ACTIVITY AND THERMOREGULATION IN THREE MEDITERRANEAN SPECIES OF LACERTIDAE

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ABSTRACT

A study was made of the thermoregulatory development and activity rhythms, both daily and annual, of three species of mediterranean Lacertidae: *Psammodromus algirus, P. hispanicus* and *Acanthodactylus erythrurus*, recording 505 cloacal temperatures (TB). Statistically significant correlations were found between the TB and the TA and TS (temperatures of the body, environment and substrate, respectively) values of the different age and sex classes established in *P. algirus* and *P. hispanicus* but not in some age and sex classes of *A. erythrurus*.

A. erythrurus, mainly the adult males, was the species that showed the greatest thermoregulatory efficiency.

Both *Psammodromus* species remain active from March to October, while the fringe-toed lizard shows an annual activity from May to September.

INTRODUCTION

The activity rhythms, and in particular thermoregulation are less well known aspects in the ecology of the Iberian Lacertidae. In the case of the species examined here, *Psammodromus algirus, Psammodromus hispanicus* and *Acanthodactylus erythrurus*, there are few works that have dealt with these topics; in this sense, only Mellado *et al.* (1985), Busack (1976 and 1978), Pough and Busack (1978), Pérez-Mellado (1981), Seva (1982) and Seva and Escarre (1980) offer some data.

Our aim in the present work was to provide a definition in these species of what could be termed "niche thermal dimension", a parameter that we believe to be of great importance apart from the by now classic definitions of niche for characterising both the autoecology of species and interactions between them.

We felt it essential to determine the daily and annual activity rhythms of the established different age and sex classes (see below) owing to the importance of the three species in communities of Iberian lizards. Regarding *P. algirus*, many basic aspects of its biology remain to be elucidated, in spite of it being one of the most abundant Lacertidae in the southernmost two thirds of the Iberian Peninsula (Arnold and Burton, 1978) and being present throughout the whole of the peninsula with the exception of the extreme northern part (Salvador, 1985). In the study zone, *A. erythrurus* is found close to the northern boundary of its distribution area in the west of the Peninsula such that we felt it interesting to gain insight into its activity cycles and thermoregulatory behaviour in this area. Finally, *P. hispanicus* is undoubtedly one of the least well known Lacertidae regarding its ecology; only recent works have offered data concerning the Spanish *Psammodromus* (Pascual, 1986).

MATERIAL AND METHODS

The study area is located to the south west of the province of Salamanca (Spain) in the neighbourhood of the village of Espeja. The zone features a greater Atlantic influence than the rest of the province, with a sub-humid mediterranean type bioclimate. Sampling was performed from May 1986 to June 1987, with a total number of sampling hours of 85 throughout the months in which the species studied were active. In the case of *P. algirus* and *A. erythrurus*, five age and sex classes were established: adult males, adult females, subadult males, subadult females and juveniles. In this sense, the specimens observed during the years in which they had been born and that had still not gone through a winter season were considered as juveniles; subadults were considered to be the specimens that were observed in the year after they had been born and that had lived through a winter season, and adults were considered to be the specimens detected after two periods of winter lethargy with reproductive capacity. In the case of *P. hispanicus*, we only considered three classes of age and sex: adult males, adult females and juveniles since, according to Pascual (1986) and to our own observations, most of the juveniles of this species reach sexual maturity during the year after hatching, after the winter period.

To determine activity rhythms, a total of 671 observations was made, 197 corresponding to *P. hispanicus*, 287 to *P. algirus* and 187 to *A. erythrurus*; these were made made during the whole of the activity period of the species studied. Using these data, we constructed plots of annual and diurnal activity during the day in different periods of the year according to the behaviour exhibited by the specimens. Regarding this we considered two types of specimens according to their behaviour: a) active specimens, involved in activities including locomotion, territorial defense, hunting or others and b) specimens showing thermoregulatory activity that in these species is usually heliothermic. The values corresponding to each hourly or monthly segment were obtained applying an index to correct the sampling differences in each period.

A total of 505 cloacal temperatures (TB) were recorded using a Scultheis thermometer, 129 in *A. erythrurus*, 215 in *P. algirus* and 161 in *P. hispanicus* Air (TA) and substrate (TS) temperatures were taken at the same moment as the TB temperatures of the specimens were made; TA was taken at 1 meter above the surface of the soil occupied by the specimen, always in the shade, and TS was taken by placing the thermometer on the substrate, also in the shade.

RESULTS

THERMOREGULATION

A. erythrurus, in all its age and sex classes, showed higher TB values than those of the other two species studied (Table I). Within the species, the adult males had the highest mean TB but with no statistically significant differences between any of the different age and sex classes (one way ANOVA test, F(4.124) = 1.65, n.s.).

The adult females comprise the age and sex class with the highest mean TB values in *P. algirus*, with highly significant differences (one way ANOVA test, F(4.210) = 7.09; $P<0.001$) between all the age classes, except among the adults (Student's t test: subadults between them t = –3.618, $P<0.001$, subadult males-adult males t = 4.65, $P<0.01$; subadult females-females t = –4.60, $P<0.001$, subadult males-juveniles t = –2.46, $P<0.02$, juveniles-adult males, t = –2.28, $P<0.05$, juveniles-adult females: t = –2.47, $P<0.02$, adult females-juveniles: n.s.).

There were also significant differences between juveniles and adults in *P. hispanicus* (F (4,158) = 7.166, $P<0.005$) but not between adults (adults intra-specimens) t = –1.38, n.s.; adults males-juveniles: t = –3.35, $P<0.001$, adult females-juveniles: t = 1.56, n.s.).

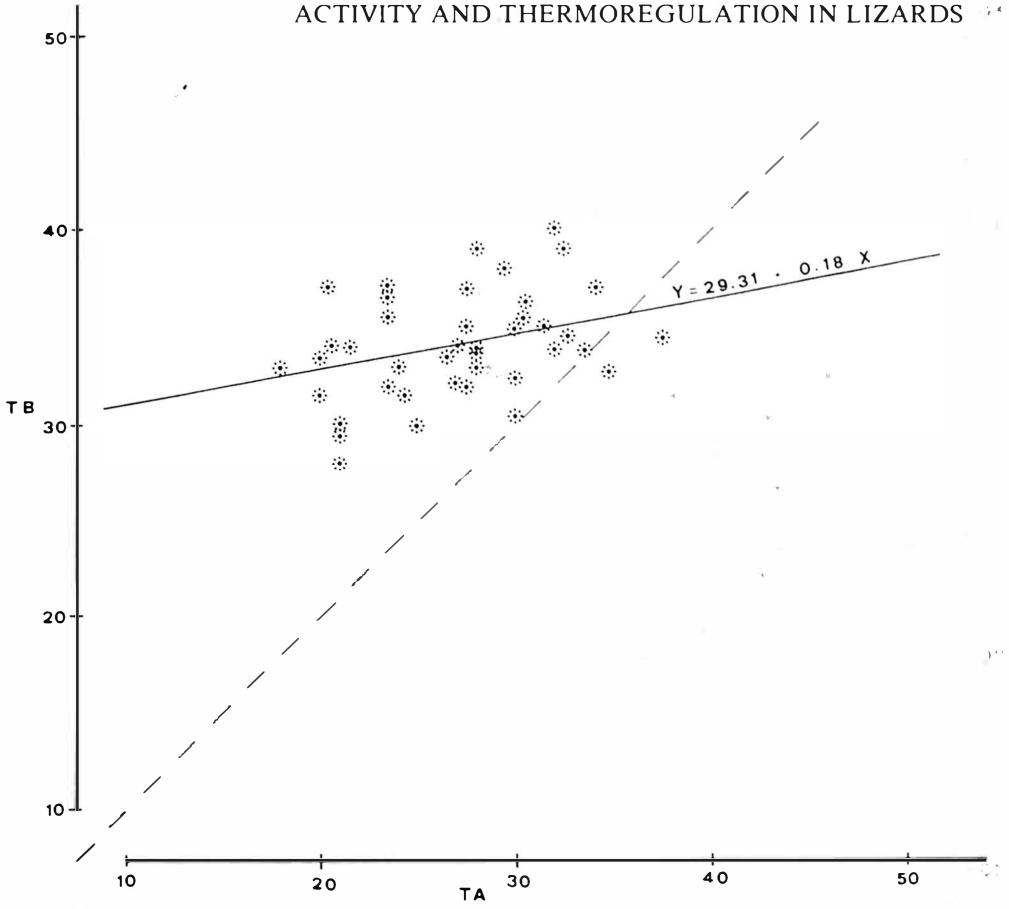
Correlations were made between TB-TA and TB-TS (see Figs. 1, 2 and 3); only in the case of *A. erythrurus* were coefficients lacking in statistical significance found, which points to the high degree of thermal independence of this species (see corresponding regressions).

HOURLY VARIATIONS AND VARIATIONS WITH MICROHABITAT OCCUPATION

Regarding the hourly time-course of the TB, TA and TS (Figs. 4, 5 and 6), in both *Psammodromus* species, the TB values reached their maxima during the first hours of the morning, probably due to thermoregulatory processes. Following this they fell sharply during the period of activity, to rise gradually thereafter during the middle hours of the day. Regarding the mean values of the TB, TA and TS in the different hourly segments, of the three species we applied the Spearman rank correlation coefficient. The results obtained were as follows: *P. algirus*: TB-TA: rs = 0.8583, $P<0.01$; TB-TS: rs = 0.5891, $P<0.05$, *P. hispanicus* TB-TA: rs = 0.5727, $P<0.05$, TB-TS: rs = 0.6906, $P<0.05$; *A. erythrurus* TB-TA: rs = 0.60, $P<0.05$; TB-TS: rs = 0.6363, $P<0.05$ and hence statistically significant in all cases.

Age class and sex	$\overline{X}$	S	CV	Range	n
* *A. erythrurus*					
adults males	34.20	2.66	7.80	29.5-40	33
adults females	33.41	3.55	10.62	26.5-39.5	26
subadults males	32.54	3.28	10.08	27-37	16
subadults females	32.76	2.55	7.78	27-37.5	19
juveniles	32.66	2.48	7.59	21.5-35.5	35
* *P. algirus*					
adults males	30.89	4.15	13.45	21-38.5	72
adults females	31.27	4.29	13.73	21.5-39.5	47
subadults males	27.19	3.60	13.24	19-32	33
subadults females	30.20	3.04	10.07	22-36.5	31
juveniles	29.23	3.05	10.43	21-38.5	32
* *P. hispanicus*					
adults males	28.94	4.31	14.91	19-38	53
adults females	30.09	3.22	10.69	22.5-36	31
juveniles	31.06	1.87	6.04	21-34.5	77

TABLE 1: Body temperatures of different age and sex classes considered.
$\overline{X}$: arithmetic mean; S: standard deviation; CV: coefficient of variation; n: sample size.



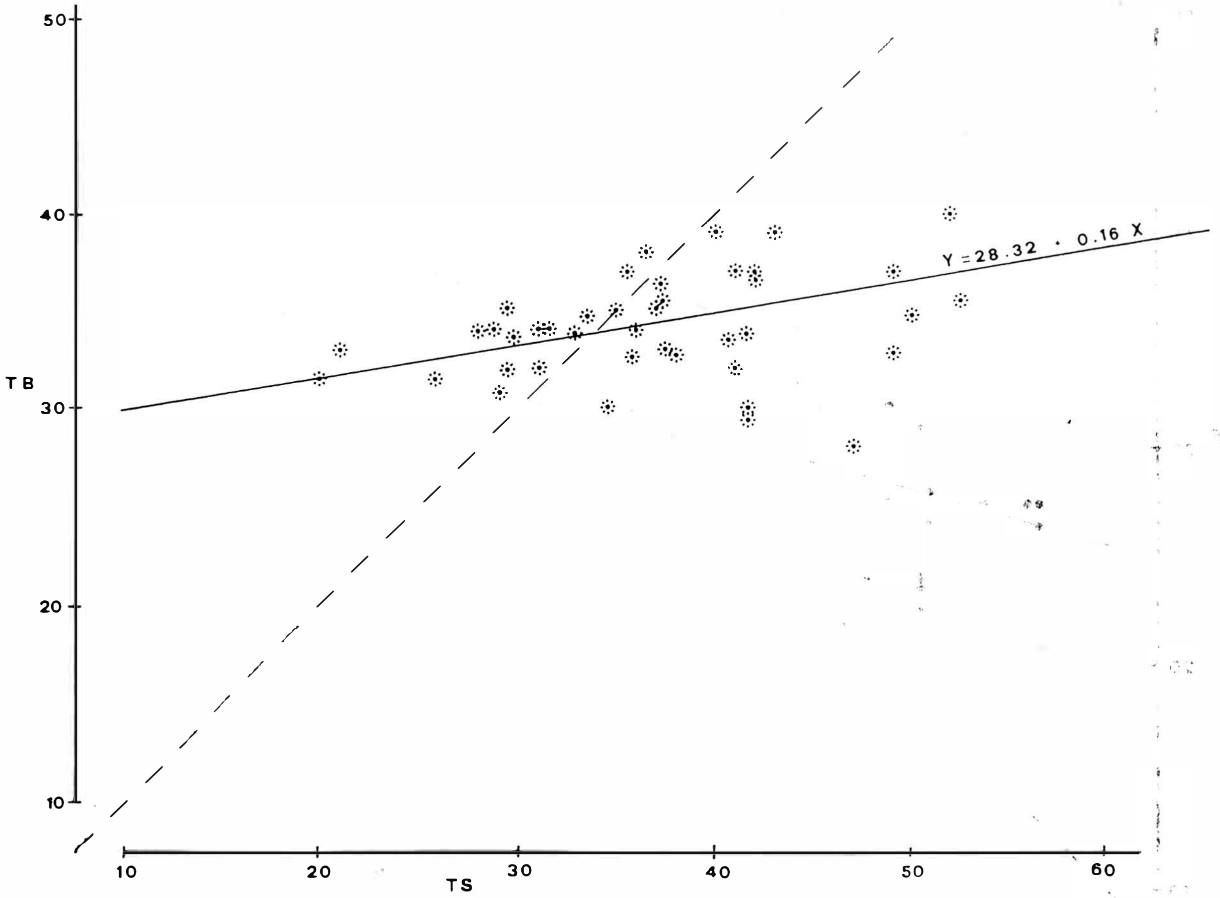


Fig. 1 Several representative examples were chosen of the relationship between body temperatures, environmental temperatures and substrate temperatures, although analyses were performed on all of the age and sex classes considered. Correlation between Body temperature (TB) and Air temperature (TA) and Substrate temperature (TS) in adults males of *A. erythurus*, both in °C. (TB-TA, r: 0.355, $P<0.05$; TB-TS, r: 0.438, $P<0.02$). The dotted line is called the line of perfect poikilothermy (absolute correlation between TB and the other temperature considered).

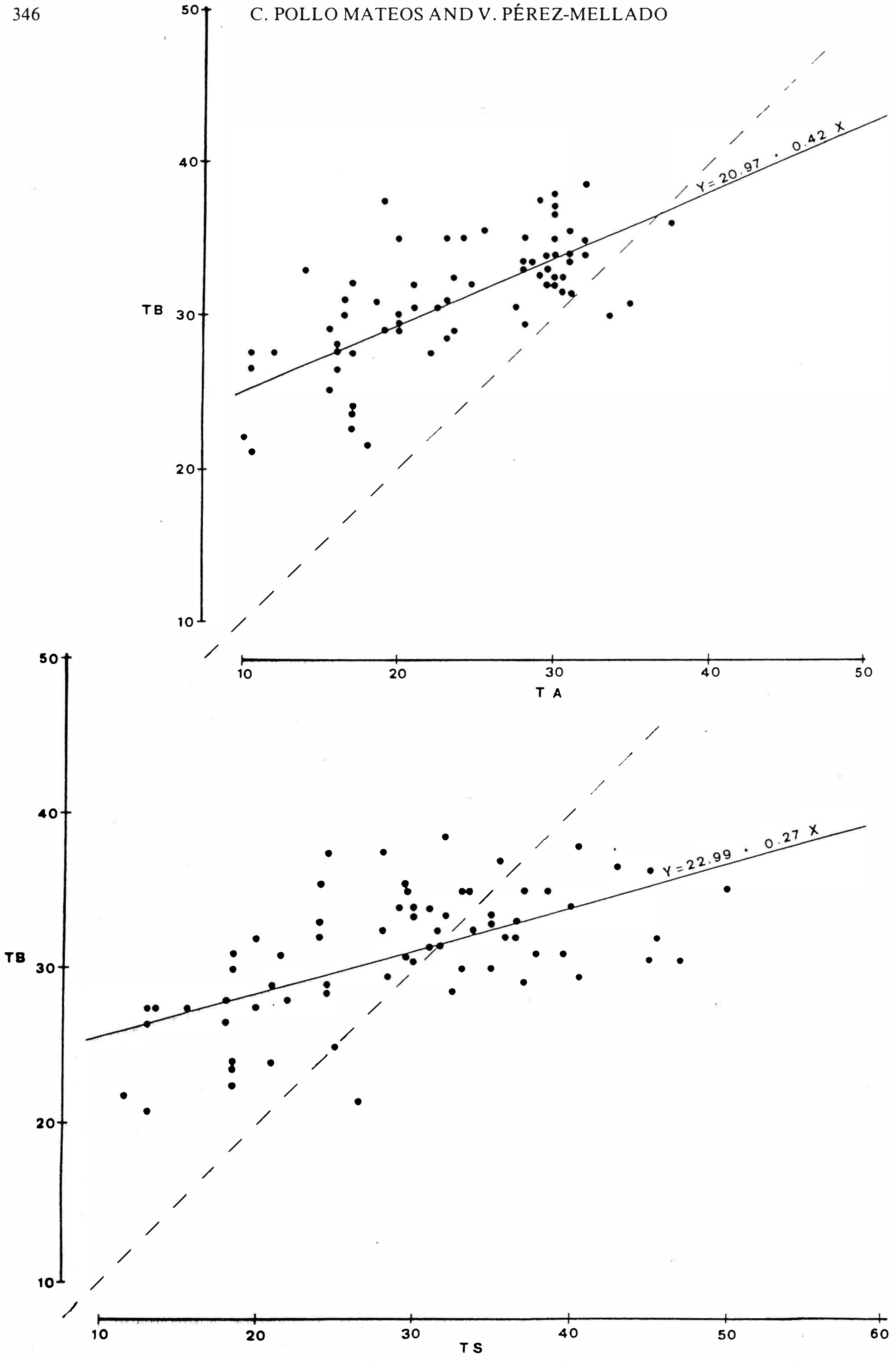


Fig. 2 Correlation between body temperature (TB) and air temperature (TA) and substrate temperature (TS) in adult male specimens of *P. algirus*, (TB-TA, r: 0.700, P<0.001; TB-TS, r: 0.594, P<0.001).

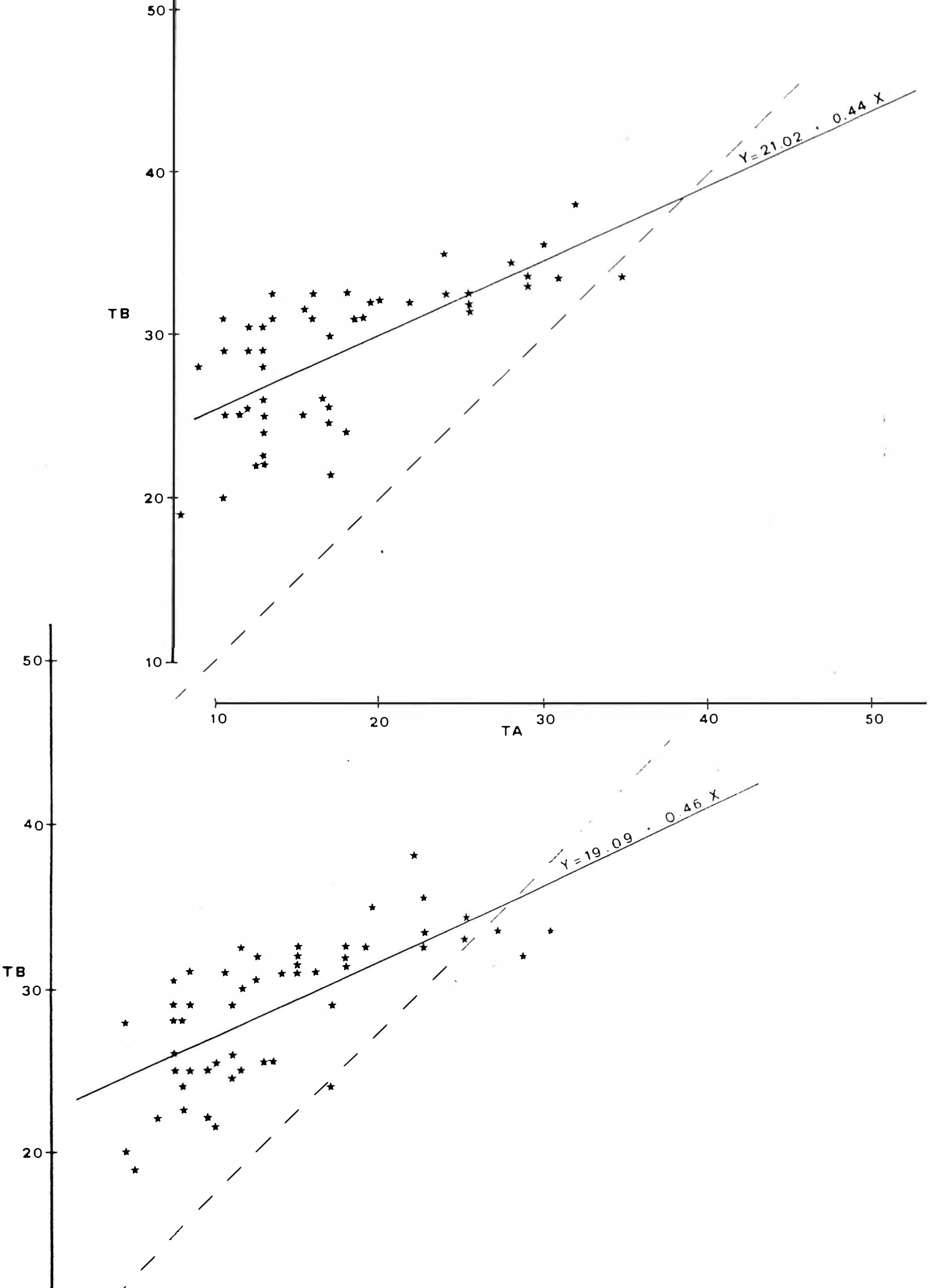


Fig. 3 Correlation between body temperature (TB) and air temperature (TA) and substrate temperature (TS) in adult male specimens of *P. hispanicus*, (TB-TA, r: 0.686, P<0.001; TB-TS, r: 0.701, P<0.001).

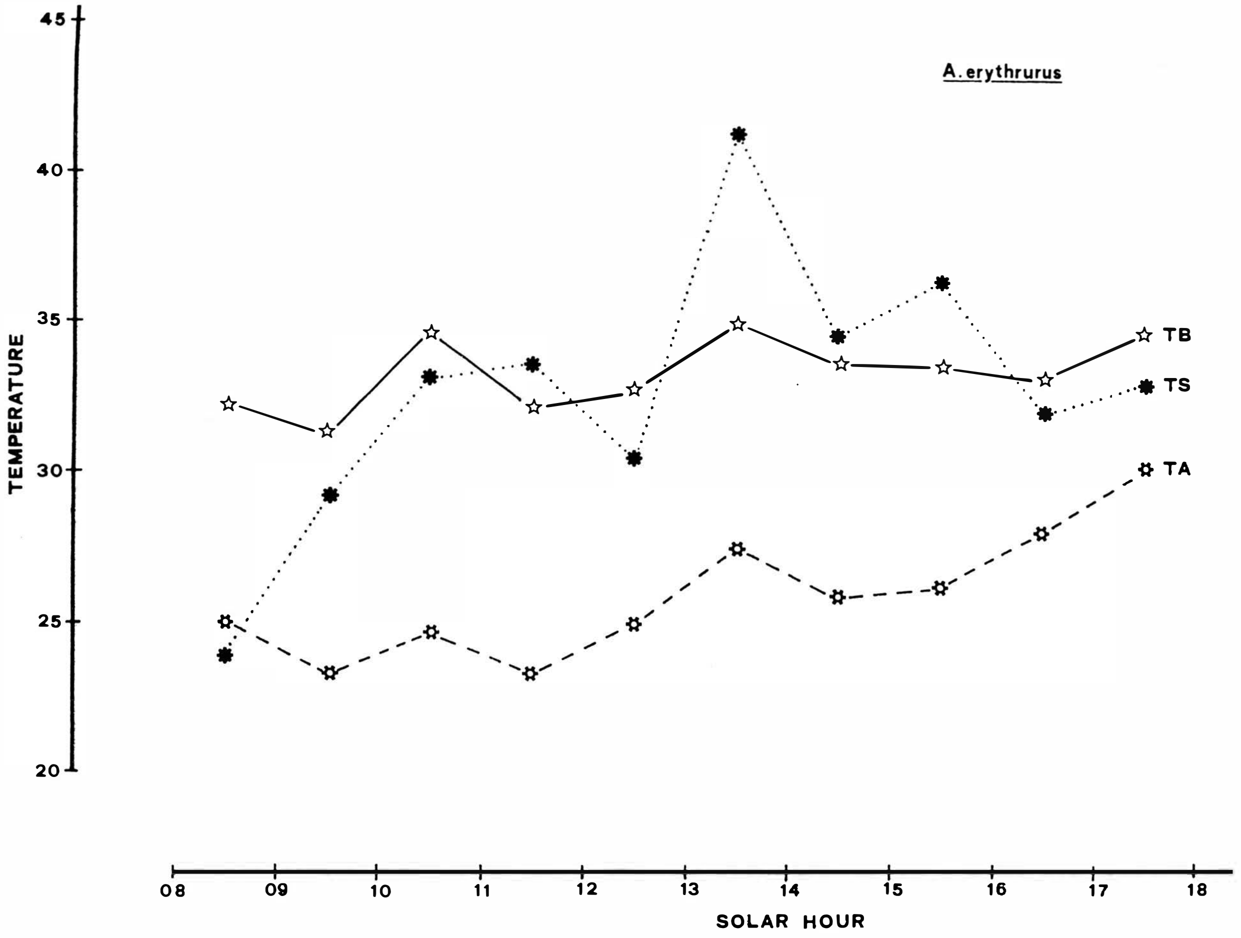


Fig. 4 Hourly variation of TB, TA and TS in *A. erythrurus* for all age classes.

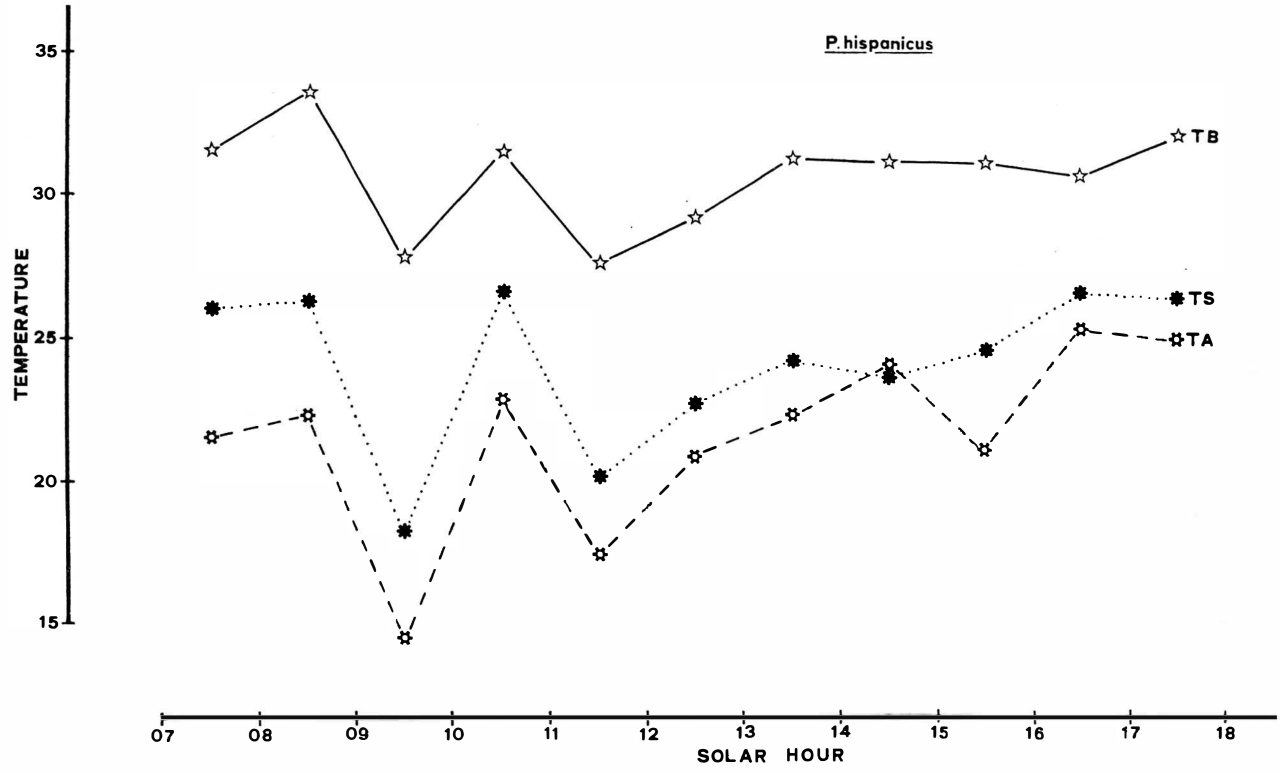


Fig. 5 Hourly variation of TB, TA and TS in *P. hispanicus* for all age classes.

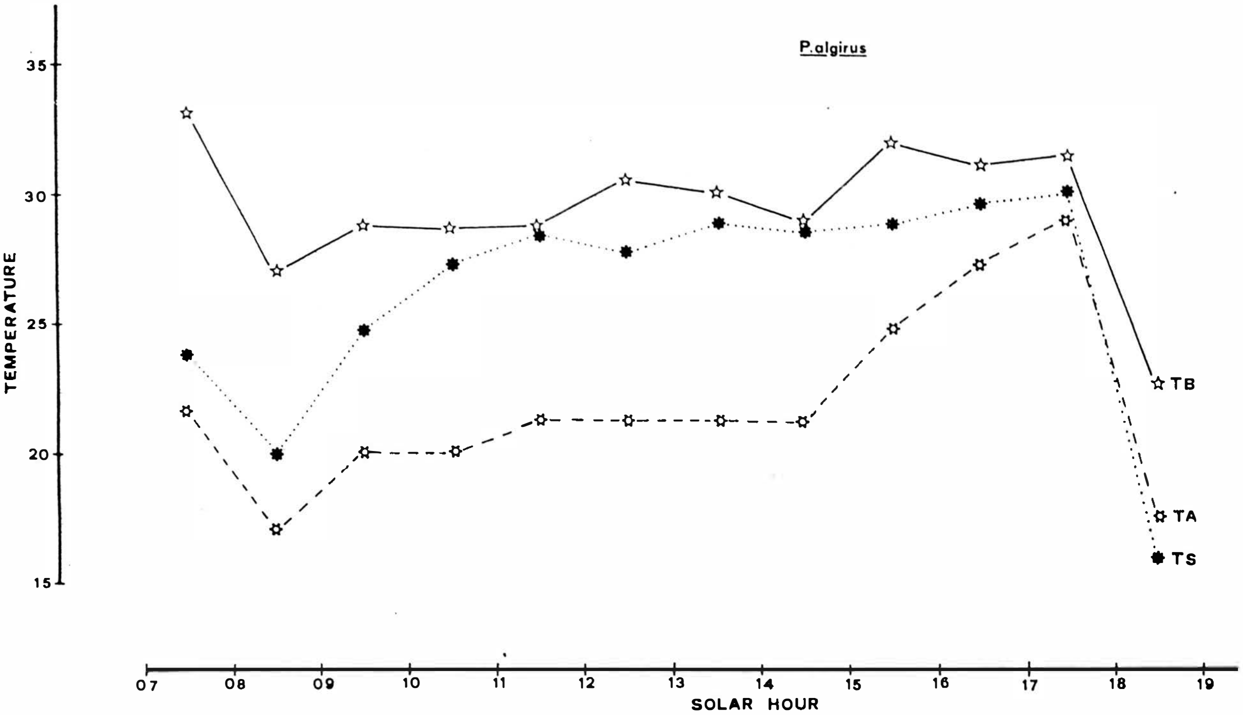


Fig. 6 Hourly variation of TB, TA and TS in *P. algirus* for all age classes.

ACTIVITY

A. erythrurus shows an annual activity period restricted to 5 months, lasting from May to September. By contrast, both *Psammodromus* species have a broader annual period of activity ranging from March to October. *P. hispanicus* has a winter lethargy period in all the populations studied, while *P. algirus* and *A. erythrurus* only show this resting period in areas where the winter season is harsh (Pérez-Mellado, 1982a) although they remain active throughout the year in zones with milder climates (Seva, 1982).

In all three species, the peak activity period in autumn is greater than in spring, undoubtedly due to the appearance of the juveniles. This is specially pronounced in the case of *P. hispanicus* where great activity is shown by this class in this period (autumn), thus allowing some specimens — hatched earlier than their fellows — to reach adult size before the winter lethargy period (Pascual, 1986).

The adults of *P. algirus* and *P. hispanicus* show a bimodal type of activity during the summer months, exhibiting a complete diapause in the middle of the day. By contrast, the adults of *A. erythrurus* show an unimodal activity (Fig. 7a and 7b) throughout the day during all the months in which they are active.

In our study area the subadults and juveniles of this species remain active throughout the day, there only appearing a slight bimodality in activity in the juveniles during the central hours of the day (Fig. 7c and 7d).

In *A. erythrurus*, the activity peak in the morning is higher than that recorded in the afternoon, both in spring and in summer.

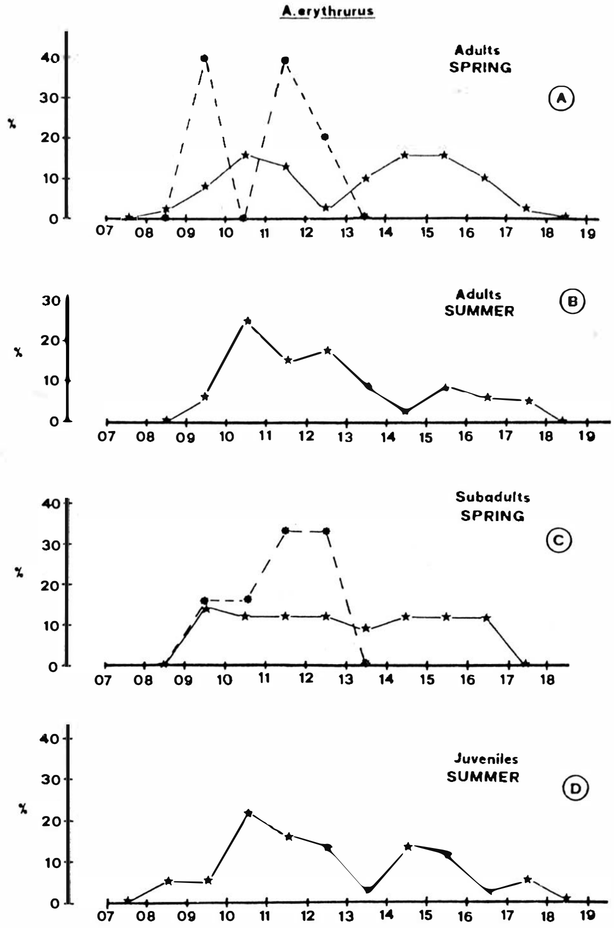


Fig. 7 Behaviour of *A. erythrurus*, throughout the day in different periods of activity, A. Adults, spring; B. Adults, summer; C. Subadults, spring and D. Juveniles, summer. On ordinates, percentage of individuals of the total number observed. Continuous line, active specimens, dotted lines, specimens under thermoregulation.

DISCUSSION

The slopes of the regression lines of *A. erythrurus* and the plots of the hourly time course of TB, TA and TS seem to show that with high substrate temperatures, the lizard exhibits lower TB values; this species must therefore possess a hypothermic mechanism that affords it a certain independence from the temperature of the microhabitats that it occupies. Such a characteristic is shared by other Saurian species that inhabit areas in which sharp differences in temperature occur during the day, such as in the case of deserts and high mountain areas (Heatwole, 1976; Avery, 1979 and Pérez-Mellado, 1981, 1982b). Regarding thermoregulatory behaviour, Seva (1982) has shown that *A. erythrurus* occupies a position close to that of reptiles adapted to life in desert regions, with TB values that are consistently higher than those of TA, as is our own case and which increases in the differences in the first and last hours of the day. This thermal independence, with a continuous daily activity but with brief periods of intermittence, is one characteristic of the thermoregulatory behaviour of reptiles inhabiting open spaces or sites with very sparse vegetation (Avery, *op. cit.*).

In all three species the processes of heliothermia in spring are delayed with respect to summer, where they can be seen at the beginning of the day. During this latter season we were unable to observe thermoregulatory behaviour in *A. erythrurus* (Fig.7b and 7d), probably due to the high temperatures of the microhabitats occupied. *P. hispanicus* shows several thermoregulatory phases in spring one during the first hours of the morning and another later on, at around 12.00 solar time. This seems to allow the lizard to be active very early; later such activity decreases but then gradually increases again towards midday.

The absence of statistically significant differences between the mean TB values and the microenvironmental temperatures of the different media suggest that the heat independence of *A. erythrurus* may be due to physiological causes that are determined genetically. In turn, both species of *Psammodromus* show regression lines that in all cases are statistically significant between TB-TA and TB-TS; this was not the case of *A. erythrurus*. In *P. algirus*, the TS value showed much lower correlations than TA in all the age classes with the exception of the subadult males. In *P. hispanicus* the adult females and the juveniles show a lower TB-TS correlation than TB-TA, opposite to what happens in the adult males in all cases being statistically significant.

The three species can therefore be considered as ectotherms able to control their TB with the thermoregulatory behaviour that they exhibit and hence able to show a broad range of voluntary TBs (eurithermy).

A. erythrurus is found close to the northern limit of its distribution; accordingly, both its annual and daily activity and its thermoregulatory behaviour are strongly affected by microclimatic characteristics which are very different to those of the microhabitats usually occupied by this species in the southern and eastern parts of the Iberian Peninsula. Pough and Busack (1978) have shown that *A. erythrurus* does not tolerate low temperatures very well, which thus limits its activity. This species therefore exhibits a thermoregulatory behaviour that affords its considerable independence from its microhabitat, characterised by strong fluctuations in TA and particularly in TS.

The other two species, not as affected by the environmental influences of the zone and probably with greater thermal tolerance, show a much greater annual and hourly activity than *A. erythrurus.*

Seva (1982), working on the sandy coast of Alicante, found that *P. algirus* has great thermoregulatory efficiency. This rather rare inhabitat for this species, but common for *A. erythrurus*, demands a finer thermoregulatory performance leading to an inversion of roles between both species with respect of our area.

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