

Patterns of shape and size sexual dimorphism in a population of *Podarcis hispanica** (Reptilia: Lacertidae) from NE Iberia

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Size and shape sexual dimorphism have long been of great interest for animal biologists and herpetologists. Although general trends do exist, every species may represent a particular case and intraspecific variation in the degree and patterns of sexual dimorphism is not rare. In the case of P. hispanica, which presents a high morphological variability and whose intraspecific taxonomy is yet not well defined, interpopulational differences could help to elucidate the morphological patterns observed. The results of a morphological analysis of a population belonging the NE form of P. hispanica* are here provided. A marked sexual dimorphism exists for the characters studied, both biometric and pholidotic, although sexual dimorphism in SVL is absent. Sexual differences in pholidotic characters, rarely examined, were marked, not only in femoral pores and ventral scales which are the characters usually studied in lizards, but also in gular scales and subdigital lamellae. The patterns of size and shape sexual dimorphism were in some cases also reflected in the analysis of static allometries. Influences of sexual and natural selection on those traits are discussed.*

Keywords: sexual dimorphism, size, shape, scaling, *Podarcis hispanica**, Iberian Peninsula.

INTRODUCTION

Sexual dimorphism is a common trait in reptiles (Schoener 1977, Cooper & Vitt 1989) and it has been shown to be related to sexual selection (Shine 1978, Perry 1996, Berry & Shine 1980, Anderson & Vitt 1990, Olsson *et al.* 2002), fecundity selection (Bonnet *et al.* 1997, Shine *et al.* 1998, Olsson *et al.* 2002) and resource par-

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tioning between the two sexes (Schoener 1977, Shine 1991, Andersson 1994, Herrel *et al.* 1999, Shine *et al.* 2002, Baird *et al.* 2003). In lacertid lizards, males are usually larger than females (Böhme 1986; Pérez-Mellado 1998a, b). However, there are species or populations where the reverse situation can be found or, simply, no significant size differences between the sexes exist (Braña 1996). Nevertheless, as a general rule in lizards, males have relatively bigger heads (Braña 1996; Herrel *et al.* 1996, 1999; Molina-Borja 2003), a pattern usually attributed to sexual selection (Carothers 1984, Hews 1990, Andersson 1994, Braña 1996, Gvozdik & Van Damme 2003). Sexual dimorphism in body size and shape in lizards might reflect differences in age distribution between the sexes or differences in body size within age classes (Stamps 1993, Stamps & Krishnan 1997), as well as differences in strategies for allocation of energy during growth (Dunham 1978, Haenel & John-Alder 2002).

*Podarcis hispanica** (*sensu lato*) is distributed throughout the Iberian Peninsula, South France and North Africa. It was once considered a single species, presenting a very high intraspecific morphological variability and its subspecific taxonomy has been revised many times (Pérez-Mellado 1998a, b; Barbadillo *et al.* 1999; Salvador 1986). However, increasing evidence advocates for a species complex. Different authors have defined a variable number of forms (Pérez-Mellado 1998a, b; Geniez 2001) and recent molecular studies (Harris & Sá-Sousa 2001, 2002; Pinho *et al.* 2003, 2004) indicate the presence of five-six morphological/genetic forms in the Iberian Peninsula.

As described in its general form, *P. hispanica** is a medium-sized species, adult males being from 38 to 70 mm and adult females from 37 to 67 mm long. (Pérez-Mellado 1998a, b; Barbadillo *et al.* 1999). It usually lives in rocky environments where it climbs frequently, but it can also be found in trees or present ground-dwelling behaviour in lack of rocks (Pérez-Mellado 1998a, b; Barbadillo *et al.* 1999). Although sexual dimorphism is not extreme, males are slightly larger than females, their heads being broader and generally more robust and their extremities longer (Pérez-Mellado 1998a, b). Females of *P. hispanica** from the Cantabrian Mountains (Northwestern Spain) have been reported to have longer trunks than males (Braña 1996). However, there are marked interpopulational differences in the species' morphology (Geniez 2001), as well as in other aspects of its biology (Pérez-Mellado 1998a, b). Consequently, aspects previously investigated in one form are not to be generalized to others without previous investigation.

Geographic differences in the *P. hispanica* complex bring forward the need for local studies on morphology to test sexual variability. The subject of this study was to describe the morphology of a population of *P. hispanica** from the area of Barcelona (NE Spain), to investigate the morphological differences between the two sexes and to elucidate the proximal mechanisms responsible for these differences.

MATERIALS AND METHODS

Study population

Specimens for this study were collected during the years 1984-1986. The sampling site was located in the Experimental Area of the Faculty of Biology of the University of Barcelona (UTM 31TDF28) and the studied population is genetically typified as belonging to the NE type of *P. hispanica** (Harris & Sá-Sousa 2002, Pinho *et al.* 2003). Lizards were collected by hand approximately at a monthly basis and an effort was made for all size classes to be included in the sampling. As both sexes in the population reach sexual maturity within the first year after their birth (Llorente 1988), a distinction was made only between adult and immature individuals. Size class and sex of the individuals were determined after dissection by the presence of enlarged follicles or oviductal eggs in females, and the size and aspect of testes and epididymes in males (Llorente 1988). A total of 59 adult males, 52 females, 7 immature males and 12 immature females were examined.

Characters studied

Eleven biometric characters and six pholidotic characters were recorded in the specimens analyzed. The following biometric characters were measured to the nearest 0.1 mm using an electronic caliper: snout-vent length (SVL), trunk length (TRL), head length (HL), head width (HW), head height (HH), mouth opening (MO) defined as the distance between the point of the snout and the end of the last supralabial scale, front foot length (FFL), femur length (FL), tibia length (TBL), total length of the 4th toe and the tarsus (4TL) and hind foot length (HFL). Bilateral characters were measured on the right side of the lizards' body when possible. Measurements were taken following the methodological recommendations on morphometry of the Lacertidae given by Pérez-Mellado & Gosá (1988). Six more pholidotic characters were studied: colar scale number (CSN), gular scale number (GSN), dorsal scales around midbody (DSN), number of transversal ventral scale lines (VSN), femoral pores at the left and right side of the body (FPNL and FPNR respectively) and subdigital lamellae at the left and right side of the body (SLNL and SLNR respectively).

Data analysis

Pholidotic characters were not normally distributed (Kolmogorov-Smirnov test) and thus were examined for differences among the four size/sex classes using non-parametric statistics. In the case of bilateral characters, the mean of the two sides was

calculated, in order to include all the information available without pseudoreplicating the data. For biometric characters, we first conducted univariate two-way ANOVAs for each character to examine the effect of size class and sex on the biometry of the lizards and the interaction between them. When the interaction size*sex was significant, Scheffé's *post-hoc* comparisons were applied to further investigate the differences between groups. The same procedure was followed using only measurements from the ten largest individuals of each sex, as to investigate for sexual size dimorphism, eliminating biases possibly introduced by differential sampling of the two sexes (Carothers 1984, Gibbons & Lovich 1990, Stamps & Andrews 1992, Smith & Nickel 2002). In this case the non-parametric Mann-Whitney U test was applied to compare between the two sexes. A discriminant and canonical variate analysis was conducted on raw data, in order to detect the variables responsible for the discrimination among the four size/sex classes.

In order to investigate differences in shape among the size/sex classes, univariate ANCOVAs were conducted for each character, using SVL as a covariate. The residuals of log-transformed biometric variables in their regression with log (SVL) were introduced in a discriminant and canonical variate analysis and the patterns of variation observed among the size/sex classes were examined.

Finally, the scaling of each of the biometric variables (log-transformed) with SVL was examined, treating separately the two sexes. Due to the presence of measurement error in both the independent and the dependent variable, ordinary least-squares regression would provide skewed values for the allometry equations (McArdle 1988, Sokal & Rohlf 1995). Thus, reduced major axis (RMA) regression was applied, using the software developed by Bohonak (2002) for this purpose. Deviations from isometry were tested using the formulas given in Clarke (1980) and homogeneity of slopes between groups was examined by inspection of the 95% confidence limits of the slopes' estimates.

RESULTS

Pholidosis

No differences were detected between immature and adult animals (Mann-Whitney U test, $P > 0.1$ for both sexes and all the examined variables), thus subsequent analyses were conducted grouping immatures and adults of each sex. Sexes differed significantly in dorsal, ventral and gular scales, femoral pores and subdigital lamellae (see statistics in Table 1).

Table 1.

Descriptive statistics for the two sexes of the studied population and results of Mann-Whitney U tests; Numbers indicate mean \pm SE, range and sample size. See materials and methods section for variables' abbreviations.

| Variable | Males | Females | Mann-Whitney Z | P-level |
|----------|------------------|------------------|----------------|-----------------------|
| CSN | 10.02 \pm 0.13 | 9.72 \pm 0.18 | | |
| | 8-12 | 7-13 | -1.233 | 0.217 |
| | 66 | 60 | | |
| GSN | 27.06 \pm 0.33 | 26.00 \pm 0.27 | | |
| | 22-33 | 21-33 | -2.371 | 1.8*10 ⁻² |
| | 65 | 62 | | |
| DSN | 59.02 \pm 0.53 | 56.92 \pm 0.43 | | |
| | 51-74 | 50-68 | -3.059 | 2*10 ⁻³ |
| | 66 | 62 | | |
| VSN | 25.47 \pm 0.14 | 29.20 \pm 0.20 | | |
| | 22-29 | 26-34 | 9.196 | 3.7*10 ⁻²⁰ |
| | 66 | 60 | | |
| FPN | 18.58 \pm 0.18 | 17.64 \pm 0.22 | | |
| | 15.5-21 | 14-21.5 | -3.139 | 1.7*10 ⁻³ |
| | 60 | 61 | | |
| SLN | 25.07 \pm 0.25 | 23.76 \pm 0.21 | | |
| | 21-29.5 | 20-27.5 | -3.713 | 2.05*10 ⁻⁴ |
| | 61 | 54 | | |

Biometry

Size variation

Table 2 shows the descriptive statistics of all the biometric variables studied for the four size/sex classes, as well as the results of the ANOVA comparisons. The *post-hoc* comparisons showed no significant differences in SVL between different sexes of the same size class. For the rest of the biometric characters studied, differences were significant among all size/sex classes (Scheffé's tests, $P < 0.05$), except between the two sexes of immature animals, which only presented significant differences in trunk length (TRL). On the other hand, the two sexes of adult lizards were significantly different for the rest of biometric characters (Scheffé's tests, $P < 0.05$), but not for TRL (Scheffé's tests, $P = 0.28$). In contrast, when analyzing the ten largest adult individuals of each sex, differences between sexes were significant for all the biometric variables including SVL (Mann-Whitney tests, $P < 0.01$ for all the variables) males being larger than females, except for TRL, which was not significantly different between the sexes (Mann-Whitney test, $P = 0.52$).

Table 2.

Descriptive statistics of the biometric variables for the four age/sex classes in the population studied and ANOVA comparisons for age and sex. Numbers indicate mean \pm SE, range and sample size. See materials and methods section for variables' abbreviations.

| Character | Adult | Adult | Immature | Immature | ANOVA (age, sex, age*sex) | | |
|-----------|------------------|------------------|------------------|------------------|---------------------------|--------|-----------------------|
| | males | females | males | females | F | d.f. | P-level |
| SVL | 50.46 \pm 0.68 | 48.83 \pm 0.63 | 26.14 \pm 1.53 | 32.57 \pm 1.77 | 252.844 | 1, 125 | <0.01 |
| | 40.50-61.10 | 41.00-56.30 | 22.10-33.20 | 22.50-38.60 | 3.525 | 1, 125 | 6.27*10 ⁻² |
| | 59 | 51 | 7 | 12 | 9.958 | 1, 125 | 2*10 ⁻³ |
| TRL | 22.94 \pm 0.38 | 24.07 \pm 0.42 | 10.32 \pm 0.92 | 14.62 \pm 1.20 | 196.444 | 1, 124 | <0.01 |
| | 17.58-29.59 | 18.47-29.37 | 7.38-14.74 | 7.93-20.19 | 11.923 | 1, 124 | 7.6*10 ⁻⁴ |
| | 59 | 51 | 7 | 11 | 4.036 | 1, 124 | 4.7*10 ⁻² |
| HL | 13.79 \pm 0.18 | 11.75 \pm 0.11 | 7.83 \pm 0.27 | 8.97 \pm 0.33 | 221.449 | 1, 125 | <0.01 |
| | 10.80-17.20 | 10.00-13.20 | 7.10-9.20 | 7.20-10.20 | 2.341 | 1, 125 | 0.13 |
| | 59 | 51 | 7 | 12 | 29.203 | 1, 125 | 3.2*10 ⁻⁷ |
| HW | 8.23 \pm 0.13 | 6.65 \pm 0.73 | 4.59 \pm 0.20 | 5.12 \pm 0.25 | 166.047 | 1, 125 | <0.01 |
| | 5.70-10.40 | 5.00-7.50 | 4.00-5.70 | 3.70-6.30 | 6.899 | 1, 125 | 9.7*10 ⁻³ |
| | 59 | 51 | 7 | 12 | 27.790 | 1, 125 | 5.7*10 ⁻⁷ |
| HH | 6.20 \pm 0.10 | 4.98 \pm 0.06 | 3.30 \pm 0.11 | 3.50 \pm 0.18 | 190.265 | 1, 125 | <0.01 |
| | 4.30-7.90 | 4.20-5.70 | 3.00-3.80 | 2.50-4.20 | 10.407 | 1, 125 | 1.6*10 ⁻³ |
| | 59 | 51 | 7 | 12 | 20.130 | 1, 125 | 1.6*10 ⁻⁵ |
| MO | 11.05 \pm 0.16 | 9.06 \pm 0.11 | 5.58 \pm 0.26 | 6.06 \pm 0.39 | 239.438 | 1, 123 | <0.01 |
| | 7.20-13.14 | 7.66-11.02 | 4.70-6.80 | 4.00-7.70 | 7.641 | 1, 123 | 6.6*10 ⁻³ |
| | 59 | 50 | 7 | 11 | 20.354 | 1, 123 | 1.5*10 ⁻⁵ |
| FFL | 17.81 \pm 0.28 | 15.12 \pm 0.19 | 9.22 \pm 0.40 | 11.13 \pm 0.50 | 183.221 | 1, 125 | <0.01 |
| | 12.40-22.50 | 11.40-17.40 | 7.90-11.10 | 8.10-13.30 | 0.703 | 1, 125 | 0.40 |
| | 59 | 51 | 7 | 12 | 24.471 | 1, 125 | 2.4*10 ⁻⁶ |
| FL | 8.21 \pm 0.14 | 6.84 \pm 0.10 | 3.82 \pm 0.22 | 4.56 \pm 0.36 | 188.112 | 1, 121 | <0.01 |
| | 5.60-10.57 | 5.64-8.70 | 3.30-4.85 | 2.60-6.30 | 1.703 | 1, 121 | 0.19 |
| | 58 | 49 | 7 | 11 | 18.993 | 1, 121 | 2.8*10 ⁻⁵ |
| TBL | 6.26 \pm 0.12 | 5.06 \pm 0.07 | 2.93 \pm 0.12 | 3.61 \pm 0.21 | 153.343 | 1, 120 | <0.01 |
| | 4.20-9.67 | 3.98-6.41 | 2.40-3.40 | 2.30-4.50 | 1.898 | 1, 120 | 0.17 |
| | 58 | 48 | 7 | 11 | 23.803 | 1, 120 | 3*10 ⁻⁶ |
| 4TL | 13.78 \pm 0.18 | 11.78 \pm 0.14 | 7.56 \pm 0.42 | 8.85 \pm 0.49 | 201.934 | 1, 117 | <0.01 |
| | 8.95-16.40 | 9.78-13.75 | 6.50-9.80 | 5.90-10.70 | 1.223 | 1, 117 | 0.27 |
| | 55 | 48 | 7 | 11 | 25.924 | 1, 117 | 1.4*10 ⁻⁶ |
| HFL | 28.03 \pm 0.33 | 23.59 \pm 0.27 | 14.47 \pm 0.65 | 16.88 \pm 0.87 | 294.356 | 1, 125 | <0.01 |
| | 21.00-33.80 | 20.10-28.40 | 6.50-9.80 | 12.40-20.10 | 2.945 | 1, 125 | 0.09 |
| | 59 | 51 | 7 | 12 | 33.657 | 1, 125 | 5.1*10 ⁻⁸ |

Table 3.

Summary of the discriminant analysis of the four size/sex classes based on raw data. See materials and methods section for variables' abbreviations.

| | Wilks' Lambda | Partial Lambda | F-remove (3.106) | P-level | Tolerance | 1-Toler. (R ²) |
|-----|---------------|----------------|------------------|---------|-----------|----------------------------|
| SVL | 0.064 | 0.680 | 16.66 | <0.001 | 0.122 | 0.878 |
| TRL | 0.051 | 0.852 | 6.14 | 0.001 | 0.305 | 0.695 |
| HL | 0.053 | 0.821 | 7.72 | 0.000 | 0.158 | 0.842 |
| HW | 0.045 | 0.953 | 1.74 | 0.163 | 0.248 | 0.752 |
| HH | 0.044 | 0.975 | 0.92 | 0.435 | 0.347 | 0.653 |
| MO | 0.046 | 0.949 | 1.91 | 0.132 | 0.166 | 0.834 |
| FFL | 0.044 | 0.991 | 0.33 | 0.801 | 0.368 | 0.632 |
| FL | 0.044 | 0.991 | 0.32 | 0.811 | 0.358 | 0.642 |
| TBL | 0.044 | 0.979 | 0.77 | 0.512 | 0.481 | 0.519 |
| 4TL | 0.046 | 0.948 | 1.96 | 0.125 | 0.503 | 0.497 |
| HFL | 0.045 | 0.958 | 1.56 | 0.202 | 0.241 | 0.759 |

| | % correct | AF | AM | IF | IM |
|-------|-----------|----|----|----|----|
| AF | 95.83 | 46 | 1 | 0 | 1 |
| AM | 96.36 | 2 | 53 | 0 | 0 |
| IM | 85.71 | 0 | 0 | 6 | 1 |
| IF | 80.00 | 1 | 0 | 1 | 8 |
| Total | 94.17 | 49 | 54 | 7 | 10 |

The discriminant analysis conducted on raw data showed a good level of discrimination between the four size/sex classes, although percentages of correct classification were notably lower for immature lizards. The biometric variables significant for the discrimination among the four groups were SVL, TRL and HL. The summary of the discriminant analysis are shown in Table 3.

Shape variation

The results of the univariate ANCOVAs for all the studied biometric characters, using SVL as a covariate, are presented in Table 4. The *post-hoc* comparisons revealed significant differences between animals of different size classes for all the variables and for both sexes. Adult individuals of different sexes were significantly different for all the characters studied (Scheffé's test, $P < 0.05$), males presenting relatively larger characters, except for TRL which was relatively longer in female lizards. On the other hand, immature individuals only presented significant differences between the sexes for TRL, HL, FFL and HFL (Scheffé's test, $P < 0.02$),

Table 4.

Results of the univariate ANCOVA comparisons between the four size/sex classes in the populations studied. See materials and methods section for variables' abbreviations.

| Character | Factor | F | d.f. | P-value |
|-----------|---------|--------|--------|-----------------------|
| TRL | age | 2.000 | 1, 123 | 0.160 |
| | sex | 11.432 | 1, 123 | 9.7*10 ⁻⁴ |
| | age*sex | 0.299 | 1, 123 | 0.585 |
| HL | age | 1.032 | 1, 124 | 0.312 |
| | sex | 44.774 | 1, 124 | 6.8*10 ⁻¹⁰ |
| | age*sex | 28.678 | 1, 124 | 4*10 ⁻⁷ |
| HW | age | 0.209 | 1, 124 | 0.648 |
| | sex | 41.010 | 1, 124 | 2.8*10 ⁻⁹ |
| | age*sex | 18.494 | 1, 124 | 3.4*10 ⁻⁵ |
| HH | age | 4.402 | 1, 124 | 0.038 |
| | sex | 39.541 | 1, 124 | 5*10 ⁻⁹ |
| | age*sex | 9.346 | 1, 124 | 2.7*10 ⁻³ |
| MO | age | 5.439 | 1, 122 | 0.021 |
| | sex | 59.452 | 1, 122 | 3.8*10 ⁻¹² |
| | age*sex | 12.411 | 1, 122 | 6*10 ⁻⁴ |
| FFL | age | 2.288 | 1, 124 | 0.133 |
| | sex | 10.557 | 1, 124 | 1.5*10 ⁻³ |
| | age*sex | 13.846 | 1, 124 | 3*10 ⁻⁴ |
| FL | age | 5.064 | 1, 120 | 0.026 |
| | sex | 11.123 | 1, 120 | 1.1*10 ⁻³ |
| | age*sex | 8.812 | 1, 120 | 3.6*10 ⁻³ |
| TBL | age | 4.440 | 1, 119 | 0.037 |
| | sex | 8.478 | 1, 119 | 4.3*10 ⁻³ |
| | age*sex | 13.219 | 1, 119 | 4.1*10 ⁻⁴ |
| 4TL | age | 16.154 | 1, 116 | 10 ⁻⁴ |
| | sex | 5.425 | 1, 116 | 0.022 |
| | age*sex | 15.780 | 1, 116 | 1.2*10 ⁻⁴ |
| HFL | age | 20.161 | 1, 124 | 1.6*10 ⁻⁵ |
| | sex | 22.216 | 1, 124 | 6*10 ⁻⁶ |
| | age*sex | 25.051 | 1, 124 | 2*10 ⁻⁶ |

whereas there were no significant differences for the rest of the characters studied (Scheffé's test, $P > 0.1$).

The discriminant analysis based on the regression residuals of log-transformed biometric variables against log (SVL) followed a similar pattern with that using raw data. In this case, the variables significant for the discrimination among the four size/sex classes

Table 5.

Summary of the discriminant analysis of the four size/sex classes based on residuals of the biometric variables in their regression with SVL (logarithmic scale). See materials and methods section for variables' abbreviations.

| | Wilks' Lambda | Partial Lambda | F-remove (3.106) | P-level | Tolerance | 1-Toler. (R ²) |
|-----|---------------|----------------|------------------|---------|-----------|----------------------------|
| TRL | 0.182 | 0.981 | 0.698 | 0.555 | 0.959 | 0.041 |
| HL | 0.219 | 0.816 | 8.024 | <0.001 | 0.760 | 0.240 |
| HW | 0.193 | 0.927 | 2.806 | 0.043 | 0.660 | 0.340 |
| HH | 0.184 | 0.973 | 0.983 | 0.404 | 0.711 | 0.289 |
| MO | 0.198 | 0.905 | 3.754 | 0.013 | 0.552 | 0.448 |
| FFL | 0.181 | 0.987 | 0.464 | 0.708 | 0.795 | 0.205 |
| FL | 0.181 | 0.990 | 0.365 | 0.779 | 0.625 | 0.375 |
| TBL | 0.183 | 0.978 | 0.789 | 0.502 | 0.655 | 0.345 |
| 4TL | 0.181 | 0.988 | 0.447 | 0.720 | 0.621 | 0.379 |
| HFL | 0.183 | 0.976 | 0.867 | 0.461 | 0.504 | 0.496 |

| | % correct | AF | AM | IF | IM |
|-------|-----------|----|----|----|----|
| AF | 91.67 | 44 | 2 | 0 | 2 |
| AM | 92.73 | 0 | 51 | 1 | 3 |
| IM | 14.29 | 1 | 5 | 1 | 0 |
| IF | 20.00 | 6 | 2 | 0 | 2 |
| Total | 81.67 | 51 | 60 | 2 | 7 |

were HL, HW and MO. Correct classification was very high for adult animals, but on the contrary a very high percentage of immature individuals was classified erroneously. The summary of the discriminant analysis on residuals is shown in Table 5.

Scaling

The regression parameters for biometric characters for each size/sex class are given in Table 6. The only character that presented significant deviations from isometry was head length (HL), which was negatively allometric (or hipometric) for the immature males and females. The examination of the slopes estimates revealed a significant deviation of adult males from the rest of the groups in some characters, namely head length (HL) and head height (HH). For head length and height, adult males presented a steeper slope than the rest of the groups. Adult males and females differed in all characters except for TRL, FL, 4TL and HFL. No differences were present in the slopes of immature animals of different sexes, nor between adult females and immature animals of either sex.

Table 6.

Intercept and slope estimates of RMA regression for biometric variables (log-transformed) with log(SVL). AF: Adult females, AM: Adult males, IF: Immature females, IM: Immature males. See materials and methods section for variables' abbreviations.

| Class | Character | N | Intercept | Intercept Confidence Limits | | Slope | Slope Confidence Limits | | R ² |
|-------|-----------|----|-----------|-----------------------------|-------|-------|-------------------------|------|----------------|
| AF | TRL | 51 | -0.86 | -1.29 | -0.44 | 1.33 | 1.08 | 1.58 | 0.58 |
| | HL | 51 | -0.14 | -0.33 | 0.05 | 0.72 | 0.61 | 0.83 | 0.71 |
| | HW | 50 | -0.60 | -0.92 | -0.28 | 0.84 | 0.65 | 1.03 | 0.41 |
| | HH | 51 | -0.76 | -1.11 | -0.28 | 0.86 | 0.65 | 1.07 | 0.27 |
| | MO | 50 | -0.55 | -0.81 | -0.29 | 0.89 | 0.74 | 1.05 | 0.65 |
| | FFL | 50 | -0.40 | -0.66 | -0.13 | 0.94 | 0.77 | 1.09 | 0.66 |
| | FL | 49 | -1.01 | -1.45 | -0.57 | 1.09 | 0.83 | 1.35 | 0.35 |
| | TBL | 48 | -0.95 | -1.36 | -0.53 | 0.98 | 0.73 | 1.23 | 0.28 |
| | 4TL | 48 | -0.39 | -0.76 | -0.02 | 0.87 | 0.65 | 1.09 | 0.28 |
| AM | HFL | 51 | -0.09 | -0.37 | 0.18 | 0.87 | 0.71 | 1.03 | 0.58 |
| | TRL | 59 | -0.76 | -1.11 | -0.41 | 1.24 | 1.04 | 1.45 | 0.61 |
| | HL | 59 | -0.56 | -0.75 | -0.38 | 1.00 | 0.89 | 1.11 | 0.83 |
| | HW | 59 | -1.04 | -1.34 | -0.75 | 1.15 | 0.98 | 1.32 | 0.68 |
| | HH | 59 | -1.31 | -1.66 | -0.95 | 1.23 | 1.02 | 1.44 | 0.60 |
| | MO | 59 | -0.90 | -1.17 | -0.63 | 1.14 | 0.98 | 1.30 | 0.72 |
| | FFL | 57 | -0.70 | -1.04 | -0.36 | 1.15 | 0.95 | 1.35 | 0.59 |
| | FL | 58 | -1.31 | -1.73 | -0.90 | 1.31 | 1.06 | 1.55 | 0.51 |
| | TBL | 58 | -1.61 | -2.10 | -1.12 | 1.41 | 1.13 | 1.70 | 0.43 |
| IF | 4TL | 55 | -0.58 | -1.00 | -0.15 | 1.01 | 0.76 | 1.26 | 0.19 |
| | HFL | 59 | -0.09 | -0.35 | 0.18 | 0.90 | 0.74 | 1.06 | 0.57 |
| | TRL | 11 | -1.04 | -1.68 | -0.39 | 1.46 | 1.03 | 1.89 | 0.85 |
| | HL | 12 | -0.03 | -0.22 | 0.15 | 0.65 | 0.53 | 0.77 | 0.93 |
| | HW | 12 | -0.63 | -1.02 | -0.23 | 0.88 | 0.62 | 1.15 | 0.82 |
| | HH | 12 | -0.86 | -1.20 | -0.53 | 0.93 | 0.71 | 1.15 | 0.89 |
| | MO | 11 | -0.87 | -1.24 | -0.51 | 1.10 | 0.86 | 1.34 | 0.91 |
| | FFL | 12 | -0.20 | -0.45 | 0.04 | 0.83 | 0.66 | 0.99 | 0.92 |
| | FL | 11 | -1.35 | -2.12 | -0.58 | 1.33 | 0.82 | 1.84 | 0.74 |
| IM | TBL | 11 | -0.93 | -1.55 | -0.31 | 0.99 | 0.57 | 1.40 | 0.69 |
| | 4TL | 11 | -0.52 | -1.01 | -0.03 | 0.97 | 0.65 | 1.30 | 0.80 |
| | HFL | 12 | -0.18 | -0.76 | 0.41 | 0.93 | 0.54 | 1.32 | 0.65 |
| | TRL | 7 | -1.15 | -1.65 | -0.66 | 1.53 | 1.18 | 1.88 | 0.96 |
| | HL | 7 | 0.04 | -0.14 | 0.23 | 0.60 | 0.47 | 0.73 | 0.96 |
| | HW | 7 | -0.38 | -1.09 | 0.32 | 0.74 | 0.24 | 1.24 | 0.65 |
| | HH | 7 | -0.31 | -1.20 | 0.57 | 0.59 | -0.03 | 1.21 | 0.15 |

| | | | | | | | | |
|-----|---|-------|-------|------|------|------|------|------|
| MO | 7 | -0.44 | -0.97 | 0.09 | 0.84 | 0.47 | 1.21 | 0.85 |
| FFL | 7 | -0.10 | -0.91 | 0.71 | 0.75 | 0.18 | 1.32 | 0.56 |
| FL | 7 | -0.81 | -0.67 | 0.04 | 0.99 | 0.38 | 1.59 | 0.71 |
| TBL | 7 | -0.62 | -1.70 | 0.47 | 0.77 | 0.00 | 1.53 | 0.24 |
| 4TL | 7 | -0.46 | -0.94 | 0.01 | 0.95 | 0.61 | 1.28 | 0.90 |
| HFL | 7 | 0.08 | -0.30 | 0.46 | 0.76 | 0.49 | 1.03 | 0.91 |

DISCUSSION

Pholidosis

The results obtained on the pholidosis of the population studied are in accordance with previous studies of the species in Catalonia (Vives-Balmaña 1982, Carretero & Llorente 1993), as well as with the pholidotic patterns reported in the most recent morphological study on the NE type of *P. hispanica** (Geniez 2001). This makes this form one of the most distinctive in scale counts, since all of its pholidotic characters are close to the upper limit of the range given in the general description of the species (Pérez-Mellado 1998a, b). For example, when compared to the form present in the NW of the Iberian Peninsula (Galán 1986), the population studied presents less ventral scales and more femoral pores in both sexes.

Concerning the sexual dimorphism present in pholidotic characters, males have significantly more gular and dorsal scales, femoral pores and subdigital lamellae, while females have more ventral scales. Sexual dimorphism in pholidotic characters is not a rare feature in lacertid lizards, although to our knowledge it has never been studied extensively. A higher number of ventral scales in females has been reported in various cases for *P. hispanica** (Galán 1986, Carretero & Llorente 1993, Geniez 2001, Sá-Sousa *et al.* 2002) and it might be related to the presence of a longer trunk in females, constrained by the need of space for the allocation of eggs. On the other hand, the observed differences in the rest of the pholidotic characters are rarely studied. Concerning the higher number of gular scales in males, the same pattern has been observed in *P. pityusensis* (Carretero *et al.* 1999). The higher number of femoral pores observed in males has also been reported or can be deduced for *P. hispanica** (Galán 1986, Carretero & Llorente 1993, Geniez 2001, Sá-Sousa *et al.* 2002). A common feature for lacertid lizards is the different aspect of femoral pores in the two sexes, they are generally bigger and have higher secretory capacity in males and are involved in individual recognition related with social or reproductive behaviours (Cole 1966, Carretero & Llorente 1993, López & Martín 2004). Consequently, it is not surprising that a sexual dimorphism in the number of femoral pores exists, at least in some species.

Finally, the absence of pholidotic differences between immatures and adults is not surprising, since pholidotic characters do not vary with age (Klauber 1943, Arnold & Bennet 1988, Carretero & Llorente 1993).

Size and shape dimorphism

In the population studied, immature animals were monomorphic, sexual dimorphism being restricted to the adult stage, as in the case of many lizard species (Cooper & Vitt 1989, Braña 1996). Concerning sexual dimorphism in adults, no significant differences in SVL were present between the sexes. This has been reported before for other populations of *P. hispanica** in NE Iberia (Vives-Balmaña 1982, Carretero & Llorente 1993). However, when the largest individuals of each sex were compared, males were found to be significantly larger than females, possibly indicating sexual differences in growth patterns or survival rates. For the rest of the characters studied, adult males presented absolutely (size) and relatively (shape) higher values than adult females, except for TRL which was found to be relatively longer in females. The shape variation observed is in accordance with sexual dimorphism patterns present in other lacertid lizards, males presenting more developed head characters, both in size and in shape, and females presenting relatively longer trunks (Braña 1996, Olsson *et al.* 2002). It has been stated elsewhere that a bigger head in males is advantageous both for male-to-male combats and for immobilisation of females during copulation (Hews 1990, Braña 1996, Olsson *et al.* 2002). Consequently, the head size and shape dimorphism observed, is probably the result of the effect of sexual selection for head dimensions in males. On the other hand, a longer trunk provides females with a reproductive advantage in terms of fecundity, since it would offer more space for egg allocation (Schoener 1977, Olsson *et al.* 2002), and would thus be an indication of natural selection.

It is interesting to note that, apart from longer trunks, females also present shorter limb lengths both in size and shape analysis. This phenomenon could be due to mechanical restrictions imposed to female lizards by the presence of a longer trunk (Carretero & Llorente 1993).

Character scaling

The results on static allometry revealed an interesting pattern for the scaling of head length and height. No significant deviations from isometry were detected in any size/sex class. However, regression slopes for adult males differed from the rest of the classes for these characters. This apparent contradiction is probably attributable to statistical restrictions. In fact, examining deviations from isometry by inspection of

slope confidence limits, at least head length could be considered hypermetric. The pattern of dimorphism observed could be an indication of sexual selection for head dimensions in adult males. Head size is known to be sexually selected in numerous lizard species (Braña 1996, Olsson *et al.* 2002). It has been stated (Hews 1990) that head height could be related to male capability for immobilising females during copulation since bite force in lacertid lizards depends on the mass of the jaw adductor muscles which are fixed on the postorbital region of the cranium (Herrel *et al.* 1996, 1999). Although sexually selected characters are usually hypermetric (Green 1992, Petrie 1992), we were not able to detect such a pattern in the population studied. However, other factors that might affect head size should not be neglected, such as the habitat preferences of this species. In fact, head dimensions in rock lizards are restricted by natural selection due to habitat use (Carretero & Llorente 1993). Having in mind both selective forces acting on head dimensions, we consider that the pattern observed for head length and height could be a strong indication for sexual selection on head size which could be more constrained in the vertical dimension.

Discrimination between classes

Size and shape discriminant and canonical analyses showed a very good discrimination between the two sexes in adults. Although the variables significant for the discrimination differed in the two analyses, percentages of correct classification were very high, in accordance with the patterns of sexual dimorphism observed in the univariate analyses. These results reflect conclusions reported on pholidosis, as sexual differences in some characters are related to size and shape (*e.g.* ventral scales). Considering the immature lizards, discrimination between the sexes was also highly correct in both analyses but less marked. However, the discrimination of immature animals presented more difficulties when shape variables were used, many individuals being erroneously classified as adults. Obviously, since the criterion used to distinguish immatures from adults is exclusively body size (determining the gonad development), once this variable is statistically extracted from the analysis, this class becomes a poorly defined group because it is composed of animals of different ages. In contrast, in the size discriminant analysis, the discrimination between immatures and adults was very good, being based on variables directly related to size (SVL, TRL, HL).

Combining the results from univariate character analysis, examination of static allometry patterns and size and shape discrimination analyses, we can confirm that sexual dimorphism in the population studied seems to be driven by sexual and natural selection for some traits, as head size in males and trunk length in females, while for others, such as extremity length, it could be constrained by biomechanical limitations.

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