

## **Sexual dimorphism of tail length in lacertid lizards: test of a morphological constraint hypothesis**

L. JAVIER BARBADILLO

*Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid,  
E-28049 Madrid, Spain*

AND D. BAUWENS\*

*Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium*

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Males of many lizard species have longer tails than similarly-sized females. We hypothesized that this dimorphism is induced by a longer non-autotomous tail part in males, which is associated with the presence of the copulatory organs at the tail base, and presumably reduces the males' ability to escape predation by tail shedding. A compensatory mechanism would be an increase of total tail length in males, to achieve equal lengths of the autotomous tail part in both sexes. A critical prediction of this 'morphological constraint' hypothesis is that the extent of dimorphism in total tail length increases with the magnitude of sexual differences in length of the non-autotomous tail base. We tested this prediction through a comparative study in a small clade of lacertid lizards. Within each of nine species, sexual differences in length of the non-autotomous tail base and in total tail length do not change with body size. All species, except one, exhibit a clear male-biased dimorphism in length of the non-breakable tail base. In all species studied, males have longer tails than females. We used the method of phylogenetically independent contrasts to explore the interspecific relation between dimorphism in length of the tail base and sexual differences in total tail length. Contrary to our prediction, we found no evidence for a positive correlation between the extent of dimorphism in both traits. Thus, constraints imposed by the male copulatory organs on tail autotomy do not seem to be a significant factor in the evolution of dimorphism in tail length in this clade of lacertid lizards.

### **Introduction**

The most prevalent explanation for sexual dimorphism is that it evolved through the action of sexual selection (e.g. Darwin, 1871; Selander, 1972; Clutton-Brock, Harvey & Rudder, 1977). However, there exist alternative hypotheses that do not invoke sexual selection (Hedrick & Temeles, 1989). First, natural selection might favour dimorphism when this promotes ecological divergence and thereby relaxes intersexual competition for food (Schoener, 1967; Shine, 1989, 1991; Houston & Shine, 1993). Second, natural selection for increased reproductive output may induce larger body sizes in females (Shine, 1988; Hedrick & Temeles, 1989).

An additional hypothesis, which has received little attention, proposes that sexual dimorphism in some characters may result from constraints directly imposed by differences in the anatomy of the sexual organs. This hypothesis, termed the 'Morphological Constraint' hypothesis by King (1989), was first formulated by Klauber (1943) and Clark (1966) to explain the longer tails of male snakes. These authors suggested that the presence of the copulatory organs (i.e. the paired hemipenes) at the

\*Address for correspondence: email: dirk.bauwens@instnat.be

base of the tail places a lower limit on tail length in males, but not in females. All else being equal, this constraint should induce longer tails in male snakes. This hypothesis, however, does not specify why the tail portion not occupied by the hemipenes should be equally long in both sexes. Nevertheless, results of interspecific comparisons are consistent with specific predictions of this hypothesis (King, 1989).

We recently (Barbadillo *et al.*, 1995) proposed a hypothesis, similar to that of Klauber (1943) and Clark (1966), for the sexual dimorphism in tail length in lizards. It identifies the male reproductive organs as a morphological constraint on an important function: the capacity to autotomize the tail. Tail autotomy is a significant component of the escape behaviour of many lizard species (Arnold, 1984, 1988). Tail shedding is an active process that occurs along an intravertebral fracture plane that is present in most vertebrae, except the most basal ones (Etheridge, 1967; Bellairs & Bryant, 1985; Arnold, 1988; Russell & Bauer, 1992; Barbadillo *et al.*, 1995). As in snakes, the copulatory organs of male lizards are housed at the base of the tail, where their presence constrains the capacity to break the tail. As a result, males of many species of lacertid lizards have a higher number of non-autotomous vertebrae, and hence a longer non-breakable tail base than conspecific females (Arnold, 1973; Barbadillo *et al.*, 1995). At equal total tail lengths, the tail portion that can be broken would therefore be shorter in males, and presumably reduce their chances to escape by autotomy (Arnold, 1988). A compensatory mechanism would be an increase of total tail length in males, such that the autotomous tail part would be of equal length in both sexes.

Thus, our hypothesis poses that dimorphism in tail length in lizards is mainly a consequence of sexual differences in the length of the non-autotomous tail base. A critical prediction of this hypothesis is that species that are highly dimorphic in length of the non-autotomous tail base should also exhibit a high extent of dimorphism in total tail length. In other words, among-species differences in dimorphism of the length of the non-autotomous base of the tail should be associated with parallel sexual differences in total tail length. We here present a test of this prediction in a clade of phylogenetically-close species of lacertid lizards. Our objectives are: (1) to document sexual dimorphism, and its ontogenetic trajectory within each species, in length of the non-autotomous tail portion and in total tail length; (2) to explore the interspecific relation between the magnitude of sexual differences in total tail length and the extent of dimorphism in length of the non-breakable tail base, using statistical methods that account for the phylogenetic relations among the species studied.

## Material and methods

### *General procedures and intraspecific analyses*

We studied dry skeletons and cleared specimens of 9 species of lacertid lizards (*Gallotia galloti*, *Psammotromus algirus*, *Ps. hispanicus*, *Lacerta monticola*, *Podarcis muralis*, *P. hispanica*, *P. bocagei*, *Acanthodactylus erythrurus*, *Lacerta vivipara*). Lizards were collected at different localities in continental Spain and on Tenerife (Canary Islands; only *G. galloti*), and deposited in the collections of the Biology Department, Autonomous University of Madrid. Clearing of specimens, and staining of their skeletons, followed methods described in Taylor (1967) and Zug & Crombie (1970). We recorded species, sex and snout-vent length (SVL; to the nearest 0.05 mm) of each lizard upon capture. For each dry skeleton, we noted the position of the first caudal vertebra with a complete fracture plane. Cleared specimens were examined under a binocular dissecting microscope with an ocular micrometer; we recorded the position of the first caudal vertebra with a complete autotomous plane and measured (to the nearest 0.01 mm) the length of the non-autotomous part at the base of the tail (LNAT; from the anterior end of the prezygapophyses of the first caudal vertebra to the first complete fracture plane). For each species and sex, we examined lizards of different age classes, attempting to cover the entire range of body lengths.

Because many of the cleared specimens had regenerated tails, information on length of the intact tail was obtained for different samples, consisting of complete ontogenetic series of lizards. For most species, data (tail length, SVL; to the nearest 0.05 mm) were taken from specimens in the collections of the Biology Department, Autonomous University of Madrid and the National Natural History Museum of Madrid. The sex of juvenile and subadult lizards was determined by examination of the gonads and/or the musculature at the base of the tail. We took X-ray photographs of the tail of many adult specimens, to verify that it was entirely intact. Data for *L. vivipara* were collected during a mark-recapture study of a natural population at Kalmthout (Belgium); we retained measurements of SVL and intact tail length at the first capture of each individual lizard. Records for *P. hispanica* were of adult lizards caught at Salamanca (Spain) and their laboratory-born progeny, which were measured at biweekly intervals until the age of 4 months; we selected the first measurement of each adult lizard, and that taken on a randomly chosen date for each young born in captivity.

Within each species, we examined sexual differences in the relations of LNAT, and of total tail length, to SVL by analysis of covariance (ANCOVA). All variables were transformed logarithmically (base 10) to achieve linearity of the relationships and homoscedasticity of the variances. We first assessed whether the assumption of equality of the slopes (i.e. parallelism of the regression lines) was met. We then calculated and compared the adjusted means of the dependent variable (i.e. LNAT or total tail length). The adjusted means account for possible sexual differences in the covariate (i.e. SVL) and therefore provide convenient summary statistics for the dependent variables within each sex and species. Subsequent interspecific comparisons were performed using the adjusted means calculated from *log-log* transformed data. The adjusted means shown in Tables II & III are backtransformed (*antilog*) values which can be interpreted directly. Note that we cannot directly estimate the length of the autotomous portion by subtracting LNAT from total tail length, because both variables were measured in different samples of lizards.

### *Interspecific analyses*

For each measured trait, we regressed the adjusted means for males to those of females. Estimates of the extent of sexual dimorphism in each species were then obtained by calculating the residuals of the regression equation. Species with positive residual scores exhibit a more prominent male-biased dimorphism than generally present in the group of species studied; in species that have negative residual scores, the difference between males and females is less salient. Regression residuals provide statistically robust estimates of the extent of sexual dimorphism and are therefore more appropriate than simple size ratios (e.g. Packard & Boardman, 1987; Ranta, Laurila & Elmberg, 1994 and references therein). To explore covariation between 2 dimorphic traits, residuals from one regression equation (e.g. dimorphism in tail length) can be analysed as a function of residuals from another regression (e.g. dimorphism in LNAT).

We use interspecific data to test predictions of an evolutionary hypothesis statistically. The existence of hierarchical phylogenetic relationships implies, however, that data for different species cannot be regarded as independent data points, so that some basic assumptions of conventional statistical methods are not met (Felsenstein, 1985; Garland *et al.*, 1992; Pagel, 1993). Consequently, the standard tabulated values of test statistics are not appropriate as critical values for hypothesis testing. Recently developed methods offer adequate remedies for this statistical problem (Harvey & Pagel, 1991). Here we use the method of phylogenetically independent contrasts (Felsenstein, 1985). This method uses phylogenetic information to obtain statistically independent data points ('contrasts') for each trait studied. These contrasts can then be used to calculate (partial) correlation and regression coefficients (Garland *et al.*, 1992). If the contrasts are appropriately standardized, then the correlation coefficients can be compared with conventional critical values (Martins & Garland, 1991; Garland *et al.*, 1992; Díaz-Uriarte & Garland, 1996).

All interspecific (partial) correlations reported herein, and calculations of regression residuals, were based on independent contrast regressions (for a detailed account of the procedures see Garland *et al.*, 1992). Putative phylogenies of the Lacertidae based on either immunological (Mayer & Benyr, 1994) or morphological (Arnold, 1989) information are not completely equivalent (Fig. 1). We therefore analysed our data using 2 phylogenetic hypotheses. Some estimates of divergence times between species are based on arbitrary choices (see Bauwens *et al.*,

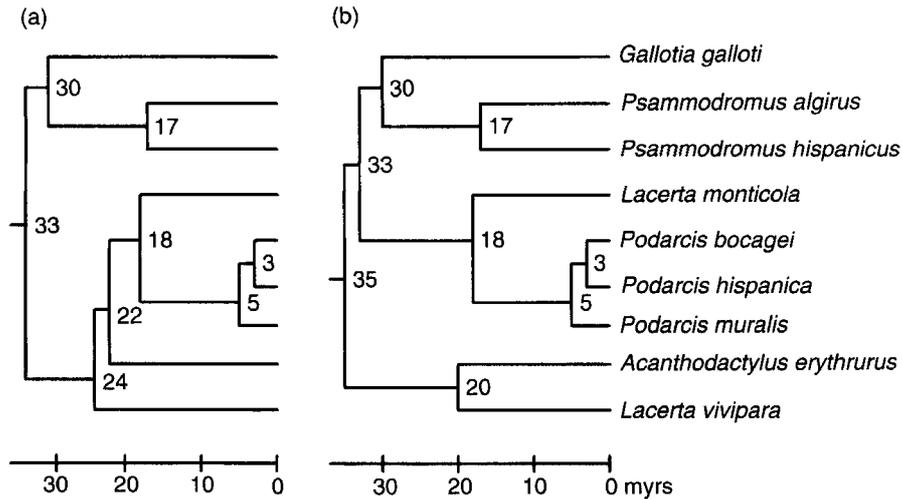


FIG. 1. Hypothesized phylogenetic relationships and estimated divergence times (numbers at nodes, in millions of years) for nine species of lacertid lizards. Branching patterns are based on: (a) immunological distances (micro-complement-fixation of albumins; Mayer & Benyr, 1994) and (b) external and internal morphological characteristics (Arnold, 1989). Divergence times for main branching patterns are based on immunological distances and were used for both phylogenetic trees. See Bauwens *et al.* (1995) for details on the reconstructions of both phylogenies.

1995). Because of this uncertainty in the assignment of separation times, we performed additional analyses on both phylogenetic trees with all branch lengths set to unit length. By analysing our data in the context of various phylogenetic hypotheses that differ in both topology and branch lengths, we evaluate the robustness of our results with respect to the phylogenetic hypotheses employed (Losos, 1994; Martins, 1996). We use combinations of subscripts 'I' or 'M' to denote results obtained with the phylogenies derived from immunological or morphological information, and subscripts 'n' or 'u' for the trees with non-unit or unit branch lengths.

We checked for adequate standardization of the phylogenetically independent contrasts by examining correlations between the absolute value of contrasts and their standard deviation (Garland *et al.*, 1992). No significant correlations were evident, so we used untransformed branch lengths in all analyses.

TABLE I

Summary statistics for the positions (vertebra number) of the tail vertebrae with the first complete fracture plane in males and females of species of lacertid lizards. Significance of sexual differences as obtained by Mann-Whitney U-tests. Data for *Ps. algirus*, *L. monticola*, *P. hispanica* and *L. vivipara* are from Barbadillo *et al.* (1995)

Species	Males			Females			Diff. sexes
	mean $\pm$ S.E.	min.-max.	n	mean $\pm$ S.E.	min.-max.	n	
<i>G. galloti</i>	6.0 $\pm$ 0.0	6-6	11	6.0 $\pm$ 0.0	6-6	16	> 0.90
<i>Ps. algirus</i>	6.7 $\pm$ 0.1	6-8	21	6.2 $\pm$ 0.1	6-7	19	< 0.005
<i>Ps. hispanicus</i>	7.0 $\pm$ 0.2	6-8	9	5.9 $\pm$ 0.2	5-7	9	< 0.005
<i>L. monticola</i>	6.9 $\pm$ 0.1	6-8	30	5.8 $\pm$ 0.1	5-6	25	< 0.001
<i>P. bocagei</i>	6.5 $\pm$ 0.1	6-7	13	5.8 $\pm$ 0.2	5-7	13	= 0.01
<i>P. hispanica</i>	7.0 $\pm$ 0.1	6-8	23	6.2 $\pm$ 0.1	5-7	19	< 0.001
<i>P. muralis</i>	6.7 $\pm$ 0.1	6-7	29	5.9 $\pm$ 0.1	5-6	22	< 0.001
<i>A. erythrurus</i>	10.6 $\pm$ 0.1	10-11	12	8.5 $\pm$ 0.1	8-9	13	< 0.001
<i>L. vivipara</i>	7.1 $\pm$ 0.1	6-8	16	5.2 $\pm$ 0.1	5-6	14	< 0.001

TABLE II

Parameter estimates of the intraspecific regression relations between length of the non-autotomous basal tail segment and snout-vent length in males and females of species of lacertid lizards. Shown are estimates for slopes ( $b \pm 1$  S.E.) and adjusted means (backtransformed values, in mm) of least square regressions on log-log transformed data, sample size ( $n$ ), and the probability of sexual differences in slopes ( $b$ ) and adjusted means ( $a$ ) as assessed by ANCOVA. Data for *Ps. algirus*, *L. monticola*, *P. hispanica* and *L. vivipara* are from Barbadillo *et al.* (1995)

	Males			Females			ANCOVA	
	$b \pm$ S.E.	Adj. mean	$n$	$b \pm$ S.E.	Adj. mean	$n$	$b$	$a$
<i>G. galloti</i>	1.032 $\pm$ 0.074	11.89	10	1.081 $\pm$ 0.035	11.30	16	> 0.50	= 0.10
<i>Ps. algirus</i>	1.143 $\pm$ 0.089	10.23	9	1.309 $\pm$ 0.122	9.16	8	> 0.20	< 0.02
<i>Ps. hispanica</i>	1.069 $\pm$ 0.280	6.97	9	0.907 $\pm$ 0.211	5.46	9	> 0.70	= 0.001
<i>L. monticola</i>	1.260 $\pm$ 0.181	10.14	11	1.083 $\pm$ 0.127	6.89	8	> 0.40	< 0.001
<i>P. bocagei</i>	1.153 $\pm$ 0.166	6.35	12	1.172 $\pm$ 0.159	5.13	13	> 0.90	< 0.001
<i>P. hispanica</i>	1.526 $\pm$ 0.133	8.43	13	1.657 $\pm$ 0.390	6.73	9	> 0.60	< 0.005
<i>P. muralis</i>	1.265 $\pm$ 0.045	8.32	13	1.138 $\pm$ 0.067	6.34	9	> 0.10	< 0.001
<i>A. erythrurus</i>	1.510 $\pm$ 0.095	20.14	12	1.254 $\pm$ 0.114	14.26	14	> 0.10	< 0.001
<i>L. vivipara</i>	1.330 $\pm$ 0.135	9.25	8	1.110 $\pm$ 0.129	5.55	8	> 0.20	< 0.001

Independent contrasts were calculated with the program PDTREE (Garland *et al.*, 1993); statistical analyses, using regression through the origin, were done with SPSS/PC + (v. 5.0). Because we test directional predictions of character correlations, we use one-tailed tests for all (partial) correlation coefficients.

## Results

In all species, except *G. galloti*, the first vertebra with a complete fracture plane was more distal from the base of the tail in males than in females (Table I). In other words, males have more non-autotomous tail vertebrae than females. In *G. galloti*, the number of vertebrae without fracture planes is invariant: all individuals examined, both males and females, possess five non-autotomous bones at the tail base. Among the other species, the sexual difference in the position of the first autotomous bone is smallest in *Ps. algirus* and *P. bocagei*, and most pronounced in *A. erythrurus* and *L. vivipara* (Table I).

Within each species, slopes of the relationships of LNAT with SVL do not differ between males and females. In all species except *G. galloti*, adjusted means are significantly higher in males (Table II). These results indicate that, within most species, the non-autotomous tail part is larger in males than in females, and that the relative magnitude of this difference remains constant over the entire range of body length. In *G. galloti*, no difference in LNAT exists between males and females, irrespective of their SVL.

Sexual dimorphism in total tail length is evident in all species. The intraspecific regression relations for males and females have similar slopes, but exhibit higher adjusted means in the males (Table III). Thus males of all species studied have longer tails than conspecific females, and the extent of this sexual difference does not change during ontogeny.

Interspecific variation in the extent of sexual dimorphism in LNAT (i.e. residuals of the interspecific independent contrast relation between adjusted means of males to adjusted means of females) is positively correlated to variation in sexual differences of the number of non-autotomous vertebrae (i.e. residuals of the independent contrasts regression between mean number in males to mean number in females) ( $r_{In} = 0.898$ ,  $r_{Mn} = 0.864$ ,  $r_{Iu} = 0.855$ ,  $r_{Mu} = 0.797$ , all  $P < 0.01$ ). Thus, sexual dimorphism in LNAT is, unsurprisingly, most pronounced in species that exhibit the largest sexual difference in

TABLE III

Parameter estimates of the intraspecific regression relations between total tail length and snout-vent length in males and females of species of lacertid lizards. Shown are mean SVL of the samples studied, estimates for slopes ( $b \pm 1 \text{ S.E.}$ ) and adjusted means (backtransformed values, in mm) of least square regressions on log-log transformed data, sample size ( $n$ ), and the probability of sexual differences in slopes ( $b$ ) and adjusted means ( $a$ ) as assessed by ANCOVA. Data for *L. vivipara* are from Barbadillo *et al.* (1995)

	Males				Females				ANCOVA	
	SVL	$b \pm \text{S.E.}$	Adj. mean	$n$	SVL	$b \pm \text{S.E.}$	Adj. mean	$n$	$b$	$a$
<i>G. galloti</i>	59.9	$0.809 \pm 0.059$	139.0	18	61.9	$0.842 \pm 0.049$	127.4	23	$> 0.60$	$< 0.001$
<i>Ps. algirus</i>	41.8	$1.175 \pm 0.042$	112.7	20	55.8	$1.161 \pm 0.065$	103.8	16	$> 0.80$	$< 0.005$
<i>Ps. hispanicus</i>	35.3	$1.371 \pm 0.069$	58.5	40	37.7	$1.303 \pm 0.062$	48.4	33	$> 0.40$	$< 0.001$
<i>L. monticola</i>	46.2	$1.184 \pm 0.033$	78.9	23	46.5	$1.122 \pm 0.053$	73.5	17	$> 0.30$	$< 0.005$
<i>P. bocagei</i>	45.7	$0.958 \pm 0.068$	92.7	25	38.3	$1.034 \pm 0.091$	83.0	13	$> 0.40$	$< 0.001$
<i>P. hispanica</i>	42.1	$1.104 \pm 0.032$	70.5	49	37.3	$1.017 \pm 0.052$	65.8	35	$> 0.10$	$< 0.001$
<i>P. muralis</i>	52.2	$1.244 \pm 0.059$	74.3	29	52.5	$1.250 \pm 0.056$	67.5	23	$> 0.90$	$< 0.001$
<i>A. erythrurus</i>	66.2	$1.033 \pm 0.027$	117.8	61	62.7	$0.954 \pm 0.041$	109.1	45	$> 0.05$	$< 0.001$
<i>L. vivipara</i>	32.0	$1.414 \pm 0.014$	43.7	212	33.3	$1.379 \pm 0.017$	39.4	197	$> 0.10$	$< 0.001$

number of non-autotomous vertebrae. In the absence of more detailed data, we cannot examine the contribution of possible sexual differences in size of the caudal vertebrae to the dimorphism in LNAT.

Contrary to the prediction of our hypothesis, the extent of sexual dimorphism in total tail length was not correlated with dimorphism in LNAT ( $r_{In} = -0.085$ ,  $r_{Mn} = -0.143$ ,  $r_{Iu} = -0.298$ ,  $r_{Mu} = -0.300$ , all  $P > 0.50$ ; Fig. 2). However, the species treated here differ considerably in absolute tail length, and these differences may mask the true underlying relationship. We therefore calculated partial

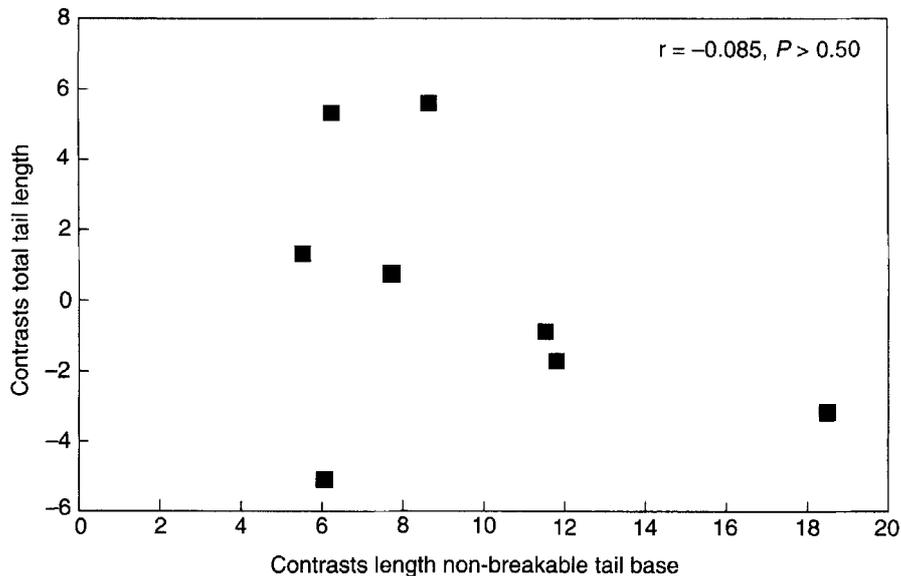


FIG. 2. Scatterplot of independent contrast relation between total tail length and length of the non-autotomous tail base. Contrasts shown were obtained with the immunological phylogeny, with non-unit branch lengths.

correlations between the dimorphism in total tail length and in LNAT, holding for the effect of absolute tail length. The results do not alter our former conclusion ( $r_{In} = -0.062$ ,  $r_{Mn} = -0.128$ ,  $r_{Iu} = -0.303$ ,  $r_{Mu} = -0.298$ , all  $P > 0.50$ ).

The species studied differ also in relative length of the tail. The extent of dimorphism in total tail length is negatively correlated with relative tail length (i.e. residuals of the independent contrast regression between tail length and SVL;  $r_{In} = -0.635$ ;  $P < 0.05$ ;  $r_{Mn} = -0.662$ ;  $P < 0.05$ ;  $r_{Iu} = -0.575$ ;  $P = 0.07$ ;  $r_{Mu} = -0.649$ ;  $P < 0.05$ ). Thus, sexual dimorphism in total tail length is most pronounced in relatively short-tailed species. After statistically removing the effect of relative tail length, partial correlations between the dimorphism in total tail length and LNAT are negative, contrary to our prediction ( $r_{In} = -0.796$ ,  $r_{Mn} = -0.786$ ,  $r_{Iu} = -0.849$ ,  $r_{Mu} = -0.821$ , all  $P > 0.99$ ). These results do not allow us to reject the null hypothesis of our one-tailed statistical tests (i.e. the correlation is zero or negative). Moreover, the negative correlations would have been considered highly significant as compared with the critical value for a two-tailed test. This provides evidence for a relation in the direction opposite to our *a priori* prediction.

### Discussion

Our comparative study demonstrates a negative correlation between tail length dimorphism and relative tail length among species of lacertid lizards: species with rather short tails for their SVL were most dimorphic in tail length. The 'Morphological Constraint' hypothesis, as formulated by King (1989), asserts that the mere presence of the male copulatory organs constrains minimum tail length in males, and that this should be more evident in relatively short-tailed species. Thus, our results corroborate a prediction of this hypothesis. However, given that the tail part housing the hemipenes comprises only 10–20% of total tail length in lacertid lizards, it is not obvious why the mere presence of the copulatory organs should constrain total tail length.

Our variant of the 'Morphological Constraint' hypothesis views tail autotomy as a function that is hampered by the presence of the male genitals. This allows formulation of a more precise and critical prediction: tail length dimorphism should increase with the magnitude of sexual differences in length of the non-autotomous tail base. Our results were not consistent with this prediction. First, sexual differences in length of the tail base are absent in *G. galloti*, yet this species exhibits dimorphism in total tail length. We also note that the extreme phylogenetic position of *G. galloti*, at least in the putative phylogeny based on immunological data (Fig. 1), may indicate that sexual dimorphism in tail length originated before and independently of the sexual differences in the non-autotomic region. However, data of other *Gallotia* and of appropriate outgroups (e.g. Xanthusidae and Teiidae) are needed to corroborate this inference. Second, and more convincingly, interspecific variation in the magnitude of sexual differences in total tail length were not correlated with the extent of dimorphism in length of the non-breakable tail base. We conclude that constraints imposed by the male copulatory organs on tail autotomy capacities do not seem to be a significant factor in the evolution of tail length dimorphism in this clade of lacertid lizards.

This conclusion may, however, be criticized because the low sample size of this study (nine species) may impede the detection of the predicted relationship. The following arguments dismiss this criticism. First, we deliberately restricted ourselves to a small clade of closely-related species, because they form a relatively homogeneous group with respect to many aspects of their general morphology and ecology. This reduces the risk that results of comparative studies are induced or confounded by among-species differences in traits that were not under study (Huey & Bennett, 1986; Losos, 1990; Harvey & Pagel, 1991; Bauwens *et al.*, 1995). Hence, our choice of species should have

increased the possibilities of detecting a pattern, despite the small sample size. Second, we opted to base our comparative analyses on detailed information of sexual differences within the different species. Thus, we gathered data on complete ontogenetic series of animals for each species. This allowed us to verify that intraspecific sexual differences do not change with ontogeny, an implicit assumption of our interspecific comparisons. Obviously, we do not escape from the trade-off between intraspecific detail and interspecific generality. Third, our results do not even suggest that a relation in the predicted direction may exist. If anything, we found evidence for a negative relation between total tail length and length of the non-breakable tail base, at least after statistically removing the effect of relative tail length. In conclusion, it seems unlikely that we failed to detect an existing positive relationship.

Failure to document predictions of an evolutionary hypothesis may indicate that the effect of its putative mechanism is nonexistent or overshadowed by that of others. Alternatively, some assumptions of the hypothesis could be false. Our version of the 'Morphological Constraint' hypothesis makes two important assumptions. The first is that the presence of the male copulatory organs effectively restricts the capacity of tail autotomy. This assumption is supported by the observation that males of most lacertids have a longer non-breakable tail base than conspecific females. In addition, detailed information for a field population of *L. vivipara* shows that more females than males autotomize their tail at very short distances from the base, reflecting the dimorphism in length of the non-autotomous tail part (Barbadillo *et al.*, 1995).

The second assumption is that abilities to escape by autotomy increase with the length of the breakable tail part. We know of no direct test of this assumption, but the following information provides some support, although alternative interpretations are possible. Skinks with experimentally reduced tails were less successful in escaping predatory attacks than lizards with intact tails (Vitt & Cooper, 1986). Predatory attacks directed to the tail, and concurrent possibilities to escape by autotomy, were more common in long-tailed than in short-tailed species of *Liolaemus* lizards (Medel *et al.*, 1988). In sceloporine lizards, populations or species subject to heavier predation have evolved longer tails (Fox, Perrea-Fox & Franco, 1994). These data suggest that longer tails may indeed improve escape abilities, either because they are more attractive, or because they are more effective as a target for predators. However, available information is insufficient to determine whether small individual differences, such as those observed in length of the breakable tail part between the sexes in lacertid lizards, have consequences on survival and fitness.

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#### REFERENCES

- Arnold, E. N. (1973). Relationships of the palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammotromus*. *Bull. Br. Mus. (Nat. Hist.) Zool.* **25**: 291–366.
- Arnold, E. N. (1984). Evolutionary aspects of tail shedding in lizards and their relatives. *J. Nat. Hist.* **18**: 127–169.
- Arnold, E. N. (1988). Caudal autotomy as a defense. In *Biology of the Reptilia* **16**: 235–273. Gans, C. & Huey, R. B. (Eds). New York: J. Wiley & Sons.
- Arnold, E. N. (1989). Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bull. Br. Mus. (Nat. Hist.) Zool.* **55**: 209–257.
- Barbadillo, L. J., Bauwens, D., Barahona, F. & Sánchez-Herráiz, M. J. (1995). Sexual differences in caudal morphology and its relation to tail autotomy in lacertid lizards. *J. Zool. (Lond.)* **236**: 83–93.

- Bauwens, D., Garland, T., Jr, Castilla, A. M. & Van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* **49**: 848–863.
- Bellairs, A. d'A. & Bryant, S. V. (1985). Autotomy and regeneration in reptiles. In *Biology of the Reptilia* **15**: 301–410. Gans, C. & Billet, F. (Eds). New York: J. Wiley & Sons.
- Clark, D. R. (1966). Notes on sexual dimorphism in tail-length in American snakes. *Trans. Kans. Acad. Sci.* **69**: 226–232.
- Clutton-Brock, T. H., Harvey, P. H. & Rudder, B. (1977). Sexual dimorphism, socioeconomic sex ratio and body weight in primates. *Nature (Lond.)* **269**: 797–800.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: Murray.
- Díaz-Uriarte, R. & Garland, T., Jr (1996). Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. *Syst. Biol.* **45**: 27–47.
- Etheridge, R. (1967). Lizard caudal vertebrae. *Copeia* **1967**: 699–721.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Fox, S. F., Perrea-Fox, S. & Franco, R. C. (1994). Development of the tail autotomy adaptation in lizards under disparate levels of predation at high and low elevations in Mexico. *Southwest. Nat.* **39**: 311–322.
- Garland, T., Jr., Dickerman, A. W., Janis, C. M. & Jones, J. A. (1993). Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**: 265–292.
- Garland, T., Jr, Harvey, P. H. & Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**: 18–32.
- Harvey, P. H. & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hedrick, A. V. & Temeles, E. J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol. Evol.* **4**: 136–138.
- Houston, D. & Shine, R. (1993). Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *J. Anim. Ecol.* **62**: 737–748.
- Huey, R. B. & Bennett, A. F. (1986). A comparative approach to field and laboratory studies in evolutionary biology. In *Predator-prey relationships: perspectives from the study of Lower Vertebrates*: 82–98. Feder, M. E. & Lauder, G. V. (Eds). Chicago: Chicago University Press.
- King, R. B. (1989). Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? *Biol. J. Linn. Soc.* **38**: 133–154.
- Klauber, L. M. (1943). Tail-length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. *Bull. Zool. Soc. San Diego* **18**: 1–60.
- Losos, J. B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**: 1189–1203.
- Losos, J. B. (1994). An approach to the analysis of comparative data when a phylogeny is unavailable or incomplete. *Syst. Biol.* **43**: 117–123.
- Martins, E. P. (1996). Conducting phylogenetic comparative studies when the phylogeny is not known. *Evolution* **50**: 12–22.
- Martins, E. P. & Garland, T., Jr (1991). Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**: 534–557.
- Mayer, W. & Benyr, G. (1994). Albumin-Evolution und Phylogenese in der Familie Lacertidae. *Ann. Naturhist. Mus. Wien* **96B**: 621–648.
- Medel, R. G., Jiménez, J. E., Fox, S. E. & Jacksic, F. M. (1988). Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* **53**: 321–324.
- Packard, G. C. & Boardman, T. J. (1987). The misuse of ratios to scale physiological data that vary allometrically with body size. In *New directions in ecological physiology*: 216–236. Feder, M. E., Bennett, A. F., Burggren, W. W. & Huey, R. B. (Eds). Cambridge: Cambridge University Press.
- Pagel, M. D. (1993). Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. *J. theor. Biol.* **164**: 191–205.
- Ranta, E., Laurila, A. & Elmgberg, J. (1994). Reinventing the wheel: analysis of sexual dimorphism in body size. *Oikos* **70**: 313–321.
- Russell, A. P. & Bauer, A. M. (1992). The *m. caudifemoralis longus* and its relationship to caudal autotomy and locomotion in lizards (Reptilia: Sauria). *J. Zool. (Lond.)* **227**: 127–143.
- Schoener, T. W. (1967). The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science (Washington DC)* **155**: 474–477.
- Selander, R. K. (1972). Sexual selection and dimorphism in birds. In *Sexual selection and the Descent of Man 1871–1971*: 180–230. Campbell, B. (Eds). Chicago: Aldine Publ. Co.
- Shine, R. (1988). The evolution of large body size in females: a critique of Darwin's 'fecundity advantage' model. *Am. Nat.* **131**: 124–131.

- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**: 419–461.
- Shine, R. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Am. Nat.* **138**: 103–122.
- Taylor, W. R. (1967). An enzyme method of clearing and staining small vertebrates. *Proc. U.S. Nat. Mus.* **122**: 1–17.
- Vitt, L. J. & Cooper, W. E., Jr (1986). Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Sc.). *Can. J. Zool.* **64**: 583–592.
- Zug, G. R. & Crombie, R. I. (1970). Modifications of the Taylor enzyme method of clearing and staining for amphibians and reptiles. *Herpetol. Rev.* **3**: 49–50.