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

José A. Díaz1, Sara Cabezas-Díaz1,2 and Alfredo Salvador3

1Dpto. de Zoología y Antropología Física (Vertebrados), Facultad de Biología, Universidad Complutense, Madrid, Spain
2Instituto de Investigación en Recursos Cinegéticos (IREC), C.S.I.C., Ciudad Real, Spain
3Dpto. 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 lizard 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*, *Uppa 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_s) 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_s records per season); hourly variations in T_s 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...
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, thergoregulatory 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*sl*) that lizards attempt to maintain in the absence of physical and biotic constraints (Licht et al., 1986) was estimated in the laboratory (Bellure 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*s (23.4 - 51.7 °C), 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 theromgradient (Gvodzik, 2002). The average T*sl* increased ca. 2 °C from May (average lower and upper limits of 30.9 and 34.7 °C, respectively) to July (32.8-36.9 °C). Following Hertz et al. (1993), we evaluated the thermal suitability of microsites with reference to the T*sl* of the corresponding season, using the mean of the absolute values of deviations of T*s from T*sl* (d*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 lizards 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 × microhabitat (G=4437, 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 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*s and d*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* (May: F*1,116* =12.4, P<0.001; July: F*1,116* =27.73, P<0.001) and d* (May: F*1,116* =6.90, P=0.009; July: F*1,116* =5.14, P=0.023), and holm oak T*s were always lower than rockrose or open areas T*s (Table 1). Thus, the thermal suitability (i.e., mean d*) of the preferred microhabitat was highest in July but not in May, when most T*s (76 %) were below T*sl*. 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*sl* (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*s were too low, the proportion of models with T*s below T*sl* was highest in holm oaks and lowest in rockroses. In July, the proportion of T*s above T*sl* was highest in rockroses and lowest in holm oaks. However, in both seasons the proportion of models with temperatures within T*sl* 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...
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 $T_s$ and larger $d_s$ 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.

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REFERENCES


TABLE 1. Operative temperatures ($T_s$: mean±SD) and their deviations from the selected range ($d_s$: mean±SD), both in °C, 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.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>May</th>
<th>July</th>
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<tr>
<td></td>
<td>$T_s$</td>
<td>$d_s$</td>
</tr>
<tr>
<td>Holm oak shrubs</td>
<td>24.9±9.2</td>
<td>8.6±6.0</td>
</tr>
<tr>
<td>Rockrose shrubs</td>
<td>27.4±10.0</td>
<td>7.6±6.1</td>
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<tr>
<td>Open areas</td>
<td>26.5±9.2</td>
<td>7.7±5.7</td>
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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.

<table>
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<tr>
<th>Microhabitat</th>
<th>May</th>
<th>July</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Below $T_{sel}$</td>
<td>Within $T_{sel}$</td>
</tr>
<tr>
<td>Holm oak shrubs</td>
<td>79.9</td>
<td>8.0</td>
</tr>
<tr>
<td>Rockrose shrubs</td>
<td>66.8</td>
<td>12.9</td>
</tr>
<tr>
<td>Open areas</td>
<td>74.4</td>
<td>7.7</td>
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