

THE EFFECTS OF POPULATION DENSITY ON TIME BUDGETS OF THE IBERIAN WALL LIZARD (*PODARCIS HISPANICA*)

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ABSTRACT

Individual time budgets under natural conditions and under increased population density conditions were studied in a population of *Podarcis hispanica* in Western Spain. We examined the effects of sex, time of day, and density on daily time budgets. Artificially increasing density indicated that demographic changes do affect time budgets, and that the animals initially respond with short-term compensatory behavior.

We found that: (1) basking was the predominant behavior in time budgets of all lizards; (2) thermoregulatory patterns are affected by high population density; (3) our results confirm the hypothesis that density of population, and not sex, is a primary factor affecting basking behavior, i.e., high population density leads to increased basking; (4) social interaction frequency increased and percentage of time resting decreased at high population density.

INTRODUCTION

Studies of time budgets, that is, the pattern of time allocated to different activities, can reveal much about the way natural selection operates to produce efficient individuals (Enoksson, 1983). Iberian lizards have been the subjects of several studies of temporal patterns of behavior related to circadian activity rhythms (Pough and Busack, 1978; Seva and Escarré, 1980; Pollo and Pérez-Mellado, 1989, 1991; Braña, 1991; Carretero and Llorente, 1995; Galán, 1995). However, the analysis of daily variations in time allocated to different behaviors has received little attention (but see Saint-Girons, 1977; Avery, 1991).

Many factors influence the time-budget regime, including *time of year* (Shine, 1980; Bauwens and Thoen, 1981; Van Damme et al., 1987; Brodie, 1989; Pollo and Pérez-Mellado, 1989; Deslippe et al., 1990; Braña, 1991), *temperature* (Avery, 1976; Busack, 1976; Pough and Busack, 1978), and *food availability* (Stamps and Tanaka, 1981; Waldschmidt, 1983). For example, female reptiles may change their basking behavior between mating and egg-laying. This may involve increasing basking frequency (Shine, 1980) or time spent basking (Schwarzkopf and Shine, 1991). By basking and retaining oviductal eggs, females may accelerate egg development, and thus increase the number of eggs that will hatch successfully (Rose, 1981). Males have also been found to move

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greater distances per unit of time during the breeding season than during the nonbreeding season in both territorial (Stamps, 1983) and non-territorial (Kingsbury, 1989) species.

Through a detailed analysis of time allocated to different behaviors, we can evaluate not only their relative importance in terms of time involved, but also the existing relations between them. Thus, the study of the pattern of time allocated to different activities, under experimental conditions of increased population density, can reveal much about stability of animal behavior in changing density conditions.

In this paper, we present the results of an experimental study of time budgets in the Iberian wall lizard in summer. We examine the effects of sex, time of day, and population density on daily time budgets.

MATERIALS AND METHODS

THE SPECIES

Podarcis hispanica (Squamata, Lacertidae) is a small (adult snout–vent length (SVL) 37–70 mm) wall lizard whose distributional range is limited to the Iberian Peninsula, Southern France, and North Africa (Pérez-Mellado, 1997, 1998). *Podarcis hispanica* is a heliothermic and saxicolous lizard that actively searches for prey. More detailed aspects of its ecology are given by Pérez-Mellado (1998). These lizards are able to regulate their body temperature (T_b) within relatively narrow limits during their active periods (Bauwens et al., 1995; Díaz et al., 1996). Behavioral thermoregulation in *P. hispanica* is mainly characterized by the adoption of basking postures and shuttling between sun and shade (Avery, 1976; Pérez-Mellado, 1983a; Bauwens et al., 1996). The preferred body temperature for our study species is 34.4 °C (based on individuals from the same site) (Bauwens et al., 1995). Preferred body temperatures appear to be very similar among populations of the same species (Van Damme et al., 1989, 1990).

FIELD DESCRIPTION

The study area was situated at the western zone of the Sistema Central of the Iberian Peninsula, at the Sierra de la Peña de Francia (elevation 1074 m), Salamanca, Spain (40°31'43.6"N, 006°07'10.2"W). This area comprised a granite afloration within an open mixed deciduous woodland dominated by oak *Quercus pyrenaica*. We delimited a plot of 1500 m² on the study area. Vegetation in our study site was characterized by oak-bush and other scrub vegetation, such as *Calluna vulgaris*, *Erica arborea*, *Erica australis*, *Erica umbellata*, *Lavandula stoechas*, and *Hallimium alyssoides*. Grassy areas were dominated by *Agrostis castellana*, *Poa bulbosa*, and *Tuberaria guttata*.

MEASUREMENT OF TIME BUDGETS

Seasonal or daily activity of reptile populations has usually been investigated by recording the number of animals active in a population, without considering the types of

behavior they are engaged in. In this sense, specimens sampled in our study were all active.

Time budgets were constructed by focal sampling (Altmann, 1974; Slater, 1978; Martin and Bateson, 1986) of adult males and females, during summer in 1992 (27–28 June and 4, 18, 25 July) and 1993 (26, 30 June and 2 July). The use of short sampling periods eliminates seasonal effects as a source of variation in the data. Moreover, focal sampling was only performed on days with similar weather conditions (sunny days, in the absence of clouds and wind). The focal individual was closely observed and followed for as long as possible, but not less than 5 minutes ($\bar{x}_{1992} = 973.88 \pm 107.18$ s, range = 300–2955 s, $n = 25$; $\bar{x}_{1993} = 502.54 \pm 50.73$ s, range = 300–982 s, $n = 26$). Each behavior category was timed with a stopwatch. For all observations, the time spent in each activity was expressed as a percentage of the total time of that observation.

Time budgets were classified according to time intervals (8:00–10:00/10:00–14:00/14:00–20:00), sex, and sampling period (summer of 1992 and summer of 1993). Immediately after the focal animal sampling, air temperature (shaded bulb, 1 cm above substrate, = T_a) (at the last site that the specimen was observed) was measured to the nearest 0.1 °C with a thermocouple connected to an electronic thermometer.

The following mutually exclusive behavior categories were recognized:

- Basking: dorsoventral flattening of the body and orientation perpendicular to the sun's rays (Avery, 1976; Castilla and Bauwens, 1991; Bauwens et al., 1996). Lizards increase net radiative heat gain through the adoption of a basking posture.
- Moving: locomotor activities.
- Resting: voluntary inactivity periods in a protected and cool retreat. This behavior is more frequent during the central hours of the day to compensate for the higher ambient temperatures (Pough et al., 1998).
- Vigilance: usually alternating bursts of locomotion with pauses during which the lizards are immobile. Lizards frequently adopted the vigilance posture during pauses, keeping their head high, their eyes raised to the maximum possible height above ground level, and only rarely moving their heads from side to side. Vigilance posture enables lizards to scan the environment more effectively, increasing the probability of detection of potential prey, potential predators, and conspecifics (Avery, 1991).
- Social interactions: an extensive repertoire of postural and other displays concerned with courtship, mating, and aggression.

The last two behavior categories were not analyzed in conjunction with the first three behavior categories. Social interactions and vigilance posture were not performed by all animals during focal sampling and, when they were present, comprised a very small percentage of the time budget. Other behaviors were recorded, such as prey capture and prey manipulation, but they were too infrequent to be included in the analyses.

DEMOGRAPHIC ANALYSES

We carried out demographic analyses in this population (Diego-Rasilla, 1999). Demographic analyses require the capture and recapture of individuals. Within each sampling period, captures and recaptures provided data for studying the evolution of demographic parameters with time. Every time an animal was captured or recaptured, we registered its age, sex, body length (SVL in millimeters, accuracy: ± 1 mm), mass (accuracy: ± 0.01 g), and other morphological and behavioral characteristics. Also, we measured body (cloacal = T_b), air (shaded bulb, 1 cm above substrate, = T_a), and substrate (shaded bulb, = T_s) temperatures to the nearest 0.1 °C with a thermocouple connected to an electronic thermometer. These data provided valuable information about social interactions and we used this information to complement data from time budgets.

During the summer of 1993 we carried out a selective manipulation of population density, releasing 63 adult males in a marked experimental plot within the study area. The individuals were captured from neighboring areas approximately 6–7 km from the study plot (Diego-Rasilla, 1999). *Podarcis* time budgets were quantified in the plot prior to the introduction of these individuals (summer 1992) and one week after their introduction (i.e., after 25/06/93). It is important to note that the post-introduction analyses excluded introduced males.

Density was estimated considering an open population model. The basic open population model suitable for this situation is the Jolly–Seber model (Jolly, 1965; Seber, 1965, 1982). This model makes a critical assumption, an equal catchability for marked and unmarked individuals (Pollock et al., 1990). In order to guarantee that all model assumptions had been met by the data we applied the goodness-of-fit test of the Jolly–Seber model (Pollock et al., 1985).

CLIMATIC DATA

The National Institute of Meteorology (Territorial Meteorological Center of Castilla y León) provided climatic data from four weather stations up to 10 km from the study site. These data revealed similar climatological characteristics throughout the study (see Results).

STATISTICAL PROCEDURES

We used standard statistical methods (Pearson correlation coefficient, *t*-test, ANOVA, Scheffé *a posteriori* test, and chi-square test) to evaluate relationships or differences among variables. The standard criterion of statistical significance was $p \leq 0.05$. Proportions were arcsin transformed to achieve normality (Sokal and Rohlf, 1981).

A multivariate ANOVA (MANOVA) was performed on all time budgets (as percentage of time devoted to behavior categories we established arcsin transformed). We previously tested the assumptions associated with this analysis: multivariate normality, homogeneity of covariance matrices, and independence (even though repeated-measures-ANOVA is robust to violations of the first two assumptions). Violations of independence produce a nonnormal distribution of the residuals, which results in invalid *F* ratios. Our residuals showed a normal distribution (Kolmogorov–Smirnov test; $p > 0.05$). In addition, we

conducted Bartlett's test of sphericity which examines the form of the common covariance matrix. Our within-subject factors failed to meet the assumption of sphericity ($\chi^2 = 63.657$, d.f. = 5, $p < 0.001$), justifying the use of the multivariate rather than univariate approach.

RESULTS

CLIMATIC DATA

A two-way ANOVA on mean monthly temperature revealed, as expected, significant differences between seasons ($F_{[3, 40]} = 66.703$, $p < 0.001$), but showed no significant differences between years ($F_{[1, 40]} = 2.151$, $p = 0.150$), nor interaction between these factors ($F_{[3, 40]} = 0.146$, $p = 0.932$). Winter (5.52 ± 0.68 °C, $n = 12$) and autumn (7.81 ± 0.55 °C, $n = 12$) showed no significant differences, and summer (19.72 ± 0.91 °C, $n = 12$) was hotter than spring (13.37 ± 0.86 °C, $n = 12$) (Scheffé *a posteriori* test, $p < 0.05$). Rainfall was higher during the spring of 1993 than during the spring of 1992 (*t*-test; $t = -2.118$, d.f. = 22, $p = 0.046$). There were no significant differences between years in summer (*t*-test; $t = -1.146$, d.f. = 2.942, $p = 0.27$), autumn (*t*-test; $t = -1.693$, d.f. = 3.448, $p = 0.11$), or winter (*t*-test; $t = 2.023$, d.f. = 22, $p = 0.06$) rainfall. Considering exclusively climatic data recorded by the weather stations during our sampling periods, there were no differences between the 1992 (22.50 ± 0.40 °C) and 1993 (21.35 ± 0.25 °C) ambient temperatures (*t*-test; $t = 2.438$, d.f. = 1.678, $p = 0.16$) nor between 1992 and 1993 rainfall (*t*-test; $t = 2.169$, d.f. = 3, $p = 0.12$). These climatic data evidence similar weather conditions during the study, which is important for comparative purposes.

Climatic data recorded in our study site during focal sampling provided valuable information about microclimatic characteristics of the site (e.g., T_a). A three-way ANOVA on T_a measured during focal sampling showed no significant differences between sexes ($F_{[1, 37]} = 0.406$, $p = 0.528$) nor between years ($F_{[1, 37]} = 0.033$, $p = 0.856$), but revealed significant differences between time intervals ($F_{[2, 37]} = 8.019$, $p = 0.001$). Air temperatures were lowest at the onset (8:00–10:00) of the day ($\bar{x} = 24.236 \pm 1.044$ °C, $n = 11$) and highest during the rest of the day ($\bar{x}_{10:00-14:00} = 27.132 \pm 0.658$ °C, $n = 22$; $\bar{x}_{14:00-20:00} = 29.531 \pm 0.519$ °C, $n = 16$) (Scheffé's *a posteriori* test, $p < 0.05$). Differences between air temperatures do not depend on year in conjunction with the time intervals ($F_{[2, 37]} = 0.703$, $p = 0.502$) or sex ($F_{[1, 37]} = 1.845$, $p = 0.183$). There were no interactions between sex and time intervals ($F_{[2, 37]} = 1.297$, $p = 0.286$) and, finally, there was no three-way interaction between these variables ($F_{[2, 37]} = 2.639$, $p = 0.085$). Thus, there were no significant differences between the summer of 1992 (27.383 ± 0.743 °C, $n = 23$) and summer of 1993 (27.162 ± 0.666 °C, $n = 26$) for air temperatures measured during focal sampling.

TIME BUDGETS

We tested the null hypothesis that sex does not affect mean percentage of time devoted to behavior categories. By examining the Wilks' value for this test (0.940) and its associated *F*-ratio and *p* value ($F_{[3, 37]} = 0.781$, $p = 0.512$), we concluded that any

Table 1
Multivariate ANOVA (MANOVA) of percentage of time spent basking, moving, and resting by *Podarcis hispanica* (data arcsin-transformed before analysis)

| Source | Wilks' Lambda | d.f. | F-value | p |
|---------------------------------------|---------------|---------|---------|-------|
| Sex | 0.940 | (3, 37) | 0.781 | 0.512 |
| Sampling period | 0.679 | (3, 37) | 5.832 | 0.002 |
| Time interval | 0.768 | (6, 74) | 1.737 | 0.124 |
| Sex : sampling period | 0.829 | (3, 37) | 2.537 | 0.072 |
| Sex : time interval | 0.808 | (6, 74) | 1.385 | 0.232 |
| Sampling period : time interval | 0.603 | (6, 74) | 3.546 | 0.004 |
| Sex : sampling period : time interval | 0.776 | (6, 74) | 1.666 | 0.141 |

differences between time budgets do not reliably depend on sex (Table 1). Subsequently, we tested the null hypothesis that time budgets do not change across different sampling periods (summer of 1992 and summer of 1993). Since the p value for this hypothesis is small ($F_{[3, 37]} = 5.832, p = 0.002$), we can confidently reject the null hypothesis and conclude that percentage of time devoted to behavior categories we established changed between both summer periods (Table 1). There were no differences between time intervals in lizard time budgets ($F_{[6, 74]} = 1.737, p = 0.124$) (Table 1). Differences between time budgets do not reliably depend on sex in conjunction with sampling period ($F_{[3, 37]} = 2.537, p = 0.072$) or time intervals ($F_{[6, 74]} = 1.385, p = 0.232$) (Table 1). We found a highly significant interaction between sampling period and time ($F_{[6, 74]} = 3.546, p = 0.004$), i.e., changes in time budgets across time intervals depends upon sampling periods (Table 1). Finally, we tested the null hypothesis that time budgets do not change with the interaction of sex by sampling period and time intervals. There was no evidence of such interaction ($F_{[6, 74]} = 1.666, p = 0.141$) (Table 1).

Factors affecting total basking time are given in Fig. 1a. Results revealed that sex had no significant effect on time budgets (see Table 1), and we therefore pooled data from adult males and females in this figure. We can see (Fig. 1a) that percentage of time devoted to basking was very similar between the summer of 1992 and the summer of 1993 at the onset of the day (8:00–10:00). However, percentage of time devoted to basking was higher in the summer of 1993 during the rest of the day (Table 2). Conversely, Fig. 1c shows that percentage of time resting was similar at the onset of the day in both sampling periods, but was lower in the summer of 1993 during the rest of the day (Table 2). Figure 1b also provides evidence of the sampling period by time interval interaction (see Table 1); the significant difference between sampling periods in percentage of time devoted to locomotor activities is remarkably high during the 14:00–20:00 time interval (Table 2). Finally, we can conclude that differences in time budgets between sampling periods were significantly higher during the 14:00–20:00 time interval. Thus, animals in the summer of 1993 spent more time basking than moving or resting, while in the summer of 1992 they balanced the time devoted to these behavior categories. Otherwise, time budgets did not show significant differences between sampling periods during the 8:00–10:00 time interval (Fig. 1, Table 2).

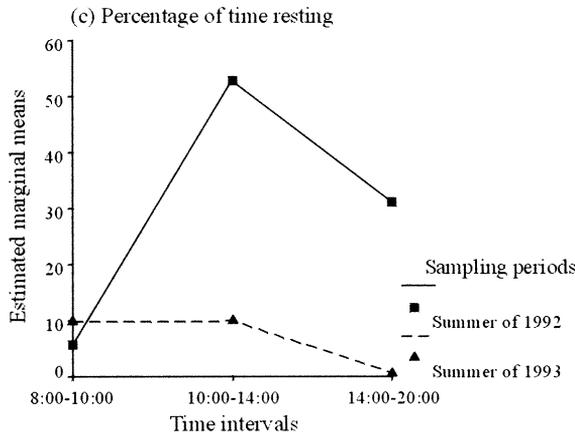
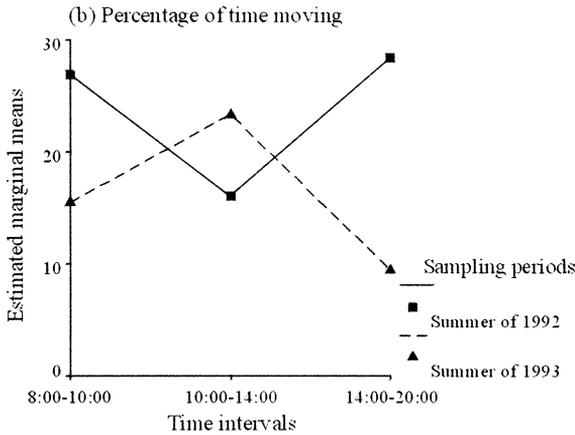
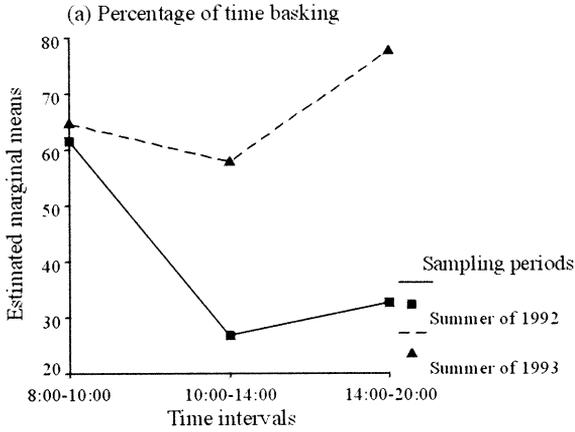


Fig. 1. Estimated marginal means of percentage of time basking (a), moving (b), and resting (c). Since adult males and females had similar time budgets (see Table 1), sexes were combined in this figure.

Table 2

Mean time budgets of animals during the sampling periods. Adult males and females had similar time budgets (see Table 1), then sexes were combined. For description of behavior categories, see Materials and Methods. Time spent in each activity is expressed as percentage of total time. Standard deviations are given in parentheses

| Time intervals | Summer of 1992 | | | | Summer of 1993 | | | | |
|---------------------|----------------|--------------|--------------|--------------|----------------|--------------|-------------|--------------|--------------|
| | 8:00–10:00 | 10:00–14:00 | 14:00–20:00 | 8:00–10:00 | 10:00–14:00 | 14:00–20:00 | 8:00–10:00 | 10:00–14:00 | 14:00–20:00 |
| Basking | 61.54(18.62) | 32.38(23.53) | 33.99(22.77) | 64.62(16.17) | 58.48(26.64) | 68.81(28.56) | 15.48(7.70) | 23.06(15.44) | 13.14(15.63) |
| Moving | 26.90(15.31) | 19.86(16.16) | 28.74(14.40) | 15.48(7.70) | 23.06(15.44) | 13.14(15.63) | 9.84(7.44) | 10.06(12.80) | 0.86(2.27) |
| Resting | 5.58(9.60) | 42.57(41.67) | 29.94(24.43) | 9.84(7.44) | 10.06(12.80) | 0.86(2.27) | | | |
| No. of observations | 8 | 7 | 10 | 4 | 15 | 7 | | | |

Table 3

Percentage of occurrence and frequency of social interactions (agonistic behavior between adult males, courtships, and matings) and other behaviors (basking, moving, resting, vigilance posture, prey capture, and prey manipulation) during sampling periods. Total density of population (No./1500 m²), error estimates (SE), and 95% confidence intervals are also reported

| | Social interaction | | | Other behaviors | | | SE | 95% confidence interval |
|----------------|--------------------|------------|--|-----------------|------------|--|-------|-------------------------|
| | Frequency | Percentage | Density (animals/1500 m ²) | Frequency | Percentage | Density (animals/1500 m ²) | | |
| Summer of 1992 | 4 | 1.61 | 244 | 244 | 98.39 | 83.76 | 20.49 | 43.59–123.92 |
| Summer of 1993 | 48 | 7.38 | 602 | 602 | 92.62 | 236.66 | 66.02 | 107.25–366.06 |

When basking, lizards generally increase their T_b up to the preferred temperature range. The associated time investment in this behavior will be highest when the preferred temperature is far above ambient temperature. We can expect a positive relationship between percentage of time spent basking and the difference between the preferred temperature and ambient temperature, although a relationship with ambient temperature is implicit in this view. To test this prediction, we obtained an index (the difference between mean preferred temperature and air temperature) to measure the disparity between the preferred and air temperatures. Our results confirm the prediction: percentage time spent basking was positively related, during the summer of 1992, to the difference between preferred and air temperature in adult males ($r = 0.921$, $p < 0.001$, $n = 9$) and adult females ($r = 0.775$, $p = 0.001$, $n = 14$), but not during the summer of 1993, in adult males ($r = -0.125$, $p = 0.684$, $n = 13$) or adult females ($r = 0.330$, $p = 0.271$, $n = 13$). These results suggest a change in the thermoregulation patterns of the population at high population density (see Table 3 for population density estimates).

There were no significant differences between adult males ($\bar{x} = 3.96 \pm 1.38\%$, $n = 8$) and females ($\bar{x} = 3.05 \pm 0.68\%$, $n = 15$) in percentage of time spent in vigilance posture during the summer of 1992 (t -test; $t = 0.560$, d.f. = 21, $p = 0.581$). We obtained similar results during the summer of 1993 (t -test; $t = -1.195$, d.f. = 14, $p = 0.252$; $\bar{x}_{\text{adult males}} = 2.99 \pm 1.08\%$, $n = 9$; $\bar{x}_{\text{adult females}} = 2.45 \pm 1.15\%$, $n = 7$).

Only thirteen animals maintained social interaction during our focal sampling. Social interaction comprised $1.24 \pm 0.56\%$ of the time budgets of these animals ($n = 6$) during the summer of 1992 and $2.06 \pm 0.75\%$ of time budgets ($n = 7$) during the summer of 1993. However, within each sampling period, captures and recaptures provided data about lizard behavior (see Materials and Methods). These data revealed a significant difference in social interaction frequency between sampling periods (Table 3) (chi-square test; $\chi^2 = 9.929$, d.f. = 1, $p < 0.01$). Social interaction was more frequent in the summer of 1993, at high population density (Table 3).

Finally, we analyzed behavior rates (i.e., the frequency of the different behavior categories per hour). For the two sampling periods, the frequency of different behaviors is independent of total time of time budgets (Pearson correlation coefficient; $p > 0.05$ in all cases). The frequency of social interaction per hour was significantly higher during the summer of 1993 ($5.13 \pm 1.75 \text{ h}^{-1}$, $n = 7$) than during the summer of 1992 ($1.10 \pm 0.42 \text{ h}^{-1}$, $n = 6$) (t -test; $t = -4.880$, d.f. = 11, $p < 0.001$). Two-way analyses of variance (ANOVA) showed that vigilance posture rates ($\bar{x}_{\text{summer of 1992}} = 19.23 \pm 2.85 \text{ h}^{-1}$, $n = 23$; $\bar{x}_{\text{summer of 1993}} = 16.77 \pm 3.45 \text{ h}^{-1}$, $n = 16$) and resting rates ($\bar{x}_{\text{summer of 1992}} = 8.63 \pm 1.80 \text{ h}^{-1}$, $n = 25$; $\bar{x}_{\text{summer of 1993}} = 10.10 \pm 1.58 \text{ h}^{-1}$, $n = 16$) did not differ significantly between sampling periods ($F_{[1, 33]} = 2.058$, $p = 0.161$; $F_{[1, 35]} = 0.054$, $p = 0.817$, respectively), nor between time intervals ($F_{[2, 33]} = 0.760$, $p = 0.476$; $F_{[2, 35]} = 0.215$, $p = 0.807$, respectively). There was no interaction between factors ($F_{[2, 33]} = 0.905$, $p = 0.414$; $F_{[2, 41]} = 1.650$, $p = 0.207$, respectively). A two-way ANOVA on basking frequency showed no significant differences between time intervals ($F_{[2, 45]} = 0.963$, $p = 0.389$), but revealed significant differences

between sampling periods ($F_{[1, 45]} = 8.735$, $p = 0.005$; $\bar{x}_{\text{summer of 1992}} = 26.52 \pm 3.08 \text{ h}^{-1}$, $n = 25$; $\bar{x}_{\text{summer of 1993}} = 42.84 \pm 4.67 \text{ h}^{-1}$, $n = 26$). There was no interaction detected between these factors ($F_{[2, 45]} = 0.965$, $p = 0.389$). Animals showed higher moving frequency during the summer of 1993 ($89.41 \pm 14.76 \text{ h}^{-1}$, $n = 26$) than during the summer of 1992 ($47.40 \pm 4.86 \text{ h}^{-1}$, $n = 25$) ($F_{[1, 41]} = 4.384$, $p = 0.043$), but there were no differences between time intervals ($F_{[2, 41]} = 0.201$, $p = 0.818$), or interaction between these factors ($F_{[2, 41]} = 0.532$, $p = 0.591$).

DISCUSSION

The problem with this type of field control is that it was carried out at different times, so control-experimental differences could also be due to time-related changes. Changes in environmental conditions are the most likely causes of differing time budgets/thermoregulatory patterns between years. Obviously, we assume that time budgets of lizards are highly sensitive to differences in weather conditions. However, we believe that this major objection has been circumvented by (1) focal sampling exclusively on sunny days, in the absence of clouds and wind, and by (2) obtaining climatic data from weather stations near the study site and recording climatic data during focal sampling. Analysis of these climatic data showed no differences in weather conditions between summers. Thus, we can assume that there was no environmental change between the two sampling periods. In addition, physical structure of the environment determines microclimatic factors (e.g., temperature, presence of shade or sunlight, wind) (Heatwole, 1977) which can introduce additional artifactual differences when a different area is used as a control. Different environments may cause differences in time budgets through changes of physiological traits in response to variations in an environmental factor (e.g., ambient temperature) (Heatwole, 1977; Díaz et al., 1996). Although climatic data recorded in weather stations do not measure the operative temperatures in lizard habitats, they do provide reliable estimates of the relative differences among different sampling periods (Bakken, 1992; Díaz et al., 1996).

Temperature-regulating behaviors have a direct effect on how well an animal can carry out essential activities (Pough et al., 1998). Behavioral thermoregulation is the main mechanism regulating T_b in reptiles (Huey, 1982; Stevenson, 1985), although physiological control may be important (Bartholomew, 1982). Thus, *P. hispanica* spend a considerable proportion of their daily time budget basking in an attempt to achieve their preferred temperature range (Bauwens et al., 1996). When the preferred temperature is far above ambient temperature, lizards must spend a high proportion of their daily time budget basking (Díaz et al., 1996). Percentage of time basking in adult males and females was positively related to disparity between the preferred and air temperatures during the summer of 1992, but not in 1993. During the summer of 1992, the animals spent a lot of time basking at low air temperatures, but very little at high temperatures, which is a conspicuous indication of behavior thermoregulation (Huey et al., 1977; Waldschmidt, 1980). The fact that (1) there were no differences between weather

conditions (data reported by The National Institute of Meteorology) not only during sampling periods, but during the whole of 1992 and 1993, (2) that there were no differences between air temperatures measured during focal sampling in 1992 and 1993, and (3) that there is no relationship between percentage of time basking and disparity between the preferred and air temperatures during the summer of 1993 suggests that thermoregulatory patterns during the summer of 1993 were affected by artificially increased population density because lizards should minimize the time spent on heating so as to prolong the time that T_b can be maintained at, or near, the preferred range (Díaz et al., 1996).

The activities of a lizard are limited in space and time by its thermoregulatory requirements (Pianka, 1969; Avery, 1978; Pough et al., 1998). The need to thermoregulate determines the total activity period, time spent moving, resting and basking, and the food consumption of *P. hispanica*. Similar results have been described in other species of lacertids (Avery, 1976; Márquez et al., 1997; Pérez-Mellado and Romero-Beviá, 1999) and iguanids (Huey and Slatkin, 1976; Hertz and Huey, 1981). Thus, during the early morning in both summers, lizards must be in the sun, and basking constituted about 63% of the time budget. During the middle of the day the environment is so hot that they must remain in the shade, as happened during the summer of 1992. However, despite the fact that there was no difference between air temperature measured during the summer of 1992 and the summer of 1993, lizards spent a high proportion of their time budget warming during the central hours of the day in the summer of 1993. Thus, during this period lizards spent similar percentages of time budget resting in the shade during the early morning and the middle of the day.

Our results support the hypothesis that density of population, and not sex, is a primary factor affecting basking behavior, since there were no differences in weather conditions between sampling periods. High population density leads to increased percentage of time basking.

During the summer of 1992, the percentage of time devoted to the different behavior categories (basking, moving, and resting) was similar at the end of the day (14:00–20:00), which may indicate an absence of strong thermal constraints (Díaz, 1991; Bauwens et al., 1996). Focal animal observations revealed that in the afternoon lizards could potentially reduce the time and cost of T_b regulation (Huey, 1974; Huey and Slatkin, 1976). Hence, they could increase time available for other activities (e.g., foraging, social interaction) (Bauwens et al., 1996). This evening phase coincides with the main hunting behavior during the day (Pérez-Mellado, 1983b), therefore moving is a relevant behavior during this time interval. Once again, lizards showed a different pattern behavior during 1993 and they remained basking most of the time, spending little time moving.

Increased time spent basking, induced by high density conditions, would dramatically curtail the time available for other activities (Avery, 1976). It allows less time for feeding and moving, and so can reduce the probability of prey capture (Avery, 1982). In this sense, Avery (1971) estimated that, in *Lacerta vivipara*, on days in which there was some sunshine, but also variable amounts of cloud cover, food consumption was around

60% of that on sunny days, in which there were long periods of uninterrupted sunshine. This is a consequence of the reduction in time available for feeding (Avery, 1976). In addition, prey capture efficiency will be increased with body temperature (Avery, 1982; Van Damme et al., 1991).

In conclusion, artificially increasing density indicated that demographic changes do affect time budgets. The frequency of social interaction, such as agonistic behaviors between adult males, courtships, and matings increased significantly as a consequence of increasing density. These behaviors had a negative effect on basking behavior, interrupting it and making it very difficult, in terms of time investment, to achieve their preferred body temperatures, increasing the total basking time necessary to maintain preferred body temperature (Ouboter, 1981; Edsman, 1990). Therefore, the high total basking time was achieved by numerous short periods of basking, i.e., high basking frequency. Hence, when faced with an environmental change, the animals should initially respond with short-term compensatory behavior (Díaz et al., 1996). Due to the body temperature dependence of ecologically important traits (Huey and Stevenson, 1979; Huey and Bennet, 1987; Huey and Kingsolver, 1989; Pough et al., 1998), the change in activity patterns could also reduce their probability of survival (Diego-Rasilla, in press).

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