

ENVIRONMENTAL INFLUENCES ON MULTI-MODAL SIGNALLING ACROSS IBERIAN ROCK LIZARD POPULATIONS

It is impossible to interpret multiple signalling outside the context of the environment, given that signal perception is highly dependent of habitat physical characteristics or social characteristics, and animals may evolve to communicate through multiple sensory modalities in response to fluctuating or heterogeneous environments. We explored whether physical or social environment may drive the use of visual or chemical sexual signals across 15 populations of *I. cyreni* lizards with microgeographic environmental differences. We found that microhabitat characteristics, such as higher cover of rocky outcrops, bare soil and farther distances from refuges, may promote chemical signalling, whereas higher cover of plants may promote visual signalling. Intrasexual competition (reflected by male head size) or territoriality (reflected by habitat heterogeneity) may promote both the development of visual and chemical signalling. Our results showed that physical and social characteristics of lizards' environment may play an important role in the evolution of multimodal signalling, and suggested that the equilibrium between each sensory modality in each population may depend on the interaction social environment and microhabitat characteristics.

Keywords: signal evolution, sexual selection, multiple signals, sensory modalities, chemical signals, visual signals, lizards

It has been known for years that multiple sensory systems (or modalities) are important for communication (Darwin 1872; Tinbergen 1959). However, the relationships among different sensory channels have been little studied but until recently (Partan and Marler 2005). Many animals produce and respond to displays made up of multiple components (for review see Rowe 1999; Candolin 2003). These signals have been described as being 'multicomponent' (Hölldobler 1995; Johnstone 1995; Kodric-Brown and Nicoletto 2001), or 'multimodal' where components occur in more than one sensory system (Guilford and Dawkins 1991; Rowe and Guilford 1999; Elias et al. 2005; Partan and Marler 2005).

Most theoretical interest has focused upon explaining multiple sexual displays,

exploring the conditions under which multiple handicaps or Fisherian traits might evolve (reviewed in Candolin 2003). However, focusing purely on the honesty of signals, omits other selection pressures over the design features of signals that enhance effective communication (Alberts 1992; Endler and Basolo 1998; Endler et al. 2005; Hebets and Papaj 2005). Many studies show that signal differences among different species or populations are consistent with the idea that selection has favoured more effective stimulation of receivers that differs under differing environments (e.g., Endler and Houde 1995; Endler and Théry 1996; Boughman 2001; Leal and Fleishman 2004). Most of these studies rely on differences in exclusively one sensory system, but accurate and efficient mate recognition and assessment

may also require that individuals of different species or populations use the sensory system best suited for their mating environments. However, the role of the environment in the evolution of sexual signals perceived under different sensory modalities remains, to our knowledge, almost unexplored.

The goal of this study was to explore whether differences in physical or social environment may drive the use of sexual signals based on different sensory systems in a lizard species with multisensory (visual and chemical) signalling. Studies using comparative methods have investigated the evolutionary histories of visual (Macedonia 2001; Ord et al. 2001; 2002; Stuart-Fox and Ord 2004; Ord and Stuart-Fox 2006; Stuart-Fox et al. 2007) and chemical signalling (Kratovichil and Frynta 2002; Pincheira-Donoso et al. 2008) in various groups of lizard species. However, no previous studies have explored the evolutionary interaction of both traits in relation to physical or social environment. Moreover, most of studies have involved comparisons across species. A within-species comparison may provide a better test of the effect of habitat as it provides greater control of other factors that can influence signalling, such as phylogenetic history (Ryan and Brenowitz 1985) or body size, which may affect the size, type, and transmission distance of visual cues (Bradbury and Vehrencamp 1998; Podos 2001). Thus we examined, across 15 populations of Carpetane rock lizards (*Iberolacerta cyreni*), the relationships between the use of chemical and visual signalling, the most prominent lizard sensory systems, and different physical and social environmental factors.

The Carpetane rock lizard, *I. cyreni* (formerly *Lacerta monticola cyreni*) is a lacertid lizard found at mountains in Central Spain, occupying sparsely vegetated rocky areas at high elevations (above 1700 m) (Martín 2005). For a variety of reasons,

I. cyreni is an excellent candidate to test environment effects on sensory systems. First, mountain topography and historical climatic changes have led to different isolated populations, which are geographically very close, but isolated by the presence at lower altitudes of surrounding pine forests where this lizard does not occur (Martín 2005). This fragmented population system is especially adequate to examine the topic of the present study because provides geographically isolated lizard populations which presumably experience varying environmental conditions (e.g., with different sun orientations, vegetation types or topographical features). Second, *I. cyreni* use both visual and chemical signals in a mating context. As in many lacertid lizards, male *I. cyreni* show conspicuous blue spots on lateral-ventral scales which reflect ultraviolet (UV) light (Arribas 2001; Thorpe and Richard 2001) and are used in male contests (Molina-Borja et al. 1998; López et al. 2004). Chemical signalling is also well-developed in this species, where scent marks from femoral pores of males convey information about social status (Aragón et al. 2001; Martín and López 2007, 2008; Martín et al. 2007) or about traits used by females in mate choice (Martín and López 2000, 2006a,b; López et al. 2002, 2003). The femoral pores could be considered as a secondary sexual trait subjected to sexual selection (Martín and López 2000) and the number of femoral pores may vary considerably among species (e.g., only two or three pores occur on each leg in *Sceloporus horridus*, whereas the others *Sceloporus* species have several times that many). An increase in the number of femoral pores implies an increase in the amount of holocrine femoral glands which secrete pheromone components (Escobar et al. 2003; Martín and López 2006a). Thus, we used population average number of blue spots as an indirect measure of the intensity of use of visual signalling, and population average number of femoral pores as

an indirect measure of the intensity of use of chemical signalling.

To examine environmental influences on sexual signalling we characterized the microhabitats available and selected by lizards in each population. The relative conspicuousness of a signal can be strongly affected by how well it transmits through the local environment, that is, how well it can be seen or smelled from a distance. For instance, habitat openness or vegetation cover affects light conditions, which may exert strong selection on visual signals such as colour patches or ornaments to maximize conspicuousness (Marchetti 1993; Endler, 1992, 1993; Endler and Thery 1996; Leal and Fleishman 2004). Predators may also exploit signals to localize prey (Endler 1978, 1980; Zuk and Koluru 1998), and habitat openness can in turn determine the vulnerability of signalers to visual predators. However, other environment characteristics, such as humidity, could drive the use of chemical signalling (Alberts 1992). For instance, hydrophobicity makes the waxy pore secretions difficult to detect by olfactory organs and humidity increases the degradation of femoral pore secretions in substrate scent marks, reducing their durability. Therefore, changes in physical habitat characteristics could drive the use of signals from one sensory system to another.

Social environment may also confer different advantages associated to each sensory modality. Spacing patterns may influence the distance over which a signal must function and social factors, as intrasexual competition, also influence signalling (Andersson 1994; Blumstein and Armitage 1997; Ord et al. 2001; 2002). In lizards, "space distribution" is mediated by refuge availability (Van Damme et al. 1989; Lemos-Espinal and Ballinger 1995; Martín and Salvador 1997) and thermoregulation requirements (Huey 1982; Sorci et al. 1996; Bashey and Dunham 1997). Thus, the distribution and abundance of refuge

and thermoregulatory appropriate microhabitats should predict male and female spatial distribution in space and time and may have promoted different social scenarios. Encounters between males during the breeding season often escalate into fights with vigorous biting (Martín and López 2007; Martín et al. 2007). Male head size clearly indicate a dimorphism in bite performance (Herrel et al. 1999), suggesting that intrasexual competition may be a driving force for the head sexual dimorphism (Olsson 1992; Stamps et al. 1997; Molina-Borja et al. 1998; Gvozdík and Van-Damme 2002; Baird et al. 2003). Thus, we also used relative head size of males as indirect measure of among population social differences (Stuart-Fox and Ord 2004).

In short, we examined the relationship between two of the most prominent display sexual traits of lizards, chemical and visual signals, and physical or social environment characteristics across 15 isolated populations of *I. cyreni* lizards with microgeographic environmental differences.

Methods

Study area

We did field work during spring-summer 2003 at 15 different localities covering the geographic distribution of Iberian rock lizards in the Guadarrama Mountains (Central Spain) (Martín 2005) (Table 1). We searched for lizards by walking between 07:00 and 14:00h (GMT) with consistent sampling effort in all microhabitats and study localities. We captured adult male and female lizards by noosing. The body size distribution of lizards in the samples reflected the adult size distributions typical for these populations.

Lizard characteristics

We weighed all captured lizards with a Pesola spring scale (to the nearest 0.1 g), and measured their snout-vent-length (SVL) with a ruler to the nearest 1 mm, and their head length, width and depth with a digital calliper to the nearest 0.05 mm. We used a principal component analysis (PCA) to reduce the three head measures (length, width and depth) and SVL (all log transformed) to a single component representing relative head size (hereafter 'head size'). We considered that higher levels of intramale competition would result in relatively greater head sizes of males, and consequently in a higher degree of sexual dimorphism.

We also counted in all captured males the number of femoral pores on the right and left hind legs with the aid of a magnifying glass, and the number of ventral blue spots on the right and left sides of the belly (2–4 counts performed per animal in both cases). Numbers of blue spots and femoral pores did not change in the same individual within the same reproductive season (unpublished data).

Microhabitat characteristics

We also recorded microhabitat data at the point where each captured male lizard was first sighted. Four 1 m transects were laid out radiating from this point along the four cardinal directions, and records made at 5, 10, 15, 25, 75 and 100 cm. We noted the presence at substrate level of grass, leaf litter, bare sandy soil, small rocks (< 25 cm), medium rocks (25-100 cm), large rocks (100-200 cm), or rocky outcrops and cliff walls (> 200 cm). Plant contacts at 5, 10, 25 and 50 cm height were also noted, using a calibrated stick, for grasses (e.g., *Festuca indigesta*, *Koeleria caudata*), ferns (e.g., *Cryptogramma crispa*, *Asplenium trichomanes*, *Dryopteris oreades*) and small herbaceous semi-perennial plants (<50 cm height; e.g., *Senecio pyrenaicus*, *Digitalis purpurea*, *Doronicum carpetanum*), large woody bushes (*Cytisus oromediterraneus* and *Juniperus comunnis*) or trees (*Pinus sylvestris*). We also noted whether the sample point was in a sunny or shaded location, the presence of canopy tree cover above each point, and the distance to the

Table 1. Male lizard average characteristics (mean ± SE) and altitude of lizards' populations.

Population	SVL (cm)	Head size (PC scores)	Femoral pores	Blue spots	Altitude (m)
Casa Derruida	75.4 ± 1.9	0.74 ± 0.3	19.1 ± 0.4	6.1 ± 0.8	1970
Cueva	72.7 ± 1.1	0.52 ± 0.2	18.6 ± 0.2	5.4 ± 0.8	1935
Siete Picos	77.5 ± 1.7	0.27 ± 0.4	18.7 ± 0.5	8.7 ± 1.0	2080
Trigo	75.5 ± 1.2	0.75 ± 0.2	18.0 ± 0.4	8.7 ± 0.7	1965
Minguete	77.6 ± 1.4	0.60 ± 0.2	18.6 ± 0.4	7.4 ± 0.8	2010
Bola	73.8 ± 1.3	-0.03 ± 0.2	17.9 ± 0.3	5.6 ± 0.9	1940
Cabrillas	73.9 ± 2.1	-0.29 ± 0.4	17.9 ± 0.3	5.6 ± 1.1	1960
Dos Castillas	75.5 ± 2.6	-0.49 ± 0.5	17.8 ± 0.4	6.4 ± 1.1	2150
Antenas	77.3 ± 1.4	0.13 ± 0.2	17.8 ± 0.3	6.3 ± 1.2	2250
Cancho Negro	80.0 ± 1.3	0.57 ± 0.2	18.2 ± 0.3	7.7 ± 0.8	2170
Valdemartín	79.3 ± 1.1	0.46 ± 0.2	18.2 ± 0.4	6.0 ± 0.9	2270
Topillo 1	71.5 ± 0.7	-0.07 ± 0.1	18.0 ± 0.3	6.6 ± 1.2	1880
Topillo 2	72.1 ± 0.8	-0.19 ± 0.2	17.7 ± 0.4	5.4 ± 1.0	1887
Valdesquí	76.3 ± 1.5	-0.01 ± 0.2	18.5 ± 0.4	3.7 ± 0.7	1960
La Peñota	82.7 ± 1.1	0.54 ± 0.2	18.5 ± 0.3	7.4 ± 1.0	1940

nearest potential refuge (rock crevice or protective vegetation cover). This procedure provided 24 sample points per lizard location and allowed us to calculate the percent cover values of each habitat variable (i.e., % contacts with each substratum, vegetation type and sunny spots, and the mean distance to the nearest refuge; for a similar sampling methodology see Martín and Salvador, 1997). To estimate the availability of microhabitats in a large area surrounding that actually used by lizards, we used a similar procedure to record the same variables as described above at 2, 3 and 4 m. along the four cardinal directions from each sample point.

We used a principal component analysis (PCA) to reduce the microhabitat variables to a smaller number of independent components. Original data (number of contacts) were normalized by means of square-root transformation. Because of the large number of "zero" observations for many variables, some transformed data were not normally distributed, but otherwise met the assumptions of a PCA. Deviations from normality do not necessarily bias the analysis, as long as the distributions are reasonably unskewed (Legendre and Legendre 1998). Thus, we considered that our transformations reduced the skew sufficiently to minimize the risk of bias in the analysis. Only principal components (PCs) with eigenvalues that explained more than 5% of the total variation were retained for further analysis. Thus, the PCA for microhabitats available and those used by lizards produced six components that together accounted for the 67.43 % of the variance (Table 2). Then we calculated the mean values of each PC for microhabitats available and used for each population to use them as predictor variables in posterior analyses. Finally, altitude captures much of the variation in factors such as temperature, humidity, and wind intensity (Escobar et al. 2001; Pincheira-Donoso et al. 2008) which may influence chemical

signalling (Alberts 1992). Thus, we noted the altitudinal midpoint for each population to be used as an additional predictor variable.

We also calculated for each population the average difference between PC scores describing microhabitat available and used by lizards. We considered that this measure may affect the intensity of intramale competition for occupying selected microhabitats, such that competition would be greater in populations where microhabitats used differed more from available ones (i.e., where preferred microhabitats represented a smaller proportion of the total available area).

Relationships between habitat and lizard characteristics

We used general linear regression models (GRM) to estimate relationships between mean numbers of blue spots or femoral pores of males and environmental variables (microhabitat PCs, altitude and head size). Each type of signal (numbers of blue spots or femoral pores) was analysed separately as the dependent variable, using as potential predictors the physical environmental variables (i.e., all the PCs extracted from microhabitat, altitude and SVL) or the social environmental variables (head size and the magnitude of the differences between microhabitat available and used for each PC).

All variables were log transformed prior to analyses. Data normality was verified by Shapiro-Wilk's tests, and tests of homogeneity of variances (Levene's test) showed that variances were not significantly heterogeneous after transformation. We used a "best-subsets" approach in conjunction with stepwise methods (Neter et al. 1985). We chose the most parsimonious model as having the lowest Akaike information criterion (AIC), and we checked its coincidence with the equivalent stepwise solution. Residuals from the final models

were normally distributed (Grafen and Hails 2002). All statistical analyses were performed with the software Statistica version 6.0. All tests were two-tailed and the level of significance was 0.05.

Results

Interpopulation variation in lizard characteristics

There were significant differences between males from different populations in snout-to-vent length, SVL (one-way ANOVA, $F_{14,200} = 5.42$, $P < 0.0001$), and in the number of blue spots ($F_{14,200} = 2.19$, $P = 0.009$), but not in the number of femoral pores ($F_{14,200} = 1.17$, $P = 0.29$) (Table 1). There were weak but positive and significant relationships between SVL of male lizards and the number of femoral pores (Pearson's correlation, $r = 0.20$, $F_{1,213} = 9.18$, $P = 0.02$) and blue spots ($r = 0.22$, $F_{1,213} = 11.53$, $P = 0.0008$). The number of femoral pores was no significantly related to the number of blue spots ($r = 0.11$, $F_{1,213} = 2.84$, $P = 0.09$).

Relative head size was significantly larger in males than in females (two-way ANOVA, sex effect: $F_{1,291} = 48.00$, $P < 0.0001$) and varied significantly between populations (population effect: $F_{1,14} = 2.34$, $P = 0.004$). The interaction between population and sex approached significance ($F_{1,14} = 1.68$, $P = 0.057$) suggesting that the magnitude of the differences in head size between males and females (i.e. sexual dimorphism) tended to differ between populations.

Interpopulation variation in habitat characteristics

There were significant differences in relation to all PCs describing habitat characteristics among populations (GLM, Wilks' $\chi^2 = 0.19$, $F_{84,2219} = 9.20$, $P < 0.0001$) and between types of microhabitat points (available vs. used by lizards; Wilks' $\chi^2 = 0.12$, $F_{6,397} = 482.31$, $P < 0.0001$). The interaction between population and type of point was significant (Wilks' $\chi^2 = 0.24$, $F_{84,2219} = 9.20$, $P < 0.0001$) showing that the magnitude of the differences between available and used habitats differed among populations. The general model showed significant overall differences between microhabitats available and used by lizards for all PCs (adjusted $R^2 > 0.11$, $F_{29,402} > 2.85$, $P < 0.0001$ in all cases) but for PC-4 (adjusted $R^2 = 0.003$, $F_{29,402} = 1.04$, $P = 0.40$). Thus, microhabitats used by lizards had significantly lower cover of *Cytisus* bushes and leaf litter (PC-1), *Juniperus* bushes (PC-2), plants (PC-3), grasses, small and medium rocks and sunny sites (PC-5), rocky outcrops and bare soil (PC-6) and are closer to refuges (PC-6) than microhabitats available.

Relationships between lizard and habitat characteristics

With respect to the physical environment, considering the average values for each population, the SVL of male lizards was not significantly related to any of the PCs describing habitats used by lizards, which were not included in the final stepwise GRM model, but SVL was significantly and positive related to population altitude midpoint (stepwise best subsets GRM, adjusted $R^2 = 0.34$, $\beta = 0.64$, $F_{2,12} = 4.67$, $P = 0.03$). Thus, habitat characteristics did not affect body length (SVL) of male lizards, but lizards were larger at higher altitude.

Table 2. Principal component analyses for microhabitats available and used by lizards. Correlations marked in bold are significant at $P < 0.0001$.

	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6
Ground level:						
Small rocks (< 25 cm)	0.14	-0.01	-0.06	-0.12	0.63	-0.19
Medium rocks (25-100 cm)	-0.09	0.29	0.06	-0.03	0.54	-0.02
Large rocks (100-200 cm)	-0.20	0.16	0.02	0.03	0.20	0.39
Rocky outcrops (> 200 cm)	0.08	-0.09	-0.09	0.01	-0.14	0.76
Bare sandy soil	0.15	0.20	0.15	0.04	0.04	0.57
Grasses	0.23	0.03	-0.01	0.04	0.76	0.16
Leaf litter	0.64	0.48	0.22	0.01	0.08	0.07
Plant contacts:						
Grass (5 cm)	0.26	-0.03	0.01	0.04	0.79	0.20
Grass (10 cm)	0.21	-0.01	0.09	0.04	0.36	0.45
Grass (25 cm)	0.08	0.05	0.19	0.03	0.07	0.35
Grass (50 cm)	-0.02	0.06	0.01	-0.99	0.02	0.02
Ferns (10 cm)	-0.02	0.06	0.01	-0.99	0.02	0.02
Ferns (25 cm)	-0.02	0.06	0.01	-0.99	0.02	0.02
Plants (5 cm)	0.07	-0.02	0.95	0.01	-0.01	0.08
Plants (10 cm)	0.03	-0.03	0.97	0.01	0.01	0.09
Plants (25 cm)	0.03	-0.03	0.97	0.01	0.01	0.09
<i>Cytisus</i> (5 cm)	0.86	0.06	0.19	0.02	0.12	0.12
<i>Cytisus</i> (10 cm)	0.87	0.09	0.19	0.03	0.15	0.13
<i>Cytisus</i> (25 cm)	0.89	0.07	0.09	0.03	0.14	0.13
<i>Cytisus</i> (50 cm)	0.88	0.05	0.01	0.01	0.11	0.12
<i>Cytisus</i> (75 cm)	0.68	0.03	-0.13	0.01	0.06	-0.02
<i>Cytisus</i> (100 cm)	0.58	-0.10	-0.12	-0.02	0.06	-0.05
<i>Juniperus</i> (5 cm)	0.01	0.93	-0.01	-0.05	0.14	0.03
<i>Juniperus</i> (10 cm)	0.01	0.94	-0.01	-0.04	0.17	0.04
<i>Juniperus</i> (25 cm)	0.02	0.95	-0.02	-0.02	0.15	0.02
<i>Juniperus</i> (50 cm)	0.04	0.86	-0.02	-0.12	0.01	0.04
<i>Juniperus</i> (75 cm)	0.19	0.40	-0.06	0.04	-0.15	0.15
Distance to refuge	0.07	-0.02	-0.06	0.03	0.50	0.76
Sunny location	0.10	0.18	0.02	-0.02	0.81	0.40
Canopy tree cover	0.01	0.01	0.02	-0.10	0.01	0.21
Eigenvalue	6.31	3.88	2.94	2.83	2.72	1.56
% Variance	21.02	12.93	9.79	9.43	9.07	5.19

The average number of femoral pores of male lizards was positively and significantly related with PC-6 describing microhabitats used by lizards (stepwise best subsets GRM, adjusted $R^2 = 0.35$, $\beta = 0.63$, $F_{1,13} = 8.46$, $P = 0.012$) (Fig. 1a). Thus, male lizards from populations with microhabitats that had higher cover of rocky out-

rocky outcrops and bare soil, and that are far from refuges, had an average larger number of femoral pores, independently of SVL variations, which was not included in the final model. We obtained similar results when considering the PCs describing available microhabitats.

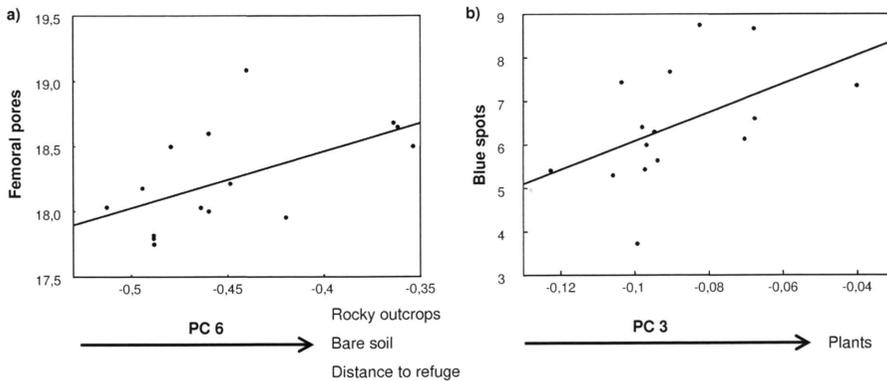


Fig. 1. Relationship between the average number of a) femoral pores and b) blue spots of males in each population and PCs for characteristics of microhabitat used by lizards.

The average number of blue spots of male lizards was positively and significantly related to PC-3 describing microhabitats used by lizards (stepwise best subsets GRM, adjusted $R^2 = 0.26$, $\beta = 0.56$, $F_{1,13} = 5.84$, $P = 0.031$) (Fig. 1b). Thus, male lizards from populations with microhabitats with higher cover of plants had an average larger number of blue spots, independently of SVL variations, which was not included in the final model. We obtained similar results when considering the PCs describing available microhabitats.

With respect to the social environment, the average number of femoral pores of male lizards was positively and significantly related with average head size and with the magnitude of the differences between microhabitat available and used explained by PC-6 (stepwise best subsets GRM, model: adjusted $R^2 = 0.60$, $F_{2,12} = 11.41$, $P = 0.001$; head size: $\beta = 0.48$, $t = 2.44$, $P = 0.03$; PC-6: $\beta = 0.44$, $t = 2.21$, $P = 0.04$) (Fig. 2). Male lizards from populations where conspecific males had average relatively greater head size and where microhabitats available and used differed more in the cover of rocky outcrops and

bare soil and in distances to refuges, had an average larger number of femoral pores.

The average number of blue spots of male lizards was positively and significantly related with average head size and with the magnitude of the differences between microhabitat available and used explained by PC-3 (stepwise best subsets GRM, model: adjusted $R^2 = 0.48$, $F_{2,12} = 7.40$, $P = 0.008$; head size: $\beta = 0.50$, $t = 2.61$, $P = 0.02$; PC-3: $\beta = 0.51$, $t = 2.66$, $P = 0.02$) (Fig. 3). Thus, male lizards from populations where conspecific males had average relatively greater head size and where microhabitats available and used differed more in plant cover had an average larger number of blue spots.

Average head size was significantly and positively correlated with the difference between microhabitats available and used described by the PC-6 (GRM, adjusted $R^2 = 0.21$, $\beta = 0.52$, $F_{1,13} = 4.93$, $P = 0.04$). Thus, populations where microhabitats available and used differed more in the cover of rocky outcrops and in distances to refuges had males with greater head size (Fig 4).

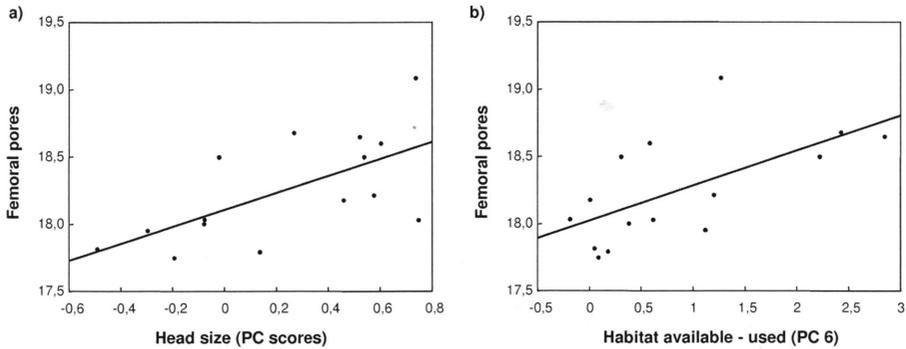


Fig. 2. Relationship between the average number of femoral pores of males in each population and a) average relative head size of conspecific males or b) differences between characteristics of microhabitats available and used by lizards (related to cover of rocky outcrops and bare soil; PC 6).

Discussion

Our results showed that different physical and social environmental characteristics may drive the divergence of chemical or visual signalling among *I. cyreni* lizard populations. We found general interpopulation differences in habitat characteristics (substrate and vegetation cover) that reflected differences in physical characteristics (e.g., temperature and humidity, visibility) which may influence the efficiency of both chemical and visual signalling (Endler and Houde 1995; Endler and Thery 1996; Alberts 1992; Leal and Fleishman 2004). Moreover, we also found interpopulation differences in the interaction between available and used habitats and in male head size (related with male aggressiveness; Herrel et al. 1999), suggesting differences in social characteristics (intensity of male intrasexual competition), which may also influence signal evolution (Andersson 1994; Blumstein and Armitage 1997; Ord et al. 2001). Recent studies have compared the relationship between two sensory types (visual and acoustic signals) elaborations across bird species (Badyaev et al. 2002; Price et al. 2006). Animals may evolve to communicate through multiple

sensory modalities in response to a fluctuating or heterogeneous environment (reviewed in Candolin 2003; Partan and Marler 2005), and different populations or species may experience varying ecological conditions that may influence the use of each sensory modality. Two primary hypotheses have been proposed to explain the use of multiple traits in mate choice: the “redundant” (or “back-up”) signal hypothesis and the “multiple messages” hypothesis (Møller and Pomiankowski 1993; Johnstone 1996; Candolin 2003; Hebets and Papaj 2005; Partan and Marler 2005). However, it is impossible to interpret multiple signalling outside the context of the environment, given that signal perception is highly dependent of habitat physical characteristics (Endler 1992; Endler and Basolo 1998; Bradbury and Vehrencamp 1998; Chiao et al. 2000) or social characteristics (Andersson 1994; Blumstein and Armitage 1997; Ord et al. 2001).

Influence of physical characteristics

Our results showed that different physical factors of the environment may drive each sensory modality, and that population equilibrium between both sensory modes should be reached depending on habitat

characteristics. Thus, we found that microhabitat characteristics, such as the higher cover of rocky outcrops, bare soil and farther distances from refuges, may promote chemical signalling in male *I. cyreni* lizards, whereas higher cover of plants may promote visual signalling.

Changes in environmental conditions (e.g., microhabitat structure or predation risk) that lead to change in signal detectability, or differences in the cost of some traits, can strongly influence both preference for traits and trait elaboration (Darwin 1871; Endler 1992; Leal and Fleishman 2004). With respect to visual signals, the habitat in which natural and sexual selection occurs is divided into microhabitats that differ in physical properties that influence colour perception, such as light intensity, light spectrum, and/or substrate colour and pattern (Endler 1993; Gomez and Théry 2004). To be effective, colour signals should be conspicuous to intended receivers, given the visual background and prevailing light conditions (Endler 1992; Fleishman and Persons 2001; Macedonia 2001; Stuart-Fox et al. 2007). Habitat openness or vegetation cover affects light conditions, which may exert strong selection on visual signals such as colour patches or ornaments to maximize conspicuousness (Marchetti 1993; Endler and Théry 1996; Zahavi and Zahavi 1997; Leal and Fleishman 2004). We found that male lizards from populations with more plant cover had more blue spots. These blue spots reflect ultraviolet (UV) light (Arribas 2001; Thorpe and Richard 2001). The conspicuousness of UV signals is particularly highlighted in dark environments, such as inside refuges or under vegetation cover, because the radiance from the background is considerably lower for the UV light than in open areas (Endler 1993; Hunt et al. 2003; Avilés et al. 2006). Therefore, in habitats with more plant cover (i.e., shadier environment) blue spots might be more efficient and advanta-

geous than in open habitats. Predators may also exploit signals to localize prey (Endler 1978, 1980; Ryan 1987), and bright colours, habitat openness or refuge availability can in turn determine the vulnerability of signallers to visual predators (Stuart-Fox and Ord 2004; Cabido et al. in press). Blue spots may increase predation risk because diurnal predators use UV wavelengths as a hunting cue (Viitala et al. 1995, Honkavaara et al. 2002; Probst et al. 2002). Thus, a lower availability of refuges or farther average distances to refuges may also influence the advantages of using blue spots, limiting the use of conspicuous visual signals and promoting the use of alternative signals such as chemical ones, as we have found. Therefore, if predation limits the use of visual signals, chemical signalling may replace visual signalling as the target of sexual selection (Darwin 1871; Shutler and Weatherhead 1990), thus explaining the positive relationship between refuge availability and number of femoral pores.

Lizards inhabiting more mesic tropical habitats vs. those in xeric habitats might use chemical signals differently because of possible differences in persistence times of the chemical signal (Gravelle and Simon 1980). A higher cover of plants offers a higher protection from predators (Martín and López 1995), but it is also related with higher humidity levels, which limits the duration of chemical signals (Alberts 1992). Therefore, in those populations where humidity is high and predation pressure is low, visual elaboration may replace chemical signals as the target of sexual selection.

Therefore, our results showed that microhabitat, through its influence both on properties of the signalling environment and predation pressure, can thus play an important role in the evolution of multimodal signalling in lizards, and suggest that the equilibrium between each sensory modality may depend on the interaction of

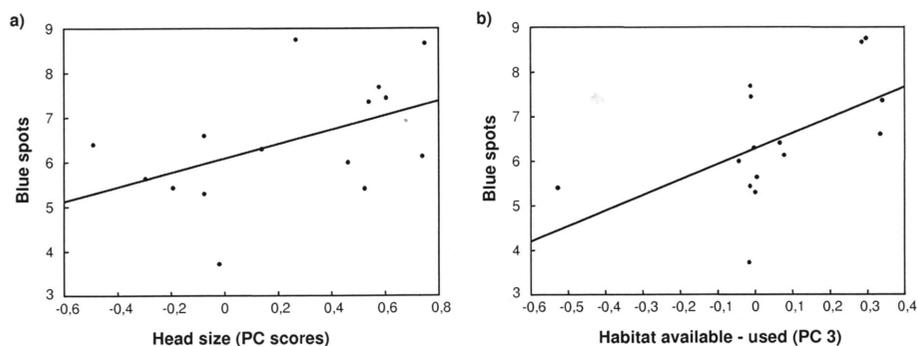


Fig. 3. Relationship between the average number of blue spots of males in each population and a) average relative head size of conspecific males or b) differences between characteristics of microhabitats available and used by lizards (related to plant cover; PC 3).

the different habitat characteristics of each population. In this sense, Hews and Benard (2001) found a negative association between visual and chemical signalling in phrynosomatid lizards. Although their results are limited because they involve only a single species-pair comparison, we did not find a significant relationship between the population average number of femoral pores and the number of blue spots. This could be due to different relationships (positive or negative) depending on the weight of the different factors in each population. For instance, social organization may promote both chemical and visual signalling (see below), that is, a positive relationship between femoral pore and blue spots number, whereas microhabitat may promote only one of them or favour a negative relationship between both. Thus, the additive and interacting whole effects of all environmental factors may hide a simple interaction between sensory modalities.

Several phylogenetically controlled comparative analyses have also found that habitat characteristics influence visual signal repertory in iguanian lizards (Macedonia 2001; Ord et al. 2001, 2002), agamid lizards (Stuart-Fox and Ord 2004) and chameleons (Stuart-Fox et al. 2007). How-

ever, Pincheira-Donoso et al. (2008) in a phylogenetically controlled comparative analysis found that environmental conditions failed to predict chemical signalling (number of precloacal pores) across several species of lizards of the *Liolaemus* genus, being the phylogenetic relationships a strong predictor of the number of precloacal pores. However, the comparison across species may suppose a lack of control of other factors different of habitat characteristics that can also influence signalling, such as body size (Bradbury and Vehrencamp 1998; Podos 2001) or variation in social organization (present study, see below; Ord et al. 2001; Ord and Stuart-Fox 2006). On the contrary, our study compares different closely related populations which have been recently isolated (*I. cyreni* only occurs above 1700 m in the top of Guadarrama mountains, alike "mountain islands") that only differ in environmental conditions (see also Leal and Fleishman 2004). In addition, Pincheira-Donoso et al. (2008) used the latitude and altitude of each species distribution as indirect measures of temperature, wind and humidity. The lack of relationships between number of femoral pores and habitat could be due to a habitat classification based in inaccurate measures, or factors that do not di-

rectly affect the efficiency of chemical signals. Our study involving multiple quantitative measures of how habitat differs physically are potentially more statistically robust as it tests for consistent trends within each habitat.

Influence of social characteristics

Our study shows that populations where microhabitats available and used differed more in the cover of rocky outcrops and bare soil and in distances to refuges, that is with higher habitat heterogeneity related with territoriality (Emlen and Oring 1977; M'Closkey et al. 1990a,b; Perry and Garland 2002), had males with greater head size which is related with higher levels of male competition (Herrel et al. 1999) and intrasexual selection (Gvozdík and Vandamme 2002; Stuart-Fox and Ord 2004). Male lizards from these populations also had an average larger number of femoral pores. In contrast, male lizards from populations with average relatively greater male head size, but where microhabitats available and used differed more in plant cover, had an average larger number of blue spots. Several comparative (Ord et al. 2001; Stuart-Fox and Ord 2004) or experimental studies (Baird et al. 1997) showed the influence of intrasexual com-

petition and social organization in the evolution of visual signalling, suggesting that signal complexity has evolved in order to improve opponent assessment under conditions of high male-male competition. Kratochvil and Frynta (2002) also showed, in a study of the relationships between male territorial behaviour and presence /absence of precloacal glands in eublepharid geckos, that species lacking these structures are less territorial. Our results suggest that intrasexual competition (reflected by male head size) or territoriality (reflected by habitat heterogeneity) may promote both the development of visual and chemical signalling. However, habitat heterogeneity due to differences in rocky cover drives chemical signalling, whereas plant cover drives visual signalling. Social systems and spacing patterns influence the distance over which a signal must function (Andersson 1994; Blumstein and Armitage 1997; Ord et al. 2001, 2002) and olfactory cues have traditionally been classified as long-distance signals (Bradbury and Vehrencamp 1998). In populations where male have to compete for rocky outcrops (which are preferably selected by *I. cyreni*; Martín and Salvador 1997) chemical cues may function to alert the receiver of the presence of the visual cues, increasing the probability of their detection and recognition (Rowe and Guilford 1999; Rowe 1999; López and Martín 2001). Moreover, chemical signal durability may be longer on rocky substrates (Gravelle and Simon 1980) that with the long-distance detection of olfactory signals may combine to decrease the costs incurred by a female during the mate selection process, and increase her probability of finding a mate (Real 1990; Jumper and Baird 1991). On the contrary, in populations where habitat heterogeneity is due to plant cover (which is avoided by *I. cyreni*; Martín and Salvador 1997), chemical signals may have less duration and visual signals may be more advantageous. These results suggest that,

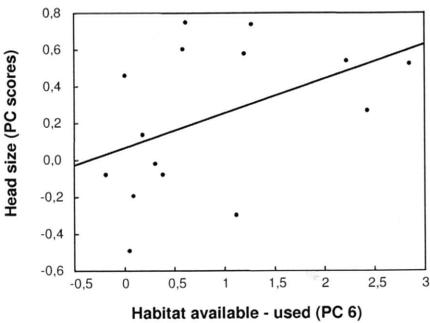


Fig. 4. Relationship between average head size and the difference between microhabitats available and used described by the PC-6.

although sexual competition promote signal complexity (e.g., a higher number of femoral pores or blue spots), habitat characteristics drives the efficiency and favours the use of each sensory mode.

In summary, our results showed that both physical and social characteristics of lizards' environment may play an important role in the evolution of multimodal signalling in lizards, and suggest that the equilibrium between each sensory modality in each population or species may depend on the interaction social environment and microhabitat characteristics.

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