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Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase?

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Lacertid lizards exhibit sexual dimorphism in size corrected values for abdomen (always larger in females) and head (larger in males) lengths. Relative abdomen length increased with SVL in females but did not in males. The mean abdomen/head ratio for juvenile lizards (sexes pooled) was lower than that of females but did not differ from that of males in any of the studied species. Therefore, the ontogenetic development of the main body segments (abdomen and head) was isometric in male lizards, whereas female abdomen exhibited positive allometric growth. Standardized independent contrasts (Felsenstein's method) of female abdomen to head ratio and of the slope of the regression of clutch size on SVL explained a significant amount of variation in sexual size dimorphism in a stepwise multiple regression model. The fact that sexual size dimorphism was best explained by variables related to female reproductive investment, together with the ontogenetic trajectories of body segments suggest that sexual size dimorphism results mainly from variation in female size. Despite the suggested prominent role of selection on female body size in determining the outcome of size dimorphism, there was also evidence of selection for increased body size in males, which were the largest sex in species with low selective pressure towards increased female size (constant clutch size or low fecundity slope over size). Evidence for intersexual food (prey size) partitioning was weaker than expected from the widespread dimorphism in body size or relative head size found among lacertid lizards. Furthermore, the development of "body segments" was in some instances inconsistent with the competitive hypothesis, the largest sex having relatively smaller trophic structures.

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Between-sex differences in body size, coloration or morphology, so-called sexual dimorphism, are widespread among reptiles (Schoener 1977, Berry and Shine 1980, Fitch 1981, Stamps 1983, Gibbons and Lovich 1990, Shine 1991) as well as other vertebrates (Selander 1972, Shine 1979, 1989, Woolbright 1983, Greenwood and Wheeler 1985, Halliday and Verrell 1986, Parker 1992, Winquist and Lemon 1994). Sexual selection, acting via between-male competition or female choice (Darwin 1871, Maynard Smith 1987), and arising from variance in mating success (McVey 1988), has been proposed as the main factor responsible for sexual dimorphism. Although this seems evident for some striking male traits (Darwin 1871, reported a number of examples across the animal lineage), recent studies have paid increasing attention to potential alternative causes of sexual dimorphism (Hamilton and Zuk 1982, Slatkin 1984, Shine 1989, 1991, Anderson and Vitt 1990, Fairbairn 1990, Emerson and Voris 1992). However, results are sometimes inconclusive because of the complex nature of the phenomenon, over which many potential causes act.

In species where males compete over females and size provides the achievement of greater reproductive success, there is a selective pressure for increased male

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body size and enlargement of combat-related structures (mainly head size in lizards; see Trivers 1976, Carothers 1984, Vitt and Cooper 1985, Hews 1990, Mouton and Van Wyk 1993). On the other hand, selection may favor fecundity through increased female size (Selander 1972, Shine 1989, Vial and Stewart 1989; but see Madsen and Shine 1994) and, furthermore, competition avoidance between the sexes could also lead to size differences (Schoener 1967, Slatkin 1984, Shine 1989). In this respect, there are numerous examples of niche (food, habitat, or both) segregation between sexes in relation to differences in sexually dimorphic attributes (e.g., in lizards: Lister 1970a, b, Schoener 1977, Busack and Jaksic 1982, Powell and Rusell 1984). Unfortunately, it is often difficult to elucidate whether sexual differences directly arose from competitive interactions or whether niche segregation was a byproduct of dimorphism promoted by sexual selection or fecundity selection.

In addition to selective pressures whose strength, and even direction, can be different for both sexes, the evolution of sexual dimorphism may be limited by physiological and ecological constraints (Clutton-Brock et al. 1977, Greenwood and Wheeler 1985, Halliday 1987, Partridge and Endler 1987), as well as by genetic correlation between the sexes for potentially dimorphic characters (Lande 1980, 1987, Hedrick and Temeles 1989). Furthermore, as juvenile individuals of dimorphic species are frequently monomorphic (see, for lizards, Bauwens and Thoen 1982, Vitt and Cooper 1985, Cooper and Vitt 1989), dimorphism in body size or shape could result from between-sex differences in growth rates or divergent trajectory in the development of particular morphometric traits (Brooks 1991). In this context, as growth occurs over time, between-sex differences in age structure due to differences in age at maturity or in subsequent adult survival could also account to some extent for apparent sexual size dimorphism (Stamps 1983, Stewart 1985).

Sexual dimorphism must then be viewed as the overall expression resulting from a balance of many selective pressures, sometimes antagonistic, and therefore its examination requires a multiple perspective. This study has two general aims: (1), to analyze the extent and direction of sexual dimorphism in lacertid lizards, mainly focusing on traits potentially showing differences in connection with male-male combat, female fecundity or trophic segregation between sexes, and (2), to study how sexual size dimorphism relates to differences in the allometry of abdomen and head growth in both sexes. The study is restricted to eight species of lizards belonging to the closely related genera *Podarcis* and *Lacerta* (Arnold 1973, 1989). This choice of taxa allowed an examination of variation in sexual dimorphism within the framework of a common morphometric model. Furthermore, the studied specimens came from essentially sympatric populations and were collected in a relatively small and rather uniform area, so they shared the within-community and environmental pressures acting on growth dynamics and body size, both at the individual and the evolutionary level. In addition, the use of sympatric populations limits the potential confusing effects of geographical variation in sexual size dimorphism, that has been reported for some species (e.g., Pianka and Parker 1975, Fitch 1981, Madsen and Shine 1993). Lacertid lizards, and specifically some of the species involved in the present study, have been reported to exhibit reproductive traits and behaviors that could lead to sexual size differences. These include polygyny and male-male competition for territory and mating (Cheylan 1975, 1990, Saint Girons 1977, Edsman 1986, Marco 1994), increased fecundity with female size (Pérez Mellado 1982, Castilla and Bauwens 1989, Braña et al. 1991, Galán 1994, Marco 1994), and higher individual egg quality (i.e., egg size coupled with hatchling size and performance) for large females (Van Damme et al. 1992, Galán 1994).

Materials and methods

This work was based on museum specimens of eight species of lacertid lizards belonging to the genera *Lacerta* and *Podarcis*, which have been considered congeneric until recently (Arnold 1973, Mayer and Tiedemann 1982, Lutz and Mayer 1985). All lizards were caught in an area of about 150 km length (east-west) and 30 to 100 km width (north-south) in the central-eastern area of Asturias and the western end of Cantabria, in the North slope of the Cantabrian Mountains (Northern Spain).

Each specimen was measured to the nearest 0.1 mm for snout-vent length (SVL) from the anterior tip of the head to the cloacal opening, head and neck length (HL) from the tip of the snout to the collar gular anterior to the forelegs, maximum head height (HH), maximum head width (HW), and abdomen length (AL) from the collar to the cloacal gap. Measurements were taken only from specimens above the minimum adult size, as determined by the occurrence of enlarged follicles or oviductal eggs for females, and by external (color, femoral secretion) and gonadal (size and aspect of testes and epididymes) examination in males. Previous work on the same populations provided conclusive information about minimum size at maturity for males of most species (Braña 1984). Additional specimens from the study area were used for raising sample size as needed in order to establish the parameters of the regressions of clutch size on female body size and prey size distributions. The number of oviductal eggs was recorded for pregnant females, and the maximum length and width of marks produced by male bites on the female sides during copulation were measured to the nearest 0.1 mm. Size measurements (total length, to the nearest 0.1 mm) were made for every prey found undamaged enough in the stomach of adult lizards; measurements were taken with calipers for prey larger than 0.5 cm, and with a micrometer on a dissecting microscope for the smaller ones.

Throughout this paper parameters of linear regressions were estimated by the ordinary least-squares technique, which has some advantages for routine use, such as the use in analyses of covariance and computation of residuals, which are uncorrelated with the X variable (Pagel and Harvey 1988, Harvey and Pagel 1991, Sokal and Rohlf 1995). However, this procedure can underestimate the slope if the assumption that Y but not X contain error is not met, especially when the coefficient of determination is low (Rayner 1985, Harvey and Pagel 1991). Therefore, to study relationships between gain in fecundity with increasing female size and sexual size dimorphism, that critically depend upon accuracy of the slope estimates, I considered both the slopes from least-squares regression and reduced major axis analysis. The reduced major axis slopes were computed as the ratio of the standard deviation of Y (clutch size) to the standard deviation of X (SVL).

Relationships among variables in juvenile lizards were used as a baseline to make inferences about the ontogenetic trajectory of abdomen to head length ratio for both sexes. I selected young-of-the-year animals, caught prior to or immediatly after their first winter emergence (before May), still showing traces of the umbilical scar. Juvenile lizards were considered as a single group within each species because sex determination is not alway certain at this age, or relies on meristic characters that are not independent of the traits of interest (e.g., number of transverse rows of ventral scales, a dimorphic trait for most lacertids [Boulenger 1920], but likely related to abdomen length and without absolute discriminant power; see, for *Lacerta vivipara*, Bauwens and Thoen 1982, Lecomte et al. 1992).

As male and female sizes (SVL) exhibited a linear relationship passing through the origin (intercept for female size as the dependent variable, $a = 3.329$, $t = 1.112$, $p = 0.309$), the ratio of male to female size (average snout-vent length) can be used as the primary measure of sexual size dimorphism (Packard and Boardman 1987). Between-sex differences in body size measurements were examined by means of analysis of covariance (ANCOVA), with SVL as the covariate, except for abdomen length and head length, which were used as the covariate for each other, as both are components of the SVL. Prior to analysis data were checked for normality and homogeneity of variances using the Kolmogorov-Smirnov and Bartlett's tests, respectively. Decimal logarithmic transformation was used when necessary to achieve normality and nonparametric tests were employed when this failed to normalize data. Except when otherwise stated, statistical tests are two-tailed, and the significance level was set at $p = 0.05$.

Across species correlations based on mean specific values for different traits can be unsuitable because of the lack of independence among data points corresponding to phylogenetically related species (Felsenstein 1985, Huey 1987, Harvey and Pagel 1991). Therefore, species cannot be treated as independent data points in correlation or regression analyses, as this could increase the likelihood of obtaining inflated estimates towards the adaptive explanation (Martins 1993, Miles and Dunham 1993). To avoid this difficulty I calculated independent contrasts for each variable, by comparing pairs of tip species or higher nodes that share a common ancestor in the phylogenetic tree, according to Felsenstein's (1985) method, thus obtaining $N-1$ independent contrasts for the N extant species. The data I used to compute correlations and regressions were contrasts standardized according to the branch lengths of the phylogenetical tree (Harvey and Pagel 1991, Garland et al. 1992), and the independent contrasts were calculated and standardized using the program PDAP developed by Jones, Dickerman and Garland. Least-squares regressions through the origin were used to obtain correlation coefficients among traits and multiple regression for size dimorphism as the dependent variable, because the expected means of standardized contrasts are zero (Martins and Garland 1991, Garland et al. 1992, Martins 1993). As only one degree of freedom is lost in regressions through the origin (Zar 1984, Garland et al. 1992) significance can be tested for $N-2$ d.f.

The framework I used for the phylogenetic arrangement of the lacertid species involved in this work was a reconstruction made by Bauwens et al. (1995; Fig. 2B), based on Arnold's (1989) phylogeny of lacertids with divergence times from immunological distances (Lutz and Mayer 1985, Mayer and Lutz 1989, 1990; extensive review of sources and approaches in Bauwens et al. 1995). Additionally I considered *Lacerta lepida* to have diverged from its putative sister group (*L. monticola* and *Podarcis* species) 20 million years before the present (mybp hereafter). This divergence time represents the upper limit of available estimates (18–20 mybp; Lutz and Mayer 1984, Böhme and Corti 1993), and allows nesting the *Archaeolacerta-Podarcis* clade at the 18 mybp level, as in Bauwens' proposal. Separation time of the species *L. schreiberi* and *L. viridis* is also unknown; however, both species lie in the *Lacerta* s. str. group, for which Lutz and Mayer (1985) reported isolation times based on immunological distances: the sibling species *L. viridis* and *L. trilineata* would have a divergence time of 3–4 my, whereas divergence for that

Table 1. Summary statistics (mean ± 1 sd, mm) of the main morphometric traits for male and female lacertid lizards (abbreviations as stated in the methods section). Between-sex differences in mean values were tested by Student's t tests (SVL) or analyses of covariance, with SVL as the covariate, except for AL and HL, used as covariates of each other. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Species	Sex	Sample Size	SVL mean ± sd	AL mean ± sd	HL mean ± sd	HH mean ± sd	HW mean ± sd
Podarcis bocagei	♂♂	41	55.30 ± 3.55	35.05 ± 2.32	20.25 ± 1.39	6.88 ± 0.58	9.21 ± 0.66
	♀♀	47	53.51 ± 3.12	36.42 ± 2.54	17.08 ± 0.78	5.47 ± 0.35	7.37 ± 0.39
			$t = 2.52$*	$F = 101.3$***	$F = 447.3$***	$F = 304.7$***	$F = 429.4$***
Podarcis hispanica	♂♂	32	50.83 ± 5.16	32.50 ± 3.36	18.11 ± 1.57	5.35 ± 0.75	7.85 ± 0.87
	♀♀	35	47.63 ± 4.01	32.31 ± 3.31	15.30 ± 0.94	4.20 ± 0.33	6.40 ± 0.40
			$t = 2.83$**	$F = 61.9$***	$F = 167.4$***	$F = 83.8$***	$F = 119.4$***
Podarcis muralis	♂♂	39	57.23 ± 3.85	36.71 ± 2.65	20.52 ± 1.34	7.23 ± 0.68	9.54 ± 0.67
	♀♀	42	57.10 ± 3.61	39.41 ± 2.92	17.69 ± 0.83	5.80 ± 0.32	7.87 ± 0.43
			$t = 0.15$	$F = 189.4$***	$F = 501.0$***	$F = 309.5$***	$F = 483.7$***
Lacerta monticola	♂♂	45	61.13 ± 3.91	38.79 ± 2.63	22.74 ± 1.65	7.72 ± 0.69	10.46 ± 0.97
	♀♀	45	62.73 ± 4.65	43.13 ± 3.60	19.60 ± 1.28	6.48 ± 0.53	8.94 ± 0.61
			$t = 1.77$	$F = 154.1$***	$F = 350.1$***	$F = 290.8$***	$F = 323.4$***
Lacerta vivipara	♂♂	18	47.91 ± 2.74	32.16 ± 2.29	15.75 ± 0.66	6.16 ± 0.44	7.64 ± 0.38
	♀♀	34	53.64 ± 3.84	38.57 ± 3.19	15.10 ± 0.84	5.62 ± 0.43	7.07 ± 0.38
			$t = 5.62$***	$F = 109.9$***	$F = 100.1$***	$F = 61.1$***	$F = 110.9$***
Laceta lepida	♂♂	12	140.78 ± 20.68	89.77 ± 12.81	51.02 ± 8.06	21.54 ± 4.31	28.27 ± 5.20
	♀♀	10	135.29 ± 16.77	91.64 ± 11.49	44.65 ± 5.51	17.77 ± 2.29	22.27 ± 2.95
			$t = 0.67$	$F = 18.1$***	$F = 16.7$***	$F = 18.7$***	$F = 36.3$***
Lacerta schreiberi	♂♂	15	102.31 ± 9.86	65.65 ± 7.07	36.66 ± 3.52	16.52 ± 2.16	20.17 ± 2.66
	♀♀	24	101.90 ± 8.25	69.57 ± 6.36	32.33 ± 2.11	13.91 ± 1.28	16.12 ± 1.46
			$t = 0.14$	$F = 92.4$***	$F = 82.1$***	$F = 54.9$***	$F = 163.7$***
Lacerta viridis	♂♂	14	107.15 ± 7.07	69.60 ± 4.45	37.55 ± 3.08	16.69 ± 1.59	20.03 ± 2.26
	♀♀	13	108.54 ± 5.48	76.21 ± 4.92	33.10 ± 1.88	14.19 ± 1.01	15.99 ± 1.24
			$t = 0.57$	$F = 65.3$***	$F = 80.8$***	$F = 63.6$***	$F = 87.3$***

pair with respect to *L. agilis* was calculated as having occurred 4–6 my ago. Lutz and Mayer (1985) indicated that this last figure could be an underestimation, as suggested by both the morphological and the electrophoretic differences, and Bauwens et al. (1995) considered as more realistic a divergence time of about 10 my for *L. agilis* and *L. schreiberi*. *L. viridis* is likely to be more closely related to *L. schreiberi* than to *L. agilis* (e.g., Arnold 1989), but less so than to *L. trilineata* (Mayer and Tiedemann 1985). It seems reasonable therefore, to assign an intermediate divergence time (5 mybp) for the pair *L. schreiberi*-*L. viridis*. The resulting phylogeny and estimated divergence times are shown in Fig. 2A.

Results

Sexually dimorphic traits

There were significant differences between sexes in mean values of all the examined traits when corrected for body size (ANCOVAs with SVL as the covariate, except for head length and abdomen length, used as covariates of each other). Males exceeded females in every head dimension, whereas the inverse was the case for abdomen length in all the studied species (Table 1). Despite the fact that abdomen length and head length adjusted for each other exhibited significant intersexual differences in all the studied species, a positive correlation between male and female abdomen to head ratio across species was close to significant (standardized independent contrasts: $r = 0.610$, $p = 0.073$, one-tailed). Males exhibited larger size (SVL) than females in the species *P. hispanica* and *P. bocagei*, and smaller in *L. vivipara*, and also marginally in *L. monticola* ($p = 0.08$). There were no significant differences in the other species.

Abdomen length positively covaried with head length in both sexes in all the studied species, but the relative increse of abdomen length with size was higher in females (the ANCOVAs showed larger slopes of the regressions of AL on HL for females; the exceptions were *L. vivipara* and *L. lepida*). The ratio between two morphometric variables can be used to infer whether an isometric (the ratio does not vary with body size) or an allometric variation ocurs (Packard and Boardman 1987). Generally, in female lacertids the ratio of abdomen length to head length significantly increased with size (SVL). The two exceptions to this pattern were *Lacerta viridis* and *L. lepida*, species with noticeably small female sample size (Table 2; see also Fig. 1). On the contrary, the ratio for males showed no variation with SVL except in *L. vivipara*. Males of this species exhibited a significant increase of the abdomen proportion over SVL, at a similar rate as females (ANCOVA for slope comparison; $F_{1,48} = 0.25$; $p > 0.1$), although at a significantly lower size adjusted level (ANCOVA for intercepts; $F_{1,48} = 103.05$, $p < 0.0001$). In general, juvenile lizards formed normal (i.e., unimodal, mesokurtic,

Table 2. Mean values (±1 sd) of the abdomen to head ratio for juvenile, adult male and adult female lizards of the eight studied species, and selected statistics for the least squares regressions of that ratio on snout-vent length for the same groups. Significance of differences among groups were tested by ANOVAs and Scheffe's tests a posteriori. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

					Regression model		
Species	Category	Sample size	Ratio mean ± sd	F	Slope	R^2	F
Podarcis bocagei	Male	41	1.73 ± 0.07	230.22***	0.001	0.000	0.013
	Female	47	2.13 ± 0.11	$F_e > (M,J)$	0.022	0.392	28.979***
	Juvenile	18	1.71 ± 0.11		0.003	0.010	0.202
Podarcis hispanica	Male	32	1.80 ± 0.08	60.72***	0.004	0.057	1.742
	Female	35	2.11 ± 0.14	$F_e > (M,J)$	0.025	0.526	36.591***
	Juvenile	14	1.78 ± 0.17		0.017	0.202	4.042
Podarcis muralis	Male	39	1.79 ± 0.07	292.78***	0.005	0.072	2.854
	Female	42	2.23 ± 0.10	$F_e > (M,J)$	0.019	0.482	37.210***
	Juvenile	30	1.77 ± 0.11		0.010	0.127	4.076
Lacerta monticola	Male	45	1.74 ± 0.10	248.78***	0.000	0.000	0.007
	Female	45	2.20 ± 0.12	$F_e > (M,J)$	0.013	0.239	13.528***
	Juvenile	24	1.68 ± 0.11		0.013	0.256	7.594*
Lacerta vivipara	Male	18	2.04 ± 0.11	151.11***	0.028	0.462	13.753**
	Female	34	2.55 ± 0.14	$F_e > (M,J)$	0.024	0.435	24.685***
	Juvenile	15	1.93 ± 0.14		0.026	0.303	5.663*
Lacerta lepida	Male	12	1.77 ± 0.09	25.29***	0.002	0.160	1.908
	Female	10	2.06 ± 0.18	$F_e > (M,J)$	0.003	0.058	0.492
	Juvenile	8	1.65 ± 0.09		0.007	0.745	17.554**
Lacerta schreiberi	Male	15	1.79 ± 0.14	54.57***	0.004	0.069	0.964
	Female	24	2.15 ± 0.10	$F_e > (M,J)$	0.008	0.405	14.975***
	Juvenile	8	1.71 ± 0.17		0.013	0.467	5.263
Lacerta viridis	Male	14	1.85 ± 0.10	160.27***	0.003	0.069	0.899
	Female	13	2.30 ± 0.13	$F_e > M$	0.007	0.215	3.021
	(#) Juvenile	3	1.77 ± 0.10		–	–	–

(#) No statistical analyses (ANOVA or regression) were performed on juvenile *L. viridis* because of the small sample size.

unskewed) abdomen to head ratio frequency distributions (the only exception was *L. monticola*, which showed a rather leptokurtic distribution [$K = 3.81$, S.E. = 0.92], although the Kolmogorov-Smirnov's test failed to detect departure from normality [$Z = 0.82$, $p = 0.51$]), whereas those of adult individuals were bimodal, with the male and female distributions hardly overlapping (see Fig. 1). Juvenile lizards of every species exhibited abdomen to head length ratios similar to that of males but significantly different from females (ANOVAs and Scheffe's tests a posteriori; Table 2). This ratio increased with SVL in juvenile of the species *L. lepida*, *L. monticola*, and *L. vivipara* (Fig. 1).

Size and size dimorphism relationships

All but one species exhibited a significant positive relationship between female SVL and clutch size (Table 3). The only exception was *Podarcis hispanica*, with an almost invariant clutch size (two eggs in 25 out of 32 pregnant females examined; mean ±1 SE, 2.20 ± 0.09; no significant relationship was found between female SVL and clutch size: $r^2 = 0.0076$; $p > 0.5$). This species also had the most extreme male-biased size dimorphism (M/F = 1.07; $t = 2.83$; $p < 0.01$). There was a positive correlation between the mean size of male bites (maximum length plus maximum width of clearly discernable marks) and female SVL in *L. vivipara* ($r = 0.624$, $n = 12$, $p < 0.05$) and also marginally in *L. monticola* ($r = 0.587$, $n = 11$, $p = 0.06$) but did not in any other species, although small sample sizes preclude definitive conclusions.

Computing standardized contrasts for each trait (Felsenstein 1985), I have found significant negative correlations between the amount of size dimorphism (mean male to female size ratio) and the abdomen to head length ratio for females ($r = -0.766$, $p < 0.05$), with the residuals from the linear regressions (through the origin) of clutch size on SVL ($r = -0.743$, $p = 0.056$), and with the slopes of these regressions ($r = -0.849$, $p < 0.02$, for slopes from least squares regression; $r = -0.758$, $p < 0.03$, for slopes from reduced major axis analysis). No significant relationships were found with SVL ($r = 0.147$; $p > 0.1$) or with the abdomen to head ratio for males ($r = -0.157$; $p > 0.1$). Clutch size contrasts were computed as the residuals from the linear regression (through the origin) on SVL, as the preliminary correlation matrix using standardized contrasts showed significant association between both variables ($r = 0.860$; $p < 0.02$). In a stepwise multiple regression with species sexual size dimorphism as the dependent variable, the slope of the regression of clutch size on SVL and the ratio of abdomen to head for females were the only predictor variables that significantly entered the model (in that order; level to enter the regression: $p = 0.1$). Results were similar with respect to variables entering the regression and amount of variance explained by using slopes from least squares regressions or reduced major axis analyses (Table 4).

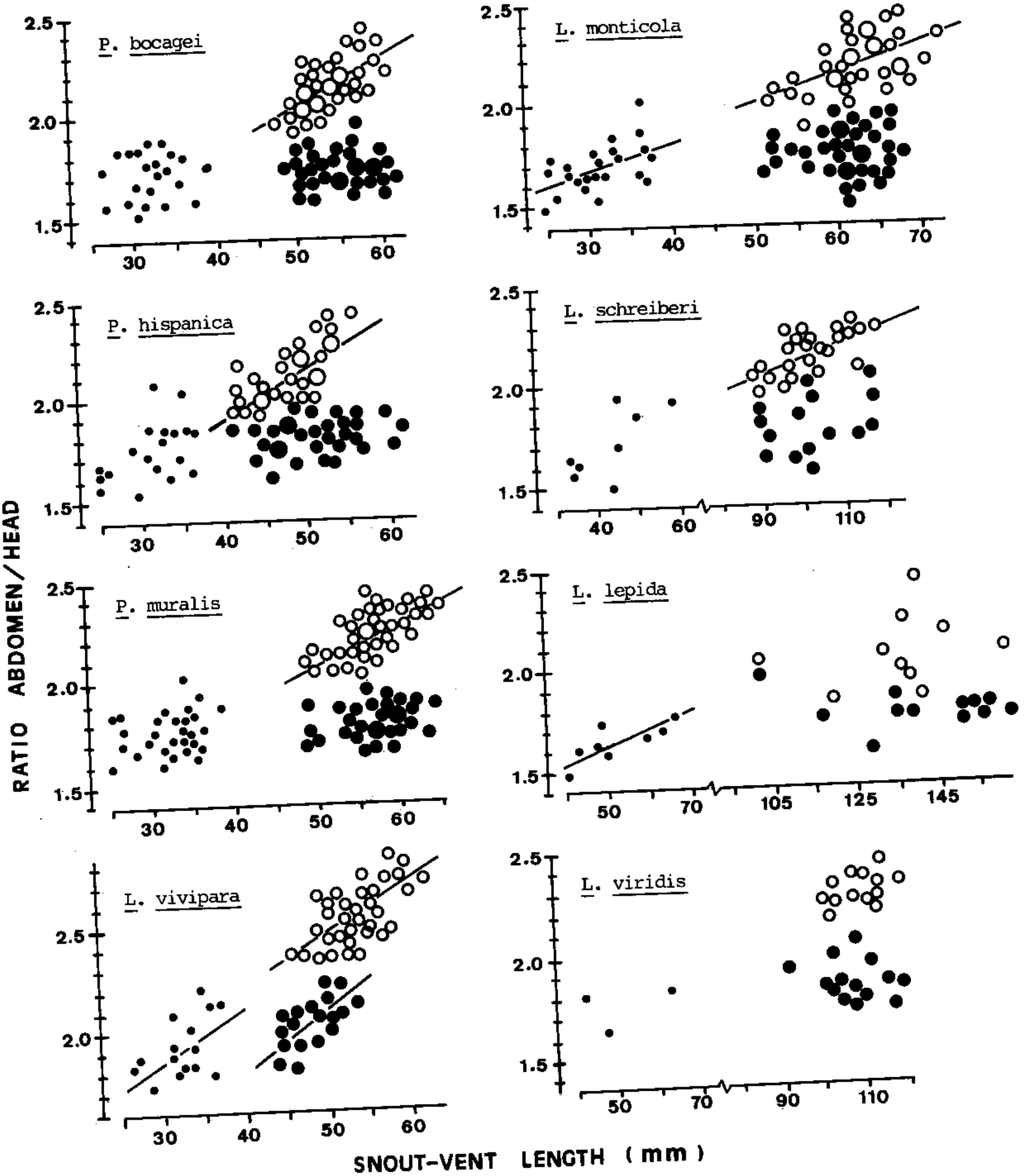

Fig. 1. Scatterplots of the abdomen to head ratio against the snout-vent length for eight species of lacertid lizards. Points refer to juvenile lizards, closed circles to adult males, and open circles to adult females; larger circles for adult specimens include three or more data points. Regression lines are shown whenever the slopes are significantly different from zero

Prey size segregation

The mean size of prey caught by the adult specimens showed between sex differences for the species *P. hispanica* ($t = 3.06$, d.f. $= 87$, $p < 0.01$), *P. muralis* (data were log transformed to achieve normality; $t = 3.57$, d.f. $= 373$, $p < 0.001$) and *L. lepida* (log transformed data; $t = 2.83$, d.f. $= 74$, $p < 0.01$); mean prey length was higher for males in all three species (Fig. 3).

Computing prey size composition at the individual level (maximum, minimum, mean, and standard deviation) for lizards with three or more measurable prey in

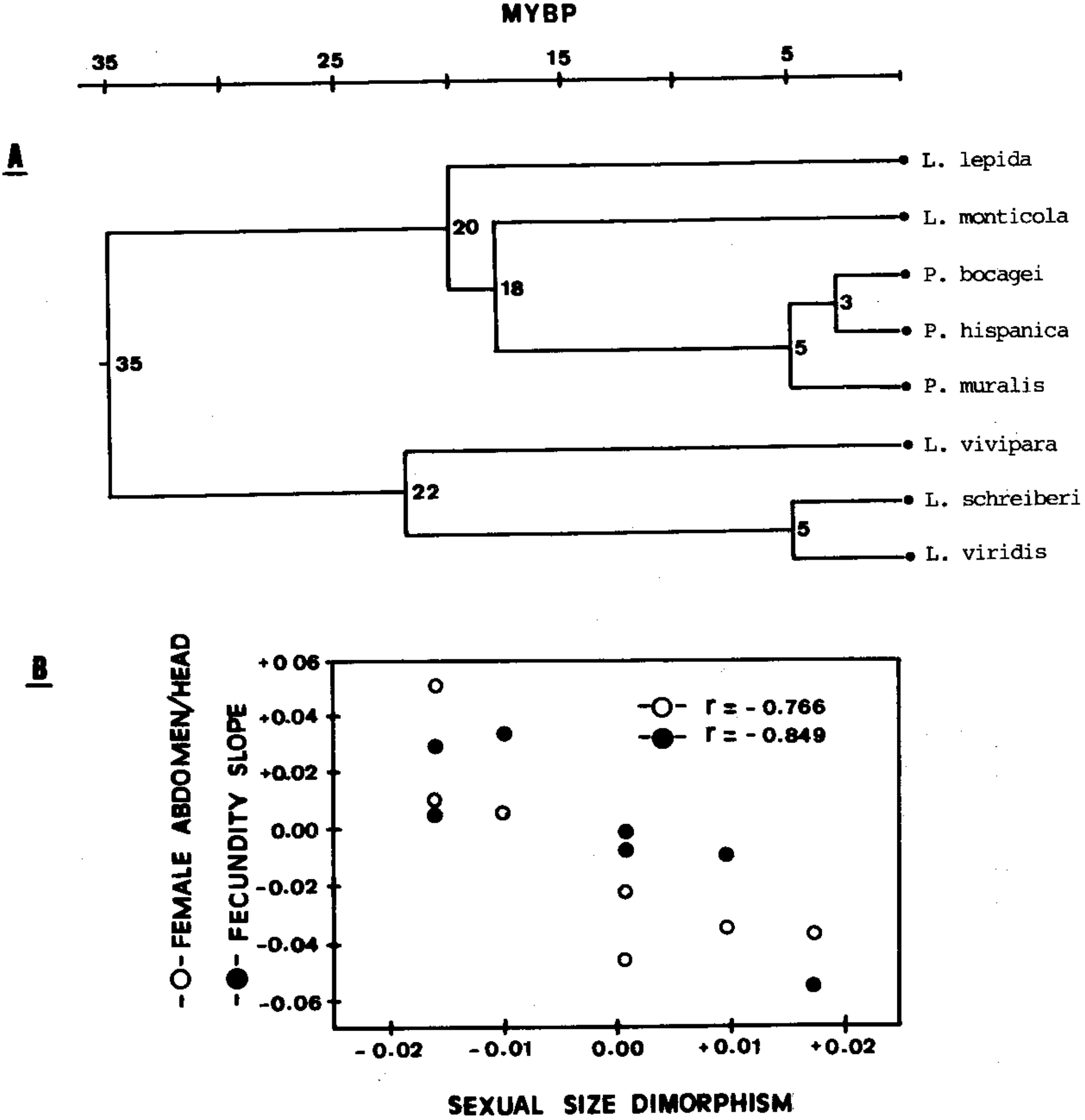

Fig. 2. (A) Phylogenetic arrangement and estimated divergence times among the eight studied species, that allow the computation of standardized independent contrasts according to Felsenstein's method. (B) Contrasts of the female abdomen to head ratio and of the slopes of the least squares regressions of clutch size on SVL are plotted against contrasts for size dimorphism.

the stomach, I have found between sex differences for minimum prey size in *P. muralis* (larger for males; $F_{1,48} = 6.03$, $p = 0.018$), and for standard deviation in *L. lepida* (higher for males; $F_{1,8} = 6.31$, $p < 0.05$). When head width was used as the covariate, these differences disappeared ($F_{1,46} = 0.99$, and $F_{1,6} = 0.43$, respectively; $p > 0.1$ in both cases), but some new ones emerged (maximum prey size and standard deviation; lower values for males in *P. muralis* and *L. monticola*; $F_{1,46} = 6.14$, $p < 0.02$, and $F_{1,46} = 7.83$, $p < 0.01$ for the first species, and $F_{1,33} = 6.85$, $p < 0.02$, and $F_{1,33} = 6.75$, $p < 0.02$, for the second one).

Discussion

Lacertid lizards exhibited between-sex differences in size corrected values for abdomen length and head dimensions. There is no evidence from previous studies that differences between sexes in adult age distribution

Table 3. Summary statistics for the least squares regression of clutch size on SVL in eight species of lacertid lizards, and reduced major axis slopes for the same samples. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Species (sample size)	Least squares regression				RMA slope
	slope	intercept	R^2	F	
Podarcis bocagei (31)	0.081	−0.904	0.208	7.598**	0.177
Podarcis hispanica (32)	0.011	1.682	0.007	0.229	0.126
Podarcis muralis (58)	0.209	−6.833	0.287	22.556***	0.390
Lacerta monticola (57)	0.310	−13.318	0.583	76.943***	0.405
Lacerta vivipara (43)	0.277	−8.734	0.455	34.273***	0.410
Lacerta lepida (4)	0.170	−12.816	0.963	53.013***	0.173
Lacerta schreiberi (10)	0.232	−12.130	0.426	5.937*	0.355
Lacerta viridis (12)	0.243	−14.473	0.437	7.776*	0.367

could account for SSD in the studied lacertid species (Castanet and Roche 1981, Pilorge and Castanet 1981, Braña 1984, Castanet 1986, Edsman 1990, Galán 1994). Despite that, I have found significant between-sex differences in mean adult size in several species, including both females larger than males and males larger than females. Larger species are not more dimorphic in body size, as is a frequent rule in vertebrates (Clutton-Brock et al. 1977, Berry and Shine 1980; review in Reiss 1989), and has also been suggested for lizards and snakes (Fitch 1981, but see Stamps 1983).

A central point of interest in the analysis of sexual size dimorphism in the lizards is the differential growth dynamics for head and abdomen between sexes. Sexual selection via male-male combats could increase head size (Carothers 1984, Vitt and Cooper 1985), whereas selection acting on clutch size or clutch volume in females might promote larger abdomen size (Shine 1989, Griffith 1990, Karlsson and Wickman 1990). In adult lacertids, abdomen and head increased with each other in both sexes, but abdomen length increased at a higher rate in females. As a consequence, the common pattern for females was an increase of the relative size of the abdomen as the SVL increased (the only exceptions were the species with the lowest female sample size: *L. viridis* and *L. lepida*), whereas only one species (*L. vivipara*) showed a significant change in the abdomen to head ratio with SVL for males. In addition, mean abdomen to head ratio of adult males did not differ from that of juveniles, and both were significantly lower than that of females in all the studied species. In fact, the linear relationship between abdomen length and head length, and the constant ratio of these measures in relation to SVL in males indicates isometry of both body segments (Packard and Boardman 1987, Harvey and Pagel 1991). In contrast, female abdomen exhibited a positive allometry (the ratio increased with SVL). The positive relationship of the abdomen ratio with SVL found in juvenile of some species may only reflect the starting of the sexual differentiation among the largest individuals.

Size dimorphism is not by itself a trait directly subjected to selection, but rather it is the result of a variety of selective forces acting on both male and female size. There is strong evidence for the prominent role of selection on female body (or abdomen) size in determining the actual outcome of size dimorphism in lacertid lizards. In fact, the abdomen to head length ratio of females together with the fecundity slope accounted for about 85% of the variation in SSD in the studied species of lacertids. As the slope of the regression of clutch size on female SVL represents the gain in fecundity per unit increase in body size, it could be considered a measure of the strength of the selective pressure towards large body size in females. Therefore, the negative correlation found between the fecundity slope and the male/female size ratio could be interpreted on the basis of the fecundity-advantage hypothesis. Furthermore, species with larger mean clutch size than expected for their body size (positive residuals) exhibited larger female size relative to male size. Variation in sexual size dimorphism associated with variation in fecundity, whether it be clutch size in a reproductive episode or lifetime egg production, has been reported in other squamate reptiles (Fitch 1981, but see Shine 1994 for snakes), as well as in insects (Wiklund and Karlsson 1988, McLain 1991). Similarly, Shine and Greer (1991) reported for Australian scincid lizards that species with invariant clutch size (= no gain in fecundity with increasing size) exhibited smaller body sizes.

Positive allometric growth of the head in males has sometimes been concluded because the males have a higher slope than females for the regression of head length on total body length. But that outcome can also result from a positive allometry of abdomen length in females, as seems to be the case for most of the lacertid lizards in this study. However, this does not exclude any role of sexual selection in determining total body size, body shape or coloration in male lacertid lizards. The fact that SSD was mainly explained by traits linked to female fecundity does not imply that males have not experienced selection for increased size, but may only mean that determinants of male body size do not differ substantially across species, so SSD would reflect relative variation in female size. In this scheme, male body size could be considered as the

Table 4. Multiple regressions through the origin for SSD as the dependent variable and the following assayed predictor variables: male abdomen to head ratio (AHM), female abdomen to head ratio (AHF), slopes of clutch size on SVL within species (fecundity slope), and the residuals of the mean specific fecundity on the across-species regression of clutch size on SVL. Data values were standardized independent contrasts (Felsenstein method), and the regression followed a stepwise model with the entry level set at $p = 0.1$. The analysis was performed by considering both fecundity slopes from least squares regressions (A) and reduced major axis (B).

Variables entered in the regression	Coefficients			Variance explained		
	$b \pm$ se	t	p	Multiple R^2	F	p
(A) 1. Fecundity slope (LS)	−0.272 ± 0.087	3.104	0.027	0.722	15.553	0.008
2. AHF	−0.158 ± 0.072	2.206	0.078	0.859	15.218	0.007
(B) 1. AHF	−0.187 ± 0.088	2.109	0.086	0.587	8.526	0.027
2. Fecundity slope (RMA)	−0.179 ± 0.087	2.042	0.096	0.775	8.600	0.024

baseline in looking at the evolution of female size, because the multiple evolutionary and environmental factors influencing body size preclude the analysis of absolute values for this trait (Shine 1988). The fact that males were not equal but larger than females in species with an almost invariant clutch size (i.e., with low selective pressure towards increased female size, therefore potentially representing a neutral control for looking into the evolution of male size) suggests an evolutionary increase of male size. Actually, there is circumstantial evidence supporting this possibility, as larger males have been reported to have higher reproductive success in some lacertids (e.g., Edsman 1990, Marco 1994), and the positive relationships of the size of male bites and female SVL in some species could be indicative in the same way. Larger heads should be advantageous in order to achieve higher reproductive success for male lizards, both in the context of male-male combat and to increase effectiveness in subduing females during copulation (Carothers 1984, Edsman 1990, Hews 1990), but a large head does not necessarily require differential (allometric) growth, as it can also be achieved by overall body growth (Shine 1989). In addition, most of the species examined showed clearly dimorphic color patterns (Arnold 1973), and males of several species exhibit showy colors whose spread and brightness seasonally vary in connection with reproductive state (e.g., *L. vivipara*, Bauwens et al. 1989; *Lacerta schreiberi*, Marco 1994; *Podarcis bocagei*, Galán 1994), so has likely developed in response to sexual selection (Cooper and Vitt 1988, Shine 1989, Vial and Stewart 1989). Díaz (1993) reported some evidence of positive correlation of brightness of male coloration and short-term reproductive success in the lacertid *Psammodromus algirus*, then providing evidence for the possible mechanism implicated in such kind of selection.

Evidence for intersexual dietary partitioning was weaker than expected from the amount of dimorphism in overall body size or in relative head size, evidently related to prey capture and manipulation (Powell and Russell 1985, Shine, 1991, Emerson and Voris 1992), as only three species showed significant differences in mean prey size (always larger for males); only one of these species (*P. hispanica*) exhibits dimorphism in snout-vent-length although all of them are dimorphic in head size and showed the expected direction in prey size differences as predicted by sexual dimorphism. Previous studies showed little between-sex prey size segregation in lacertids, even when the studied species were dimorphic in SVL or head dimensions (e.g., Marco Llorente and Pérez Mellado 1988, Castilla et al. 1991, Pérez Mellado et al. 1991). Moreover, there are in the present study two species (*P. muralis* and *L. monticola*) for which maximum prey size and prey size variability (standard deviations) did not differ between sexes, but values adjusted for head width were significantly lower in males. The simultaneous evolution of larger total body size in females and larger relative size of the structures responsible for prey capture in males, a rather frequent pattern in lizards (Boulenger 1920, 1921, Fitch 1981, Cooper and Vitt 1989; examples in this work), means that the main dimorphic trait (head size) could act on prey size distribution in a compensatory direction with respect to total body size, rather than reinforcing intersexual dietary divergence. This pattern of functionally divergent evolution of "body segments" (from the trophic view) may actually be a strong indication against food partitioning as promoter of sexual dimorphism. On the contrary, an ecological cause of sexual dimorphism would be more plausible when body size and relative size of the trophic apparatus are consistent with the observed differences in prey size distribution (Selander 1972, Shine 1989, Camilleri and Shine 1990). Even in this case (actually limited to the species *P. hispanica* in this study), there is no reason to discard the hypothesis of dimorphism primarily determined by sexual selection that results in (or even is reinforced by) trophic divergence between the sexes (Slatkin 1984, Shine 1989), as the observed direction of size differences was in agreement with the expected under the hypothesis of sexual selection causation.

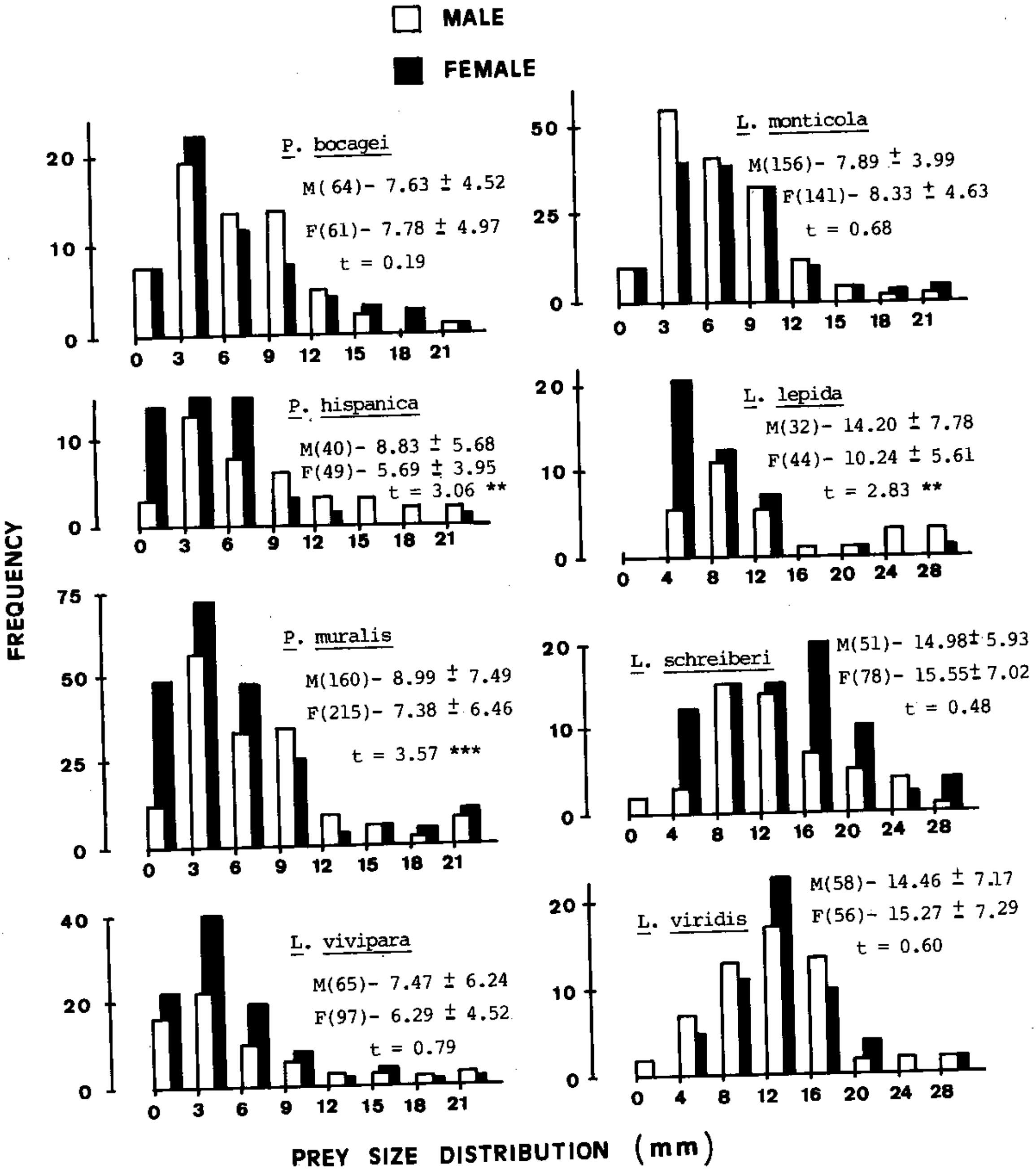

Fig. 3. Frequency distribution of prey sizes for males and females of lacertid lizards. Figures represent, for every species, sample size (in brackets), mean prey size (±1 sd) for males and females, and *t* statistics for between sex differences in mean prey lengths (**: $p < 0.01$, ***: $p < 0.001$).

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