Thermal and temporal patterns of two Mediterranean Lacertidae

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Abstract: The thermal and the temporal dimensions of the niche were analyzed for two lacertid lizards, the Large Psammodromus (*Psammodromus algirus*) and the Fringe-toed Lizard (*Acanthodactylus erythrurus*), in a dune ecosystem in NE Spain. Uniform sampling was carried out in order to obtain comparative results. 134/79 cloacal temperatures and 202/116 observations were recorded for each species, respectively. Both species proved to be heliotherms with similar degree of thermoregulation. However, *A. erythrurus* showed higher body temperatures than *P. algirus* because of its use of higher environmental temperatures. Annual differences were also recorded but only the second species showed intraspecific variation. In relation to these results, the annual activity was different between species and size classes. Only the immature specimens of *P. algirus* were active all year and the rest of animals showed a winter diapause period. The daily activity of *P. algirus* lasted from 3-4 hours in winter to 12 hours in summer. In contrast, the daily range of *A. erythrurus* was 2-3 hours shorter. In summer, the pattern of population activity was bimodal in *A. erythrurus* but not in *P. algirus*. During the rest of the year the daily activity was unimodal in all cases. Thermoregulatory behaviour was mainly observed at low air temperatures and this was very rare in *A. erythrurus*. The thermal environment, the physiological constraints but also the non-thermal selective pressures could explain the different temporal strategies of the lizards in this locality.

Key words: Thermal ecology, activity, Lacertidae, *Psammodromus algirus*, *Acanthodactylus erythrurus*.

INTRODUCTION

Psammodromus algirus (Large Psammodromus) and *Acanthodactylus erythrurus* (Fringe-toed Lizard) are two medium-sized lacertids living together in many open Mediterranean areas of Iberian Peninsula and NE Africa (BARBADILLO, 1987). *P. algirus* is more North-spread than *A. erythrurus*, also reaching the SE of France (FRETEY, 1987).

This study is a part of a wider work carried out in a zone of coastal dunes where these species are especially abundant (SEVA, 1984). The thermal and temporal dimensions of the niche of these species have been previously studied in continental areas (POLLO & PÉREZ-MELLADO, 1989).

This study attempts to analyse these features in a warm climate zone, deducing the thermal and activity patterns of every species and determining the inter-intraspecific variation.

MATERIAL AND METHODS

The study area was a mosaic habitat of dunes and moist zones covered by psammophile and halophile vegetation in the delta of the Ebro river (see description in CARRETERO & LLORENTE, 1993b). The climate is littoral Mediterranean, with a long dry season in summer (mean annual rainfall = 548 mm, mean temperature = 16.6°C; see PANAREDA & NUET, 1973).

Psammodromus algirus and *Acanthodactylus erythrurus* are the only saurian species living in this area (abundance ratio: 2:1). Only two size classes (adult and immature) were distinguished for each species since both reached their sexual maturity mostly at the first year of age (unpublished data). See CARRETERO & LLORENTE (1993b) and CARRETERO & LLORENTE (in press) for the limit sizes of the classes.

A monthly sampling was carried out from March 1988 until February 1989 on 100% sunny days without strong wind. A surface of 0.35 Ha (35x100 m) was surveyed in the search for active lizards along all the period of activity (from 6 to 18 hours GMT). A 30 minute transect was done every hour between hour+15' and hour+45'. Prospection effort was kept constant for hours and months (TELLERÍA, 1986).

Usual techniques in thermal ecology were used (AVERY, 1982) with captured animals. Cloacal temperature (TB) in shade was measured no more than 15-20 seconds after the first observation. Air temperature (TA) 50 cm above the ground and substrate temperature (TS) in the place of first sight, were recorded, both also in shade. These temperatures were taken using a digital thermometer with a K type thermocouple (resolution 0.1°C, reading time 1'). Additionally, relative humidity was registered using a metal-band analogic hygrometer with an

	N	X	S	CV	lim(95%)	range
P. algirus						
pooled						
TB	134	31.44	4.27	13.58	±0.72	18.7-41.0
TA	134	22.49	5.06	22.49	±0.86	12.0-33.8
TS	134	26.81	7.62	28.43	±1.29	11.3-45.6
males						
TB	17	31.59	5.93	18.78	±2.82	18.7-41.0
TA	17	22.69	5.51	24.28	±2.62	15.0-33.8
TS	17	28.28	7.69	27.19	±3.65	18.2-42.1
females						
TB	22	34.66	2.57	7.42	±1.07	30.1-38.5
TA	22	25.29	4.54	17.97	±1.90	15.8-32.9
TS	22	29.06	5.78	19.90	±2.42	20.9-45.6
immatures						
TB	95	30.67	3.91	12.76	±0.79	22.6-37.8
TA	95	21.80	4.91	22.52	±0.99	12.0-31.2
TS	95	26.02	7.90	30.37	±1.59	11.3-44.9
A. erythrurus						
pooled						
TB	79	33.10	3.25	9.81	±0.72	24.4-39.4
TA	79	24.09	3.77	15.66	±0.83	14.0-30.6
TS	79	28.72	5.81	20.23	±1.28	18.9-43.2
males						
TB	13	34.29	2.74	7.99	±1.49	30.7-38.6
TA	13	24.33	3.46	14.22	±1.88	17.1-27.7
TS	13	30.94	8.11	26.21	±4.41	18.9-43.2
females						
TB	6	32.05	3.18	9.93	±2.55	29.1-37.6
TA	6	23.63	3.66	15.49	±2.93	19.1-29.7
TS	6	25.68	4.47	17.41	±3.58	18.9-31.6
immatures						
TB	60	33.10	3.33	10.07	±0.84	24.4-39.4
TA	60	24.09	3.90	16.19	±0.99	14.0-30.6
TS	60	28.72	5.24	18.26	±1.33	19.1-41.3

Table 1: Temperatures of the Lacertidae from the Ebro Delta. TB = body temperature. TA = air temperature. TS = substrate temperature. N = sample. X = mean. S = standard deviation. CV = coeficient of variation.

error of ±1%.

The analysis of covariances, ANCOVA (SOKAL & ROHLF, 1981) was used to compare the TB values among groups correcting the effect of environmental temperatures.

Moreover, the number of lizards seen (included those not captured), their class, the hour and the month of the location were registered. Intersexual variation in activity patterns was not considered since sex determination was sure only in captured adults. It should be cosidered that the activity results obtained here derive from two different origins: the total number of lizards and their presence above ground. Besides, individual activity may differ from population.

The behaviour of the individuals observed was divided into two types:

1- Active animals (including locomotion, defence, hunting or breeding).

2- "Basking" animals (in heliothermia).

For the study by seasons, months were grouped as follow:

Winter = December + January + February
Spring = March + April + May
Summer = June + July + August
Autumn = September + October + November

The class "adults" included captured males and females plus non-captured animals which could not be sexed but whose body sizes were large enough.

RESULTS

Temperatures

The descriptive statistics of TB, TA and TS for the captured animals (134 *P. algirus* and 79 *A. erythrurus*), considering the pooled population and the classes, are shown in Table 1. Some interspecific variation was recorded. The TB values adjusted for TS were higher in *A. erythrurus* than in *P. algirus*

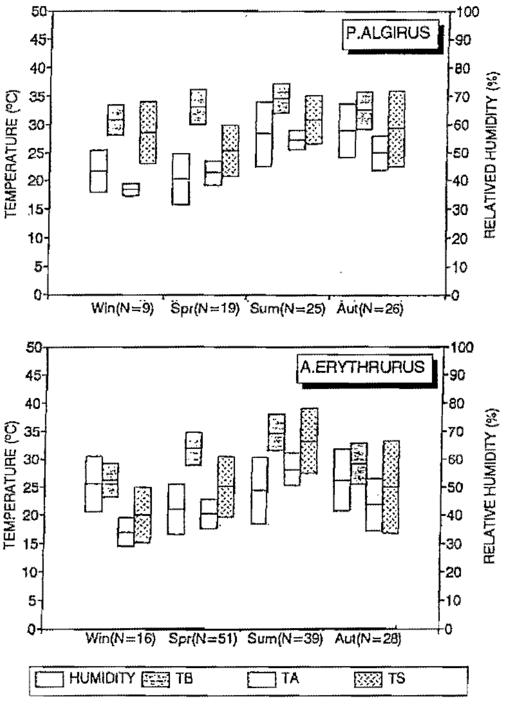

Figure 1: Seasonal variation of the temperatures and the humidity in *P. algirus* (above) and *A. erythrurus* (below) of the Ebro Delta. Horizontal lines represent mean and standard deviation intervals respectively.

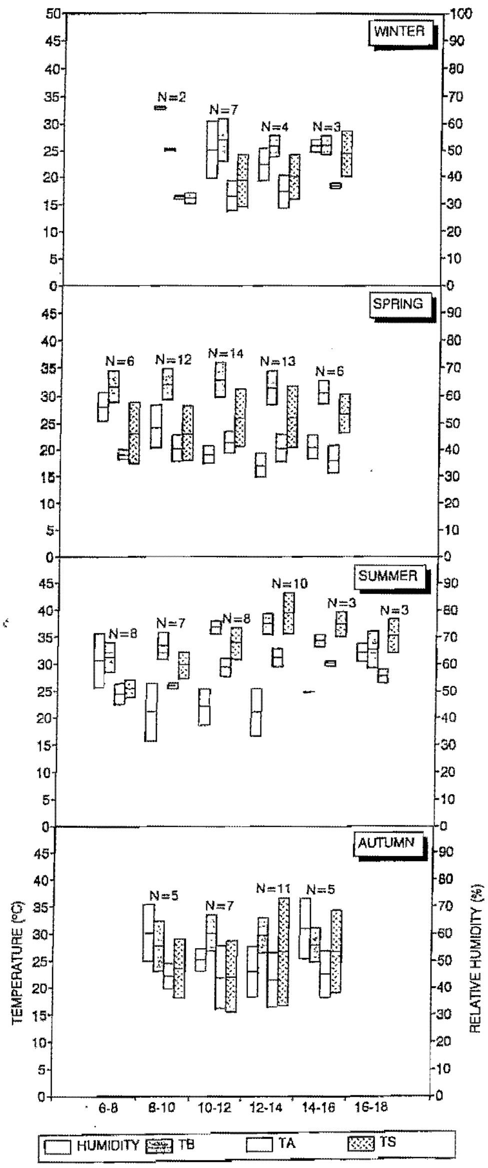

Figure 2: Daily variation of the temperatures and the humidity in *P. algirus*. Data accumulated by seasons and two-hour intervals. Horizontal lines represent mean and standard deviation intervals respectively.

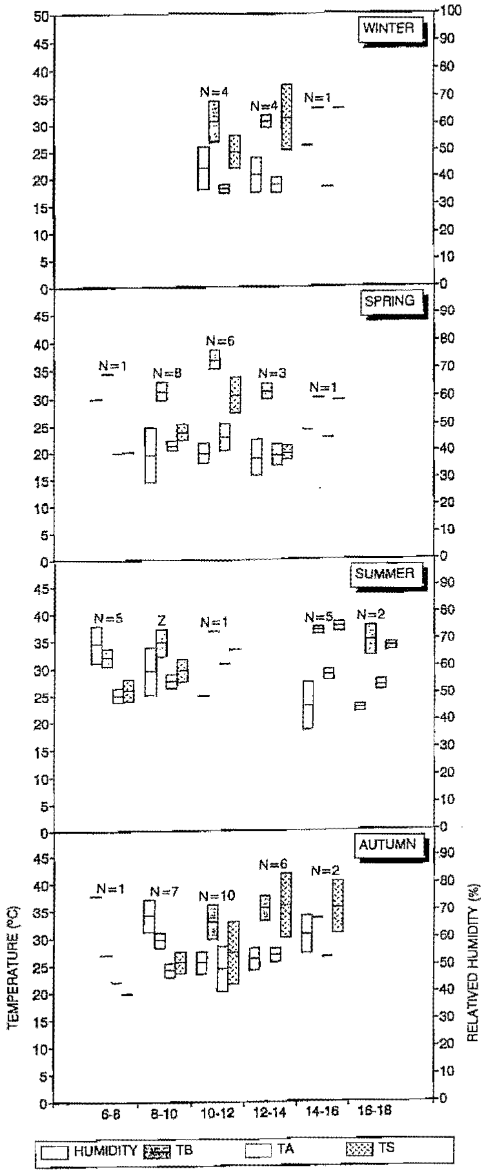

Figure 3: Daily variation of the temperatures an the humidity in *A. erythrurus*. Data accumulated b seasons and two-hour intervals. Horizontal line represent mean and standard deviation interval respectively.

(ANCOVA, $F = 5.089$, $p < 0.05$, for the adjusted means to TS). Nevertheless, the adjusted values for TA did not show differences.

The only intraspecific variation detected was that *P. algirus* females had significantly higher TBs than immatures (ANCOVA, $F = 3.95$, $p < 0.01$, for the adjusted means to TA) o r males (ANCOVA, $F = 8.50$, $p < 0.01$, for the adjusted means to TS). No differences were found in *A. erythrurus*.

The general pattern of annual variation consisted of higher values in summer than in the rest of year (see Figure 1). The increasing order of temperatures was TB, TS and TA. TS approached TB in summer. *P. algirus* showed higher TB-TA residuals in spring than in the rest of the year (ANCOVA, $F = 19.45$, $p < 0.01$, for the adjusted means, no slope differences). If we considered the TB-TS residuals, the pair winter-autumn was higher than the pair spring-summer (ANCOVA, $F = 14.00$, $p < 0.01$, for the adjusted means; no slope differences). In all cases, *A. erythrurus* showed a higher TB value in winter than in the rest of the year. Moreover, it was found that, adjusting for TS, the spring value was higher than summer one (ANCOVA, $F = 8.79$, $p < 0.01$, adjusted means for TA; ANCOVA, $F = 5.52$, $p < 0.01$, adjusted means for TS; no slope differences). No differences in environmental humidity were found among species or seasons.

The daily variations of TB, TA, TS and relative humidity are represented in Figures 2 (*P. algirus*) and 3 (*A. erythrurus*), grouped in periods of two hours. In both cases TB was the higher temperature and followed the TA values with a maximum at midday. TS increased during the day reaching its maximum at the end of the afternoon. In summer, this allowed TS to surpass TC. The humidity tended to be higher at the begining and at the end of the day.

Nevertheless, the differences in temperature were not statistically significant. However, some differences in humidity were detected corresponding to low values at midday. It was observed for *P. algirus* (one way ANOVA, $F_{spring} = 20.66$, $F_{summer} = 7.09$; $p < 0.01$) and for *A. erythrurus* (one way ANOVA, $F_{summer} = 5.76$, $F_{autumn} = 15.32$; $p < 0.01$).

The thermal relations between TB and TA (Table 2) had significant regressions in all the cases except the *A. erythrurus* females. All the slopes were different (t test, $p < 0.01$) from 0 (perfect thermoregulation) and 1 (absolute thermoconformity). All the correlations between TB and TS (Table 2) were also significant (slope

	N	R	SIG. R	regression line
P. algirus				
pooled	134	0.74	**	TC = 0.62 TA + 17.30
		0.68	**	TC = 0.38 TS + 21.13
males	17	0.65	*	TC = 0.70 TA + 15.61
		0.81	**	TC = 0.63 TS + 13.76
females	22	0.65	**	TC = 0.37 TA + 25.25
		0.63	**	TC = 0.28 TS + 26.46
immatures	95	0.76	**	TC = 0.61 TA + 17.32
		0.67	**	TC = 0.33 TS + 22.00
A. erythrurus				
pooled	77	0.53	**	TC = 0.46 TA + 21.97
		0.34	**	TC = 0.34 TS + 23.16
males	11	0.71	**	TC = 0.56 TA + 20.47
		0.75	**	TC = 0.25 TS + 26.40
females	6	0.52	n.s.	
		0.85	*	TC = 0.60 TS + 16.38
immatures	60	0.43	**	TC = 0.43 TA + 22.37
		0.57	**	TC = 0.36 TS + 22.51

Table 2: Correlations and regression lines between body (TB) and air (TA) or substrate (TS) temperatures in the two species of the Lacertidae from the Ebro Delta (* $p < 0.05$, ** $p < 0.01$, n.s. not significant).

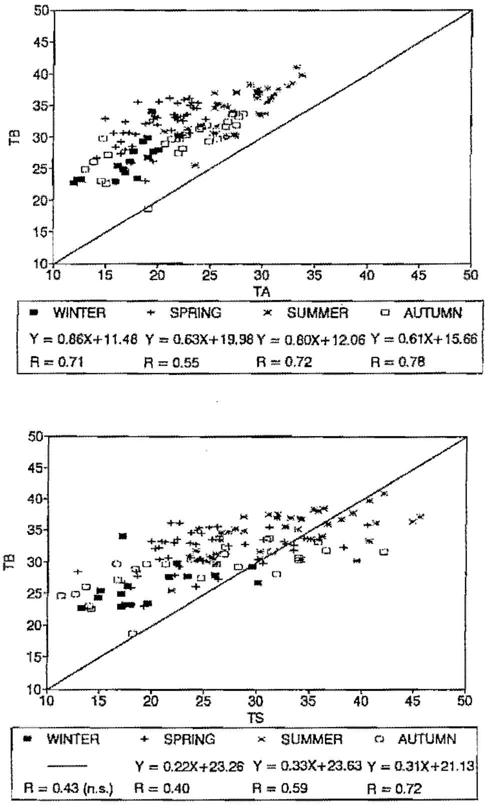

Figure 4: Seasonal variation in the TB-TA (above) and TC-TS (below) relations of *P. algirus*.

different from 0 and 1, t test, $p < 0.01$) in both species and their classes.

The TB-TA slope was higher than TB-TS one in *P. algirus* but not in *A. erythrurus* (parallelism test, $p < 0.01$ when significant). The comparison of the TB-TA (and TB-TS) slopes between both species did not detect significant differences (parallelism tests). Generally, the value of the coefficient of correlation R was higher in the TB-TA regression than in the TB-TS one for the same group. The only intraspecific difference in slope was found in *P. algirus*. The males of this species had lower slope of TC-TS regression than the rest of classes (parallelism test, $p < 0.01$).

The analysis of the slope variation among seasons for the two species (Figures 4 and 5) did not show significant differences. The TB-TA slopes of winter and summer in *P. algirus* and those of summer and autumn in *A. erythrurus* were not significantly different from 1 (t test, $p < 0.01$).

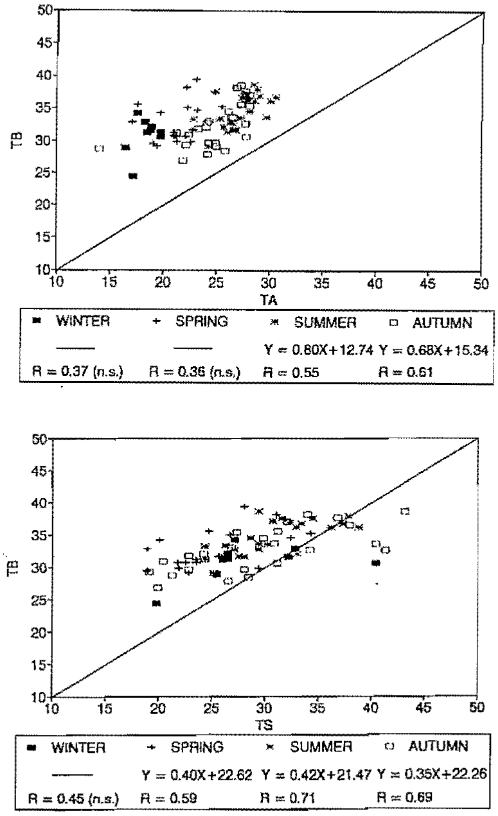

Figure 5: Seasonal variation in the TB-TA (above) and TC-TS (below) relations of *A. erythrurus*.

Activity

202 *P. algirus* and 100 *A. erythrurus* were observed (including captures). The patterns of annual activity of both species were clearly different (Figure 6). *P. algirus* had two equal maxima in spring and autumn. It was found during all the year although the activity decreased in winter. However, *A. erythrurus* interrupted its activity in January and their maxima were in late spring-summer and late summer-autumn. The second one was higher than the first.

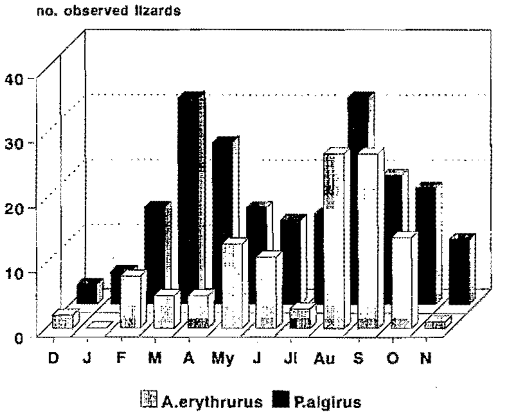

Figure 6: Annual activity of the whole populations of the two Lacertidae.

When this pooled activity was divided by classes, several intraspecific differences appeared. No sex differences were considered because of the small sample.

The adults of *P. algirus* (Figure 7) showed a clear diapause period in winter which lasted form November to February. In March, immediately after the diapause, the adults were mostly males. Immatures were active in winter when weather conditions were suitable and they were absent in mid summer.

Both classes of *A. erythrurus* (Figure 8) had a winter diapause but they did not have equal activity. So, immatures had three more months of activity than adults. These were very scarce in mid summer.

The pattern and the range of daily activity were also different among seasons and between species (Figures 9 and 10).

The total number of active individuals of *P. algirus* (Figure 9) followed a very restricted unimodal distribution (3-4 hours) in winter. In spring and autumn, the pattern was also unimodal but it was wider than in winter. The aestival activity becames more uniform and was

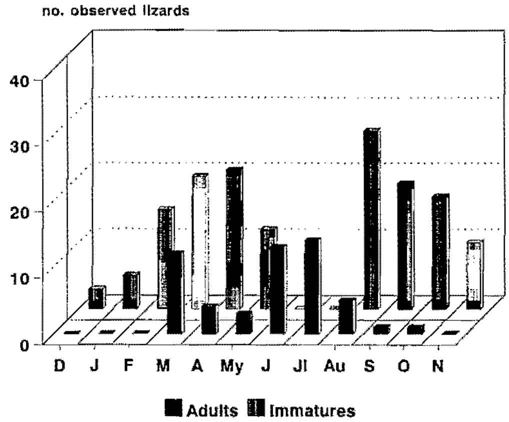

Figure 7: Annual activity of the classes of *P. algirus*.

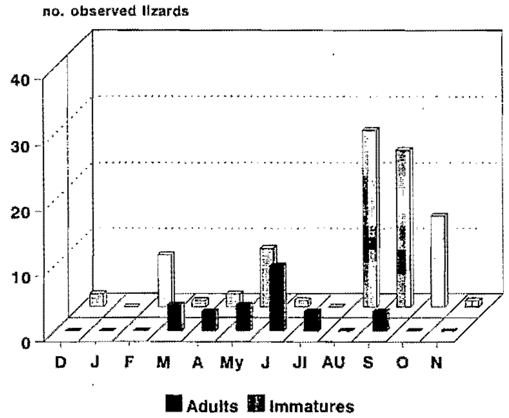

Figure 8: Annual activity of the classes of *A. erythrurus*.

slightly bimodal. The "basking" animals appeared in the coldest hours, i.e. all day in winter and the beginning and at the end of the activity in summer. In spring and autumn, the distribution of these animals followed a bimodal curve with a minimum at midday.

A. erythrurus (Figure 10) showed a more conspicuous pattern with a narrower range than *P. algirus*. Only few individuals were seen in winter at midday. The pattern was unimodal in spring and autumn and strongly bimodal in summer. The activity in the afternoon was always lower than in the morning. The individuals in heliothermia were scarce and appeared at the beginning or the end of the activity in spring and autumn.

The same results divided by classes (Figures 9 and 10) showed only slight differences. When the sample was sufficient, immatures of both species showed more uniform patterns of activity than adults. Generally, the immatures were also the first lizards seen in the morning.

DISCUSSION AND CONCLUSIONS

The first remarkable feature in the results is the high degree of thermophilia in *Acanthodactylus erythrurus*, typical of this genus (Avery, 1982). This is especially remarkable in comparision to *Psammodromus algirus* at the same site. This difference could be associated with the Northern range of distribution in every species (see Barbadillo, 1987) consequence of a cost-benefit optimization of energy and the reproductive success (Saint-Girons & Saint-Girons, 1956). Seva (1984) points out that this trait is determinant for the latitudinal variation in the abundance ratio between these two species in coastal sandy areas.

Working in central Spain, Pollo & Pérez-Mellado (1989) also find differences between these two species but other authors (Seva & Escarré, 1980; Seva 1982) do not find them in the coast of SE Spain (see also Carretero & Llorente, 1991). The cause of this disparity should be attributed to the environment more than to endogenous factors (Malhotra & Thorpe, 1993). In the localities near the Northern boundary of *A. erythrurus* (Central Spain, NE Spain) the TB of this species remains constant in comparison to the Southern localities (Busack, 1976; Seva, 1982, 1984; Pough & Busack, 1978) but reduces its activity range. In contrast, *P. algirus* decrease its TB and remains active. So, the increment of TB to the South in this species is a consequence of the availability of different environmental temperatures (see Pianka, 1970).

The high TB found in the females of *P. algirus* have already been registered (Pollo & Pérez-Mellado, 1989; see also Carretero & Llorente, 1991). Other reproductive factors different from pregnancy (Beuchat, 1986; Heulin, 1987; Braña, 1993) may be involved in this marked difference, which is independent of the thermal environment. The small size effect detected here (see Carretero & Llorente, 1993a, for the discussion of an example) may be in relation to the high environmental temperatures.

Considering now the annual variation (Huey & Pianka, 1977), the high relative values of TB

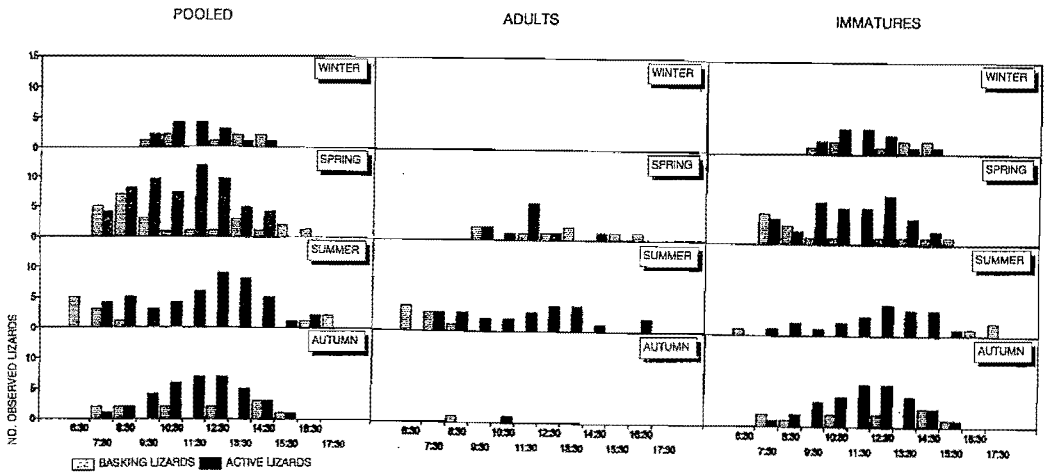

Figure 9: Daily activity considering seasons and classes in *P. algirus*.

in winter should be interpreted as a compensation for the low environmental temperatures (especially in the substrate), but below the selected TB. The situation in summer is inverse. The surprisingly high TB in spring, higher than in autumn, could correspond to a longer period devoted to heliothermia (see activity) during reproduction.

The daily variation of TB confirms the dependence of the environment in the ectotherm species. In the hours with low environmental temperatures, TB decrease but thermal compensation mediated by insolation increase (see activity). At midday, Tb is the highest, near the environmental temperatures, and insolation behaviour is scarce.

As in the deserts, sand can accummulate a great amount of caloric energy during the day (CLOUDSLEY-THOMPSON, 1991) and is an important source of heat for both species in the late afternoon when TA decrease. So, some individuals, especially *P. algirus*, have been observed at the end of the day in tigmothermia with low air temperatures. This fact can also decrease the number of active animals in summer (Figures 6, 7 and 8).

Humidity is a factor afecting the activity of reptiles (BRADSHAW, 1986; HEATWOLE & TAYLOR, 1987; CLOUDSLEY-THOMPSON, 1991) including the Mediterranean Lacertidae (SEVA, 1982; CARRETERO & LLORENTE, 1993a). Although the sample is small, the results indicate the importance of daily variations. In summer, midday is not only the hottest period but also the driest. The humidity could be a stimilus to maintain the activity in unfavourable temperatures, especially at the begining of day when dew is drunk (HEATWOLE & TAYLOR, 1987). Conversely, the water loss is an associated cost to activity when the temperatures are favourable in helio- and eurythermal reptiles (BOWKER, 1993).

The slope of the regression line points out how much TB depends on the environmental temperatures, TA or TS (see HUEY & SLATKIN, 1976). In the case of *P. algirus*, TA, or the solar radiation, is the main (not the only) influence of TB. This confirms this species as heliotherm (AVERY, 1979). However, TB of *A. erythrurus* depends equally on the air and substrate temperatures. In both species but especially in the second one, tigmothermia appears as another compatible behaviour particularly in open areas (PÉREZ-MELLADO, 1992). In this case of *A. erythrurus*, a special tactic is followed (SEVA, 1988), increasing TB gaining heat from substrate inside the burrow before going out and reducing the vulnerability during the basking period and the water loss (see also NAGY, 1991). However, the heat conductance from the substrate does not have a significant role in areas with a dense vegetal coverage as the Mediterranean forests, where *P. algirus* appears to be strictly heliotherm (CARRASCAL & DÍAZ, 1989; DÍAZ, 1991, 1992).

The thermoregulatory efficiency showed by both species was similar. This contrast with the results of POLLO & PÉREZ-MELLADO (1989) who consider *A. erythrurus* to be more independent of TA and a good thermoregulator.

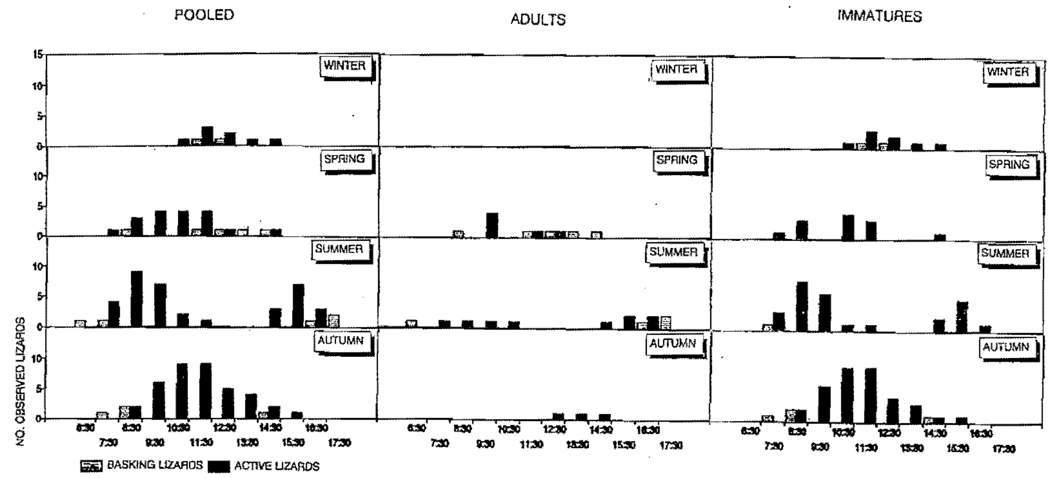

Figure 10: Daily activity considering seasons and classes in *A. erythrurus*.

Other studies corroborate these conclusions in the genus *Acanthodactylus* (BUSACK, 1975; POUGH & BUSACK, 1978; PÉREZ-MELLADO, 1992). However, other authors (Seva, 1984; CARRETERO & LLORENTE, 1991) even indicate *P. algirus* in the Mediterranean coast to be the more efficient than *A. erythrurus*. It is not necessary to invoke physiological differences to explain these changes. The buffer effect of the sea in the temperatures, prevent coastal areas from reaching extreme temperatures. Consequently, no high temperatures are reached and lizards are not found in hipothermia (see results) as in the continental climate. When the thermal stress decrease it is not strange that the high thermoregulatory potentiality does not become apparent (see MALHOTRA & THORPE, 1993). Nevertheless, *A. erythrurus* is inactive at low environmental temperatures while *P. algirus* remains active devoting most of its time to insolation (see results).

The slight tendency in the adults to thermoregulate more than immatures could be explained in terms of ethological or physiological differences (see CARRETERO & LLORENTE, 1993a). The ecological consequence is that immatures are more thermoconformers (and generally these TBs are lower) than adults. In comparison to adults, the growing lizards invest more in seaching for food than in thermoregulation (see AVERY, 1984; CASTILLA & BAUWENS, 1991). It has been demonstrated (LEE, 1980) that thermoregulatory efficiency depends on the physiological considition of the animal (fat reserves) adjusting to a cost/benefit model (HUEY & SLATKIN, 1976; HUEY, 1982). Annual results show than a long-term thermoregulation may take also place (see DAMME *et al.*, 1987; CARRETERO & LLORENTE, 1993a). A different range of body temperatures is the main way of thermal modulation in the lizard species of the Ebro Delta (AVERY, 1978; BOWKER *et al.*, 1986; HERTZ, 1992). It has been considered to be more conservative than the variation of thermoregulatory efficiency (AVERY, 1982; GILLIS, 1991). The latter is more dependent on the environment and both species present changes at geographical level.

The activity of the diurnal lizards in temperate regions is highly dependent on temperature since favourable periods are scarce (GRANT & DUNHAM, 1988). However, it should always be considered as a result of a compromise between positive (feeding, drinking, reproduction) and negative (predation, competition) pressures (HUEY, 1982; PIANKA, 1986; HEATWOLE & TAYLOR, 1987). Compared to other temperate regions, Mediterranean ecosystems are warm enough allow different strategies of activity in the same environment. This is an example. *Psammodromus algirus* remains active all the year exploiting the scarce resources in winter (CARRETERO & LLORENTE, 1993b). This has been recorded on the Mediterranean coast and in the South of Spain (AMORES *et al.*, 1980; SEVA, 1984; MELLADO & OLMEDO, 1987; CARRETERO & LLORENTE, 1991). However, this species shows a diapause period in zones under the continental influence (MELLADO *et al.*, 1975; PÉREZ-MELLADO, 1982, POLLO & PÉREZ-MELLADO, 1989) in association with extreme temperatures in winter. Immatures are usually the only individuals active in this season, while adults remain inactive following a more conservative strategy (maybe under physiological control). The early appearance of males seems to be general in those members of the familiy Laceridae which have a winter diapause (NULAND & STRIJBOSCH, 1981; NICHOLSON & SPELLERBERG, 1989; SALVADOR, 1987) and it is thought to be in relation to territorial marking. The larger number of individuals was found, as expected, in the periods of reproduction and new-births. The postreproductive decrese in summer has been explained as a way of escaping predation (ROSE, 1981; ETHERIDGE & WIT, 1993) and avoiding a dry, resource scarcity period (FUENTES, 1976). *Acanthodactylus erythrurus* follows a more conservative strategy, especially marked in the adults. In the Northern boundary of its range, the activity patterns must be adjusted to the environmental constraints. So, the diapause has been detected in other Northern areas (POLLO & PÉREZ-MELLADO, 1989) but not in warmer localities (BUSACK, 1976; BUSACK & JACKSIC, 1982; SEVA, 1984). Nevertheless, the interruption of activity is longer in this species, as a consequence of physiological limits because the Fringe-toed lizard stops feeding at low temperatures (BUSACK, 1976). Its high voluntary temperatures could also produce energetic and hydric deficits that could only be balanced when there is abundance of food (Bowker, 1993; ETHERIDGE & WIT, 1993). The interpretation on the maximum of activity is the same as in the former species with a slight delay in the first one. The patterns of daily activity registered here are those typical of the diurnal lizards in warm-temperate zones (AVERY, 1978; ADOLPH & PORTER, 1993): bimodal in the warm season and unimodal the rest of the year. Thermoregulation appears in the coldest hours (see DÍAZ, 1991, 1992; CARRETERO & LLORENTE, 1993b). However, two comments have to be made.

1-The activity of *P. algirus* is not clearly bimodal possibly due to its capacity to use shaded microhabitats of plants (see Seva, 1984; CASAS-ANDREU & GURRIOLA-HIDALGO, 1993) if the summer temperatures are moderate. However, a marked bimodal pattern appears in the places where the summer is very hot (CARRASCAL & DÍAZ, 1989; POLLO & PÉREZ-MELLADO, 1989).

2-Basking was rarely observed in *A. erythrurus* because thermoregulation begins inside the burrow (see above). The behaviour is not rare in desert lizards (MCGINNIS & DICKSON, 1967) and confirms the conservative condition of this species.

The activity pattern of inmmatures in comparison to adults seems to be general (see CARRETERO & LLORENTE, 1993b for an extensive discussion). Their high surface/volume index in comparison to adults (HAILEY, 1982) and some ethological constraints can produce the same result. As seen above, immatures behave as opportunists and increase the range of activity devoting less time to thermoregulation and more to feeding. When growing is not so important both are inverse (AVERY, 1984; CASTILLA & BAUWENS, 1991). Other possibilities such as the minimization of competence or predation of the conespecific adults (MELLADO *et al.*, 1975; ROSE, 1981) cannot be ruled out *a priori*.

Hence, not only a thermal explaination, but also a general energetic model of costs and benefits should explain the activity strategies of lizards in Ebro Delta. This model should consider lizards under pressure from two opposite forces: on one hand, the energy demands for maintenance, growing and reproduction; on the other hand, the biotic (competence, predation) and abiotic constraints (STEPHENS & KREBS, 1986).

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REFERENCES

ADOLPH S. C. & PORTER, W. P. (1993): Temperature, activity and lizard life histories. *Am. Nat.*, 142(2): 273-295.

AMORES, F.; FRANCO, A.; HIRALDO, F. & MELLADO, J. (1980): Actividad invernal de reptiles en el Suroeste español. *Actas II Reunión Iberoamericana de Conservación y Zoología de Vertebrados*. Cáceres (Spain).

AVERY, R. A. (1978): Activity patterns, thermoregulation and food consumption in two sympatric species (*Podarcis muralis* and *P. sicula*) from central Italy. *Journal of Animal Ecology*, 47: 143-158.

AVERY, R. A. (1979): *Lizards: A study in thermoregulation*. Studies in Biology 109. E. Arnold Pub. Ltd. 56 pp.

AVERY, R. A. (1982): Field studies of body temperatures and thermoregulation. pp. 93-

166, *in*: C. GANS & F. H. POUGH (eds.) *Biology of the Reptilia. Vol. 12. Physiology C*. Academic Press. London.

AVERY, R. A. (1984): Physiological Aspects of Lizard Growth: The Role of Thermoregulation. *Symp. zool. Soc. Lond.*, 52: 407-424.

BARBADILLO, L. J. (1987): *La guía de Incafo de los Anfibios y Reptiles de la Península Ibérica, Islas Baleares y Canarias*. INCAFO Madrid. 694 pp.

BEUCHAT, C. (1986): Reproductive influences on the Thermoregulatory Behavior of a Live-bearing Lizard. *Copeia*, 1986(4): 971-979.

BOWKER, R. G. (1993): The thermoregulation of the lizards *Cnemidophorus exanguis* and *C. velox*: some consequences of high body temperature. pp. 117-132, *in*: J. W. WRIGHT & L. J. VITT (eds.), *Biology of Whiptail Lizards (genus* Cnemidophorus*)*. Oklahoma Mus. Nat. Hist. Norman, Oklahoma.

BOWKER, R. G.; DAMSCHROEDER, S.; SWEET, A. M. & ANDERSON, D. K. (1986): Thermoregulatory behavior of the North American lizards *Cnemidophorus velox* and *Sceloporus undulatus*. *Amphibia-Reptilia*, 7: 335-346.

BRADSHAW, S. D. (1986): *Ecophysiology of Desert Reptiles*. Academic Press. Sydney. 324 pp.

BRAÑA, F. (1993): Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos*, 66: 216-222.

BUSACK, S. D. (1975): Biomass estimates and thermal environment of the fringe-toed lizard *Acanthodactylus pardalis*. *Brit. J. Herpetol.*, 5(4): 457-459.

CARRASCAL, L. M. & DÍAZ, J. A. (1989): Thermal ecology and spatio-temporal distribution of the Mediterranean lizard *Psammodromus algirus*. *Holarct. Ecol.*, 12: 137-143.

CARRETERO, M. A. & LLORENTE, G. A. (1991): Thermal ecology of three lacertid lizards in a Mediterranean beach. Communication presented to the 6th O.G.M. Societas Europaea Herpetologica. Budapest (Hungary).

CARRETERO, M. A. & LLORENTE, G. A. (1993a): Ecología térmica y actividad en una población costera de *Psammodromus hispanicus*. *Rev. Esp. Herp.*, 7: 21-32.

CARRETERO, M. A. & LLORENTE, G. A. (1993b): Feeding of two sympatric lacertids in a sandy coastal area (Ebro Delta, Spain). pp. 155-172, *in*: Böhme, W.; Pérez-Mellado, V.; Valakos, E. & Maragou, P. (eds.). *Lacertids of the Mediterranean Region*. Hellenic Zoological Society.

CARRETERO, M. A. & LLORENTE, G. A. (in press): Morfometria de *Psammodromus algirus* i *Acanthodactylus erythrurus* al Delta de l'Ebre. *Butll. Parc Natural Delta de l'Ebre*, 8.

CASAS-ANDREU, G. & GURRIOLA-HIDALGO, M. A. (1993): Comparative ecology of two species of *Cnemidophorus* in coastal Jalisco, Mexico. pp. 133-155, *in*: J. W. WRIGHT & L. J. VITT (eds.), *Biology of Whiptail Lizards (genus* Cnemidophorus*)*. Oklahoma Mus. Nat. Hist. Norman, Oklahoma .

CASTILLA, A.M. & BAUWENS, D. (1991): Thermal biology, microhabitat selection, and conservation of the lizard *Podarcis hispanica atrata*. *Oecologia (Berl.)*, 85: 366-374.

CLOUDSLEY-THOMPSON, J. L. (1991): *Ecophysiology of Desert Arthropods and Reptiles*. Springer Verlag. Berlin. 203pp.

DAMME; R. VAN; BAUWENS, D.; CASTILLA, A. M. & VERHEYEN, R. F. (1987): Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. *Herpetologica*, 43(4): 405-415.

DÍAZ, J. A. (1991): Temporal patterns of basking behaviour in a Mediterranean lacertid lizard. *Behaviour*, 118(1-2): 1-14.

DÍAZ, J. A. (1992): Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus*. *Herpetologica*, 48(3): 293-300.

ETHERIDGE, K. & WIT, L. C. (1993): Factors afecting activity in *Cnemidophorus*. pp. 151-162, *in*: J. W. WRIGHT & L. J. VITT (eds.), *Biology of Whiptail Lizards (genus* Cnemidophorus*)*. Oklahoma Mus. Nat. Hist. Norman, Oklahoma.

FRETEY, J. (1987): *Guide des Reptiles de France*. Hatier, Paris. 255pp.

FUENTES, E. R. (1976): Ecological convergence of lizard communities in Chile and California. *Ecology*, 57: 3-17.

GILLIS, R. (1991): Thermal biology of two populations of Red-chinned Lizards (*Sceloporus undulatus erythrocheilus*) living in different habitats in Southcentral Colorado. *J. Herpetol.*, 25(1): 18-23.

GRANT, B. W. & DUNHAM, A. E. (1988): Thermally imposed constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, 69(1): 167-176.

HAILEY, A. (1982): Choice of substrate and heating rate in *Lacerta vivipara*. *British Journal of Herpetology*, 6: 207-213.

Heatwole, H. T. & Taylor, J. (1987): *Ecology of Reptiles*. Surrey Beatty & Sons Pty Limited. 325pp.

Hertz, P. E. (1992): Evaluating thermal resource partitioning. By sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. *Oecologia*, 90: 127-136.

Heulin, B. (1987): Temperature Diurne d'Activité des Males et des Femelles de *Lacerta vivipara*. *Amphibia-Reptilia* 8: 393-400.

Huey, R. E. (1982): Temperature, physiology, and the ecology of reptiles. pp. 25-91, *in*: C. Gans & F. H. Pough (eds.) *Biology of the Reptilia. Vol. 12. Physiology C.* Academic Press. London.

Huey, R. B. & Pianka, E. R. (1977): Seasonal variation in the thermoregulatiry behavior and body temperature of diurnal Kalahari lizards. *Ecology*, 58: 1066-1085.

Huey, R. B. & Slatkin, M. (1976): Costs and benefits of lizard thermoregulation. *Quaterly Rev. Biol.*, 51: 363-384.

Lee, J. C. (1980): Comparative thermal ecology of two lizards. *Oecologia (Berl.)*, 44: 171-176.

Malhotra, A. & Thorpe, R. S. (1993): An experimental field study of a eurytopic anole, *Anolis oculatus*. *J. Zool. Lond.*, 229: 163-170.

McGinnis, S. M. & Dickson, L. L. (1967) Thermoregulation in the Desert Iguana *Dipsosaurus* dorsalis. *Science*, 156: 1090-1091.

Mellado, J.; Amores, F.; Parreño, F. F. & Hiraldo, F. (1975): The structure of a Mediterranean lizard community. *Doñana. Acta Vertebrata*, 2(2): 145-160.

Mellado, J. & Olmedo, G. (1987): Actividad invernal en poblaciones de lagartos de la zona subtropical. *Mediterránea Ser. Biol,*. 9: 5-13.

Nicholson, A. M. & Spellerberg, I. F. (1989): Activity and home range of the lizard *Lacerta agilis* L. *Herpetological Journal*, 1: 362-365.

Nuland, G. J. Van & Strijbosch, H. (1981): Annual Rhythmics of *Lacerta vivipara* Jacquin and *Lacerta agilis agilis* L. (Sauria, Lacertidae) in the Netherlands. *Amphibia-Reptilia*, 2: 83-95.

Panareda, J. M. & Nuet, J. (1973): El clima i les aigües dels Països Catalans. pp. 69-102, *in*: *Geografia física dels Països Catalans*. Ed. Ketres, Barcelona.

Pérez-Mellado, V. (1982): Estructura de una taxocenosis de Lacertidae (Sauria, Reptilia) del Sistema Central. *Mediterránea Ser. Biol.*, 6: 39-64.

Pérez-Mellado, V. (1992): Ecology of lacertid lizards in a desert area of eastern Morocco. *J. Zool. Lond.*, 226: 369-386.

Pianka, E. R. (1970): Comparative autoecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology*, 51: 703-720.

Pianka, E. R. (1986): *Ecology and Natural History of Desert Lizards*. Princeton University Press. New Jersey. 207pp.

Pollo, C. J. & Pérez-Mellado, V. (1989): Activity and thermoregulation on three mediterranean species of Lacertidae. *Herpetological Journal*, 1: 343-350.

Pough, F. H. & Busack, S. D. (1978): Metabolism and activity of the spanish fringe-toed lizards (Lacertidae: *Acanthodactylus erythrurus*). *J. Thermal Biology*, 3: 203-205.

Rose, B. (1981): Factors afecting activity in *Sceloporus virgatus*. *Ecology*, 62(3): 706-716.

Saint-Girons, H. & Saint-Girons, M. C. (1956): Cycle d'activité et thermorégulation chez les reptiles (Lezards et Serpents): *Vie et Milieu*, 7: 133-226.

Salvador, A. (1987): Actividad del lagarto verdinegro (*Lacerta schreiberi*) (Sauria: Lacertidae). *Mediterránea Ser. Biol.*, 9: 41-56.

Seva, E. (1982): *Taxocenosis de lacértidos en un arenal costero alicantino*. Tesis doctoral. Universidad de Alicante. 317pp.

Seva, E. (1984): Reparto de recursos entre dos especies psammófilas de saurios, *Acanthodactylus erythrurus* y *Psammodromus algirus*. Arenal costero de Alicante. *Mediterránea Ser. Biol.*, 7: 5-25.

Seva, E. (1988): Estímulos térmicos y conductas de adquisición de calor en la actividad de *Acanthodactylus erythrurus* (Sauria: Lacertidae): Comunicacion presentada al II Congreso Nacional de Herpetología. Salamanca (España).

Seva, E. & Escarré, A. (1980): Distribución espacial y temporal de *Acanthodactylus erythrurus* (Sauria, Lacertidae) en un arenal costero alicantino. *Mediterránea Ser. Biol.*, 4: 133-162.

Sokal, R. R. & Rohlf, F. J. (1981): *Biometry*. W. H. Freeman and Company, San Francisco. 776pp.

Stephens, D. W. & Krebs, J. R. (1986): *Foraging theory*. Monographs in Behaviour and Ecology. Princeton University Press. Princeton. 247pp.

Tellería, J. L. (1986): *Manual para el censo de los vertebrados terrestres*. Raices. Madrid.