Comparative thermal ecology of the sympatric lizards
Podarcis tiliguerta and *Podarcis sicula*

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ABSTRACT

We studied field body temperatures (T_b) in sympatric populations of the Mediterranean lizard species *Podarcis tiliguerta* and *P. sicula* Both species have identical activity rhythms, experience highly similar ambient conditions and maintain body temperatures around identical mean values However, *P sicula* regulates its T_b more precisely than *P. tiliguerta*, as indicated by the lower value of the regression slope of T_b on air and substrate temperatures, the lower variance in T_b s, and the absence of diurnal variation in T_b s in the former species. Available data of selected T_b s suggest that both species have highly similar thermal preferences Both species differ in microhabitat use: *P tiliguerta* was almost exclusively seen on rocks and stone-walls, often at perch heights > 50 cm and at short distances to patches of shade; *P sicula* basked on rocky surfaces but foraged on ground in open meadows, often at distances of > 5 m to deep shade. Microhabitat occupation did not seem to influence thermoregulatory precision in the latter species We suggest some hypotheses that may explain the observed interspecific difference in precision of thermoregulation.

KEYWORDS: thermoregulation, *Podarcis tiliguerta*, *Podarcis sicula*

RÉSUMÉ

On a étudié la température corporelle (T_b) au champ de deux populations sympatriques de *Podarcis tiliguerta* et *P. sicula*, espèces de lézards méditerranéennes Ces deux espèces ont des rythmes d'activité identiques, connaissent des conditions ambiantes très similaires et maintiennent leur température corporelle à des valeurs moyennes identiques Néanmoins, *P. sicula* régule sa T_b plus précisément que *P. tiliguerta*, comme l'indiquent les valeurs plus basses de la courbe de régression de T_b sur les températures de l'air et du substrat, la variance moins élevée de T_b s et l'absence de variation diurne de T_b s chez la première espèce. Les données disponibles sur une T_b s donnée suggèrent que les deux espèces ont des préférences thermiques très similaires Les deux espèces diffèrent quant à l'utilisation du microhabitat : *P. tiliguerta* a été vue presque exclusivement sur des rochers et des murs de pierre, souvent à des hauteurs supérieures à 50 cm et à courte distance de taches d'ombre; *P. sicula* se chauffe sur des surfaces rocheuses mais chasse sur le sol dans des prairies ouvertes, souvent à des distances de plus de 5 m de la pleine ombre L'occupation du microhabitat ne semble pas influer sur la précision de la thermorégulation chez cette dernière espèce Nous proposons quelques hypothèses qui pourraient expliquer la différence interspécifique observée dans la précision de la thermorégulation

INTRODUCTION

The thermal characteristics of the environment have a pronounced impact on the ecology and behaviour of ectotherms. Most reptiles attempt to buffer changes in ambient heat loads by behavioural adjustments in order to keep their body temperatures between lower and upper threshold temperatures (BERK & HEATH, 1975; BARBER & CRAWFORD, 1977; HUEY, 1982; VAN BERKUM *et al*, 1986). The importance of maintaining a constant body temperature relies on its direct influence on physiological and whole-animal performances (HUEY & STEVENSON, 1979; HUEY, 1982). Recent theoretical reflections (MAGNUSON *et al*, 1979; TRACY & CHRISTIAN, 1986) have led to consider the thermal environment, which translates to body temperature, as an important resource that can be exploited in the same way as the space or food components of a reptile's niche.

Lizards from the family Lacertidae are an important component of the European reptile fauna. Most species of this familly are highly similar in basic ecological characteristics such as diet composition, foraging behaviour, activity times and thermoregulatory behaviour (ARNOLD, 1987). Differential habitat utilisation is the main factor separating the niches of the distinct species; this is especially evident when two or more lizards occur sympatrically (ARNOLD, 1987). Lacertid lizards hence seem well suited for studying the possible influence of exploitation of the thermal environment and of interspecific interactions on body temperatures achieved in the field. Published studies indicate that the between-species variation in activity body temperatures is rather small (see ARNOLD, 1987 and references therein). However, with the exception of AVERY (1978) and ARNOLD (1987), no comparative studies of the thermal relations in sympatric species are available.

We here report a study of body temperatures, thermoregulatory behaviour and aspects of habitat utilisation in the lizards *Podarcis tiliguerta* and *P. sicula* that are sympatric in parts of the Mediterranean island of Corsica. Our main aim is to examine to what extent both species differ in body temperatures maintained during activity in the field. Interpretation of our results proved to be difficult in the absence of information on the ecological relations between both lizards. Our conclusions are therefore mainly directed towards suggesting working hypotheses for future studies.

MATERIAL AND METHODS

ANIMALS

Podarcis tiliguerta is a small (adult body size: 45-65 mm; mass: 2-6 g) wall lizard that is endemic to the Mediterranean islands of Corsica and Sardinia and some adjacent smaller islets. *P. tiliguerta* is the most ubiquitous lizard on Corsica, where dense populations can be found in a wide range of habitats (rockworks, stony walls, ruins, roadsides, maquis, wood fringes and clearings) from sea-level up to more than 1,800 m altitude.

Podarcis sicula is a robust wall lizard (adult body size: 60-80 mm; mass: 5-10 g) with a broader distribution: it inhabits Italy, the east Adriatic coastline, European Turkey and islands in the Tyrrhenian Sea. Two subspecies occur on Corsica: *P. sicula cetti* in the extreme south (near Bonifacio) and *P. sicula campestris* in the northern, western and eastern parts of the island. Both forms seem primarily restricted

to coastal areas up to an altitude of 400 m, where they can be found in meadows, roadsides, woodfringes, maquis, cultivated lands and city parks

Both species are diurnal, shuttling heliotherms that bask to achieve body temperatures that are well above ambient. Like most other European lacertids (see ARNOLD, 1987), they actively search for arthropods that form the bulk of their diet.

FIELD STUDY

We studied *P. tiliguerta* and *P. sicula campestris* at a study area situated ca 5 km SW of Calvi (42° 32′ N, 8° 43′ E; département Haute-Corse, Corsica, France), at elevations 0-70 m, between the shoreline and the coastal road between Calvi and Galeria. This site is an unkempt meadow with small rocky outcrops, stone piles, stone walls and several small ruins standing scattered over the area. Vegetation consists mainly of grasses and small herbal plants, some shrubs (*Rubus sp.*, *Cistus criticus*, *C. monspeliensis*) and trees (*Pistacia lentiscus, Quercus ilex*). The study area is surrounded by typical Corsican maquis. Both *Podarcis* share this habitat with the secretive little lizard *Algyroides fitzingeri*, two geckos (*Tarentola mauritanica* and *Hemidactylus turcicus*) and the predatory snake *Coluber viridiflavus* which was frequently observed here.

We visited the site from 7-16 and 27-28 May 1988. Data were collected between 7 hrs. 30-18 hrs. 00 (Mean European Time), covering the entire daily activity period of the lizards at that time of the year. We randomly walked the study area and captured active adult lizards (*P. tiliguerta*: body length > 45 mm; *P. sicula*: body length > 60 mm) with a noose. We immediately measured body (cloacal, $= T_b$), air (shaded bulb, ± 3 cm above substrate, $= T_a$) and substrate temperatures (shaded bulb, $= T_s$) to the nearest 0.1°C with a thermocouple connected to a quick-reading electronic thermometer (DGT Digital thermometer). We also noted time of day, sex, weather conditions (sunny, cloudy/variable — respectively ≥ 5 or < 5 min of continuous sunshine before observation), amount of solar radiation at the spot of first sighting (full sun, sun filtered by vegetation, shade, overcast), whether or not the lizard was basking, and microhabitat characteristics. Microhabitats were characterized by three parameters: habitat type (stone walls, isolated rocks, meadow, bushes), height above ground (< 25 cm, 25-50 cm, 50-100 cm, > 100 cm), and transit distance to the nearest spot of deep shade (< 0.5 m, 0.5-1 m, 1-2 m, 2-5 m, > 5 m).

SELECTED BODY TEMPERATURES

Selected (or "preferred") body temperatures of 15 male *P. tiliguerta* that had been transported to our laboratory, were measured in a laboratory thermogradient (see VAN DAMME *et al.*, 1989 for details)

Estimates of selected temperatures of *P. sicula* were obtained from laboratory temperature recordings reported by AVERY (1978)

RESULTS

THERMAL PREFERENCES

Selected body temperatures of adult male *P. tiliguerta* in a laboratory thermogradient averaged 35.47°C ($s = 1.27$, range: 33.0-38.2, $n = 40$).

Body temperatures recorded in the laboratory for *P. sicula campestris* from Tuscany (Italy) by AVERY (1978) averaged 34.79°C (range: 31.2-38.8, $n = 27$). As the latter author did not report the distribution of the temperature readings, we cannot assess the statistical difference between both data sets.

TEMPERATURE RELATIONS AND ACTIVITY RHYTHMS

We found no differences in body temperatures between sexes in either of the species (ANOVA, $P>0.50$) and therefore lumped data in subsequent analyses

Availability of direct sunshine influences T_b of both lizards: T_b s recorded during sunny periods were significantly higher than those measured under cloudy or variable conditions (t-tests, both $P<0.05$; table I). Further analyses are therefore based on sunny weather data only

Statistics of body and ambient temperatures are shown in table I. Mean body, air and substrate temperatures did not differ between both species. However, the variance of T_b was significantly higher in *P. tiliguerta*, whereas the variances of T_a and T_s did not differ between species (table I).

The slope of the regression line relating T_b on T_a, an estimate of the precision of thermoregulation (HUEY & SLATKIN, 1976), was significantly different from zero in *P. tiliguerta* ($P<0.01$) *but not in P. sicula* ($P>0.60$), and is significantly steeper
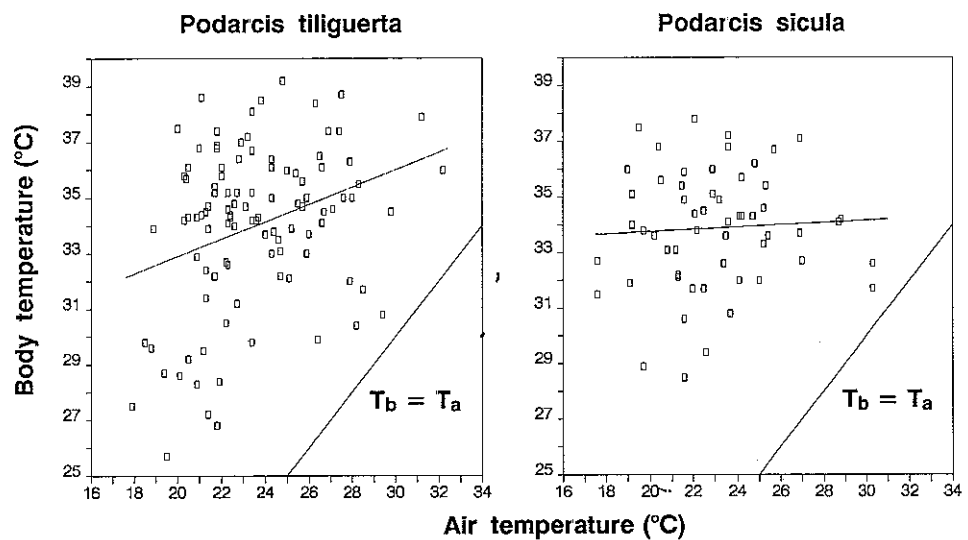

FIG. 1 — Relations between body (T_b) and air (T_a) temperatures in *P. tiliguerta* and *P. sicula* Equations of regression lines are: *P. tiliguerta* $T_b=0.310\ T_a+26.70$; *P. sicula* $T_b=0.039\ T_a+32.98$. Data for periods of uninterrupted sunshine only

in the former species ($F=3.378$, $P=0.05$; fig. 1). Identical results were obtained for the relation between T_b and T_s. These data indicate that T_b s of *P. tiliguerta* are more closely coupled to ambient temperatures than are T_b s of *P. sicula*, and suggest that the latter species exhibits a higher precision of thermoregulation.

The number of *P. sicula* observed per person hour was highest during the early morning and late afternoon hours, whereas activity of *P. tiliguerta* seemed to peak during the afternoon. These apparent differences in activity rhythms are, however, not significant ($G=14.860$, 9 df, $P>0.05$).

Hourly mean T_b exhibited significant diurnal variation in *P. tiliguerta* ($F = 2.320$, $P = 0.02$; fig. 2). In *P. sicula*, we found no differences among hourly
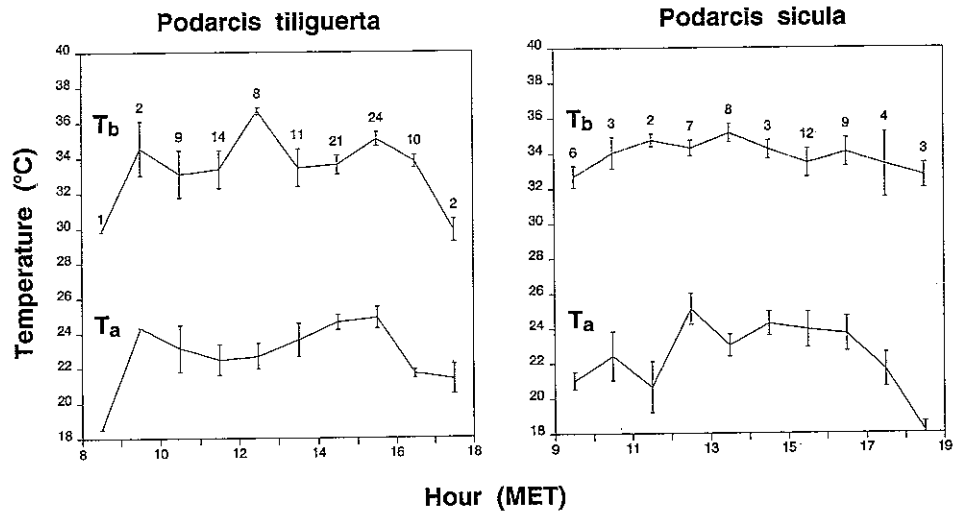

FIG. 2 — Diel variation in body (T_b) and air (T_a) temperatures in *P. tiliguerta* and *P. sicula*. Shown are hourly means (± 1 SE) and sample sizes. Data for periods of uninterrupted sunshine only.

mean T_b s ($F = 0.771$, $P > 0.60$; fig. 2) despite obvious variation in T_a ($F = 2.832$, $P < 0.01$) and T_s ($F = 3.000$, $P < 0.01$).

When weather conditions changed from sunny to cloudy, *P. tiliguerta* exposed themselves for some time on rocky substrates in a basking-like posture, whereas *P. sicula* retreated rapidly. The proportion of *P. tiliguerta* observed during cloudy weather (31/133) was significantly higher than in *P. sicula* (5/62) ($G = 6.172$, $P = 0.01$).

The proportion of animals seen basking showed a typical diurnal variation in both species, with more lizards basking in the morning and afternoon hours. We found no difference between species in the relative number of basking lizards (*P. tiliguerta*: 47/102, *P. sicula*: 19/56, $G = 2.196$, $P > 0.10$).

MICROHABITAT USE

Although both species shared the same habitat, some clear-cut differences in microhabitat use were evident ($G = 73.469$, 3 df, $P < 0.001$; table II). At our study area, *P. tiliguerta* was largely a climbing species that was almost exclusively seen on rocks and man-made stone-walls and rarely descended to the surrounding vegetation. *P. sicula* was seen both on rocky surfaces and in open meadows (table II). Most (13/19) *P. sicula* that basked were seen on rocky substrates, whereas the majority of the non-basking lizards (30/37) were in vegetated habitats ($G = 12.957$, $P < 0.001$). This lizard seems to use rocks and stone walls as basking sites, while it forages mainly on ground among grassy vegetation. When disturbed,

TABLE I — Statistics (mean±1 SD, range in parentheses) of body (T_b), air (T_a) and substrate (T_s) temperatures and slopes (±1 SE) for the regressions of body versus air and of body versus substrate temperatures for P tiliguerta and P sicula recorded under cloudy and sunny weather

	P tiliguerta	P. sicula	P variances	P means
Cloudy				
T_b	30.20±3.06	30.85±0.79	<0 001	>0.70
	(23 6-36.8)	(30 2-31 8)		
N	31	5		
Sunny				
T_b	34.02±2 90	33.89±2 12	<0 01	>0 70
	(25.7-39 2)	(28 5-37 8)		
T_a	23.58±2 89	22.96±2 89	>0 40	>0 20
	(17 9-32 2)	(17 6-30 3)		
T_s	27.17±3 52	26 96±3 39	>0 40	>0 70
	(18.7-37 3)	(21.3-37.2)		
Slope T_b-T_a	0 310±0 095	0 039±0 099		=0.05
Slope T_b-T_s	0 405±0 072	0.117±0 082		<0.02
N	102	57		

TABLE II — Number of individuals (percentage in parentheses) of P. tiliguerta and P sicula observed in different microhabitats, perch height (cm) classes and transit distances (m) to nearest spot of deep shade. Data for periods of uninterrupted sunshine only

	Microhabitat			
	Rock	Wall	Meadow	Bush
P tiliguerta	64 (63)	34 (33)	2 (2)	2 (2)
P sicula	17 (30)	4 (7)	34 (60)	2 (2)

	Perch height			
	<25	25-50	50-100	>100 cm
P tiliguerta	32 (35)	21 (23)	28 (31)	10 (11)
P. sicula	43 (80)	5 (9)	4 (7)	2 (4)

	Distance to shadow				
	<0.5	0.5-1	1-2	2-5	>5 m
P tiliguerta	89 (87)	3 (3)	4 (4)	3 (3)	3 (3)
P sicula	22 (39)	0 (0)	0 (0)	6 (11)	29 (51)

ground-dwelling P. sicula may flee over distances of several meters to stone piles or take refuge in holes at ground-level

As a consequence of the differences in microhabitat use, the height distribution also differs among both species ($G = 27.919$, 3 df, $P < 0.001$): while most P. sicula were seen on or near the ground, a large proportion of P tiliguerta was active on more elevated places (table II).

The microhabitats used by both species also differed in the availability of shadow: the shortest transit distance from a lizard in full sun to a patch of deep

shadow was significantly larger in *P. sicula* than in *P. tiliguerta* ($G = 59.555$, 4 df, $P < 0.001$; table II).

In order to examine whether differences in microhabitat utilisation influence temperature relations, we grouped the distinct microhabitats into two categories: habitats with stony substrates ("rock" + "wall") where lizards were generally at some height above ground, and vegetated microhabitats ("meadow" + "bush") where lizards were encountered at ground level. Neither mean values or variances of air and substrate temperatures differed between the two habitat categories (table III). Body temperatures of both lizard species did not differ with respect to microhabitat, although the variance in T_b s of *P. sicula* tended to be highest on stony substrates. Nevertheless, the regression slopes of T_b on T_a for *P. sicula* were very similar in both habitat categories ("rock + wall": $b = 0.096 \pm 0.242$, $n = 20$; "meadow + bush": $b = 0.039 \pm 0.104$, $n = 36$; ANCOVA: $F = 0.021$, $P > 0.50$). The scarcity of observations of *P. tiliguerta* in vegetated microhabitats precluded a similar analysis for this species.

TABLE III. — *Statistics (mean ± 1 SD, range in parentheses, sample size) of body (T_b), air (T_a) and substrate (T_s) temperatures for* P *tiliguerta and* P. *sicula recorded in two distinct microhabitat categories. Data for periods of uninterrupted sunshine only*

	Rock and wall	Meadow and bush	P variances	P means
T_b P *tiliguerta*	33.98 ± 2.93 (25.7-39.2) 98	34.95 ± 1.97 (32.7-36.8) 4	>0.20	>0.50
T_b P *sicula*	34.08 ± 2.54 (28.9-37.5) 20	33.83 ± 1.89 (28.5-37.8) 36	>0.05	>0.60
T_a	23.43 ± 2.88 (17.9-32.2) 118	23.11 ± 2.99 (17.6-30.3) 40	>0.40	>0.50
T_s	27.17 ± 3.57 (18.7-37.3) 118	26.82 ± 3.19 (21.3-34.2) 40	>0.20	>0.50

DISCUSSION

Our study contrasts activity body temperatures of two congeneric lizards that occur sympatrically, have identical activity rhythms, and hence experience highly similar ambient conditions. The most striking finding is that although both species maintain their T_b s around identical mean values, *P. sicula* regulates its body temperature more precisely than *P. tiliguerta*. This is evidenced by the lower value of the regression slopes of T_b on T_a and on T_s, the lower variance in body temperatures, and the absence of diurnal variation in T_b s in the former species. In addition, *P. tiliguerta* was the most frequently seen species under suboptimal (cloudy) conditions. This lizard hence seems to tolerate voluntarily a wider range of T_b s than its congener.

Differences between species in the precision of regulated temperatures may result from differences in the range of preferred body temperatures. The available data did not allow a statistical treatment of the preferred temperatures. However, considering the similarity of the average values and the wide overlap of the ranges, it seems appropriate to conclude that both species exhibit very similar zones of preferred temperatures.

An ectotherm's body size influences its heat balance with the environment As the species studied here differ in body mass (*P. tiliguerta*: 2-6 g; *P. sicula*: 5-10 g), we should examine to what extent observed differences in thermoregulatory precision reflect differences in their size. In a simulation study, STEVENSON (1985) showed that differences in the predicted daily range of T_b s will be small or non-existent over the body size span that we encountered. In addition, behaviour rather than size seems to limit the daily T_b-range for animals less than 10 kg (STEVENSON, 1985). This conclusion is supported by the observation that variance in T_b s is not different among various species of varanid lizards, which cover a huge range of body sizes (30 g-45 kg; D. KING, in litt.). Hence, both empirical and theoretical evidence suggest that the small difference in size between both species studied here is unimportant in eliciting the observed differences in thermoregulatory precision

The precision of thermoregulation is thought to be determined by the balance between its costs and benefits (HUEY & SLATKIN, 1976). Thus, the observed difference in thermoregulatory precision should be reducible to differences in costs and/or benefits between the two species. A great variety of internal and external factors have been shown to influence these costs and benefits (review in HUEY, 1982). The available data, which are purely descriptive, do not allow an appraisal of the importance of all of these factors, but we can suggest some hypotheses and possibly test them.

A first factor that influences thermoregulatory precision is investment (of time) in thermoregulatory behaviours. A reduction of the time invested in regulatory behaviours by *P. tiliguerta* could explain its lower degree of thermoregulatory precision. The relative number of lizards observed basking, a crude index of the time invested in behaviours that tend to increase T_b, did not differ significantly between both species, and was actually slightly higher in *P. tiliguerta*. This result dismisses the importance of variation in time investments as a main factor influencing the observed difference in thermoregulatory precision.

Microhabitat structure, particularly the availability of patches with different thermal characteristics, affects the time and energy expended in thermoregulatory behaviours and may therefore be an important determinant of the precision of regulated temperatures. The availabity of patches of sun in shaded forests determines thermoregulatory precision in *Anolis* (RUIBAL, 1961; RAND, 1964; HUEY, 1974; HUEY & SLATKIN, 1976; LEE, 1980) and the availability of shade may be important in open habitats (ASPLUND, 1974; McFARLAND, 1976) In our study area, *P. sicula* alternated its activities between rocky substrates and open meadows and occupied a wider range of microhabitats than *P. tiliguerta*, which was restricted to rocky surfaces. The following reasons support the view that differential habitat utilisation is not an important determinant of the observed differences in thermal relations. First, we found no differences in temperature characteristics between the distinct microhabitats. Second, rocky substrates provide lizards with ample opportunities to shuttle between sun-warmed surfaces and patches of shade provided by crevices

and holes between piled stones The variable orientation of their surfaces should facilitate the adoption of postural adjustements that alter net radiation intake These microhabitats hence seem to be more favourable in terms of thermoregulatory abilities than the structurally less heterogenous open meadows We therefore would expect a higher extent of thermoregulatory precision in *P. tiliguerta*, while the opposite result was obtained. Finally, thermoregulatory precision, as indexed by the regression slope of T_b on T_a, was similar in *P sicula* occuring in different microhabitats.

Cost-benefit considerations (HUEY & SLATKIN, 1976) predict that raising the rate of food intake, and hence of the time available for non-foraging behaviours, should be associated by an increase in thermoregulatory precision. Lizards that live in food-rich habitats, or that exploit the available resources more efficiently, are therefore expected to regulate their temperature more precisely than lizards occuring in less productive environments. Empirical evidence for such a relation has been provided by LEE (1980) who showed that well-nourished *Anolis sagrei* exhibit higher thermoregulatory precision than poorly-nourished individuals. In the absence of data on the rates of food intake by both *Podarcis* species, we cannot examine this hypothesis.

Exploitation competition between species with similar temperature preferences should have the same effect as a decrease in the productivity of the habitat, and is expected to reduce thermoregulatory precision (HUEY & SLATKIN, 1976; MAGNUSON *et al*, 1979). Shifts in habitat occupation in the presence of congeneric species are often considered as evidence of competition (JENSSEN, 1973; LISTER, 1976; MEDEL *et al*, 1988), although this must be interpreted with caution (ADLER, 1985). Data available for a solitary population of *P. tiliguerta* at a high altitude location (VAN DAMME *et al*, 1989) indicate that it occupies a wider range of microhabitats and is frequently active at ground level. These data might indicate that *P sicula* depresses microhabitat use of *P tiliguerta*, although unknown differences in microhabitat availability may obscure this interpretation Other authors also suggested that habitat occupation by *P. tiliguerta* is restricted in the presence of *P sicula* (LANZA, 1955; ARNOLD & BURTON, 1978). We hypothesize that restriction of the microhabitats occupied by *P tiliguerta*, possibly resulting from competitive interactions with *P sicula*, may reduce its rate of food intake and lead to less carefull thermoregulation. Experimental studies, involving replacement of *P sicula*, are needed to test this suggestion.

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