

SOURCES OF COLOUR PATTERN VARIATION IN MEDITERRANEAN *PSAMMODROMUS ALGIRUS*

by

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ABSTRACT

Colour pattern and its relation to sex, size and season were investigated in three coastal populations of *Psammodromus algirus* from NE Spain. Eight pattern variables, as well as body size and reproductive parameters, were recorded for 430 specimens. Results show that yellow head pattern was present in both males and females and depended on body size and locality. Furthermore, its seasonal variation was associated with reproductive activity in males. Orange infralabials appear almost exclusively in adult males. Blue ocelli constitute a potential size signal in intraspecific interactions, especially in males. The attainment of sexual maturity modified tail colour (antipredatory) and dorsolateral stripes (cryptic). Bright spots on hindlimbs varied between sites. Colour pattern is interpreted as a trade-off between different selective pressures including crypsis and intraspecific interactions. Most pattern variation is due to body size differences and only secondarily to sexual dimorphism. A hypothesis invoking differences in social system is proposed to explain the striking differences between these populations and those from Central Spain.

KEY WORDS: colour pattern, Lacertidae, *Psammodromus algirus*, sexual dimorphism.

INTRODUCTION

Colour patterns in reptiles have been interpreted as an adaptive compromise between often conflicting selective pressures arising from social, predatory, antipredatory, thermoregulatory and other functions (reviewed in COOPER & GREENBERG, 1992). However, such compromises are poorly documented and most explanations of chromatic variation are more often speculative. Recent studies emphasise the role of colour variation in lizard behaviour (OLSSON, 1993, 1994a, b; CARPENTER, 1995a, b; MAYNARD-SMITH, 1996; SINERVO & LIVELY, 1996). However, little is known about the nature of this variation and its relation to other morphological features.

Lacertid lizards are usually brightly coloured and 38% of the species studied show chromatic sexual dimorphism (COOPER & GREENBERG,

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1992). Although olfactory stimuli are also clearly involved, visual cues play a determinant role in the social behaviour of these lizards (KRAMER, 1937; KITZLER, 1941; COOPER & GREENBERG, 1992). This is the case for the lacertid *Psammodromus algirus*, the most common lizard in the Mediterranean regions of the Iberian Peninsula, SE France and NW Africa. It occupies a wide variety of open or semi-open habitats (BARBADILLO *et al.*, 1999) associated with medium-high plant cover (CARRASCAL *et al.*, 1989). A pattern variation described for the males of this species (MELLADO & MARTÍNEZ, 1974), has been reported to be associated with differences in behaviour (DÍAZ, 1992; SALVADOR *et al.*, 1996a). However, during an ecological study of three populations in NE Spain, preliminary observations on colour pattern differed from these results. Since data on reproductive condition and biometry were already available (CARRETERO & LLORENTE, 1993, 1993/94, 1997b), this paper aims to: 1) describe the pattern variation of the populations analysed associated with sex, body size, season and locality; 2) correlate this variation with body and reproductive condition; and 3) discuss the possible differences with other populations previously studied.

MATERIALS AND METHODS

The study sites were three coastal sandy areas of NE Spain (not more than 250 km apart) covered by psammophile vegetation (25-50%): Aiguamolls de l'Empordà (U.T.M. grids 31TEG1075/0975/0974), Torredembarra (31TCF6857) and the Ebro Delta (31TCF1810) (for environmental data see CARRETERO & LLORENTE, 1997b). During 1986 and 1987, a total of 430 *Psammodromus algirus* were collected in monthly samplings and sacrificed humanely. Snout-vent length (SVL) of the lizards was measured with a digital calliper to the nearest 0.01 mm and several pattern variables were recorded (see below). Sex and sexual maturity were determined after dissection by inspection and measurement of the reproductive organs (testis/ovary weight, epididymis diameter and weight of fat bodies (for details see CARRETERO & LLORENTE, 1997b). Two size classes were distinguished: adult (>55 mm for both sexes in the three sites) and immature (see CARRETERO & LLORENTE, 1993, 1993/1994, 1997b). Adult males and females were not dimorphic in body size but larger in Aiguamolls de l'Empordà than in the other two sites (CARRETERO & LLORENTE, 1997b). Only immatures remained active throughout the year while adults showed winter diapause (CARRETERO & LLORENTE, 1995, 1997b). The reproductive period lasted from March-April to July (CARRETERO & LLORENTE, 1997b).

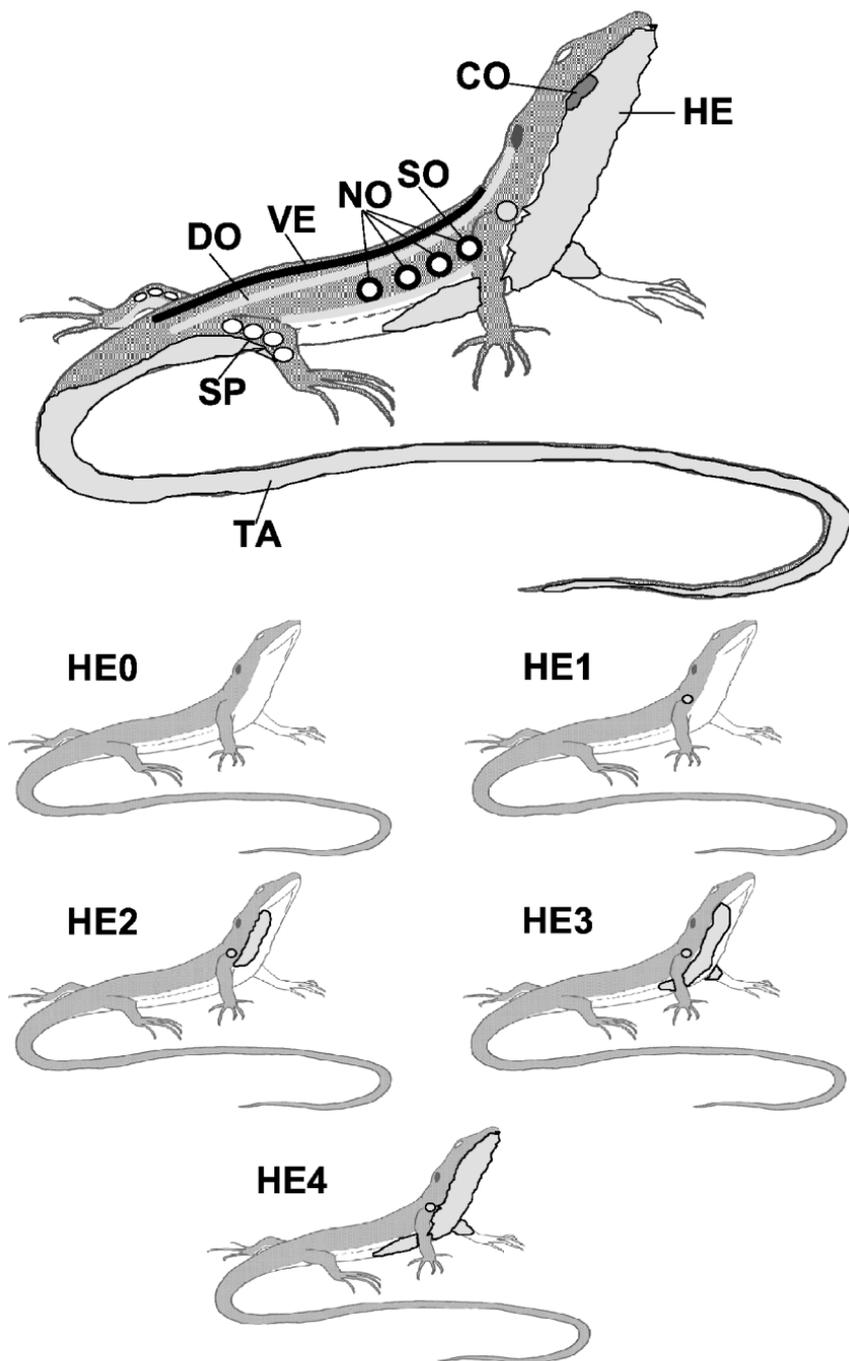


Fig. 1. Representation of the pattern variables analysed (see table 1).

TABLE 1
Colour pattern variables analysed.

Var.	Description and variable states
HE	Extension of the yellow head pattern (HE0 = absent/HE1 = spot over the forelimb/HE2 = HE1 + throat sides/HE3 = HE2 + forelimbs/HE4 = HE3 + chin + chest).
HE*	Rearrangement of HE (HE0 + 1 = low-pigmentation/HE2 + 3 + 4 = high-pigmentation).
CO	Presence of orange commissures (<i>i.e.</i> rear infralabial scales) (CO0 = no/CO1 = yes).
NO	Total (both sides) number of blue ocelli on the flanks (NO0 = none/NO1 = 1-2/NO2 = 3-4/NO3 = 4-6/NO4 = 6).
SO	Total (both sides) number of blue scales composing all these ocelli (SO0 = none/SO1 = 1-4/SO2 = 5-8/SO3 = 9-16/SO4 = 16).
TA	Presence of orange tail colouration (TA0 = absent/TA1 = weak/TA2 = marked).
VE	Presence of dark vertebral stripe (VE0 = absent/VE1 = weak/VE2 = marked).
DO	Colour of the dorsolateral stripes (DO0 = white, whitish/DO1 = yellowish/DO2 = bright yellow).
SP	Presence of bright spots on hindlimbs (SP0 = absent/SP1 = weak/SP2 = marked).

Eight colour pattern variables showing intraspecific variation were analysed (see fig. 1 and table 1 for description and character states). Univariate comparisons were made with log-linear models. Influence of body size was tested in two ways: categorical variables were used as factors for an ANOVA of SVL and quantitative variables were correlated with SVL using Spearman R. Multivariate analysis was performed through Multiple Correspondence Factorial Analysis (MCFA, LEBART *et al.*, 1984) due to the categorical nature of most variables. This analysis presents both individual and variable states simultaneously (BISQUERRA, 1989). The estimations of the variance explained by the factorial axes were calculated from the transformed eigenvectors by Benzecri's method (BENZECRI, 1979; BISQUERRA, 1989). The possible differences between the centroids of the groups (sites, seasons, sexes, and size classes) were evaluated using MANOVA of the factorial axes projections (CARRETERO & LLORENTE, 1997a).

RESULTS

The results of the log-linear analyses of different factors on colour pattern are shown in table 2. Table 3 shows the degree of dependence of each variable on body size.

Head pattern. The extension of the bright yellow area was highly variable among adults but, with rare exceptions, it did not appear in immature individuals. Adults of both sexes that showed the most extensive colour patterns were larger than the others (fig. 2; tables 2 and 3). Intersexual differences appeared in Torredembarra, females being the most coloured.

In order to detect possible seasonal differences in adults and due to the low sample size, head patterns were dichotomously grouped into low- and high-pigmented (table 1). Seasonal and site variation in this trait was significant (table 2). Most high-pigmented males and females

TABLE 2

Log-linear models analysing sex, class and site variation of the categorical pattern variables. See table 1 for the meaning of the variable abbreviations.

Log-linear models		Interaction with:								
Var.	log-linear model	site			sex			class		
		χ^2	d.f.	<i>p</i>	χ^2	d.f.	<i>p</i>	χ^2	d.f.	<i>p</i>
HE	HE-class/ class-site/ sex	5.13	2	n.s.	4.34	1	0.04	160.61	1	$1.02 \cdot 10^{-36}$
CO	CO-sex/ CO-class/ class-sex	0.6	2	n.s.	34.58	1	$4.12 \cdot 10^{-36}$	109.99	1	$1.08 \cdot 10^{-25}$
TA	TA-class/ TA-sex	1.59	2	n.s.	10.87	1	$9.81 \cdot 10^{-4}$	30.29	1	$3.74 \cdot 10^{-8}$
VE	site/VE/sex	0.33	2	n.s.	0.13	1	n.s.	1.8	1	n.s.
DO	DO-class/ class-site/ class-sex/ DO-site	19.62	2	0	1.03	1	n.s.	158.87	1	$2.07 \cdot 10^{-36}$
SP	SP-site/class	14.64	2	0	0.07	1	n.s.	0.91	1	n.s.
		site			sex			season		
HE* (adults)	HE* -site/HE* -season/ sex-season	8.43	2	0.01	0.68	2	n.s.	14.69	2	0.002

TABLE 3
Relationships between pattern variables and body size.

Var. class	Aiguamolls E.			Torredembarra			Ebro Delta			
	d.f.	<i>F</i>	<i>p</i>	d.f.	<i>F</i>	<i>p</i>	d.f.	<i>F</i>	<i>p</i>	
ANOVA SVL by states										
HE	Ad.%%	4,25	6.05	0.001	4,23	4.47	0.008	4,27	6.00	0.001
	Ad.&&	4,28	5.60	0.001	2,24	5.96	0.002	4,25	7.00	$6 \cdot 10^{-4}$
	Im.%%	1,47	4.84	0.033	1,51	3.45	n.s.	–	–	–
	Im.&&	1,27	14.01	$8 \cdot 10^{-4}$	3,42	3.16	0.034	–	–	–
CO	Ad.%%	1,28	15.60	$4 \cdot 10^{-4}$	1,26	19.47	10^{-4}	1,30	4.21	0.05
	Ad.&&	1,31	5.60	0.001	1,27	0.50	n.s.	1,28	6.70	0.015
	Im.%%	–	–	–	1,51	3.45	n.s.	–	–	–
	Im.&&	–	–	–	–	–	–	–	–	–
TA	Ad.%%	2,27	5.95	0.007	2,25	6.34	0.006	2,29	7.66	0.002
	Ad.&&	2,30	7.48	0.002	2,26	1.73	n.s.	2,27	8.93	0.001
	Im.%%	1,47	0.02	n.s.	1,51	6.64	0.013	2,38	9.31	$5 \cdot 10^{-4}$
	Im.&&	2,26	0.70	n.s.	1,44	4.01	n.s.	1,28	2.76	n.s.
VE	Ad.%%	2,27	0.46	n.s.	2,25	0.98	n.s.	2,29	2.62	n.s.
	Ad.&&	2,30	1.79	n.s.	2,26	0.66	n.s.	2,27	0.79	n.s.
	Im.%%	2,46	0.30	n.s.	2,50	5.99	0.005	2,38	0.32	n.s.
	Im.&&	2,26	4.14	0.027	2,43	1.09	n.s.	2,27	0.54	n.s.
DO	Ad.%%	2,27	5.03	0.014	2,25	0.83	n.s.	2,29	0.16	n.s.
	Ad.&&	1,31	0.76	n.s.	2,26	3.20	n.s.	2,27	4.22	0.025
	Im.%%	1,47	6.01	0.018	1,51	23.92	10^{-4}	2,38	3.60	0.037
	Im.&&	2,26	3.57	0.042	1,44	6.69	0.013	1,28	19.42	10^{-4}
SP	Ad.%%	2,27	0.12	n.s.	2,25	3.69	0.039	2,29	0.95	n.s.
	Ad.&&	2,30	0.60	n.s.	2,26	0.46	n.s.	2,27	0.64	n.s.
	Im.%%	2,46	0.03	n.s.	2,50	0.54	n.s.	2,38	1.81	n.s.
	Im.&&	2,26	2.78	n.s.	2,43	1.26	n.s.	2,27	0.88	n.s.
Correlations with SVL										
		n	Rs	<i>p</i>	n	Rs	<i>p</i>	n	Rs	<i>p</i>
NO	Ad.%%	30	0.16	n.s.	28	0.44	0.019	32	0.52	0.002
	Ad.&&	33	-0.07	n.s.	29	0.30	n.s.	30	0.09	n.s.
	Im.%%	49	0.43	0.002	53	0.58	$6 \cdot 10^{-6}$	41	0.32	0.042
	Im.&&	29	0.11	n.s.	46	0.41	0.004	30	0.25	n.s.
SO	Ad.%%	30	-0.06	n.s.	28	0.44	0.02	32	0.36	0.042
	Ad.&&	33	-0.09	n.s.	29	0.21	n.s.	30	0.03	n.s.
	Im.%%	49	0.44	0.001	53	0.58	$5 \cdot 10^{-6}$	41	0.35	0.024
	Im.&&	29	0.11	n.s.	46	0.42	0.004	30	0.30	n.s.

were observed in spring (fig. 3). When analysing the patterns of seasonal variation in the three populations separately, males (fig. 4) and females (not represented) from Aiguamolls lost yellow pigmentation earlier than those from the other localities. Moreover, in adult males, significant

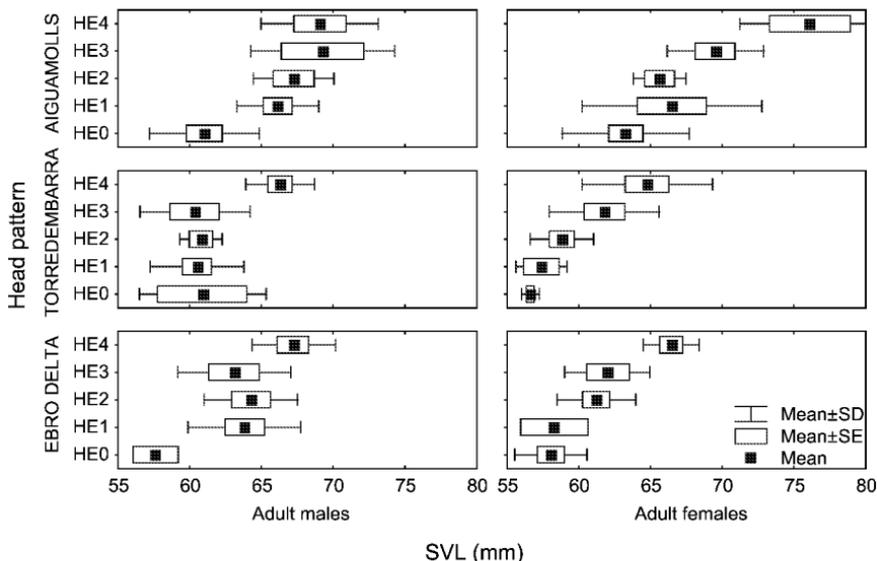


Fig. 2. Variation of head pattern in relation to body size (SVL) of the adults of both sexes in the three populations studied. See table 1 for the description of pattern categories.

correlations (on a monthly basis) between head pattern and relative testis weight, epididymis diameter and weight of fat bodies (residuals with SVL, both log-transformed) were only found in Aiguamolls ($R_s = 0.45$, 28 d.f., $p = 0.01$; $R_s = 0.43$, 28 d.f., $p = 0.01$; $R_s = -0.45$, 28 d.f., $p = 0.01$; respectively). In adult females, a significant negative correlation between head pattern and relative weight of fat bodies was also found in the same locality ($R_s = -0.40$, 31 d.f., $p = 0.01$) but no correlation with ovary weight was detected.

Commissures. Orange infralabials occurred almost exclusively in adult males (table 2). Only a low number of adult and one immature females showed that feature, and pigmented males were usually larger than non-pigmented (table 3). Neither site nor season had any influence on this character.

Ocelli. Both the number of ocelli and the number of scales composing them were higher in adults than in immatures of the same sex. Adult males showed more ocelli and more blue area on their body sides than adult females (3-way ANOVA site, sex and class; number of ocelli; sex $F_{1,418} = 107.70$, $p = 1.32 * 10^{-22}$, class $F_{1,418} = 201.06$, $p < 0.000001$, sex \times class $F_{1,418} = 69.35$, $p = 1.19 * 10^{-15}$; number of scales; sex

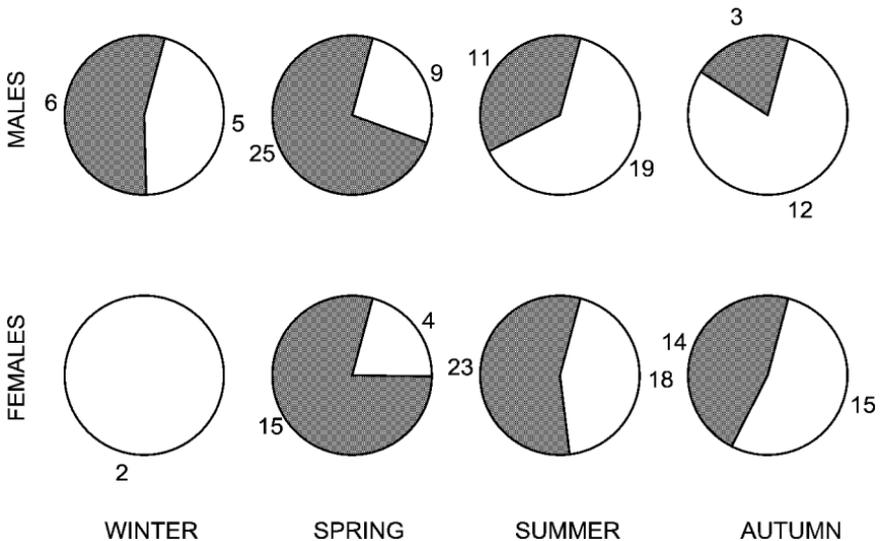


Fig. 3. Seasonal variation of the head pattern of adult males and females (three populations pooled). Numbers: sample; solid area: high-pigmented lizards (see table 1).

$F_{1,418} = 114.85$, $p = 7.68 * 10^{-24}$, class $F_{1,418} = 198.28$, $p < 0.000001$, sex \times class $F_{1,418} = 75.77$, $p = 7.43 * 10^{-17}$, no other results significant). Both variables were correlated with body size in males but not in females (table 3). No other variation was found.

Tail colour. The orange tail colour was strongly and negatively correlated with body size (tables 2 and 3). Colour persisted more in females than in males of the same size. No other variation was found.

Vertebral stripe. A great deal of individual heterogeneity was detected in all the classes. Some large lizards even lacked this stripe. However, neither seasonal nor site variation was observed (table 2).

Dorsolateral stripes. The colour of the dorsolateral stripes changed from white to yellow after attaining sexual maturity (table 2). Furthermore, the stripes of females from Aiguamolls were less intensely yellow than the others. No seasonal or sexual differences were detected.

Spotted hindlimbs. The bright spots appearing on hindlimbs varied between populations but not between classes and was independent of body size and season (tables 2 and 3). Individuals belonging to all classes were more spotted in Ebro Delta than in the other populations.

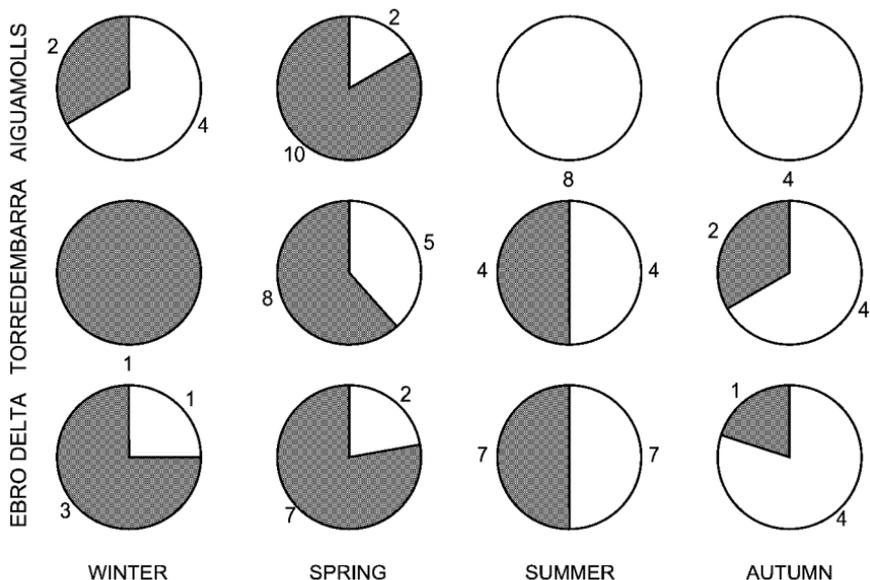


Fig. 4. Seasonal variation of head pattern of adult males in the three populations studied. Numbers: sample; solid area: high-pigmented lizards (see table 1).

Global analysis of the variables. The representation of the pattern variables and the individuals by means of Multiple Correspondence Factorial Analysis (MCFA) appears in figure 5. Only the projections on the first two factorial axes were considered since together they explained 94.1% of total variance (table 4). The relative contribution of each pattern variable to the inertia explained by both axes is also shown in table 4. The variables HE, CO, TA and VE were associated with the first axis but not with the second. In contrast, the variables NO and SO (ocelli) were mainly associated with axis 2 and secondarily with axis 1. Axis 1 was more strongly correlated with SVL than axis 2 ($R^2 = 0.38$, $p < 0.0001$, 457 d.f. vs. $R^2 = 0.01$, $p < 0.02$, 457 d.f.). Thus, axis 1 depended on body size whereas axis 2 depended on sexual dimorphism.

MANOVA was performed on the first two axis projections using site, season, sex and class as classification factors. Since adults were almost completely inactive in winter, this season was excluded from the analysis. Results showed significant differences in overall colour pattern when considering all four factors separately (table 5). Moreover, interactions season*sex and sex*class were detected. When analysing the first five axes results were essentially the same, but the significance of site variation increased and the interaction site*season*class appeared. Immatures (negative values of axis 1 in fig. 5) were more homogeneous than adults

TABLE 4

Percentages of the variance explained by the first two axes of the Multiple Correspondence Factorial Analysis (MCFA) and relative contribution of each pattern variable to the inertia explained by each axis.

	Axis 1	Axis 2
Variance explained	84.7	9.4
variable		
HE	15.4	1.8
CO	14.6	3.5
NO	18.3	42.3
SO	18.5	43.0
TA	14.7	4.1
VE	15.5	3.2
DO	2.6	0.4
SP	0.3	1.6

TABLE 5

Multivariate Analysis of the Variance (MANOVA) performed on the axes 1-2 and 1-5 of the Multiple Correspondence Factorial Analysis (MCFA). The winter sample was excluded because not all classes were active during this season.

Effect	Axes 1-2			Axes 1-5		
	Wilk's lambda	d.f.	<i>p</i>	Wilk's lambda	d.f.	<i>p</i>
site	0.95	4604	0.002	0.87	10598	$1.24 \cdot 10^{-5}$
season	0.95	4604	0.006	0.93	10598	0.02
sex	0.86	2302	$3.11 \cdot 10^{-10}$	0.86	5299	$8.09 \cdot 10^{-9}$
class	0.47	2302	< 0.000001	0.45	5299	< 0.000001
site*season	0.99	8604	n.s.	0.92	20992	n.s.
site*sex	1	4604	n.s.	0.99	10598	n.s.
season*sex	0.97	4604	0.04	0.95	10598	n.s.
site*class	0.99	4604	n.s.	0.98	10598	n.s.
season*class	0.93	4.604	0.0002	0.9	10598	0.0008
sex*class	0.8	2302	$4.27 \cdot 10^{-15}$	0.8	5299	$2.43 \cdot 10^{-13}$
site*season*sex	0.96	8604	n.s.	0.93	20992	n.s.
site*season*class	0.96	8604	n.s.	0.89	20992	0.02
site*sex*class	0.97	4604	n.s.	0.95	10598	n.s.
season*sex*class	0.98	4604	n.s.	0.96	10598	n.s.
site*season*sex*class	0.99	8604	n.s.	0.95	20992	n.s.

(positive values) which diverged in axis 2. Along that axis, adult males tended to reach positive values whereas adult females remained close to zero, as did immatures.

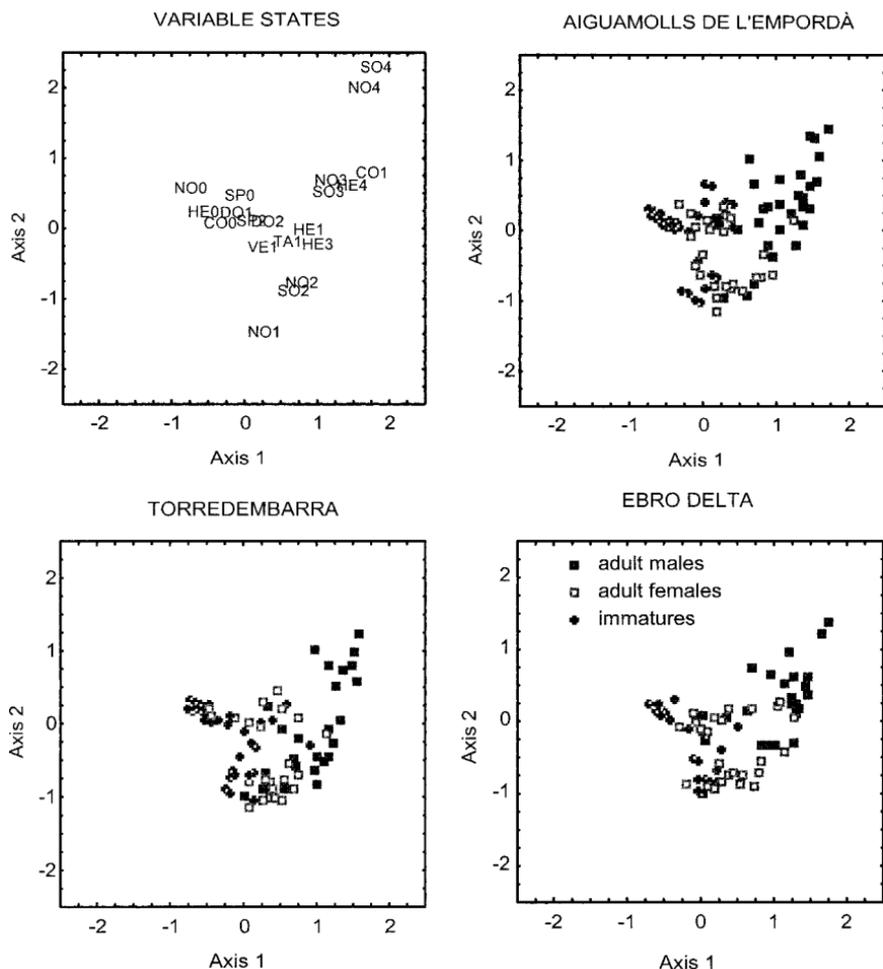


Fig. 5. Plot of the pattern variables and individuals of the populations and classes of *Psammodromus algirus* by means of the Multiple Correspondences Factorial Analysis (MCFA) using the first two axes. See table 1 for the meaning of the variable state abbreviations.

DISCUSSION

Results indicate that some previous statements on colour pattern of *Psammodromus algirus* observed in Central Spain are not general to the Mediterranean populations analysed here. The main divergence observed concerns head pattern. Orange heads were described from Morocco by GALÁN (1931), who observed pigmented and non-pigmented adults

living together and erroneously associated this variation with taxonomical differences. MELLADO & MARTÍNEZ (1974), analysing a sample of lizards from SE Spain, concluded that reddish-orange colouration of variable extension occurred exclusively in males and was related to sexual activity. Finally, DÍAZ (1993), analysing animals from Central Spain, confirmed this hypothesis and detected a correlation between the extension of colour and body size (DEARING & SCHALL, 1994). Moreover, DÍAZ *et al.* (1994) and SALVADOR *et al.* (1996c) detected an association with testis development and testosterone levels in the same populations (see also LEMOS-ESPINAL *et al.*, 1996). However, some females showing light orange colouration had already been reported even in Central Spain (Pollo, unpubl.).

Present results show that, at least in populations from NE Spain, the main head pattern is bright yellow (see also PÉREZ-QUINTERO, 1996) and is equally (or even more) frequent in females than in males. Both sexes show essentially the same pattern of seasonal variation and size dependence. Head pattern is associated with body condition in both sexes but with reproductive condition only in males (DÍAZ, 1994; LEMOS-ESPINAL *et al.*, 1996).

The significance of yellow throats is difficult to interpret. Since bright colourations are potentially costly in terms of survival (MARLER & MOORE, 1988; but see OLSSON, 1993), when present, they probably result from other selective pressures such as social or reproductive interactions (COOPER & GREENBERG, 1992). The ventral position of these marks means that they remain hidden except when the lizard raises its forebody in the presence of a conspecific (MELLADO & MARTÍNEZ, 1974; PÉREZ-MELLADO & GALINDO-VILLARDÓN, 1986; GALÁN, 1995). Relationships between nuptial male colouration and other parameters such as fighting ability and reproductive success have been demonstrated in other lacertids (OLSSON, 1994a) suggesting that this may act as a status signal minimising male-male aggression. Testosterone treatment applied to males from Central Spain induced bright head colours, increased their aggressive behaviour against other males and made them overlap spatially more females (SALVADOR *et al.*, 1996c). However, no evidence was provided that females either recognised those males or selected them by this trait (SALVADOR *et al.*, 1996c; MARTIN & FORSMAN, 1999; see also COOPER & BURNS, 1987; COOPER & VITT, 1993). The abundance of pigmented females in the populations studied reinforce such results. However, this female pattern does not fit completely any of the functions proposed by COOPER & GREENBERG (1992) since it is found also in males.

In NE Spain, orange colouration, when present, is restricted to the rear infralabial scales in the largest males. It is noteworthy that the pigmented area is only exposed when the mouth is open. This trait could be equivalent to that found in the least pigmented lizards from Central Spain (MELLADO & MARTÍNEZ, 1974; DÍAZ, 1993). Several authors (SALVADOR *et al.*, 1996c; SALVADOR & VEIGA, 2001) propose a polygynous mating system for *P. algirus* in Central Spain based on the territoriality of the dominant, brightly-coloured males which overlapped the home ranges of females and subordinate males, all dull-coloured. If such a model is also valid in NE Spain, two explanations for the significance of head pattern could apply. First, if the yellow is equivalent to orange in Central Spain, then a parallel female hierarchy should occur. Second, if only orange signals dominance, then all the adult males in NE Spain would be non-territorial (SALVADOR *et al.*, 1996c) and the function of yellow colour would remain unsolved. Both possibilities would imply a different breeding system (monogamy or other) in these coastal populations. Similar situations have been reported for other lacertids, invoking different selective pressures, especially density (THORPE & BROWN, 1989; THORPE, 1996; THORPE *et al.*, 1996; BAUWENS & CASTILLA, 1998; GALÁN, 1995, 2000).

In contrast with the previous characters, the blue blotches appearing on the body sides are permanently visible for other lizards and remain constant throughout the year. This trait could be used as a generic size signal in intraspecific interactions (not necessarily between adults nor related to breeding), probably avoiding direct aggression (OLSSON, 1994a). The stronger association between ocelli and body size, which is more evident in males than in females, suggests that size recognition is more important in males and extends outside the breeding period. Histological evidence indicates that this could be due to morphological constraints. In contrast with yellow, orange and red pigmentations, blue colour in Lacertidae is mainly due to iridophores (KLAUSEWITZ, 1964), which produce structural colours and are more stable than chromatophores. This would not prevent some seasonal variation in shine and hue of the ocelli (as reported by SEVA, unpubl., in *P. algirus*; see also MORRISON *et al.*, 1995, 1996) but it would keep constant the number of scales composing them, at least between two consecutive skin renewals. This would also explain why manipulations of throat colour in a male *P. algirus* did not succeed in shifting the responses of conspecifics from those expected for his size (MARTIN & FORSMAN, 1999).

Conspicuous caudal marking is common in other ground-dwelling lizards found in open habitats where they can easily be sighted by predators (ARNOLD, 1988). Although other alternatives have been pointed out

(COOPER & VITT, 1985; COOPER & GREEBERG, 1992), the main function of bright tail colouration is to enhance the effectiveness of caudal autotomy as antipredator behaviour (*i.e.* distracting predator towards the rear part of the body, ARNOLD, 1988). The restriction of this trait to immatures may reflect their greater vulnerability to predation. On the other hand, the loss of colour at maturity may be due to the negative effects of tail loss on reproduction (VITT & COOPER, 1986). Moreover, tail loss has been reported to decrease the size of home range and to reduce access to females and the reproductive success in adult male *Psammotromus algirus* (SALVADOR *et al.* 1996a, b). These findings correspond with the faster loss of tail colour in males than in females observed here.

The presence of a vertebral stripe is not the rule in *P. algirus* (BARBADILLO *et al.*, 1999) but it is common in the populations living in steppes and coastal sandy areas (SEVA, unpubl.; BONIS & GENIEZ, 1996; pers. obs.). Striped morphs in lizards are usually associated with crypsis in grassy habitats (VAN DEN WINDEN, 1995; but see FORSMAN & SHINE, 1995 for alternative explanations). In fact, gramineae and rushes were the main refuges selected by adult *P. algirus* in the study areas (CARRETERO & LLORENTE, 1997a). Immatures were always darker and less striped than adults, used greater diversity of microhabitats (CARRETERO & LLORENTE, 1997a) and were probably under different predation pressures (see BEATSON, 1976; KING, 1993). The presence of dorsolateral stripes could also intensify the dorsal crypsis (*i.e.* the striped pattern). Nevertheless, yellow stripes seem to be a signal for sexual maturity, especially for males. With regard to the presence of spotted hindlimbs, since no evident adaptive explanation can support the high frequencies found in the lizards from Ebro Delta, it is tentatively attributed to local genetic variation.

The MCFA analysis provides an acceptable representation of the overall colouration pattern in these populations. Most of the colour variation (about 85%) can be explained in terms of body size changes (axis 1), not only from immatures to adults, but also within adults. On the other hand, sexual dimorphism (axis 2) was due to features appearing in males and absent in females and immatures. They represented only a minor part (<10%) of the pattern differences found since, as already stated above, some features which proved to be dimorphic in Central Spain (MELLADO & MARTÍNEZ, 1974), are quite similar for both sexes in NE Spain. Finally, site and seasonal differences are very small (included in the remaining 5%). It must be remembered that no sexual size dimorphism was detected in the studied populations (CARRETERO & LLORENTE, 1997b). In contrast, MELLADO & MARTÍNEZ (1974) found males to be larger than females. Although chromatic and sexual size dimorphism

appear together, it remains unclear if colour is due to size or both are the consequence of a third factor. Evidence found here is contradictory. Orange restricted to commissures may well result from the small body size of the specimens from NE Spain (CARRETERO & LLORENTE, 1997b). However, as suggested above, other different factors must be considered to explain the yellow pigmentation present in both sexes.

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