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

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ABSTRACT

We studied field body temperatures *(T)* in sympatric populations of the Mediterranean lizard species *Podarcis tiliguerta* and *P sicula* Bath species have identical activity Ihythms, experience highly similar ambient conditions and maintain body tempe1atures around identical mean values However, *P silula* regulates its *Tb* more precisely than *P tiliguerta,* as indicated by the lower value of the regression slope of *Tb* on air and subst1ate temperatures, the lower variance in *Tb s,* and the absence of diurnal variation in *1* s in the farmer species Available data of selected *Tb s* suggest that bath species have highly similax theimal preferences Bath species differ in microhabitat use: *P tiliguerta* was almast exclusively seen on rocks and stone-walls, aften at perch heights > 50 cm and at short distances to patches of shade; *P sicu!a* basked on rocky surfaces but foraged on ground in open meadows, aften at distances of> 5 m to deep shade. Microhabitat occupation did not seem to influence thermoregulatory precision in the Jatter species We suggest some hypotheses that may explain the observed interspecific difference in precision of thermoregulation

KEYWORDS: theimoregulation, *Podarch tiliguerta, Podarcis silula*

RÉSUMÉ

On a étudié la température corporelle *(Tb)* au champ de deux populations sympatriques de *Podarcis tiliguerta* et *P. sicula,* espèces de lézards méditerranéennes Ces deux espèces ont des Iythmes d'activité identiques, connaissent des conditions ambiantes très similaires et maintiennent leur température corporelle à des valeurs moyennes identiques Néanmoins, *P sicu!a* régule sa *Tb* plus précisément que *P tiliguerta,* comme l'indiquent les valeurs plus basses de la courbe de régression de *Tb* sur les températures de l'air et du substrat, la variance mains élevée de *1 s* et !'absence de vaiiation diurne de *Tb s* chez la première espèce. Les données disponibles suI une *Tb s* donnée suggèrent que les deux espèces ont des préferences thermiques très similaires Les deux espèces diffèient quant à l'utilisation du microhabitat : *P. tiliguerta* a été vue presque exclusivement suI des toChers et. c!s murs de piene, souvent à des hauteurs supérieures à- 50 cm et à Courte distance de taches d'ombre; *P. siqda* se· chauffe SUI des surfaces rocheuses mais chasse sur Ie sol dans des prairies ouvertes, souvent à des distances de plus de 5 m de la pleine ombre 'occupation du microhabitat ne semble pas influe1 suI la précision de Ia thermorégulation chez cette deinière espèce Nous proposons quelques hypothèses qui pouiraient expliquer la différence interspécifique observée dans la précision de la thermorégulation

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INIRODUCUON

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 behaviournJ adjustments in order to keep their body temperatures between lower and upper threshold temperatures (BERK & HEAIH, 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 & SIEVENSON, 1979; HUEY, 1982). Recent theoretica! 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 łom 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 lizar ds *Podarcis tiliguer ta* 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. Inter pretation of om results proved to be difficult in the absence of information on the ecological relations between both lizards. Om conclusions are therefore mainly directed towards suggesting working hypotheses for future studies

MAIERIAL AND MEIHODS

ANIMAI.S

***Podard s tiliguerta* is a small (adult body size: 45-65 mm; mass: 2-6 g) wall lizar d that is endemie 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, 1uins, roadsides, maquis, wood fringes and clearings) from sea-level up to more than 1,800 m altitude**

***Podard s 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 Tynhenian 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 primarîly restricted**

to coastal areas up to an altitude of 400 m, where they can be fOund in meadows, roadsides, woodfi:inges, maquis, cultivated lands and city parks

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

F'IElD SIUDY

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, Fxance), at elevations 0-70 m, between the shoreline and the coastal road between Calvi and Gale1ia 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. Bath *Podarcis* share this habitat with the secretive little lizard *Alg yroides fitzingeri,* two geckos *(Tarentola mauritanica* and *Hemidact ylus turcicus)* and the predatory snake *Coluber viridijlavus* which was frequently observed here

We visited the site fi:om 7-16 and 27-28 May 1988 Data were collected between 7 hrs 30-18 hrs 00 (Meao European 1ime), coveiing 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,= *Tb),* air (shaded bulb, ± 3 cm above substrate, = *TJ* and substrate temperatures (shaded bulb, = *T*J to the nearest 0 1°C with a thermocouple connected to a quick-reading electronic thermometer (DGI Digital thermometer) We also noted time of day, sex, weather conditions (sunny, cloudy/variable -respectively 5 or <S 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 <leep shade (< 0 5 m, 0 5-1 m, 1-2 m, 2-5 m,> 5 m)

SElECTED BODY IEMPERAIURES

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 obtaîned h'Om laboratory temperature recordings reported by AVERY (1978)

RESULI'S

HERMAI PREF ERENCES

Selected body temperatures of adult male *P. tiliguer ta* in a laboratory thermo-g:r adient averaged 35 47°C (s = 1 27, range: 33 0-38.2, *n= 40)*

Body temperatures recor ded in the laboratory for *P sicu/a campestris* hom Tuscany (Italy) by AvERY (1978) averaged 34 79'C (range: 31 2-38 8, n = 27). As the Jatter author <lid not report the distribution of the temperature readings, we cannot assess the statistica] difference between both data sets

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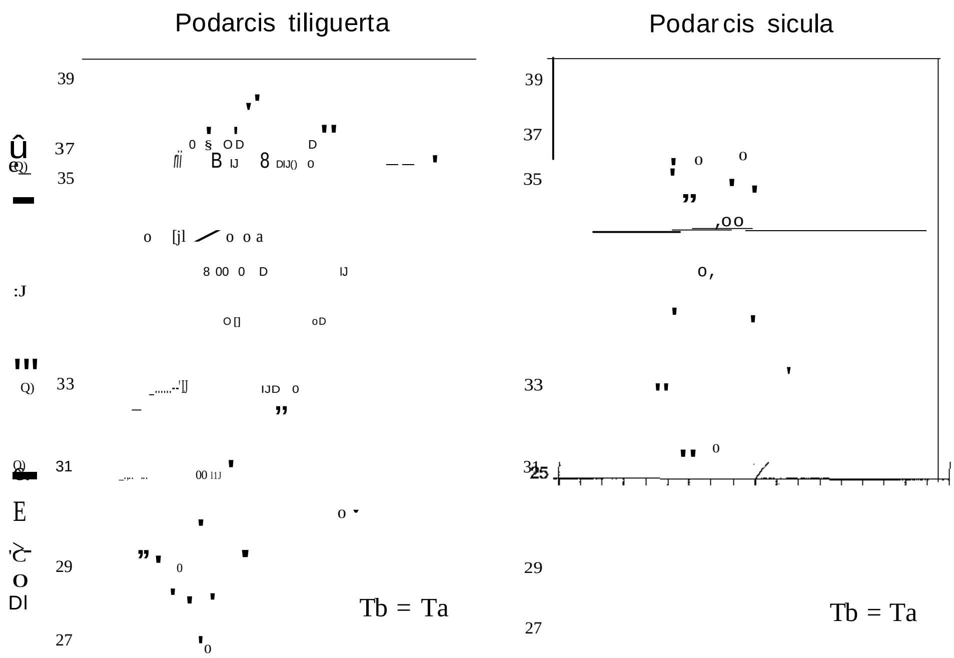
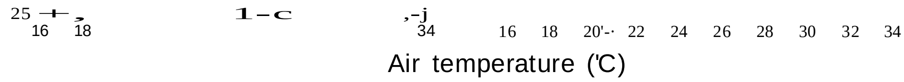
We found no diflereuces in body temper àtures between sexes in either of the species (ANOVA, $P > 0$ 50) and therefore lumped data in subsequent analyses

Availability of dir ect sunshine influences *T,* of both lizards: *T,s* rec01ded during sunny periods were significantly higher than those measured under cloudy or variable conditions (t-tests, both $P < O$ 05; table IJ . Further analyses are therefore based on sunny weathet data only

Statistics of body and ambient temperatures ate shown in table I. Mean body, air and subst1ate temperatures <lid not differ between both species However, the variance of *T,* was significantly higher in *P tiliguerta,* wher eas the variances of *T,* and *T,* <lid not diffor between species (table 1).

The slope of the regression line relating *T* on *I"'* an estimate of the precision of thermoregulation (HUEY & SrAIKIN, 1976), was significantly different from zero in *P tiliguerta (P <O..ûl) but not in P sicula* (P> 0.60), and is significantly steeper



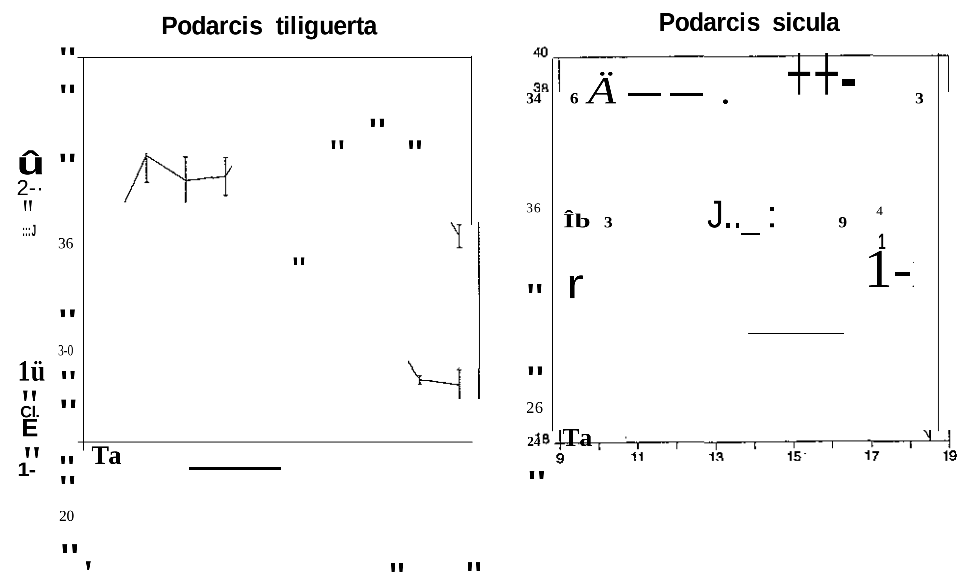


F1G 1 – Relations between body *(Tb)* and air (I) temperatures in *P tiliguerta* and *P silula* Equations of regression lines are: *P tiliguerta* $11_{,}$= 0 310 *T* + 26 70; *P sicula* $Il_{,}$= 0 039 *Ta* + 32 98 Data fCn pe1iods of unintenupted sunshine only

in the former species (F = 3378, *P=0.05;* fig. !). Identical results were obtained for the relation between *T,* and *I,* These data indicate that *T,s* of *P tiliguer ta* are more closely coupled to ambient temperatures than are *T,s* of *P sicu/a,* and suggest that the Jatter species exhibits a higher precision of thermoregulation

The number of *P sicula* observed per person hour was highest during the early morning and late af temoon hours, whereas activity of *P tiliguer ta* seemed to peak during the aftemoon.. These apparent differences in activity rhythms are, however, not significant (G = 14 860, 9 df, *P >0.05)*

Hourly mean *10* exhibited significant diurnal variation in *P tiliguer ta* (F= 2 320, *P*= 0 02; fig 2) In *P sicula,* we found no differences among hourly



Hour (MET)

FIG 2 Diel variation in body *(T)* and air *(T;J* temperatures in *P tilîguerta* and *P. sicula* Shown are hourly means (± 1 SE) and sample sizes Data for periods of uninterrupted sunshine only

mean *T() s* (F= 0.771, *P>0 60;* fig. 2) despite obvious variation in *T,* (F= 2 832, *P <0.01)* and *T,* (F= 3 000, *P <O* 01).

When weather conditions changed !rom sunny to cloudy, *P tiliguer ta* exposed themselves for some time on rocky substrates in a basking-like posture, whereas *P sicula* retreated rapidly. The proportion of *P tiliguer ta* observed during cloudy weather (31/133) was significantly higher than in *P sicula* (5/62) (G = 6 172, *P=O* 01)

The proportion of animals seen basking showed a typical diumal variation in both species, with more lizards basking in the morning and aftemoon hours. We found no difference between species in the r elative nurnber of basking lizards (P. *tiliguerta:* 47/102, *P sicula:* 19/56, G=2..196, *P >0.10)*

MICROHABIIAI USE

Although both species shared the same habitat, some clear-cut diflerences in microhabitat use were evident (G = 73.469, 3 df, *P <O* 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 sunounding vegetation. *P s icu/a* 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 <O* 001) This lizard seems to use rocks and stone walls as basking sites, while it forages mainly on ground among grassy vegetation When disturbed,

BlE I – *Statistic s (mean± 1 SD, 1ange in parenthe<Jes) of body (Tb), aiI (1) and substrate (T) temperatures and slopes (± 1 SE) /or the regrenions of body versus air and of body versus substrate temperatw e s for* P tiliguerta *and* P sicula *recorded under cloudy and sunny weather*

	P *tiliguerta*	*P. sicula*	p variances	p means
Cloudy				
T,	JO 20 ± J.06 (23 6-J6.8)	JO 85± 0.79 (JO 2-JI 8)	<0 OOI	>Ü 70
N	J I	S		
Sunny				
T,	J4 02 ± 2 90 (25 7-J92)	JJ .89 ± 2 12 (28 5-J7 8)	<0 01	>0 70
T	2J.58 ± 2 89 (17 9-J2 2)	22.96± 2 89 (17 6-JO 3)	>0 40	>0 20
I;	27.11± J 52 (18.7-J7 J)	26 96 ± J .39 (21.3-J72)	>0 40	>0 70
Slope *'IbI"*	0 JlO ± O 095	0 OJ9 ±0 099		0.05
Slope *Tb-Is*	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 (6J)	J4 (JJ)	2 (2)	2 (2)
p silula	17 (JO)	4 (7)	J4 (60)	2 (2)
	Perch height			
	< 25	25-50	50-100	>100 cm
p tiliguerta	J2 (J5)	21 (2J)	28 (J I)	10 (Il)
p sicula	4J (80)	5 (9)	4 (7)	2 (4)
	Distance to shadow			

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	<Ü.5	0.5-1	1-2	2-5	>S m
p tiliguerta	89 (87)	3 (J)	4 (4)	J (J)	J (J)
p sicula	22 (J9)	0 (0)	0 (0)	6 (I l)	29 (51)

ground-dwelling *P sicu/a* may flee ovet distances of several meters to stone piles 01 take refüge in holes at gr ound-level

As a consequence of the diflerences in rnicrohabitat use, the height distribution also differs among both species (G 27 919, 3 df, *P* <*O* 001): while most *P. sicula* were seen on or near the ground, a large propo1tion of *P tiliguerta* was active on more elevated places (table II)

The microhabitats used by both species also diffot ed in the availability of shadow: the shmtest transit distance !rom a lizard in füll sun to a patch of <leep

shadow was significantly larger in *P sicu/a* than in *P tiliguerta* (G = 59.555, 4 df, *P<O* OOI; 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 bath lizard species did not differ with respect to microhabitat, although the variance in *T,s* of *P sicula* tended to be highest on stony substrates.. Nevertheless, the regression slopes of 70 on *T.* for *P sicu/a* were very similar in both habitat categories ("rock + wall": *b* = 0.096 ± 0.242, *n* = 20; "meadow + bush": *b=0 039 ± 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

lABl.E lil. – ***Statistics (mean± 1 SD, range in parentheses, sample sîze) of body (1/,), air ('I) and substrate (1) temperatures /or* 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
Tb P tiliguerta	33 98 ± 2 93 (25 7-392) 98	34 95± 1 97 (32 7-36 8) 4	> 0 20	>0 50
11,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	23.43± 2 88 (17 9-32 2) 118	23.11 ±2 99 (17 6-30 3) 40	>0 40	> 0 50
1;	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 bath species maintain heir *T,s* around identical mean values, *P. sicula* regnlates its body temperatme more precisely than *P tiliguetta* This is evidenced by the lower value of the regression slopes of *T,* on *T.* and on *T"* the lower variance in body temperatures, and the absence of diurnal variation in *T,s* in the former species In addition, *P tiliguetta* was the most frequently seen species under suboptimal (cloudy) conditions. This lizard hence seems to tolerate voluntarily a wider range of *T,s* than its congener

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Diffärences between species in the precision of regulated temperatur es may result from differences in the range of prefoned body temperatures The available data did not allow a statistica! treatment of the preforred 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 ver y similar zones of preferred temperatures

An ectotherm's body size influences its heat balance with the environment As the species studied her e differ in body mass *(P. ti/iguerta:* 2-6 g; *P sicula:* 5-10 g), we should examine to what extent observed diffär ences in thermoregulatory precision reflect differences in !heir size.. In a simulation study, SrnvENSON (1985) showed that diffärences in the predicted daily range of T_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,-range for animals less than 10 kg (SIEVENSON, 1985). This conclusion is supported by the obser vation that variance in T_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 empirica! and theoretica! evidence suggest that the small difference in size between both species studied here is unimpor tant in eliciting the observed diffärences in thermoregulatory precision

The precision of thermoregulation is thought to be determined by the balance between its costs and benefits (HuEY & SLAIKrN, 1976). Thus, the observed diffor-ence in thermoregulatory pr ecision should be reducible to difforences in costs and/or benefits between the two species. A gr eat variety of internal and external factors have been shown to influence these costs and benefits (r eview 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 r egulatory behaviours by *P tiliguer ta* could explain its lower degr ee of thermoregulatory precision. The r elative 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 tiliguer ta*. Ihis result **dismisses the importance of variation in time investmen ts as a main factor influenc**ing the observed difference in thermoregulatory precision

Microhabitat structur e, particularly the availability of patches with diff er ent thermal characteristics, affects the time and ener gy expended in thermoregulatory behaviours and may therefore be an impor tant determinant of the precision of regulated temperatures. The availabity of patches of sun in shaded forests determi-nes thermoregulatory precision in *Anolis* (RurnA1, 1961; RAND, 1964; HUEY, 1974; HuEY & SLATKIN, 1976; LEE, 1980) and the availability of shade may be impor tant in open habitats (AsPIUND, 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 r ocky surfaces The following reasons support the view that difforential habitat utilisation is not an important determinant of the observed differ ences 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 sur faces and patches of shade provided by crevices

and holes between piled Stones The variable orientation of heir surfaces should facilitate the adoption of postUial adjustements that alter net radiation intake These rnicrohabitats hence seem to be more favourable in terms of thermoregulatory abilities than the s!lucturally less heterogenous open meadows. We therefore would expect a higher extent of thermoregulatory precision in *P tiliguer ta,* while the opposite result was obtained. Finally, thermoregulatory precision, as indexed by the regression slope of T_b on T_o was similar in *P sicula* occuring iu different mier ohabitats.

Cost-benefit considerations (HUEY & S1A1KrN, 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 ther efore expected to regulate heir temperature mor e precisely than lizards **occuring in less pt oductive environments. Empitical evidence for such a relation** has been provided by LEE (1980) who showed that well-nourished *Anolis sagrei* exhibit higher thermoregulatory pr ecision than poor ly-nour ished individuals. In the absence of data on the rates of food intake by bath *Podar cis* species, we cannot examine this hypothesis

Exploitation competition between species with similar temper atUie preforences should have the same effect as a decrease in the productivity of the habitat, and is expected to reduce thermoregulator y precision (HUEY & SLAlKrN, 1976; MAGNUSON *et al* , 1979}. Shifts in habitat occupation in the pr esence of congeneric species ar e aften considered as evidence of competition (JENSSEN, 1973; lrs1ER, 1976; MEDEL *et al* , 1988), although this must be interpreted with caution (ADLER, 1985}. Data available for a solitary population of *P tiliguer ta* at a high altitude location (VAN DAMME *et al* , 1989) indicate that it occupies a wider range of microhabitats and is frequently active at gr ound level These data rnight indicate that *P sicula* depresses microhabitat use of *P tiliguer ta,* although unknown differences in microhabitat availability may obscure this inter pretation Other authors also suggested that habitat occupation by *P tiliguer ta* is r estricted in the presence of *P sicula* (LANZA, 1955; ARNOLD & BuR roN, 1978) We hypothesize that resuiction of the microhabitats occupied by *P tiliguer ta,* possibly resulting fr om competitive interactions with *P sicula,* may reduce its rate of food intake and lead to less carefüll thermoregulation. Experimental studies, involving r eplacement of *P sicula* , are needed to test this suggestion

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