SEASONAL CHANGES IN THE THERMAL ENVIRONMENT DO NOT AFFECT MICROHABITAT SELECTION BY *PSAMMODROMUS ALGIRUS* LIZARDS

JOSÉ A. DÍAZ[1], SARA CABEZAS-DÍAZ[1,2] AND ALFREDO SALVADOR[3]

[1]*Dpto. de Zoología y Antropología Física (Vertebrados), Facultad de Biología, Universidad Complutense, Madrid, Spain*

[2]*Instituto de Investigación en Recursos Cinegéticos (IREC), C.S.I.C., Ciudad Real, Spain*

[3]*Dpto. de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, C.S.I.C., Madrid, Spain*

We studied the thermal consequences of microhabitat selection by *Psammodromus algirus* lizards by combining data on the frequency of use and relative availability of three different types of microhabitats, with information about the environmental operative temperatures, and their deviations from the lizards' selected thermal range, available in these microhabitats. In both seasons, lizards preferred holm oak shrubs and avoided rockrose shrubs and open areas. However, the thermal suitability of holm oaks was highest in July but lowest in May. We suggest that microhabitat preferences were more related to other aspects of lizard ecology (e.g. antipredator behaviour) than to thermal requirements.

Key words: lizard, operative temperatures, predation risk, thermoregulation

It is well known that lizards actively select the microhabitats they use according to their type of substrate, elevation, slope, plant cover, and other structural features (Arnold, 1987; Carrascal *et al.*, 1989; Díaz & Carrascal, 1991). Changes in microhabitat selection may also counteract the temporal variation or spatial heterogeneity of the thermal environment (Porter *et al.*, 1973; Christian *et al.*, 1983; Adolph, 1990), and many studies have emphasized the thermoregulatory consequences of habitat selection by ectotherms (Christian *et al.*, 1983; Grant & Dunham, 1988; Adolph, 1990; Huey, 1991; Bauwens *et al.*, 1996; Gvodzik, 2002). In fact, the physiological consequences of habitat selection are of paramount importance for ectotherms because the environmental temperatures available vary spatially over time, and this variation translates into body temperatures that affect short-term physiological performance, thereby determining their long-term ability to grow, survive and reproduce (Huey, 1991).

Thermoregulatory responses to environmental seasonality have also been reported for a number of liz-ard species (Van Damme *et al.*, 1987), sometimes including notable shifts in microhabitat use (Christian *et al.*, 1983; Schäuble & Grigg, 1998). However, if microhabitat selection is more dependent on other factors such as predation risk, social behaviour, etc., it may remain constant despite seasonal variations in the thermal suitability of microhabitats. Here, we report that *Psammodromus algirus* lizards in a Mediterranean open forest do not modify their patterns of habitat selection despite significant seasonal variation in the thermal characteristics of different types of microhabitats.

Psammodromus algirus is a medium-sized (adult snout-vent length ca. 60-90 mm), terrestrial, widely-foraging, lacertid lizard common in Mediterranean forests of the Iberian Peninsula. Our study was conducted at 'El Pardo' (Madrid, central Spain: 40º31'N, 03º47'W; 650-700 m elevation), a holm oak (*Quercus ilex*) broad-leaved, perennial forest whose shrub layer is dominated by holm oak offshoots and rockroses (*Cistus ladanifer*), alternating with open areas covered by annual herbs and/or bare ground. The undergrowth of holm oaks and rockroses forms well defined vegetation patches, with an average cover of more than two-thirds of the total surface. We distinguished three types of microhabitat: holm oak shrubs, rockrose shrubs, and open areas. The site has a mean annual temperature of 12.5 ºC and a mean annual rainfall of 686 mm, but meteorological conditions vary widely among seasons (e.g. mean temperature and precipitation are 15.0 ºC and 54.0 mm in May vs. 23.4 ºC and 14.8 mm in July). Several predators, including birds (e.g. *Buteo buteo*, *Falco tinnunculus*, *Otus scops*, *Athene noctua*, *Upupa epops* and *Lanius excubitor*) and snakes (*Malpolon monspessulanus* and *Elaphe scalaris*) are common at the study site.

Field sampling took place in the spring (May) and summer (July) of the 1997 activity season. Data were collected on sunny days between 0700 and 2000 hr (Mean European Time), covering the whole daily activity period of *P. algirus*. In both seasons, we simultaneously collected data about operative temperatures (T_es) and microhabitat selection. Data on operative temperatures were obtained using unpainted hollow copper cylinders (length=5 cm, diameter=1 cm) whose adequacy was experimentally confirmed (Walsberg & Wolf, 1996) following the procedures outlined by Belliure *et al.* (1996). In each season, copper models were distributed at random locations (1-9 m; distance determined by one-digit numbers from a table of random numbers) along the transects employed to measure the lizards' use of microhabitats. Temperatures were recorded at hourly intervals (final sample size of 1,170 T_e records per season); hourly variations in T_e were large enough to ensure that repeated measurements of the same model could be taken as independent data (Díaz & Cabezas-Díaz, 2004). When each model was placed on the ground for the first time, we also recorded its microhabitat location (holm oak

Correspondence: J. A. Díaz, Dpto. de Zoología y Antropología Física (Vertebrados), Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain. *E-mail*: jadiaz@bio.ucm.es

patch, rockrose patch, or open area, depending on the presence or absence of those shrub species within a 1 m-radius circle centered on the model location). The random distribution of models with respect to microhabitats provides the null hypotheses against which lizards' selectivity can be evaluated (Bauwens *et al.*, 1996; Díaz, 1997). Microhabitat use by lizards was determined by noting the location when first seen of all individuals sighted. We also noted the sex and size (adult or subadult; juveniles absent at this time of year) of all lizards seen. Because previous analyses showed that neither microhabitat use, thermoregulatory behaviour, nor body temperature vary significantly with the size or sex of the lizards (Díaz, 1997), all subsequent analyses are based upon pooled samples. In both seasons, the high population densities of *P. algirus*, combined with our effort to visit different areas each sampling day, reduced the probability of resampling individuals.

The selected temperature ranges (T_{sel}) that lizards attempt to maintain in the absence of physical and biotic constraints (Licht *et al.*, 1966) was estimated in the laboratory (Belliure *et al.*, 1996; Díaz & Cabezas-Díaz, 2004) using standard precautions. Thus, food and water were supplied *ad libitum*, the photothermal gradient employed offered a wide range of $T_e s$ (23.4 - 51.7 ºC), and body temperature was measured at different times of day on lizards of both sexes. Selected temperature ranges were estimated for each lizard as the central 80% of all body temperatures measured in the thermogradient (Gvodzik, 2002). The average T_{sel} increased ca. 2 ºC from May (average lower and upper limits of 30.9 and 34.7 ºC, respectively) to July (32.8-36.9 ºC). Following Hertz *et al.* (1993), we evaluated the thermal suitability of microsites with reference to the T_{sel} of the corresponding season, using the mean of the absolute values of deviations of $T_e s$ from T_{sel} ($d_e s$). Previous studies show that this species thermoregulates behaviourally in the field with great efficiency (Díaz, 1997; Díaz & Cabezas-Díaz, 2004).

The selection of microhabitats and its seasonal variation were analysed by means of a log-linear analysis (Heisey, 1985) of the contingency table of lizard and model observations, classified according to season and microhabitat type (Fig. 1). The final model obtained included the interactions season × microhabitat (partial association: G=12.41, df=2, P=0.002) and model or lizard x microhabitat (G=44.37, df=2, P<0.001); this is the simplest model that includes enough interactions to adequately explain the data, so that the observed and expected values do not differ significantly (G=3.404, df=3, P=0.333). The first interaction merely implies that the cover of holm oak shrubs at the sampled locations slightly decreased, and the cover of open areas slightly increased, from May to July. The second interaction is more relevant, because it shows that the number of lizards observed within or near the edge of holm oak shrubs was greater than expected (they chose shrub oaks
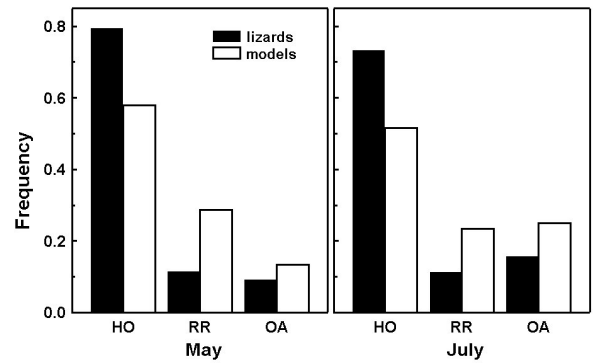

FIG. 1. Microhabitat selection by *P. algirus* in May and July: frequency of use (lizards, black bars) and relative availability (randomly distributed models, white bars) of three different types of microhabitats: holm oak shrubs (HO), rockrose shrubs (RR), and open areas (OA). Sample sizes are 341 in May and 340 in July for lizards, and 150 in May and 120 in July for models.

about 76% of the time, although this microhabitat accounted for about 56% of the available habitat), whereas the opposite was true for rockrose shrubs and open areas. Remarkably, the three-way interaction was not significant (G=0.30, df=2, P=0.862). Thus, lizards were selective in their use of microhabitats, but their preferences did not change seasonally.

We examined the thermoregulatory consequences of microhabitat selection using ANOVA contrasts to compare the $T_e s$ and $d_e s$ of holm oak shrubs (positively selected by lizards; contrast coefficient=2) against those of rockrose shrubs and open areas (avoided by lizards; contrast coefficients=-1). In both seasons, between-microhabitat differences were significant both for T_e (May: $F_{1,1167}$=12.4, P<0.001; July: $F_{1,1167}$=27.73, P<0.001) and d_e (May: $F_{1,1167}$=6.90, P=0.009; July: $F_{1,1167}$=5.14, P=0.023), and holm oak $T_e s$ were always lower than rockrose or open areas $T_e s$ (Table 1). Thus, the thermal suitability (i.e., mean d_e) of the preferred microhabitat was highest in July but not in May, when most $T_e s$ (76 %) were below T_{sel}. However, holm oak patches were actively selected in spring (Fig. 1) despite having the lowest thermal suitability in that season.

We also considered the percentage of operative temperatures in each type of microhabitat that fell below, within, and above T_{sel} (Table 2). These frequencies differed significantly among microhabitats both in May (G=20.1, df=4, P<0.001) and in July (G=31.4, df=4, P<0.001). In May, when most $T_e s$ were too low, the proportion of models with $T_e s$ below T_{sel} was highest in holm oaks and lowest in rockroses. In July, the proportion of $T_e s$ above T_{sel} was highest in rockroses and lowest in holm oaks. However, in both seasons the proportion of models with temperatures within T_{sel} was low in all microhabitats (Table 1). This implies that lizards must be using other mechanisms of temperature regulation (such as the selection of sunlit or shaded patches, or shuttling between sun and shade; Díaz & Cabezas-Díaz, 2004) to thermoregulate effectively within each of the three microhabitat types, and that the contribution of

TABLE 1. Operative temperatures (T_e: mean±SD) and their deviations from the selected range (d_e: mean±SD), both in ºC, of microhabitats classified as holm oak shrubs, rockrose shrubs, or open areas, depending on the presence or absence of those shrub species within a 1 m radius circle centered on the model location. N = sample size.

Microhabitat	May			July		
	T_e	d_e	N	T_e	d_e	N
Holm oak shrubs	24.9±9.2	8.6± 6.0	716	33.3±12.6	7.8±8.0	646
Rockrose shrubs	27.4±10.0	7.6± 6.1	286	37.4±13.0	8.3±8.3	264
Open areas	26.5± 9.2	7.7±5.7	168	37.3±14.5	9.6± 9.0	260

such mechanisms to thermoregulation is much more important than the choice of what microhabitat they use.

Thus, our data produced three important results concerning the thermal consequences of microhabitat selection. First, habitat preferences did not change seasonally despite seasonal variations in the thermal environment. This is in contrast with previous studies that have found temperature-related seasonal shifts in microhabitat use (Huey *et al*., 1977; Christian *et al*., 1983; Christian & Bedford, 1995). Second, the observed pattern of selection was not always consistent with differences among microhabitats in thermal suitability. In both study seasons lizards used holm oak shrubs more often than expected on the basis of their availability, despite the fact that in May holm oaks had lower T_es and larger d_es than rockrose shrubs or open areas. Third, the importance of microhabitat selection as a thermoregulatory mechanism is probably less than previously thought, at least in temperate forests. We can therefore conclude that other aspects of the ecology of lizards should play a larger role than thermoregulation in determining the observed pattern of microhabitat selection.

Social behaviour might be one of these factors. However, social interactions in this species (territorial chases, courtship, mate guarding, copulations, etc.) take place only in spring. Thus, the observed constancy of microhabitat preferences cannot be attributed to the influence of social interactions. Prey availability might also influence microhabitat selection, because there may be more arthropods in the leaf litter beneath holm oaks, and this difference may be persistent between seasons. Another important factor might be predation risk. Mediterranean lizards in general, and *P. algirus* in particular, are important prey for a large number of predators, many of which can be found at the study area. Holm oak shrubs, with their prickled leaves and dense cover, could be selected for providing refuge against predators. Díaz

(1992) showed that the choice of compass directions around holm oaks allowed basking lizards to minimize the escape distance towards the nearest shrub, thus reducing predation risk. It has also been shown that the approach and escape distances of lizards from a deciduous oak forest were larger at the times of year when oaks were unleaved (Martín & López, 1995). Thus, predation risk could explain the preference of lizards for holm oaks and their avoidance of open areas (where dense herb cover might still offer some refuge) and especially of rockrose patches (with practically no cover at the ground level). Obviously, in summer the selection of holm oaks would also allow lizards to reduce the risk of overheating. We therefore suggest that microhabitat preferences, which did not change seasonally in the evergreen forest we studied, could be mainly related to antipredator behaviour rather than to thermal requirements.

REFERENCES

Adolph, S. C. (1990). Influence of behavioral thermoregulation on microhabitat use by two Sceloporus lizards. *Ecology* **71**, 315-327.

Arnold, E. N. (1987). Resource partition among lacertid lizards in southern Europe. *Journal of Zoology* (B) **1**, 739-782.

Bauwens, D., Hertz, P. E. & Castilla, A. M. (1996). Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* **77**, 1818-1830.

TABLE 2. Percentage of operative temperatures in each type of microhabitat that fell below, within, and above the lizards' selected thermal range. Sample sizes are shown in Table 1.

Microhabitat	May			July		
	Below T_{sel}	Within T_{sel}	Above T_{sel}	Below T_{sel}	Within T_{sel}	Above T_{sel}
Holm oak shrubs	79.9	8.0	12.1	56.5	14.2	29.3
Rockrose shrubs	66.8	12.9	20.3	39.8	12.5	47.7
Open areas	74.4	7.7	17.9	46.9	12.7	40.4

Belliure, J., Carrascal, L. M. & Díaz, J. A. (1996). Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. *Ecology* **77**, 1163-1173.

Carrascal, L. M., Díaz, J. A. & Cano, C. (1989). Habitat selection in Iberian *Psammodromus* species along a Mediterranean successional gradient. *Amphibia-Reptilia* **10**, 231-242.

Christian, K. A., Tracy, C. R. & Porter, W. P. (1983). Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* **64**, 463-468.

Christian, K. A. & Bedford, G. S. (1995). Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology* **76**, 124-132.

Díaz, J. A. (1992). Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus*. *Herpetologica* **48**, 293-300.

Díaz, J. A. (1997). Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Functional Ecology* **11**, 79-89.

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

Díaz, J. A. & Cabezas-Díaz, S. (2004). Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Functional Ecology* **18**, 000-000.

Grant, B. W. & Dunham, A. E. (1988). Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* **69**, 167-176.

Gvodzik, L. (2002). To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. *Canadian Journal of Zoology* **80**, 479-492.

Heisey, D. M. (1985). Analyzing selection experiments with log-linear models. *Ecology* **66,** 1744-1748.

Hertz, P. E., Huey, R. B. & Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* **142**, 796-818.

Huey, R. B. (1991). Physiological consequences of habitat selection. *American Naturalist* **137**, S91-S115.

Huey, R. B., Pianka, E. R. & Hoffman, J. A. (1977). Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology* **58**, 1066-1075.

Licht, P., Dawson, W. R., Shoemaker, V. H. & Main, A. R. (1966). Observations on the thermal relations of western Australian lizards. *Copeia* 1966, 97-111.

Martín, J. & López, P. (1995). Influence of habitat structure on the escape tactics of the lizard Psammodromus algirus. *Canadian Journal of Zoology* **73**, 129-132.

Porter, W. P., Mitchell, J. W., Beckman, W. A. & DeWitt, C. B. (1973) Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* **13**, 1-54.

Schauble, C. S. & Grigg, G. C. (1998) Thermal ecology of the Australian agamid *Pogona barbata*. *Oecologia* **114***, 461-470.

Van Damme, R., Bauwens, D. & Verheyen, R. F. (1987). Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. *Herpetologica* **43**, 405-415.

Walsberg, G. E. & Wolf, B. O. (1996). A test of the accuracy of operative temperature thermometers for studies of small ectotherms. *Journal of Thermal Biology* **21**, 275-281.