due to the fact that small variations in T_b have less pronounced effects on organismal performance at low than at high T_b, since performance curves are asymmetrically skewed toward low T_b (Huey and Stevenson 1979, Huey 1982, Huey and Kingsolver 1989). According to the data in Bauwens et al. (1995), the Resume Basking T_b values of both species were within the temperature range allowing lizards to run at ≥80% of their maximal sprint capacity. Specifically, they fell within the broad, flat zone of the thermal sensitivity curve below the thermal optimum for sprinting. Shade Seeking T_b values were also within the 80% thermal performance breadths of both species. However, the Shade Seeking T_b of *P. algirus* was somewhat higher than its optimal temperature for sprinting (34.3°C), whereas that of *A. erythrurus* was almost coincident with its thermal optimum for sprinting (38.0°). It is, therefore, not surprising that both species differed in their Shade Seeking T_b values (upper set points of temperature regulation).

Heating and cooling rates were also different in the two species. *A. erythrurus* warmed more slowly and cooled faster than *P. algirus*. A proximate cause for the relatively lower heating rate in *A. erythrurus* could be its higher reflectance due to a paler coloration (Norris 1967, Porter 1967, Pearson 1977). The darker coloration of *P. algirus*, conversely, could favor a more rapid absorption of solar radiation in its forest, sun–

TABLE 7. Mean and standard error for the variables describing thermoregulatory behavior and locomotor performance of *A. erythrurus* and *P. algirus* in a laboratory thermogradient, and results of Mann-Whitney *U* tests comparing the two species. Sample size, 13 individuals for each species.

	A. erythrurus		*P. algirus*			
	$\bar{X}$	1 SE	$\bar{X}$	1 SE	*Z*	*P*
% time basking	49.6	5.0	39.7	1.7	1.18	0.238
Basking rate (no./min)	0.7	0.3	0.9	0.1	2.00	0.045
Bask duration (s)	58.1	9.2	26.7	1.8	2.67	0.008
% time basking in hot end	17.0	2.7	30.3	2.6	2.97	0.003
% time in deep shade	8.2	2.3	25.1	1.8	3.59	<0.001

shade patchy habitat, and facilitate a rapid elevation of T_b after longer stays in the shade. Reflectance curves for both species would be needed to test these ideas in an appropriate biophysical model.

The low heating rate of *A. erythrurus* and its relatively low increase with increasing T_e levels, could be seen as physiological traits favoring thermoregulation in hot, xeric habitats with low vegetation cover. A shuttling heliotherm chasing prey in open, sunny areas would need a relatively low heating rate to prolong the time spent within its preferred thermal range without being forced to shuttle continuously between sun and shade. This would allow lizards to ambush prey while motionless in the sun. On the other hand, the fast cooling rate of *A. erythrurus* would allow a rapid readjustment of T_b if it surpassed the preferred thermal range, which might occur accidentally in hot, sparsely vegetated environments. The selection of basking site thermal properties also seemed consistent with interspecific differences in heat exchange rates. Thus, in a laboratory thermogradient, *P. algirus* basked more often in the warmest end, which was avoided by *A. erythrurus*. These results show a pattern of basking site selection that is consistent with high-temperature avoidance in hot environments (Bradshaw 1986).

Our data suggest a complex set of interactions among preferred T_b levels, rates of heat gain and heat loss, and selection of basking sites that has led to different behavioral and physiological solutions for regulating T_b in contrasting thermal environments. The two patterns found in these two species are: (1) a lower preferred T_b, a lower tolerance of maximum T_b values, a faster heating rate, a slower cooling rate, and a selection of basking sites with higher temperatures in the forest-dwelling species (*P. algirus*); and (2) the opposite for all these variables in the species inhabiting warm Mediterranean areas with low vegetation cover (*A. erythrurus*).

Movement rate (moves per minute) and percentage time moving, which are usually viewed as indices of foraging intensity in lizards (Huey and Pianka 1981, McLaughlin 1989), differed significantly between *A. erythrurus* and *P. algirus*. Locomotor capacities shown by these two species are also consistent with previous results on the physiological correlates of foraging modes. Thus, Huey et al. (1984) found that sit-and-wait lacertids from the Kalahari usually had relatively high sprint speeds. Accordingly, maximal sprint speed is higher in *A. erythrurus* than in *P. algirus* (Bauwens et al. 1995). Our choice of species seems appropriate for a conservative test of the covariation of thermoregulation and movement intensity, as interspecific differences in movement behavior were significant but relatively small.

Our data suggest that the thermal consequences of inhabiting a certain type of habitat can be counterbalanced by behavioral and physiological means that, in turn, affect movement (and, hence, foraging) behavior. Shuttling heliothermy involves movements between sun and shade (Cowles and Bogert 1944), but these movements, and interspersed periods of stationary basking, can vary both in frequency and duration (Spellerberg 1972, Díaz 1991, Carrascal et al. 1992). At the same time, a heliothermic forager should select where and how long to stay in different thermal patches while searching for food, in order to maintain its T_b within its optimal performance range (Huey and Stevenson 1979, Avery et al. 1982, Huey 1982, Van Damme et al. 1991).

In the laboratory thermogradient, *P. algirus* (the more mobile species) basked more often, but for shorter periods and at warmer patches, than did *A. erythrurus*. For *P. algirus*, which moves ≈20% of its activity time, and may experience relatively low T_e in the deep shade of forest habitats, accurate thermoregulation would require an efficient selection of basking sites for rapid warming. This would compensate for relatively long periods of searching in the shade. Our results are consistent with these suggestions, both in the lab thermogradient (where *P. algirus* selected the warmest end for basking and spent longer times in the cool end) and in the field (where its time spent moving was randomly distributed with respect to sun and shade). This strategy would be enhanced by the physiological traits noted, and it would be favored in thermally heterogeneous environments such as the broad-leaved forests preferred by *P. algirus* (Díaz and Carrascal 1991). Moreover, heating and cooling rates in *P. algirus* become equal after the early period of morning warm-up, and this coincidence gives rise to a higher frequency of shorter basking periods (Díaz 1991). Thus, sustained locomotion may be required to maintain T_b levels within the preferred thermal range, even if movements are random with respect to sun and shade (Carrascal and Díaz 1989) and are simultaneously used for food searching.

On the other hand, scarcity of protective cover, escape abilities of fast-moving prey, and/or high predation risk in xeric shrubsteppes would promote the evolution of high maximum speeds, high physiologically optimal temperatures for sprinting, and high preferred temperatures (Bauwens et al. 1995). This would explain the higher Shade Seeking and Selected T_b values shown by *A. erythrurus*, which is the fastest of the 13 lacertid species examined by Bauwens et al. (1995). Selection of not-too-hot basking sites and relatively low heating rates would help *A. erythrurus* to counteract environmental heat loads and to retard exceeding its preferred T_b levels. The negative correlation between movement rate and operative temperature found in *A. erythrurus* (Fig. 1) suggests that, in this species, extreme sit-and-wait behavior may function as a heat avoidance strategy. In fact, the variance of moving rates was significantly higher in *A. erythrurus* than in *P. algirus*. This asymmetrical distribution of variation in the amount of searching movements, with higher flexibility in the less active forager, is consistent with the results reported by Pietruszka (1986; but see Huey and Pianka 1981).

In summary, results of this study provide empirical evidence that thermoregulation and foraging mode should not be regarded as isolated tasks but as interacting behaviors, strongly dependent one on each other and giving rise to patterns of association that are coherent on functional grounds. However, we do not intend to test whether or not the traits studied are integrated in adaptive syndromes, because of the inherent limitations of comparing only two species from different habitats (see Garland and Adolph 1994). An obvious alternative to the adaptive-syndrome hypothesis could be, for instance, that all differences in thermal biology reflect ancestry in different habitats, and are evolutionarily independent of foraging mode. Our approach lacks the historical perspective that is needed to discriminate between these hypotheses. The generality of the patterns described in this paper could be tested in future studies that should compare additional species of this or unrelated lizard clades. A multispecies, explicitly phylogenetic approach (Huey 1987, Harvey and Purvis 1991, Garland et al. 1992) would lead to the detection of rates and directions of evolutionary change in both thermal biology and foraging mode, thus allowing discrimination between (co)-adaptive and independent-evolution hypotheses (Huey 1987). Such an approach should complete the synthesis attempted here of two areas of lizard ecology that have traditionally been treated as separate, but that clearly are related.

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LITERATURE CITED

Anderson, R. A., and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia **49**:67–72.

Anderson, R. A., and W. H. Karasov. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. Ecological Monographs **58**:79–110.

Arnold, E. N. 1973. Relationships of the Palaearctic lizards assigned to the genera *Lacerta, Algyroides,* and *Psammodromus.* Bulletin of the British Museum of Natural History (Zoology) **25**:289–366.

———. 1983. Osteology, genitalia, and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). Bulletin of the British Museum of Natural History (Zoology) **44**:291–339.

———. 1987. Resource partitioning among lacertid lizards in Southern Europe. Journal of Zoology (Supplement) **1**: 739–782.

———. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. Bulletin of the British Museum of Natural History (Zoology) **55**:209–257.

Avery, R. A., J. D. Bedford, and C. P. Newcombe. 1982. The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. Behavioral Ecology and Sociobiology **11**:261–267.

Avery, R. A., and B. H. MacArdle. 1973. The morning emergence of the common lizard *Lacerta vivipara* Jacquin. British Journal of Herpetology **5**:363–368.

Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist **32**:194–216.

Bakken, G. S., and D. M. Gates. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. Pages 255–290 *in* D. M. Gates and R. B. Schmerl, editors. Perspectives of biophysical ecology. Springer-Verlag, New York, New York, USA.

Bakken, G. S., W. R. Santee, and D. J. Erskine. 1985. Operative and standard operative temperature: tools for thermal energetics studies. American Zoologist **25**:933–943.

Barbadillo, L. J. 1987. La guía Incafo de los Anfibios y Reptiles de la Península Ibérica, Islas Baleares y Canarias. INCAFO, Madrid.

Bauwens, D., T. Garland, Jr., A. M. Castilla, and R. Van Damme. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. Evolution **49**:848–863.

Bennett, A. F. 1980. The thermal dependence of lizard behaviour. Animal Behaviour **28**:752–762.

Bradshaw, S. D. 1986. Ecophysiology of desert reptiles. Academic Press, London, UK.

Carrascal, L. M., and J. A. Díaz. 1989. Thermal ecology and spatio-temporal distribution of the Mediterranean lizard *Psammodromus algirus.* Holarctic Ecology **12**:137–143.

Carrascal, L. M., P. López, J. Martín, and A. Salvador. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. Ethology **92**:143–154.

Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert lizards. Bulletin of the American Museum of Natural History **83**:265–296.

Díaz, J. A. 1991. Temporal patterns of basking behaviour in a Mediterranean lacertid lizard. Behaviour **118**:1–14.

———. 1993. Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammodromus algirus.* Canadian Journal of Zoology **71**:1104–1110.

Díaz, J. A., and L. M. Carrascal. 1991. Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. Journal of Biogeography **18**:291–297.

Díaz, J. A., and L. M. Carrascal. 1993. Variation in the effect of profitability on prey size selection by the lacertid lizard *Psammodromus algirus.* Oecologia **94**:23–29.

Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. Ecological Monographs **49**:129–149.

Garland, T., Jr., and S. C. Adolph. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiological Zoology **67**:797–828.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology **41**: 18–32.

Grant, B. W., and A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami.* Ecology **69**:167–176.

Harvey, P. H., and A. Purvis. 1991. Comparative methods for explaining adaptations. Nature **351**:619–624.

Heatwole, H., and J. Taylor. 1987. Ecology of reptiles. Surrey Beatty, Canberra, A.C.T. Australia.

Hertz, P. E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. Ecology **73**:1405–1417.

Hertz, P. E., R. B. Huey, and E. Nevo. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. Evolution **37**:1075–1084.

Hillman, P. E. 1969. Habitat specificity in three sympatric species of Ameiva (Reptilia: Teiidae). Ecology **50**:476–481.

Huey, R. B. 1982. Temperature, physiology and the ecology of reptiles. Pages 25–91 *in* C. Gans and F. H. Pough, editors. Biology of the Reptilia. Volume 12. Academic Press, New York, New York, USA.

———. 1987. Phylogeny, history, and the comparative method. Pages 76–101 *in* M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, editors. New directions in ecological physiology. Cambridge University Press, New York, New York, USA.

Huey, R. B., A. F. Bennett, H. John-Alder, and K. A. Nagy. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Animal Behaviour **32**:41–50.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. TREE **4**:131–135.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology **62**:991–999.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and the ecology of ectotherms: a discussion of approaches. American Zoologist **19**:357–366.

Licht, P., W. R. Dawson, V. H. Schoemaker, and A. R. Main. 1966. Observations on the thermal relations of western Australian lizards. Copeia 1966:97–111.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist **100**:603–609.

Magnusson, W. E., L. J. de Paiva, R. M. da Rocha, C. R. Franke, L. A. Kasper, and A. P. Lima. 1985. The correlates of foraging mode in a community of Brazilian lizards. Herpetologica **41**:324–332.

Martín, J., P. López, L. M. Carrascal, and A. Salvador. 1995. Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*). Canadian Journal of Zoology **73**:1065–1068.

McLaughlin, R. L. 1989. Search modes of birds and lizards: evidence for alternative movement patterns. American Naturalist **133**:654–670.

Mellado, J. 1980. Utilización del espacio en una comunidad de lacértidos del matorral mediterráneo de la Reserva Biológica de Doñana. Doñana, Acta Vertebrata **7**:41–49.

Norris, K. S. 1967. Color adaptation in desert reptiles and its thermal relationships. Pages 162–229 *in* W. W. Milstead, editor. Lizard ecology: a symposium. University of Missouri Press, Columbia, Missouri, USA.

Norusis, M. J. 1992. SPSS for Windows 5.0. SPSS, Chicago, Illinois, USA.

Pearson, O. P. 1977. The effect of substrate and of skin color on thermoregulation of a lizard. Comparative Biochemistry and Physiology **58A**:353–358.

Pérez-Mellado, V. 1992. Ecology of lacertid lizards in a desert area of eastern Morocco. Journal of Zoology (London) **226**:369–386.

Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology **47**:1055–1059.

Pietruszka, R. D. 1986. Search tactics of desert lizards: how polarized are they? Animal Behaviour **34**:1742–1758.

Pollo, C., and V. Pérez-Mellado. 1989. Activity and thermoregulation in three mediterranean species of Lacertidae. Herpetological Journal **1**:343–350.

Porter, W. P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. Ecological Monographs **37**:273–296.

Regal, P. J. 1983. The adaptive zone and behavior of lizards. Pages 105–118 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.

Salvador, A. 1982. A revision of the lizards of the genus *Acanthodactylus* (Sauria, Lacertidae). Bonner Zoologische Monographien **16**:1–167.

———. 1985. Guía de Campo de los Anfibios y Reptiles de la Península Ibérica, Islas Baleares y Canarias. Santiago García, editor. Leon, Spain.

Schoener, T. W. 1969. Models of optimal size for solitary predators. American Naturalist **103**:277–313.

Spellerberg, I. F. 1972. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. III. Behavioural aspects of thermoregulation. Oecologia **11**:1–16.

Spotila, J. R., P. W. Lommen, G. S. Bakken, and D. M. Gates. 1973. A mathematical model for body temperature of large reptiles: implications for dinosaur ecology. American Naturalist **107**:391–404.

van Berkum, F. H. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. Evolution **40**: 594–604.

Van Damme, R., D. Bauwens, A. M. Castilla, and R. F. Verheyen. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. Oecologia **80**:516–524.

Van Damme, R., D. Bauwens, and R. F. Verheyen. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Functional Ecology **5**:507–517.

Vitt, L. J., and J. D. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. American Naturalist **112**:595–608.

Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist **24**:107–120.