

## THERMAL ECOLOGY AND ACTIVITY CYCLE OF *PODARCIS MILENSIS* IN A SANDY COASTAL AREA

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### ABSTRACT

Field body temperatures ( $T_b$ s), activity cycles, and preferred body temperatures maintained in a laboratory thermogradient ( $T_{sel}$ ) were studied for *Podarcis milensis*, a small, endemic, lacertid lizard occurring in Milos Archipelago, Greece. *P. milensis* is active all year round; overall maximum activity level is recorded in spring, and minimum activity in winter. Daily activity patterns range from unimodal (winter) to strongly bimodal (summer). Body temperature of adults of the examined population ( $n = 188$ ) averages  $31.3\text{ }^\circ\text{C}$  (range  $21.5\text{--}38.4\text{ }^\circ\text{C}$ , SD  $3.27\text{ }^\circ\text{C}$ ); mean monthly  $T_b$ s are grouped together into "seasons". The species actively thermoregulates, and effectiveness of thermoregulation for the month of August is high, 0.95. The thermoregulatory behavior, microhabitat utilization, and activity cycle of this population are all discussed in the specific context of our study system: the harsh thermal environment of an insular sand dune.

### INTRODUCTION

An ectotherm gains the energy needed to sustain its physiological state and activity through a number of different paths, namely, direct solar radiation, convection, or conduction (Pough et al., 1998). This energy exchange between the organism and its environment provides ectotherms, including lizards, the opportunity to regulate their body temperature quite accurately. Nevertheless, a combination of phylogenetic history, body size, as well as of costs and benefits, defines when, how, and to what extent a lizard will thermoregulate (Huey, 1982, 1987). Accuracy of thermoregulation has been found to be affected by a number of factors such as the presence of competitors (Lister, 1976), predators (Greenberg, 1976), or even by the trophic availability of the environment (Lee, 1980). Thus, it is plausible that a certain species could attain different thermoregulating behaviors in different habitats (Huey, 1974, 1982).

Thermoregulation patterns for lizards that inhabit the Mediterranean basin are more or less known for species found in the Iberian Peninsula (e.g., Castilla and Bauwens,

1991; Martín-Vallejo et al., 1995; Pérez-Quintero, 2001). However, basic data on the thermal requirements of lizards of the eastern Mediterranean, which is characterized by a different monthly rainfall regime, more extensive semiarid climate, and a much drier summer season (Daget, 1977; Nahal, 1981) are scarce and sporadic (e.g., Valakos, 1990; Grbac and Bauwens, 2001; Scheers and Van Damme, 2002).

Here, we report on the results of a one-year study on the thermal biology and the activity cycles of a small endemic *Podarcis* species that is found in the Milos Archipelago in Greece (Milos, Kimolos, Polyaiagos, Antimilos, and islets). Our aim was twofold: (1) to present novel data for a species with a completely unknown thermal biology, and (2) to discuss ways through which these animals cope with the harsh thermal environment of a sand dune.

## MATERIALS AND METHODS

### STUDY ANIMAL

*Podarcis milensis* is a small (adult SVL: 42–70 mm), diurnal, sexually dimorphic lacertid lizard that occupies nearly all the habitats on Milos Island, from the seashore to stone walls and cultivated areas (Arnold, 2002). The species has no real competitors, as it is the only small lacertid in the area. This particular population is characterized by a long breeding season (Adamopoulou and Valakos, 2000).

### STUDY AREA

The study area, which is a sandy back-dune ecosystem situated between Lake Achivadolimni and the beach, offers a habitat low in structural diversity. Fifty-two percent of the study plot (plot dimensions 70 × 30 m) is covered by vegetation that consists mainly of *Juniperus oxycedrus* ssp. *macrocarpa* (62.23% of the vegetation, but only three individuals) and *Coridothymus capitatus* (22.54%, but more than 100 individuals) (Adamopoulou, 1999); other plant species are present in much smaller percentages. Mean *Juniperus* height is 255 cm while mean *Coridothymus* height is 23.58 cm. The rest of the plot is an open area of bare sand. Lizards are found under or near the *C. capitatus* and are rarely seen on bare sand.

### ACTIVITY CYCLE

Field data were collected every month during the course of a year, from sunrise to sunset. The activity cycle was determined by the number of individuals seen to be active along a specific 70-m line transect (in a 4-m-wide belt, 2 m on each side of the survey line) that was walked by the same observer every hour. We defined lizards that were seen either moving or standing still, yet obviously being active, e.g., walking or “patrolling”, as “active”: Upon sighting a lizard, sex and age were recorded (males, females, subadults, and juveniles). For the practiced observer sexes and ages are easily recognized from external characteristics (colors/ patterns/ size of animals).

### FIELD BODY TEMPERATURES ( $T_b, s$ )

Lizards were easily caught using a tenebrionid larva as bait (lizards would grab it and not leave it; right after capture the bait was released from their mouth almost intact). Their body temperature ( $T_b$ ) was taken immediately after capture with a quick-reading thermometer (Cloacal Quick Reader Thermometer, Miller & Co., New York). Shaded air ( $T_a$ , 5 cm above the ground) and substrate ( $T_s$ ) temperatures were taken at the spot where the lizard was caught. Time of day, general climatological conditions, age and sex of the lizards, as well as the type of substrate where they were first seen were all recorded.

### SELECTED BODY TEMPERATURES ( $T_{sel}$ )

Selected body temperatures ( $T_{sel}$ ) were measured in the laboratory on animals collected at the study site.  $T_{sel}$  estimates the temperatures that lizards would try to achieve in the absence of any physical and biotic constraints (Licht et al., 1966). Selected body temperatures were measured in spring, summer, and fall, on a photothermal gradient that was created in a  $100 \times 25$  cm terrarium with light bulbs hanging above. The temperature in the gradient ranged from 18 to 50 °C. In each series of experiments we recorded body temperatures of active lizards, using the same thermometer as that in the field. The selected temperature range was then calculated as the central 50% of all selected temperature recordings in the thermogradient (Hertz et al., 1993).

### EFFECTIVENESS OF THERMOREGULATION ( $E$ )

Data on operative temperatures ( $T_{cs}$ ) (which represent the equilibrium temperature of an inanimate object that approximates the study animal in size, shape, and color, Bakken, 1992) were obtained using 25 hollow copper models in August 1998 (given that during this month temperature constitutes the major restricting factor for lizard activity). Models were placed in the five different microhabitats that characterize the study site: open sun, partial shade, or full shade under the *Coridothymus* shrub, or partial shade or full shade under the *Juniperus* shrub. Model temperatures were recorded every hour; at the same time, lizards were captured and their body temperatures were recorded. Data were then treated as follows:

- a. Measurements taken between 8:00 and 11:00 were used to estimate the effectiveness of thermoregulation, since this is when lizards are principally active in August. Apparently, by sampling  $T_{cs}$  during these hours, our estimates of mean accuracy of thermoregulation ( $d_b$ ) and effectiveness of thermoregulation ( $E$ ) will give us information on temperature regulation during activity times only. Because we sampled  $T_{cs}$  within a set of specific microhabitats, in order to generate the available distribution of  $T_{cs}$  in the habitat we weighted the relative abundance of each microhabitat in the study site using the following, previously calculated, percentages of area of each microhabitat: full sun (bare sand) = 48%, partial shade under *Coridothymus* shrub = 9%, full shade under *Coridothymus* = 2%, partial shade under *Juniperus* shrub = 12%, and full shade under *Juniperus* = 21%.

- b. Measurements taken between 8:00 and 19:00 were used to map the thermal environment of the microhabitats available to the lizards.

The models we used were unpainted copper cylinders closed at both ends except for a small hole allowing insertion of the sensing tip of the thermometer (length = 5 cm, wall thickness = 1 mm, diameter = 1 cm). The thermal responses of lizards and models were compared by measuring the equilibrium temperatures of models and restrained live lizards under an identical heat source. The equilibrium temperatures for lizards and models were highly correlated,  $r = 0.993$ . The resulting regression equation ( $T_c = -1.478 + 1.079 * \text{measured copper temperature}$ ;  $n = 25$ ,  $R^2 = 0.985$ ,  $p < 0.05$ ) was used to correct the copper temperatures measured in the field and thus to more closely approximate the temperature of the lizard itself (namely, account for the effect of differences in solar radiation, absorbance, etc.). The  $T_c$  values presented hereafter were thus computed by entering field measurements (copper temperatures) into the above equation.

We then used the following indices to address the subsequent points on the thermoregulatory ability of the lizard:

1. Thermal quality of a habitat:  $d_e$  = mean of the absolute values of deviations of  $T_c$  from  $T_{sel}$  ( $d_e = [T_c - \text{upper limit of } T_{sel}]$  for  $T_c$  above  $T_{sel}$  and  $d_e = [\text{lower limit of } T_{sel} - T_c]$  for  $T_c$  below  $T_{sel}$ ).
2. Accuracy of thermoregulation:  $d_b$  = same as above but substituting  $T_b$  for  $T_c$ .
3. Effectiveness of thermoregulation (E) for the time period 8:00–11:00 was calculated using the formula (for details, see Hertz et al., 1993):  $E = 1 - (\bar{d}_b/\bar{d}_c)$ . Effectiveness ranges from 0 to 1. E will approach zero when animals don't thermoregulate (they select microhabitats randomly with respect to  $T_c$ ). Conversely, when they carefully thermoregulate, E will approach 1 (Hertz et al., 1993).

The range of  $T_{sel}$  (25–75%) for summer was  $T_{sel \min} = 32.1 \text{ }^\circ\text{C}$ ,  $T_{sel \max} = 35 \text{ }^\circ\text{C}$ .

## RESULTS

### TEMPERATURE REGULATION

Overall data on body temperatures ( $T_b$ s) of *P. milensis* are given in Table 1. Mean body temperature for all the animals was  $31 \text{ }^\circ\text{C}$  while mean body temperature for adults only was  $31.3 \text{ }^\circ\text{C}$ . Body temperatures were significantly higher than both air ( $t$ -test:  $t = 12.49$ ,  $df = 434$ ,  $p < 0.05$ ) and substrate ( $t$ -test:  $t = 7.67$ ,  $df = 434$ ,  $p < 0.05$ ) temperatures.

Body temperatures of adults differed significantly from those of subadults and juveniles (ANOVA,  $F_{3,214} = 5.56$ ,  $p < 0.05$ ). Differences disappeared when ANCOVA was performed with SVL as a covariate. Monthly body temperatures of adults were grouped together (Tukey test) into the following "seasons": winter = December/January (mean  $T_b = 24.9 \text{ }^\circ\text{C}$ , range =  $21.5\text{--}28.4 \text{ }^\circ\text{C}$ ); spring = February–April (mean  $T_b = 30.4 \text{ }^\circ\text{C}$ , range =  $25.2\text{--}36 \text{ }^\circ\text{C}$ ); summer = May–August (mean  $T_b = 33.8 \text{ }^\circ\text{C}$  range =  $30.4\text{--}38.4 \text{ }^\circ\text{C}$ ); fall = September–November (mean  $T_b = 28.3 \text{ }^\circ\text{C}$ , range =  $23.4\text{--}33 \text{ }^\circ\text{C}$ ). Regression of body temperatures ( $T_b$ s) on air temperatures ( $T_a$ ) for the total number of animals on an annual basis was described by the equation:  $T_b = 19.57 + 0.45 * T_a$  ( $r = 0.79$ ,  $R^2 = 0.64$ ,

Table 1

Overall statistical data on body temperatures ( $T_b$ s) of *Podarcis milensis* on Milos Island, according to sex and age

Sex/age	n	Mean value (°C)	Range (°C)	SD
Males	67	31.4	21.5–36.2	3.55
Females	121	31.3	24–38.4	3.12
Adults (total)	188	31.3	21.5–38.4	3.27
Subadults	23	28.7	22–35	4
Juveniles *	7	28.5	26–32	2.56
Total	218	31	21.5–38.4	3.45

\* 5 of the 7 were captured in fall.

$p < 0.05$ ,  $n = 218$ ). The picture was the same when only adults ( $T_b = 19.8 + 0.45 * T_a$ ,  $r = 0.8$ ,  $R^2 = 0.65$ ,  $p < 0.05$ ,  $n = 188$ ) or subadults ( $T_b = 17.69 + 0.48 * T_a$ ,  $r = 0.69$ ,  $R^2 = 0.48$ ,  $p < 0.05$ ,  $n = 30$ ) were examined. Slopes of the regression equations of  $T_b$  vs.  $T_a$  differed both from 0 ( $t = 18.75$ ,  $p < 0.05$ ) and 1 ( $t = -22.91$ ,  $p < 0.05$ ). Significant correlation was also found for  $T_b$  vs.  $T_s$  ( $r = 0.77$ ,  $R^2 = 0.59$ ,  $p < 0.05$ ). Regression equations of  $T_b$  vs.  $T_a$  for the different seasons when adult animals were examined didn't differ between them (ANCOVA,  $F_{3,180} = 1.9$ ,  $p > 0.05$ ).

#### SELECTED BODY TEMPERATURES ( $T_{sel}$ )

Selected body temperatures of adult animals (spring: mean  $T_{sel} = 33.3$  °C, range = 27–37.4 °C,  $n = 194$ ; summer: mean  $T_{sel} = 33.3$  °C, range = 26.6–37.6 °C,  $n = 188$ ; and fall: mean  $T_{sel} = 32.9$  °C, range = 25–37 °C,  $n = 153$ ) did not differ as a function of season (ANOVA,  $F_{2,532} = 1.8$ ,  $p > 0.05$  for all animals,  $F_{2,272} = 0.81$ ,  $p > 0.05$  if we use males only and  $F_{2,257} = 1.91$ ,  $p > 0.05$  for females only), but did differ between the two sexes (mean male  $T_{sel} = 33.4$  °C, mean female  $T_{sel} = 33$  °C,  $t$ -test,  $t = 2.43$ ,  $df = 533$ ,  $p = 0.01$ ). Male body temperature differed from female only during fall (ANOVA,  $F_{1,151} = 4.4$ ,  $p < 0.05$ , mean male  $T_{sel} = 33.2$  °C, mean female  $T_{sel} = 32.5$  °C, but for the other seasons, spring:  $F_{1,192} = 3.2$ , mean male  $T_{sel} = 33.6$  °C, mean female  $T_{sel} = 33.1$  °C, and summer:  $F_{1,186} = 0.8$ , mean male  $T_{sel} = 33.5$  °C, mean female  $T_{sel} = 33.2$  °C, for both seasons  $p > 0.05$ ). The mean value of all temperatures measured in the laboratory (of all seasons) did differ from the mean value of all temperatures measured in the field ( $t$ -test,  $t = 7.28$ ,  $df = 709$ ,  $p < 0.0001$ ). The mean value of  $T_{sel}$  for each season also differed from the mean value of  $T_b$  of the particular season (summer:  $t$ -test,  $t = -2$ ,  $df = 276$ ,  $p < 0.05$ ; spring:  $t = 9.89$ ,  $df = 248$ ,  $p < 0.0001$ ; and fall:  $t = 11.27$ ,  $df = 181$ ,  $p < 0.0001$ ).

#### EFFECTIVENESS OF THERMOREGULATION

Data on the effectiveness of thermoregulation are given in Table 2 and Fig. 1. In order to calculate effectiveness of thermoregulation one needs to know (1) the selected

Table 2

Data on weighted operative ( $T_{e,s}$ ) and body ( $T_{b,s}$ ) temperatures, on deviation of  $T_{e,s}$  from selected body temperatures, namely  $d_{e,s}$ , and deviation of  $T_{b,s}$  from selected body temperatures,  $d_{b,s}$ , for *Podarcis milensis* during August

Variable	n	Mean value (°C)	Range (°C)	SD
$T_{e,s}$	1840	31.2	24.4–39.5	4.38
$d_{e,s}$	1840	3	0–7.7	2.29
$T_{b,s}$	40	33.5	31–36	0.22
$d_{b,s}$	40	0.1	0–1.1	0.5

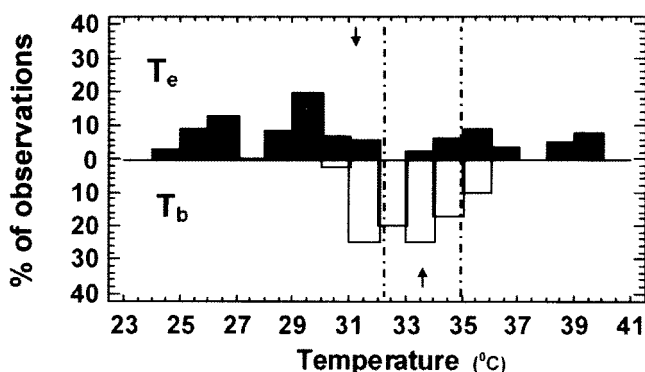


Fig. 1. Distribution of weighted operative ( $T_{e,s}$ ) and body temperatures ( $T_{b,s}$ ) of *Podarcis milensis* during August of 1998 (8:00–11:00). Vertical lines define the 25–75% of the selected body temperatures ( $T_{sel}$ ) measured in the laboratory (32.1–35 °C). Arrowheads indicate mean  $T_{e,s}$  or mean  $T_{b,s}$  (as in Table 2).

body temperatures for the same period,  $T_{sel}$ ; (2) the mean deviations  $d_b$  and  $d_e$  of body and operative temperatures, respectively, from the selected ones,  $T_{sel}$ ; and (3) lizard body temperatures ( $T_b$ ) during the same hours. The range of  $T_{sel}$  (25–75%) for summer was  $T_{sel\ min} = 32.1$  °C,  $T_{sel\ max} = 35$  °C.

As previously mentioned, in order to have the distribution of all available operative temperatures in the habitat we weighted the  $T_{e,s}$  measurements. Then, we calculated the effectiveness of thermoregulation (E):  $E = 1 - (\bar{d}_b/\bar{d}_e) = 1 - 0.15/2.97 = 0.95$ . Accordingly, in August, *P. milensis* individuals thermoregulated with high efficiency, equal to 0.95.

In addition, measurements were used to delineate the thermal environment that lizards “face”, via  $T_{e,s}$ , in the five predominant microhabitats of the site between 8:00 and 11:00 (Fig. 2). During this time, the partial shade of either *Coridothymus* or *Juniperus* offered  $T_{e,s}$  closer to the selected  $T_{sel}$ .

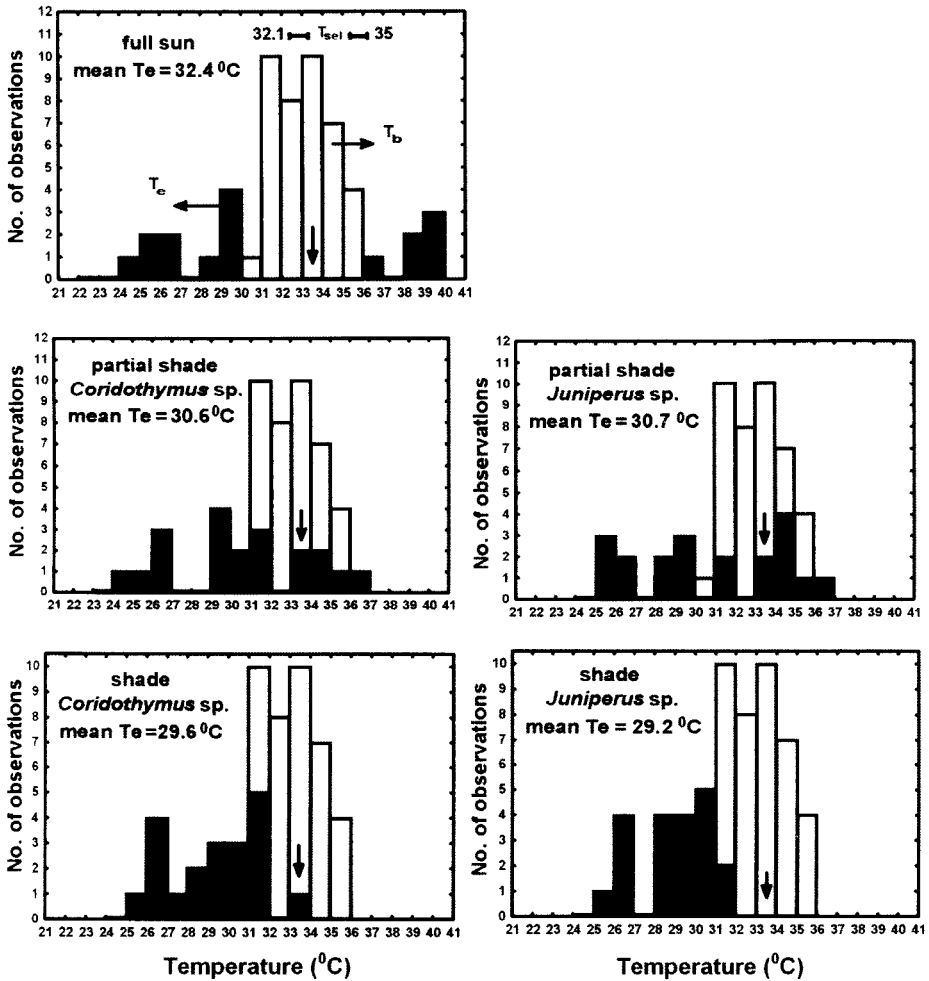


Fig. 2. Distribution of operative ( $T_e$ ) and body temperatures ( $T_b$ ) of *Podarcis milensis* during August of 1998 (8:00–11:00) in each of the five different microhabitats. Data for  $T_b$ s are the same for all microhabitats and are shown in white over the  $T_e$  distribution in the top figure (full sun) while behind  $T_e$ s for all other figures. Arrowheads indicate mean  $T_b$ .

*THERMAL PROPERTIES OF MICROHABITATS*

Maximum temperatures, reaching  $50^\circ\text{C}$ , were attained on bare sand, while minimum temperatures, in full shade, were attained under the shrubs for both plant species (Fig. 3); body temperatures of lizards for the same hours ranged from  $31\text{--}37^\circ\text{C}$ ). Intermediate values were recorded in the partial shade at the periphery of the plants. At the *Juniperus* edges, however, from midday on, size and density of the foliage seemed to create a

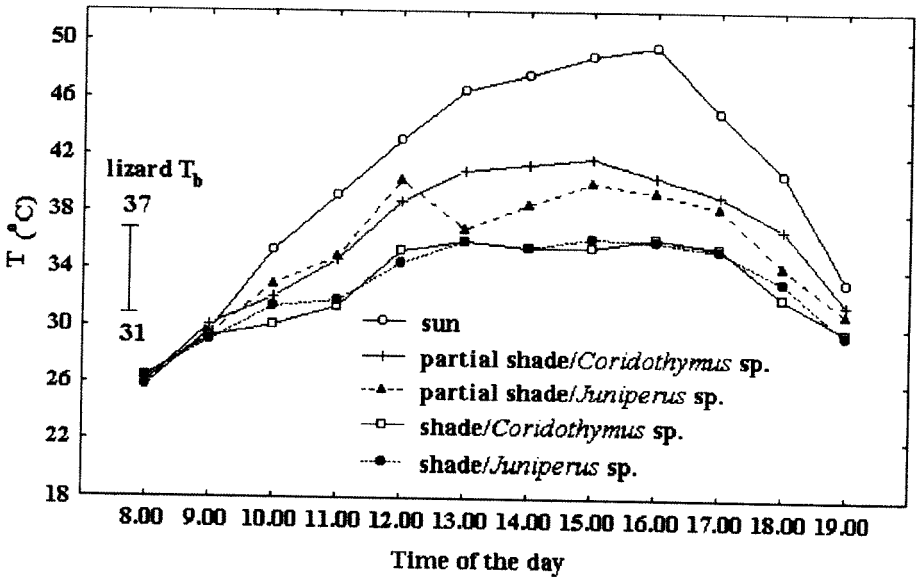


Fig. 3. Daily variation of model temperatures ( $T_e$ ) in five different microhabitats in Milos Island during a day in August. Lizard body temperatures for the same period, on the same day, ranged from 31 to 37 °C.

“cooler” environment than the one recorded for the *Coridothymus* edges. The thermal environment showed up almost identical when measured under the two plants (shade). Note that during a microhabitat recording on a typical summer morning, 84.62% of the lizards was first seen at the *Coridothymus* edges and the rest, 15.38%, equally divided between *Juniperus* edges and Poaceae (Adamopoulou, unpubl. data). On bare sand (full sun) no lizard was recorded.

#### ACTIVITY CYCLES

In total the presence of 238 *P. milensis* was recorded (males = 67, females = 105, subadults and juveniles = 66). Grouping of months into seasons followed the grouping of body temperatures (fall = September–November, 70 animals recorded; winter = December, January, 27 animals recorded; spring = February–April, 81 animals recorded; and summer = May–August, 60 animals recorded).

The population remained active all year round. The daily activity of different sexes and ages for each season is given in Fig. 4. A unimodal pattern that was prevalent in winter gradually, through spring, became strongly bimodal in summer, to return to unimodality again in winter through the transitional state of fall. Summer activity in the afternoon was always much lower than in the morning and almost entirely confined to subadults.



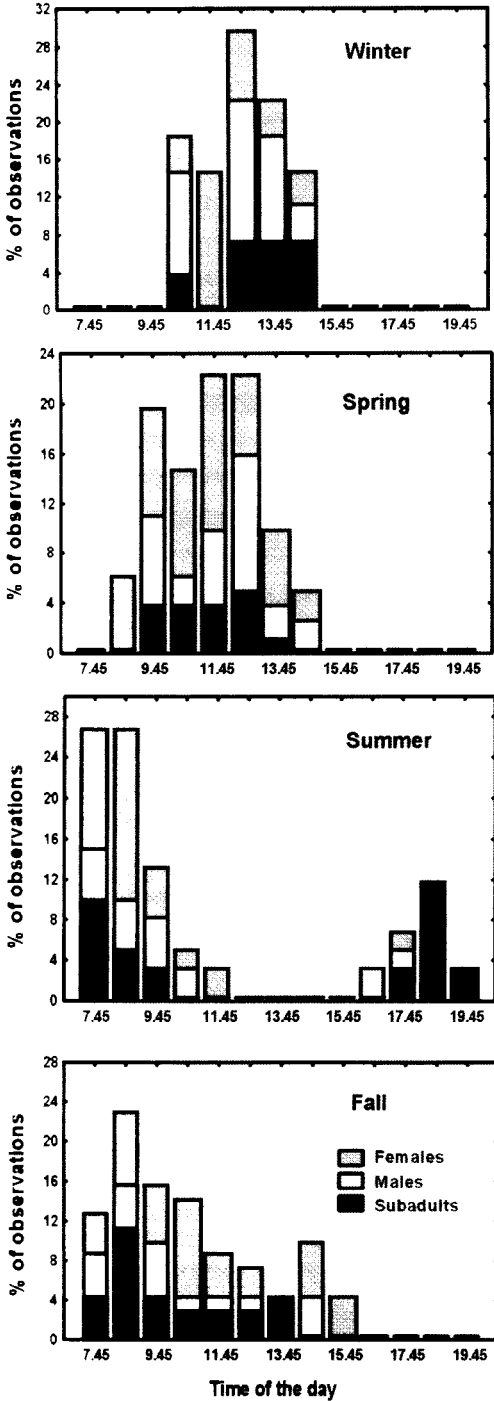


Fig. 4. Diel activity of *Podarcis milensis*, according to sex and age for each season. % of observations: percentage of individuals of each group relative to the total number of individuals of all groups. Sample sizes as follows for each season: Winter: males = 11, females = 9, subadults = 7; spring: males = 26, females = 41, subadults = 14; Summer: males = 14, females = 24, subadults = 22; fall: males = 16, females = 31, subadults = 23.

## DISCUSSION

According to our results *P. milensis* appears to actively thermoregulate to maintain its body temperature, thus following the general pattern of the thermal ecology encountered in the genus *Podarcis* (e.g., Avery, 1982; Arnold, 1987). In addition, body temperatures of active *P. milensis* agree with the general range of temperatures recorded in other *Podarcis* species inhabiting Greece (*P. erhardii* in Naxos Island: mean  $T_b = 29.9$  °C, range = 20.4–41.3 °C for all seasons; Valakos, 1990, *P. peloponnesiaca* in Peloponnisos: mean  $T_b = 31.1$  °C, range = 18.6–38 °C, for March–November, Maragou, 1997).

In August, during activity time (8:00–11:00), lizards experience  $T_b$ s with very high accuracy (most  $T_b$ s are around  $T_{sel}$ ) and clearly thermoregulate (most  $T_b$ s are closer to  $T_{sel}$  than  $T_c$ s are). Additionally, mean  $d_b$  is smaller than mean  $d_c$ , which is a simple indicator that animals behave nonrandomly with respect to the thermal environment. Animals thermoregulate carefully and successfully, as  $E$  is sufficiently high and close to 1 (Hertz et al., 1993). Besides, even in the view of the traditional measure of thermoregulation via regression slopes (Huey and Slatkin, 1976), our data also suggest behavioral thermoregulation.

Lizards, however, especially during spring and fall, don't seem to attain the  $T_{sel}$  measured in the laboratory. We did not find any seasonal differences in  $T_{sel}$  implying acclimatization, as happens in a number of lizards (review in Christian and Bedford, 1995). The observed seasonal shifts in field  $T_b$ s without changes in the selected range may well be a response to environmental seasonality (e.g., Van Damme et al., 1987). Alternatively, the costs and benefits of achieving  $T_{sel}$  may be different between seasons because of the different ecological requirements related to several parameters, such as availability of food resources, intensity of social behavior, seasonally related predation risk, etc. (see, e.g., Schauble and Grigg, 1998; Grbac and Bauwens, 2001).

In the study area, alteration of small bushes with clearings provides lizards with an ideal mosaic of microhabitats. Reptiles, in general, thermoregulate by choosing the "appropriate" habitats and activity times (Huey and Pianka, 1977; Pianka, 1986). Sandy substrates, due to wind (note here that our study site is facing north and lies only 100 meters from the sea) and solar radiation, offer a thermal mosaic that a lizard can take advantage of by moving in accordance with the prevailing microclimatic conditions (Cloudsley-Thompson, 1991). In such areas, microhabitat selection is a determinant factor of lizard activities in general. Indeed, field observations support the above. During activity recording, only a very small percentage of the animals was ever seen basking in bare sand under the full sun (5.8%,  $n = 238$ ), and this was done almost exclusively during midday of winter months. Most of the other times lizards were either moving between shrubs or standing at their edges. In addition, aged males were often seen, early in the morning when air temperature was still low, lying in their sandy burrows (with the head facing outside the hole), presumably augmenting in this way their  $T_b$  using the heat of the burrow. This observation brings us to another speculation. Body temperatures of *P. milensis* seem to depend equally on air and substrate temperatures, which could imply

occasional thigmothermy, namely an alternative tactic that concerns augmentation of body temperature via contact with the substrate. Similar behavior has been noted in other lizard species that inhabit sandy environments; lizards warm up inside the sandy burrows till they reach the “desirable” body temperature, then they come out, thereby diminishing predation risk during morning thermoregulation (e.g., for genus *Acanthodactylus* in Morocco, see Pérez-Mellado, 1992, or for Spain, Carretero and Llorente, 1995).

*P. milensis* remains active all year. This is also recorded from other *Podarcis* species in the Mediterranean (see Pérez-Mellado, 1983, for *P. hispanica*; Foà et al., 1992, for *P. sicula*; Galán, 1995, for *P. bocagei*). Daily activity patterns are more or less typical of diurnal lizards inhabiting warm and/or temperate zones, showing a clearly bimodal pattern in the warm season and a unimodal one during the cool days (Avery, 1978; Adolph and Porter, 1993). Note, however, that during summer, lizards, though seemingly inactive (since we can't record them during transects) in fact remain active near the roots of the shrubs (pers. observations—see below). On the same topic, two other points need to be mentioned. The first is that subadults and juveniles prolong their activity for more hours compared to adults during summer, an observation noted also in other lacertid populations that occur in the Mediterranean (Foà et al., 1992; Carretero and Llorente, 1995). They “broaden” their temporal activity range, devoting perhaps more time than adults to other activities such as hunting for food, an activity essential for good growth rates (Castilla and Bauwens, 1991). Usually the more time juveniles allocate searching for food, the more they will consume daily and thus the faster they will grow (Avery, 1984; Sinervo and Adolph, 1989). The second point concerns female activity. More females than males, in all seasons except winter, are active, while the diel activity pattern of both sexes remains more or less the same. Different reasons, individually or together, could be responsible for this phenomenon. *P. milensis* males show the characteristics of territorial behavior (Adamopoulou, unpubl. data). From the onset of the reproductive period males become less “active” or more “stationary”, possibly due to their engagement in patrolling their territories and/or their females. This, however, does not explain the observed differences in fall. Then again, the reproductive period of this population is particularly extended: sexual activity, depending on the weather conditions, begins in January and finishes in August. During this period, according to their age and physiological state, females lay 1 to 3 eggs more than once (up to 4 times) (Adamopoulou and Valakos, 2000). Each reproductive episode needs energy, and more energy is gained through intensive foraging. It is thus quite possible that females show increased mobility in relation to males because of their augmented energy demands in general. Note, however, that in other lizard populations females reduce activity during the mating season so as to reduce the predation risk associated with being gravid (e.g., Cooper et al., 1990). Last of all, one cannot rule out the possibility that the sex ratio of the population is female biased (Adamopoulou, 1999).

Temperature is a key environmental variable for any ectotherm, and therefore habitat selection, as determined by the microclimates that the animal experiences, is very important for its thermal biology and ultimately for its ecological performance (Huey,

1991). In our context, *P. milensis* could easily face the risk of overheating. In the harsh environment of the sand dune, small tufts of vegetation (in this case *Coridothymus*) are the only available shelter from the sun and wind. In addition to protecting the lizards, they offer the opportunity of continuous activity even at midday, when high air and substrate temperatures prevail (for similar behavior of lacertids, see Ouboter, 1981; Pérez-Mellado, 1992). During August, for example, until 11:00 the partial shade of either *Coridothymus* or *Juniperus* bush is the most favorable microhabitat for the lizards (Fig. 2), while after noon, the full shade of these plants offers them the most hospitable temperatures ( $T_e$ s) (Fig. 3) that enable maintenance of activity. It is therefore no surprise that lizards seem to show no activity between 12:00 and 16:00 during the summer transects (see Fig. 4, summer). Our field observations in fact show that during this time lizards are active (mostly foraging) under the foliage of the bushes (pers. observations).

The significance of vegetation coverage in sandy, arid environments as a principal regulator of arthropod and reptile populations has been emphasized by many investigators (e.g., Cloudsley-Thompson, 1991; Anderson, 1993; Cooper and Whiting, 2000). In this study, shrubs are extremely important for the sustenance of the lizard population since (a) they are critical for thermoregulation purposes; e.g., early in the morning lizards bask under the partial shade of the foliage till they are warm enough to hunt; (b) they provide lizards with a secure environment to avoid enemies while thermoregulating; and (c) bushes represent “food islands”, since arthropods (lizards’ principal food, Adamopoulou and Legakis, 2003) also need to stay away from the high temperatures of the bare sand. To sum up, in the structurally poor environment of the sand dune, *P. milensis* seems to thoroughly exploit the available thermal regime through microhabitat choice, selection of time of activity, and, possibly, thigmothermy.

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