Thermal biology, microhabitat selection, and conservation of the insular lizard *Podarcis hispanica atrata*

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Summary. We studied aspects of the thermal biology and microhabitat selection of the endangered lizard *Podarcis hispanica atrata* during autumn in the field and laboratory. Body temperatures *(Tb)* of active lizards were within a narrow range, were largely independent of ambient temperatures, and exhibited little die! variation. Activity *Tbs* largely coincided with the selected temperatures maintained in a laboratory thermogradient and with *Tbs* that maximize running performance. Alternation of basking with other activities and shuttling between sun and shade were obvious aspects of thermoregulatory behaviour. Lizards shifted microhabitat use throughout the day. During early morning and late afternoon, basking lizards were restricted to rocky sites surrounded by shrubs. Near midday lizards used a wider array of microhabitats, and many moved in open grassy sites. Juveniles maintained lower activity *Tbs,* had lower selected temperatures, and basked less frequently than the adults. Juveniles occupied open grassy patches more often than the adults. We discuss the relevance of our results for the conservation of this extremely rare lizard and the management of its habitats.

Key words: Body temperature – Habitat selection – Locomotor performance – Conservation – *Podarcis*

The maintenance of relatively high and constant body temperatures by behavioural thermoregulation is a conspicuous aspect of lizard biology (Avery 1982; Huey 1982). Interactions between an ectotherm and its thermal environment may constrain activity rhythms and habitat use (e.g. Porter et al. 1973; Porter and James 1979; Christian et al. 1983; Waldschmidt and Tracy 1983; Grant and Dunham 1988; Huey et al. 1989; Adolph

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1990), and may conflict with requirements for food and reproduction or the avoidance of competitors and predators (Huey and Slatkin 1976; Huey 1982). These processes might be especially evident in small insular lizard populations, such as those of several lacertids (mainly *Podarcis* spp.) inhabiting islets in the Mediterranean Sea. Because the islets are extremely small (most are 10-100 ha, some < 1 ha; see Pérez-Meflado 1989), the spatial heterogeneity of vegetation structure is aften restricted. Moreover, the islets are subject to strong tempora! changes in both abiotic and biotic (food availability, predation pressure) conditions.

Podarcis hispanica atrata is a small (adult snout-vent length 52-74 mm) wall lizard whose distributional range is limited to some small islets (total area ca. 20 ha) in the Columbretes archipelago (Spain) in the Mediterranean. This endangered lizard (Corbett 1989) has been the subject of several taxonomically oriented studies (Boscá 1916; Eisentraut 1930; Klemmer 1961), but its life-history is little known (Castilla et al. 1987). We recently undertook a short-term field study of this lizard, to gather information relevant to its conservation. This paper reports studies of the thermal ecology and habitat selection patterns during autumn. In particular, we examine: (1) die! and size-linked variations in body temperature *(Tb)* and thermoregulatory behaviour; (2) die!shifts in microhabitat utilization as a possible thermoregulatory mechanism, and (3) relation of activity *Tbs* to thermal preferences (selected body temperatures in a laboratory photothermal gradient) and the range of *Tbs* that maximizes sprint speed. We discuss the relevance of our results to the conservation of this lizard.

Materials and methods

Study area

The Columbretes islands (39° 54' N, 0° 41' E) are an archipelago of small islets of volcanic origin situated in the Mediterranean ca. 50 km off the coast of Castellón (province of Castellón, Spain). The

study was carried out on "Columbrete Grande", the largest (13 ha) and the only inhabitable islet. The climate of the archipelago is characterized by an average annual temperature of 16.8° C and low rainfall (265 mm/year). Most precipitation occurs during autumn. Daily fluctuations in ambient temperature are low during spring and autumn (Gisbert 1987).

The vegetation consists mainly of perennial shrubs *(Suaeda vera, Lobularia maritima),* herbs *(Lavatera mauritanica, M alva parvijfora)* and patches of grasses. The vegetative cover of *Lavacera mauritanica* and *Malva par vijf.ora* exhibits dramatic seasonal fluctua tions, and depends strongly on precipitation levels. Due to heavy rainfall during the fortnight preceding our visit to the islands, an explosive growth of *L. mauritanica* and *M. parviflora* occured. Trees are absent, except for one introduced individual of *Ficus carica.*

Activity p atterns and body temperatures in thefield

The field study was conducted between 27 September and 12 October 1989. Observationson behaviour and microhabitat utilization were made white one of us walked along a fixed 850-m transect. The route was walked at known times for a total of 24.5 search hours between 0700 and 1700 hours (Mean European Time), which covered the entire daily activity period of lizards at that time of the year. Upon sighting each lizard that appeared undisturbed, we recorded : date, time, size (age) class [juvenile: < 48 mm snout-vent length (SVL) ; adult: SVL > 52 mm], sex of adults, behaviour (resting; basking = dorsoventral flattening of the body and perpendicular orientation to the sun; walking; unknown), distance to the nearest spot of deep shade, and microhabitat features. Microhabitats were characterized by two parameters: substrate type (rock/stone, sand, grass, herbs) and dominant plant species *(Suaeda vera, Lobu/aria maritima, Lava tera mauritanica* or *Malva parviflo ra,* grass, no vegetation). Only observations of lizards whose size class and sex were assessed unequivocally were included in data analyses.

We estimated the relative abundance of rnicrohabitat categories by noting their presence at 5-m intervals along the transect line.

During separate searches along the route, we captured a total of 197 lizards by noose or hand and imrnediately measured body temperature (cloaca!= T_b), air ternperature (shaded bulb, 3 cm above substrate, $= T$) and substrate temperature (shaded bulb, $= T$) to the nearest 0.1 $^\circ$C with a thermocoup le connected to a quick-reading electronic thermometer (DGT-Therma 3). We also noted time of day, age class, sex, weather condition s (sunny, cloudy/variable – either 5 or < 5 min of continuous sunshine before capture) and exposure to sunlight (full sun, sun filtered by vegetation, shade, overcast).

Selection of microhabitat features

We also surveyed a 750-m² study plot, with habitat characteristics representative of the whole island, where we quantified structural features of the microhabitat at sighting places of adult lizards (sexes pooled). As preliminary observations suggested die! \ ariation in habitat occupation, we sampled microhabitats of adult lizards that were observed during the time intervals 0700--0800, 0800- 1000 and 1600-1700 hours *(n*= 12 for each interval).The range of microhabitats potentially available to the lizards was estimated by sampling 26 sites that were the nodes of 5-m equidistant grid lines, covering the entire study plot.

For each habitat sample we located 5 points: the initia! spot where the lizard was first sighted, and the endpoin ts of two orthogonal 4-m lines that intersected at the sighting spot. The direction of these lines was determined haphazardly by throwing a pen on the ground. The lizard sighting location served as the centre of a circle with a 10-cm radius; the encompassing points were each the centre of a 50-cm radius circle. Within each circle we estimated following 11 variables: (1-4) percentage cover at ground level of rock/stone, sand, grass and herbs; (5-8) percentage cover of the

vegetation layers with heights < 10 cm, 10-25 cm, 25-50 cm and > 50 m ; (9) maximum height of the vegetation; (10) distance to the nearest rock and (11) distance to the nearest patch of vegetation that would potentially provide shelter to predators. Three additional variables were calculated: (12) total vegetation cover: sum of the vegetation cover over the four layers; (13) vertical diversity: calculated over the four vegetation layers with the Shannon-Wiener formula ; (14) horizontal diversity: calculated over the habitat variables that cover the ground (rock/stone, sand, grass, herbs) with the Shannon-Wiener formula.

We deduced two descriptions of the microhabitat from this information. Habitat structure at the initia!location of the lizard was estimated using exclusively the data from the smaller, centra! sampling circle (O= 10 cm). We calculated mean values for each 'ariabie at the 5 sampling points to quantify the average habitat structure within a circle of radius 2.5 m surrounding the spot where the lizard was seen. In this way we attemptcd to provide a description of microhabitat features within a substantial portion of the lizard 's home range. The two data sets were used separately in data analyses.

We performed a principal component analysis on the correlation matrix of the habitat variables to reduce the dimensionality of the habitat space. We used one-way analysis of variance (ANOVA) and Tukey's a posteriori tests to evaluate differences among lizard observation sites and availability samples, both for the original variables and the scores on the principal components.

Se/ected body temperatures

On 13 October 1989 we transported 36 lizards (12 males, 12 females, 12juveniles) to the Department of Animal Biology, University of Salamanca. Average (± 1 SD) lengths (SVL) and masses *(M)* were: males: SVL = 68.0 ± 3.4 mm, M = 7.63± 0.75 g; females: SVL= 61.9 ± 3.6 mm, M = 4.76 ± 0.81 g; juveniles: SYL = 37.6± 4.0 mm, M = 1.16 ± 0.33 g. They were housed five to each cage (age classes separated) in terraria (100 x 50 x 40 cm) filled with sand .stones and grasses. A 150-W light bulb suspended above one end created a gradient of air temperatures ranging from 20 to 60° C. Food (mealworms and fly larvae) and water were provided ad libitum. We recorded body temperatur es of active lizards, using the same thermom eter as that in the field, with a minimum time interval of 1 h between two measurements of an individual lizard. These *Tb* readings were considered as estimates of selected (or "preferred") body temperatures. The selected temperature range is defined as the centra! 80% of all selected temperature recordings. We assume that selected body temperatu res represent the temperatures that lizards would attempt to achieve in the field in the absence of physical and biotic restrictions (Licht et al. 1966)

Thermal sensitivity of sprint speed

We determined sprint speed in adult males and females (males: SYL= 68.0 ± 3.4 mm, M= 7.63 ± 0.75 g, *n* = 12; females: SYL = 63.6 ± 2.0, M= 5.16 ± 0.58, 11=8) at a fixed sequence of body temperatures (35°, 30°, 25°, 37.5°, 32.5°, 40° C). Lizards selected for this experiment had intact or completely regenerated tails. Body temperature of lizards was controlled by placing them in an incubator at the appropriate test tcmperature for at least 1 h. Subsequently we chased an individual lizard through a racetrack (220 x 15 cm) similar to that described by Huey et al. (1981). The track was placed at a 15° incline, as preliminary tests indicated that this improved running performance. Running times were recorded by nine sets of photocells positioned at 25-cm intervals along the track. The photocells were connected to a microcomputer that calculated sprint speed over each 50-cm section of t he track. Each lizard was run three times at each test temperature . From these t hree trials, we selected the fastest 50-cm track interval

and used this value as an cstimate of a lizard's maximum sprinting ability at that temperature. Lizards were raced three times per day and were given a 1-h rest between subsequent races. The lizard's Tb was measured ju st before each run.

Following the running experiment, we determined the critica! thermal maximum (CTMax) in 10 adult lizards (5 males, 5 females), as an estimate of the upper temperature at which locomotion is possible. Animals were heated continuously in an incubator at an approximate rate of 1° C/min. while we observed their behaviour. The body temperature associated with a transient loss of righting response was used as an indicator of CT$_{Max}$ (Brattstrom 1971). At the conclusion of this experiment, all lizards were returned to the island and released at their site of capture.

To quantify the thermal dependence of sprint speed, wc standardized performances among lizards by dividing an individual's speed at each temperature by the maximum value recorded for that individual. A speed of 0 cm/s was assigned to the critica! thermal maximum temperature, using the average value for all individuals. We plotted speed against Tb and used the procedure described by \an Berkum (1986) to connect data points and to construct a minimum convex polygon for each individual. These polygons were then used to estimate the width and limits of the 80% and 95% performance breadths (TPB$_{80}$, TPB$_{95}$ = body temperature range over which speed is at least 80% or 95% of its maximum) and the optima! body temperature (T_o = temperature at maxima! performance; estimated by midpoint ^{o}Of the TPB$_{95}$) for each individual lizard.

Results

Activity and thermoregulatory behaviour

Prevailing weather conditions strongly determined daily activity patterns. Lizards did not emerge on overcast days. On days with changeable weather, lizards retreated during prolonged cloudy periods, but they quickly resumed activity when sunshine was again available.

The number of lizards observed per person-hour at different times of day differed slightly among age/sex groups (males – females: $G=17.75$, $P=0.04$; adults – juveniles: $G = 17.47$, $P=0.04$, Fig. 1). Note the high overal l sighting frequency (ca. l lizard per 3 min observation time), reflecting high lizard abundance and detectability.

The relative number of lizards seen in full sun, filtered sun, and shade varied throughout the course of the day. Most lizards were in full sun early and late in the day, while a relatively high proportion of lizards was observed i n filtered sun and shade during the centra! hours (0800-1400 hours). The proportion of lizards seen in full sun was similar in both age classes (adults: 71% of n = 117; juveniles: 67% of n = 33; $G = 0.27$, $P>0.80$).

The proportion of animals seen basking was highest at the onset (0700-0900 hours) and end (1600-1700 hours) of the day, and lowest at midday. Overall, the relative number of basking lizards was highest in the adults (adults: 45% of n = 330; juveniles: 24% of $n = 147$; $G= 18.82$, $P<0.001$).

Most lizards were observed near shaded sites, as indicated by the short transit distances to shadow (\O = 12 cm, range: 1-250 cm, $n=356$). This distance was similar in both age classes (two-way ANOVA of log distance: F= 0.61, df = 1,336, $P > 0.40$), but increased
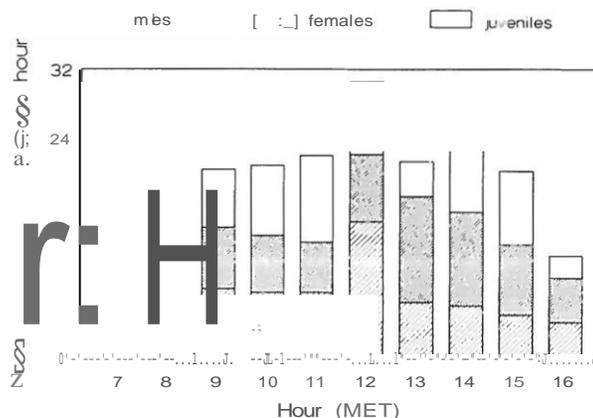

Fig. 1. Number of lizards observed per person hour at different times of day (Mean European Time)

Table 1. Statistics of body (Tb), air (T_o) and substrate $(T.)$ temperatures recorded during the field study in the distinct age/sex classes, and selected temperatures (T_1 in a laboratory thermogradient. Med $\pm Q_{3-1}$: median $\pm$ interquartile range

		Adult males	Adult females	Juveniles
	. $\pm$ SE	34.2$\pm$ 0.3	34.0$\pm$ 0.2	32.6$\pm$ 0.3
	Med $\pm Q_{3-1}$	34.7$\pm$ 3.2	34.3$\pm$ 2.3	32.8$\pm$ 2.0
	Min -max	26.6-39.3	29.4 -38.3	27.1 -35.3
	n	94	69	33
T :	\' $\pm$ SE	23.5$\pm$ 0.2	23.6$\pm$ 0.2	23.2$\pm$ 0.3
"	Med $\pm Q$ _ _	23.2 $\pm$ 1.9	23.4$\pm$ 2.1	22.7$\pm$ 1.3
	Min-max	20.2-31.1	20.8 –30.2	21.2-27.4
	n	94	69	33
T :	. $\pm$ SE	28.5$\pm$ 0.3	28.5$\pm$ 0.3	27.6$\pm$ 0.4
=	Med $\pm Q_{3-1}$	28.2$\pm$ 4.8	28.5$\pm$ 3.3	28.1$\pm$ 3.0
	Min-max	21.2-35.7	23.8- 33.4	24.3-31.0
	n	94	69	33
	HSE	34.2$\pm$ 0.1	34.7$\pm$ 0.2	33.6$\pm$ 0.1
	Med $\pm Q_{3-1}$	34.4$\pm$ 2.5	34.9$\pm$ 2.6	33.7$\pm$ 2.0
	Min-max	19.2-38.7	29.7-38.1	26.9 -37.3
	II	277	123	167

slightly during the course of the day (F= 5.05, df = 9,336, P < 0.001).

Field body temperatures

Tbs recorded during sunny weather were not different from these observed under cloudy/variable conditions (!-test: t = 0.385, 195 df, $P >0.70$) , and we therefore pooled all data for further analyses. Tbs differed among age/sex classes (one-way ANOVA : $F = 6.496$, df = 2, 194, P < 0.001). Juveniles maintained lower Tbs than adult males and females, but adult males and females had similar Tbs (Tukey's a posteriori test ; Table 1). In view of the observed difference in Tbs among lizard age classes, data for ju veniles and adults (sexes lumped) will from now on be treated separately. As indicated by the low interquartile ranges (Q_{3-1}, see Table 1), variation in Tb
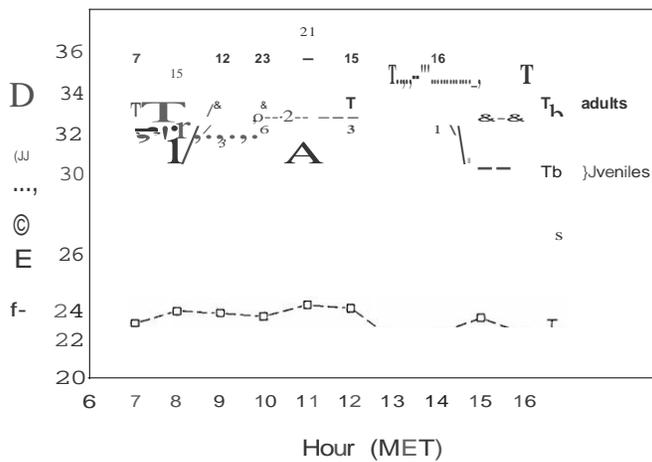
Fig. 2. Body temperatures of adults and juveniles (mean ± 1SE) and mean air (T_a) and substrate temperatures (T) at different times of day
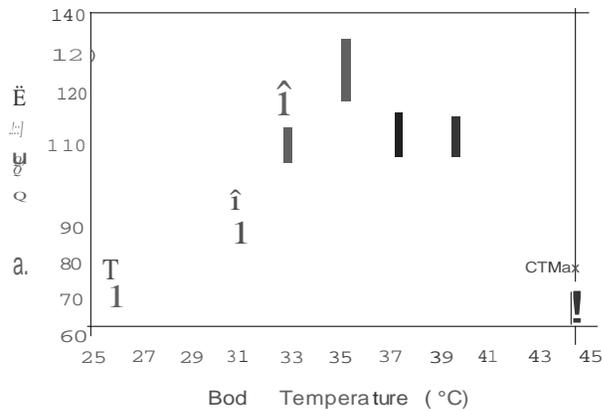

Fig. 3. Sprint speed of adult *Podarcis hispanica atrata* at various body temperatures. Values are means ± 1 SE. CT_M = critical thermal maximum temperature. n = 20 at all body temperatures

was very low in all lizard groups. Air and substrate temperatures did not differ among age/sex classes (one-way ANOVA: $P > 0.20$ in both cases; Table 1).

Slopes of the regression lines of Tb on T are low for both adults ($b = 0.203$, SE = 0.099) and juveniles ($b = -0.013$, SE = 0.217) and are not significantly different (ANCOVA: $F = 0.640$ df = 1,193, $P > 0.50$). The intercept value is significantly higher for the adult sample (ANCOVA: $F = 11.955$, df = 1,194, $P < 0.001$). Comparable results were obtained for the relations between Tb and T_a (adults: $b = 0.283$, SE = 0.061; juveniles: $b = 0.116$, SE = 0.174; difference among slopes: $F = 0.661$, df = 1,193, $P > 0.50$; difference among intercepts: $F = 9.873$, df = 1,194, $P < 0.01$). Thus adults maintained higher Tbs than juveniles, even after accounting for the effects of air and substrate temperatures.

A two-way ANOVA detected significant effects on rnriation in Tb of hour of day (F = 2.918, df = 9,176, $P < 0.01$) and age class ($F = 16.725$, df = 1,176, $P < 0.001$), but no significant interaction effect between time of day and age (F = 0.848, df = 9,176 $P > 0.50$). This indicates that die! fluctuations in Tb were similar in both age groups: juveniles maintained consistently lower Tbs (Fig. 2). Despite the detection of a statistically significant die! variation in Tb, the coefficient of variation for hourly mean Tbs was low in both adults (2.5 %) and juveniles (4.8 %), indicating that lizards maintained a rather constant Tb throughout their daily activity period (Fig. 2). Diurnal fluctuations of T_a and T'' though statistically significant, were remarkably small (Fig. 2).

Selected temperatures

Lizard age/sex groups had significantly different selected temperatures (one-way ANOVA: F = 9.809, df = 2,564, $P < 0.001$; Table 1). The multiple range analysis evidenced significant differences among adult males, females and juveniles (Tukey's a posteriori test, $P < 0.05$).

A comparison of field Tbs with selected body temperatures reveals that 67%, 71% and 75% of the field Tbs

Table 2. Parameters of the thermal sensitivity of sprint speed in adult lizards (sexes lumped). Maximum sprint speeds (Vm''; cm/s), optimal temperatures (T_o), the 80% and 95% thermal performance breadths (TPB_{80}, TPB_{95}) and their lower limits (L_{80}, L_{95}), and the critical thermal maximum temperature (CT_{MaJ} (°C) are shown

	Mean ± SE	Range	n
v_{max}	159.0 :1:9.9	96.7-259. 1	20
Tp_o	35.52 ± 0.47	32.4- 39.2	20
TPB_{80}	5.80 ± 0.60	2.9- 12.5	20
L_{80}	32.47 :1: 0.57	28.2- 37.0	20
TPB_{95}	1.61 ± 0.20	0.7- 3.7	20
L_{95}	34.71 ± 0.49	30.9- 38.6	20
CT_{Max}	44.45 ± 0.14	44.0- 45.1	10

for juveniles, adult males and females respectively, feil into the selected temperature range (the centra! 80% of the selected temperatures; see Materials and Methods). These percentages do not differ significantly (G-tests with Yates' correction, $P > 0.10$ in all cases) from the expected 80% under the null-hypothesis of an exact match between the field Tbs and the selected temperature range.

Thermal dependence of sprint speed

A two-way ANOVA (repeated measurements) revealed a significant effect of temperature (F = 4.873, $P < 0.001$) but not of sex (F = 0.896, $P > 0.30$) on absolute sprint speed. Males and females did not differ significantly in CT_{Max} (t = 0.21, $P > 0.80$) or in maximum sprint speed (1 = 0.83, $P > 0.40$), and we therefore pooled data for adult males and females. Sprint speed increased within the interval 25°-35° C and then decreased slightly again at higher Tbs (Fig. 3). Parameters derived from the temperature sensitivity curves are shown in Table 2.

Mean field and selected temperatures (Table 1) were very similar to the optima! Tb for sprinting (Table 2). We estimated relative sprint performance in the field by integrating Tb data with results of the thermal dependence of sprint speed. Approximately 77% of all Tb readings for

Table 3. Percentages of juvenile and adult lizards observed on distinct substrate types and vegetation categories

Substrate:	Rock/stone	Sand	Grass	Herbs		n
Juveniles	63	21	13	3		152
Adults	83	**11**	3	4		351

Vegetation:	Suaeda	Lobularia	Malva	Grass	No veg.	n
Juveniles	38	13	10	30	10	152
Adults	53	12	5	13	17	351
Available	39	13	6	13	29	344

adult lizards were within the TPB_{80} (32.5°-38.3° C), 21 % feil below and 2 % were above this range. Thus most lizards were active at *Tbs* that enabled them to run quickly.

Microhabitat selection

Age classes differed in substrate occupation (G= 29.92, 3 df, $P < 0.001$; Table 3). Most adults were observed on stony or sandy substrates, whereas a relatively large number of juveniles was seen on grass. Virtually all lizards of both groups were on stony substrates during the early morning and late afternoon hours.

Neither juveniles nor adults occupied vegetation categories in proportion to their availability (adults: $G = 19.92$, 4 df, P< 0.001; juveniles: G= 35.56, 4 df, $P < 0.001$; Table 3). We saw more juveniles than expected in grass, whereas adults selected *Suaeda* shrubs. Lizards of all age classes avoided sites without vegetation, mostly extensive areas of peeled volcanic rocks. The occupation of *Suaeda* vegetation by the adults peaked at the onset and end of the daily activity period.

Structural features of sites occupied by adult lizards at different times of the day and of available microhabitats are summarized in Table 4. Note that more variables exhibited significant differences between occupied and available sites for the centra) sampling circle (= initia) lizard sighting spot) than for the whole-habitat sample.

Principal component analysis was used to obtain a more integrated picture of the habitat attributes. The first three principal components accounted respectively for 50.3%, 18.4% and 9.4% of the variance of the raw data for the full microhabitat sample, and for 42.1%, 18.6% and 10.7% of the variance for the centra! sampling circle. The principal components (PC) derived from both data

Table 4. Summary (mean ± 1 SE) of structural habitat features at lizard observation sites during three time intervals and availability samples. Values for the total habitat sample and the lizard sighting spot are given separately (see text). ANOVA indicates differences among availability and the three time samples. $n = 12$ for lizard observation sites during each time interval; $n = 26$ for availability samples

	Observcd			Available	ANOVA
	0700-0800 hours	0800-1000 hours	1600-1700 hours		
Total sample					
% cover herbs	40.5 ± 4.7	47.2 ± 4.0	31.2 ± 4.6	42.1 ± 4.3	NS
grass	8.3 ± 2.1	32.7 ± 5.3	17.3 ± 5.4	22.6 ± 2.9	<0.01
rock	43.2 ± 6.9	16.6 ± 6.7	45.6 ± 4.1	27.1 ± 4.3	<0.01
sand	8.1 ± 3.5	3.6 ± 1.2	6.0 ± 2.3	8.2 ± 2.0	NS
% veg. < 10 cm	55.0 ± 4.5	80.0 ± 7.1	49.0 ± 4.9	64.3 ± 4.6	<0.01
10-25 cm	45.6 ± 5.5	47.1 ± 4.4	32.2 ± 4.6	41.9 ± 4.5	NS
25-50 cm	31.4 ± 5.0	27.3 ± 3.7	21.6 ± 5.1	25.1 ± 3.7	NS
>50 cm	5.9 ± 2.0	8.4 ± 2.3	4.0 ± 1.2	5.9 ± 1.6	NS
Tot. veg. cover	137.9 ± 14.8	161.8 ± 13.6	106.8 ± 13.1	137.2 ± 12.8	NS
Max. veg. height	35.6 ± 3.5	37.8 ± 4.0	32.4 ± 4.9	35.8 ± 3.1	NS
Distance veg.	21.8 ± 3.8	31.8 ± 8.8	52.8 ± 10.5	56.2 ± 10.0	NS
Distance rock	13.8 ± 8.9	62.7 ± 24.3	5.0 ± 4.1	56.5 ± 16.1	NS
Vertical div.	0.50 ± 0.04	0.49 ± 0.06	0.48 ± 0.04	0.58 ± 0.03	NS
Horizontal div.	0.80 ± 0.06	0.78 ± 0.08	0.63 ± 0.10	0.74 ± 0.06	NS
Sig/11ing spot					
% cover herbs	8.7 ± 4.5	27.1 ± 11.2	7.1 ± 3.9	40.2 ± 6.1	<0.01
grass	2.1 ± 2.1	41.4 ± 119	1.7 ± 1.7	21.7 ± 5.5	<0.001
rock	66.7 ± 11.6	30.3 ± 12.6	85.4 ± 8.5	27.1 ± 6.0	<0.001
sand	22.6 ± 11.1	1.3 ± 0.9	5.8 ± 5.8	11.0 ± 4.2	NS
% veg. < 10 cm	41.8 ± 10.1	68.5 ± 12.3	8.8 ± 4.0	61.9 ± 5.8	<0.001
10-25 cm	51.7 ± 10.3	28.0 ± 10.7	18.3 ± 6.4	37.6 ± 6.1	NS
25-50 cm	38.8 ± 10.8	0.0 ± 0.0	15.0 ± 5.9	23.5 ± 5.8	<0.01
:.-50 cm	7.1 ± 5.0	0.0 ± 0.0	1.7 ± 1.1	10.8 ± 4.9	NS
Tot. veg. cover	139.3 ± 26.1	96.5 ± 19.7	43.8 ± 15.I	133.7 ± 19.7	<0.01
Max. veg. height	35.3 ± 7.9	14.3 ± 2.9	28.9 ± 11.3	35.5 ± 4.7	NS
Distance veg.	7.1 ± 5.1	40.8 ± 8.6	51.7 ± 17.3	64.6 ± 16.3	NS
Distance rock	13.8 ± 8.9	62.7 ± 24.3	5.0 ± 4.2	56.5 ± 16.1 "	=0.05
Vertical div.	0.75 ± 0.14	0.37 ± 0.09	0.45 ± 0.15	0.78 ± 0.09	<0.05
Horizontal div.	0.31 ± 0.12	0.31 ± 0.12	0.19 ± 0.08	0.65 ± 0.07	<0.05

sets exhibited no qualitative and only slight quantitative differences: the correlation coefficients between original variables and principal components had similar values and significance levels. The first PC was strongly positively correlated with percent cover by herbs at ground level, percent cover of all four vegetation layers, total vegetation cover, maxima! vegetation height and vertical diversity, and was negatively correlated with percent cover by stones/rocks at ground level and the distance to the nearest vegetation patch. This represents a gradient from microhabitats with extensive cover by stones/rocks and sparse vegetation, towards sites with high, abundant, and structurally complex vegetation. The second principal axis was positively correlated with percent cover by grasses at ground level, percent cover of vegetation < 10 cm high and distance to the nearest rock, and exhibited a strong negative correlation with percent cover by stones/rocks at ground level. Thus, PC2 describes a gradient from sites with much cover by stones and rocks to locations with much low, grassy vegetation. The third PC showed strong positive correlations with percent cover by sand at ground level and horizontal diversity.

We examined habitat occupation by considering the projections (= scores) of the different samples on the component axes. For the whole-habitat samples, scores on PCl and PC3 did not differ significantly between available and occupied sites (ANOVA : PCl : $F = 1,769$, df = 3,6 1, $P > 0.10$; PC3: $F = 1,610$, df = 3,61, $P > 0.10$). Microhabitats occupied during the intervals 0700-0800 hours and 1600-1700 hours obtained significantly lower scores on PC2 (ANOVA: $F = 4.807$, df = 3,61, $P < 0.005$; Fig. 4A). Thus, during the early morning and late afternoon hours, lizards preferentially occupied sites with high cover by rocks/stones and limited (grassy) vegetation near ground level. Near midday, they were found in a wider range of habitats, including those with much low, grassy vegetation (Fig. 4A).

A more strongly delineated picture of microhabitat choice emerges upon considering habitat features at the initia! lizard sighting spot. Occupied and available sites obtained differing scores on both PC! and PC2 (ANOVA : PCl : $F = 3.125$, df = 3,61, $P < 0.05$; PC2: $F = 13.516$, df = 3,61, $P < 0.001$), but not on PC3 (ANOVA : $F = 1.609$, df = 3,61, $P > 0.10$). Lizards were not observed on sites with extremely high PCl scores, i.e. the most abundantly vegetated microhabitats (Fig. 4B). During early morning and late afternoon, lizard observations were restricted to spots positioned in the lower left corner of the PC1-PC2 space, i.e. these with extensive cover of rocks/stones and sparse vegetation at ground level. Coverage by the distinct vertical vegetation layers was rather high, especially during early morning (Table 4). Virtually all of the samples at these times were of lizards basking in an inclined or vertical position on stones/rocks located under overhanging vegetation (mainly *Suaeda vera).* Near midday, many lizards were sighted at locations with extensive grass cover (Fig. 4B) and with no vegetation > 25 cm in height (Table 4), and most were moving actively, presumably searching for food.
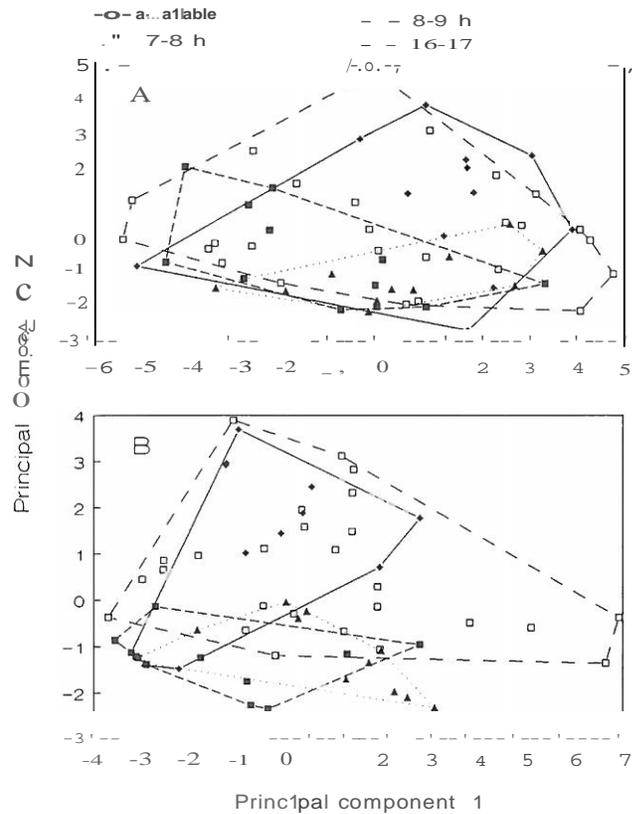

Fig. 4A, **B.** Projections of the different habitat samples on the PCl-PC2 space obtained by principal components analyses. A Values for the whole habitat sample. **B** Values for the lizard sighting spot (see text)

Discussion

Body temperatures and thermoregulatory behaviour

Body temperatures of active *P. hispanica atrata* were confined to a narrow range, were largely independent of air and substrate temperatures, and exhibited little die! fluctuation. Such a set of features is commonly considered as indicating a high degree of thermoregulato ry precision (Huey and Pianka 1977; Huey and Slatkin 1976; Huey 1982). Moreover, *Tbs* recorded in the field closely matched selected body temperatures in the Iaboratory, and most field *Tbs* feil within the TPB$_{80}$ for sprint speed. Hence, active lizards precisely regulated their *Tb* within a narrow zone which coincided with the selected temperature range and with the body temperature range that maximizes sprint performance.

Direct behavioural observations provide information on the mechanisms of thermoregulation (Heath 1964; Huey and Pianka 1977). The adoption of basking postures and shuttling between sun and shade are the most conspicuous aspects of behavioural thermoregulation in *P. hispanica atrata.* Lizards alternated periods of overt basking with bouts of other activities. The relative number of basking lizards was highest during the early morning and late afternoon hours, even though the proportion of ground surface in sun must be low then

(Huey and Pianka 1977). Through the adoption of a basking posture (dorsoventral flattening of the body and orientation perpendicular to the sun's rays), lizards increase the absorption of radiant heat to compensate for the lower ambient temperatures and the low radiation loads at these times of the day.

Ontogenetic shift in body temperatures

An interesting finding is that juveniles maintained lower activity Tbs than adults. This ontogenetic shift in Tb cannot be attributed to proximate environmental effects, as we found a parallel difference in selected temperatures, indicating that size classes differ in thermal preferences. A possible explanation is provided by the complex effects of body size on the heat balance of ectotherms. Due to their larger surface area to volume ratio, smaller lizards have: (1) higher heating and cooling rates; (2) greater convective heat loss (Muth 1977; Crawford et al. 1983; Porter and Tracy 1983); (3) a smaller heat capacity or thermal inertia (Stevenson 1985). In a given thermal environment, smaller lizards will therefore experience lower equilibrium temperatures than larger lizards (Porter et al. 1973; Porter and James 1979; Porter and Tracy 1983). This could favour the evolution of size-linked differences in the selected body temperature (Paulissen 1988). However, whether the body size range found in *P. hispanica atrata* is sufficiently large to elicit differences in equilibrium temperatures (see e.g. Crawford et al. 1983; Stevenson 1985), and to induce different thermal preferences is unclear. In the absence of measurements of operative temperatures or of relevant micrometeorological and morphological variables (Porter and Tracy 1983), we cannot at present evaluate this possibility. Few other studies have examined size-related differences in selected temperatures within single lizard species. Juvenile and adult *Cnemidophorus sexlineatus* exhibited identical thermal preferences (Paulissen 1988). Van Damme et al. (1986) found that subadult *Lacerta vivipara* had lower selected temperatures than adults during the months April-June, when size differences between the age classes were largest, but not during July-September, when the subadults progressively approached the adults' size. Interestingly, *L. vivipara* and *P. hispanica atrata* are closely related (Arnold 1973).

Because of their lower selected temperatures and their rapid heating rates, field-active juveniles should achieve their thermal preferendum with fewer associated costs than the adults. The relative number of lizards observed basking, a crude index of the time invested in behaviours that tend to increase $Tb,$ was lowest in the juveniles. This result suggests that juveniles invest less time in thermoregulatory behaviour and consequently may have more time aYailable for foraging than the adults. We indeed observed more juveniles than adults in grass, the vegetation category preferentially used by (foraging) adults during the centra! hours of the day. An obvious advantage of an increase in foraging time is a rise in the amount of daily food intake and of growth rates (Avery 1984; Sinervo and Adolph I989). Fast growth

rates would permit the juveniles to attain or approach adult size at the onset of the next activity season.

Microhabitat selection

Lizards shifted their use of structural features of the microhabitat during the day. To what extent is this pattern of habitat choice attributable to thermal constraints and/or to other factors (e.g. food availability, predation, social interactions)? Measurements of operative temperatures (Bakken and Gates 1975) in distinct microhabitats are needed to evaluate constraints imposed by the thermal environment (e.g. Christian et al. 1983; Waldschmidt and Tracy 1983; Grant and Dunham 1988; Adolph 1990). Nevertheless, the observed shift in microhabitat occupation is interpretable, at least in part, in terms of thermoregulatory mechanisms. During the first and last hours of their daily activity period, when basking frequency was highest, adult lizards were confined to sites with many rocks/stones and limited vegetation cover near ground level. These microhabitats should be favourable basking sites as close contact with sun-warmed rocks or stones enhances conductive heat gain, and the variable orientation of their surfaces facilitates postural adjustments that increase net radiation intake. At the same time, the presence of overhanging vegetation at these sites may reduce the conspicuousness of basking lizards and diminish their risks of predation. Other microhabitats are probably thermally less favourable during early morning, either because of the absence of sunlit spots (densely vegetated sites) and/or high moisture levels, and hence cool ambient temperatures, due to the presence of dew (grass).

Following the morning basking period, during which Tbs rise quickly, lizards utilize a wider range of microhabitats. Many adults were actively moving in grassy, open sites with few upright shrubs. Whether these sites are occupied because they provide the best thermal conditions at these times of the day, or because they offer a higher food availability, is unclear. Casual observations of feeding lizards and tentative impressions on insect abundance inclines us towards the latter possibility.

Patterns of microhabitat selection were more conspicuous for the initia! lizard sighting spot than for the surrounding vegetation structure. Also, many of the lizard sighting spots from the early morning and late afternoon hours feil outside the range of the microhabitat availability samples in the PC1-PC2 space (Fig. 4B). These observations suggest that suitable basking locations are not readily available and are precisely selected out of the available sites within a lizard's home range.

Conservation implications

Our findings bear some relevance to the conservation of this endemie lizard and the management of its habitat. Thermoregulation is of fundamental importance to the ecology of lizards, as their Tbs directly influence physiological and whole-animal performances, and ultimately

affect fitness (Huey and Stevenson 1979; Huey 1982; Hertz et al. 1988). Understanding of the *Tb* dependence of ecologically important traits (Huey and Stevenson 1979) provides a framework for evaluating activity *Tbs* and hence the outcome of the complex interactions between a lizard and its thermal environment. We have shown that activity *Tbs* of *P. hispanica atrata* coincide with the body temperature range that maximizes sprint performance, at least during the study period. As thermal conditions at the study area exhibit dramatic seasonal changes, these may induce shifts in activity temperatures and thermoregulatory behaviours (e.g. Huey and Pianka 1977; Christian et al. 1983; Van Damme et al. 1987). Nevertheless, our study was performed during the period of autumnal bird migration, which is presumably associated with an increased predation pressure. Under such conditions, the ability to perform at maximum speed might be of crucial importance to survival (Christian and Tracy 1981). We tentatively conclude that the actual conditions on the island allow careful thermoregulation within the *Tb* range that is conducive to maximum locomotor performance. The information presented here should permit anticipation (and correction) of long-term consequences of any disturbance of the lizards behaviour, through measuring its short-term effect on *Tbs* and hence on predictions of ecological performance.

A second relevant observation is the daily shift in microhabitat occupation, although its proximate causes are presently not fully understood. We provide quantitative descriptions of the structural features of distinct microhabitats that were used by the lizards at different times of day. The maintenance of an appropriate small-scale heterogeneity in vegetation structure should be taken into account in the design of plantation programmes that attempt to reduce soil erosion, the most acute landscape conservation problem on the island.

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