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Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootoca vivipara*: a test of two hypotheses

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Abstract

Zootoca vivipara is a small lizard that shows sexual dimorphism in head size. Males have larger heads than females of the same body size. By observing matings and aggressive interactions between males in the laboratory, we investigated whether this sexual dimorphism could be the result of intra- and/or intersexual selection. Winners of male–male interactions had larger heads than losers. During mating attempts, males with larger heads succeeded in grasping a female faster than males with smaller heads. It follows that head size in *Z. vivipara* may affect male reproductive success both through intrasexual competition (fighting ability) and through intersexual selection (grasping ability). This suggests that sexual selection may be the cause for the sexual dimorphism in head size in this species.

Key words: sexual dimorphism, sexual selection, agonistic interactions, copulation, Lacertidae, Squamata, *Zootoca vivipara*

INTRODUCTION

In many lizards males have larger heads than females. Sexual dimorphism in head size may evolve because larger heads: (1) are advantageous in contests between males (Carothers, 1984; Vitt & Cooper, 1985; Anderson & Vitt, 1990; Hews, 1990; Molina-Borja, Padron-Fumero & Alfonso-Martin, 1998); (2) enable males to successfully grasp and hold a female during copulation (Hews, 1990; Braña, 1996; Herrel, Van Damme & De Vree, 1996; Herrel, Spithoven *et al.*, 1999); or (3) allow males to eat bigger and harder prey items than females, thus reducing intersexual competition for food (Schoener, 1967; Stamps, 1977; Preest, 1994).

The effect of head size on the outcome of aggressive encounters between males and on the duration of copulation was studied in the lizard *Zootoca vivipara*. Males of this species have larger heads than females of the same body size (Wermuth, 1955; Dély, 1981; Šmajda & Majláth, 1999). One study showed that there was no dietary divergence between sexes of lacertid lizards (Braña, 1996), and therefore it seems unlikely that sexual dimorphism functions to reduce intersexual competition for food. On the other hand, encounters between males during the breeding season often escalate into fights with vigorous biting (Verbeek, 1972; Heulin, 1988), suggesting that intrasexual competition may be a driving force for the evolutionary increase in male head size. Also, to immobilize a female during mating, the male must grasp the female by the flank and retain this mouth-hold throughout copulation, which may last 35–45 min (Verbeek, 1972; Bauwens & Verheyen, 1985; Heulin, 1988). This may be another reason why having a large, powerful head could be beneficial to male *Z. vivipara.*

The following hypotheses were tested: (1) winners of male–male interactions have larger heads than losers; (2) males with larger heads can subdue females more easily and copulate for longer.

MATERIAL AND METHODS

Study species and housing

Zootoca vivipara is a small (snout–vent length 45–65 mm) insectivorous lizard. Males emerge earlier from hibernation than females (Nuland & Strijbosch, 1981). At the onset of the mating period, males synchronously shed their skins and become sexually active for *c.* 2 weeks (Bauwens, Van Damme & Verheyen, 1989). Older females become sexually receptive shortly after leaving hibernacula, but mating is delayed in younger females (Bauwens & Verheyen, 1985). The receptivity period of females lasts *c.* 5 days. Reproductive behaviour is simple

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and without courtship (see Verbeek, 1972; Bauwens, Nuijten *et al.*, 1987 for details).

At the end of March (males) and the beginning of April 1999 (females), 42 adult lizards (21 males and 21 females) were captured near Kalmthout, Belgium (51°25′N, 4°25′E; see Bauwens & Thoen, 1981 for further details). The lizards were transported to a nearby field station. It was assumed that lizards were taken randomly and that the sample is therefore representative of the body-size distribution of adults in the population studied. None of the females captured had copulated in that season, as evidenced by the absence of a typical U-shaped mating scar on the belly (Bauwens & Verheyen, 1985).

Lizards were housed individually in cages $50 \times 30 \times 30$ cm high. The bottom of each cage was covered with sand and some dry grass. Heat was provided with 100 W reflector bulbs for 5 h daily (10:00–15:00). The whole housing room was illuminated with natural light. Food (crickets *Acheta domestica*) and water in small dishes was always available. Supplementary water was provided daily by spraying water on the grass and walls of the cages.

Morphometry

Each lizard was individually marked by toe-clipping and the following measurements were taken with digital callipers to nearest 0.1 mm: body length (BL, distance from posterior margin of the collar to vent), head length (HL, measured from tip of rostrum to posterior margin of occipital), head width (HW, distance between posterior eye corners), jaw length (JL, measured from tip of rostrum to posterior margin of the last upper labial) and jaw width (JW, distance between posterior margins of the last upper labials).

Behavioural observations

Experiments were performed between 28 March and 11 April 1999 from 10:00 to 15:00. Trials were carried out in 2 cages measuring $80 \times 55 \times 30$ cm high each, divided into 2 equally-sized compartments by a removable non-transparent partition. The bottom of the cages was covered with sand. Each compartment was provided with a spotlight (100 W) above its centre, to allow thermoregulation. All trials were observed from behind a 1-way mirror. The mirror was positioned slightly above the lizards, so that they were unlikely to see any reflection.

Male–male interactions were observed before and during the mating period. Before the experiments, males were randomly divided into pairs. Each male was used in 1–3 trials but never with the same male. Males were kept undisturbed at least 24 h between successive trials to minimize any possible effects of the outcome of previous trials on their performance in subsequent trials. Each pair of males was placed in adjacent compartments (the side was determined by tossing a coin) 15 min before a trial, and allowed to habituate to their new environment. Trials started by raising the partition slowly, so the lizards were not disturbed, and their behaviour was recorded during the next 15 min. After some pilot observations, 4 readily recognizable events were focused on: throat inflation (increase in the size of throat region by puffing up), bite (a strong closing of the mouth on some part of an adversary), freeze (motionless posture), and flight (rapidly retreat). If a male had a significantly (binomial test) higher number of freezes and flights than his opponent, then he was considered the loser of that trial.

For the mating experiments, males and females were randomly assigned to pairs so that each lizard was used only once. Approximately 15 min before a trial, the male and the female were placed in adjacent compartments (the side was determined by tossing a coin) and allowed to habituate to the test terrarium. When the male had begun the first basking bout after the habituation time, trials were started by raising the partition. The duration of the following time intervals were measured with a digital stopwatch: capture time (time elapsed between removal of the partition and the moment at which the male succeeded in grasping the female), handling time (between the initial bite hold and the insertion of a hemipenis into the female's cloaca), and copulation time (between insertion and extraction of hemipenis from the cloaca). After the experiments, all lizards were released at the place of capture.

Statistical analyses

Data were checked for normality and homoscedasticity before statistical testing. For significant departures from normality or homoscedasticity, data were transformed (Box-Cox transformation; Sokal & Rohlf, 1995). Absolute values of morphometric measurements were compared between the sexes using *t*-tests for independent samples and the relative ones using analysis of covariance (ANCOVA) with BL as the covariate. For heterogeneity of slopes, the separate slopes design was applied (StatSoft, 2000). Scaling of head and jaw lengths and widths to body length (all ln transfomed) was modelled by reduced major axis regression (Sokal & Rohlf, 1995). Regression slopes of head measurements to body length between the sexes were compared using a procedure by Clarke (1980).

To remove the confounding effect of different body size on head size, residual scores were used from a log–log regression of head-size measurements on BL as relative head-size measurements (Reist, 1985). Differences in absolute and relative head lengths between winners and losers were tested using paired *t*-tests. Multiple regression analysis was applied to evaluate the effects of absolute and relative values of morphometric traits (male head length, width, jaw length and width) on capture, handling and copulation time. The total number of interactions and biting per trial between the

Table 1. Absolute values (mean ± SE, minimum–maximum) of body and head sizes in male and female *Zootoca vivipara* and their comparisons using Student's *t*-test (*t*) and ANCOVA (*F*) with body length as the covariate. All values are mm. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Trait	Males ($n = 21$)	Females ($n = 21$)	t	$F_{1,38}$
Body length	32.9 ± 0.6	36.2 ± 0.6		
	27.2 – 37.8	31.6 – 44.1	3.84***	
Head length	10.5 ± 0.6	9.7 ± 0.1		
	9.5 – 11.5	9.1 – 10.4	5.13***	4.24*
Jaw length	8.9 ± 0.1	8.0 ± 0.1		
	7.8 – 9.8	7.5 – 8.9	6.09***	5.46*
Head width	5.6 ± 0.1	5.3 ± 0.1		
	4.7 – 6.3	4.9 – 5.7	2.20*	9.94**
Jaw width	7.2 ± 0.1	6.7 ± 0.1		
	6.2 – 8.3	6.1 – 7.8	3.09**	6.70**

Table 2. Slope and intercept estimated from reduced major axis regressions for each trait against body length with the homogeneity of slopes-test (*t*) between male and female *Zootoca viviparis* ($n = 21$ for each sex). *$P < 0.05$, **$P < 0.01$, NS $P > 0.05$

	Females		Males		
Y	a	b	a	b	*t*
Head length	0.645	0.454	−0.203	0.731	2.61*
Jaw length	−0.142	0.618	−0.532	0.777	1.16 NS
Head width	−0.371	0.569	−2.066	1.083	3.18**
Jaw width	−0.888	0.776	−1.757	1.067	1.23 NS

pre-mating and mating period was compared using 1-way ANOVA in the visual generalized linear model (VGLZ) module. All statistical analyses were performed using Statistica for Windows 5.5 (StatSoft, 2000). For multiple comparisons of correlation coefficients the sequential Bonferroni test (Sokal & Rohlf, 1995) was used to correct experimental error rate. Otherwise, the significance level of $\alpha = 0.05$ was used for all statistical tests. Because of relatively low sample size, statistical power (1-β) was also calculated for tests results that were important for inferring conclusions. $1\text{-}\beta = 0.80$ at $\alpha = 0.05$ (Cohen, 1988) was chosen as an acceptable statistical power to correctly reject the null hypothesis.

RESULTS

Sexual dimorphism in head size

Males had larger heads and jaws than females, both in absolute terms and relative to BL (Table 1). The most prominent sexual differences were found in HL and HW. Slopes of HL and HW were steeper for males than those for females, whereas slopes of JL and JW were not significantly different (Fig. 1, Table 2). All head and jaw measurements were highly intercorrelated, except for JW in females (Table 3).

Table 3. Correlation coefficients of head size measurements in the both sexes of *Zootoca vivipara*. *, significant result at α corrected using the sequential Bonferroni test. HL, head length; HW, head width; JL, jaw length; JW, jaw width

Variables		Males ($n = 21$)		Females ($n = 21$)	
		r	*P*	*r*	*P*
JL	HL	0.83	< 0.0001*	0.79	< 0.0001*
HW	HL	0.79	< 0.0001*	0.67	0.001*
HW	JL	0.82	< 0.0001*	0.54	0.011*
JW	HL	0.67	0.0009*	0.35	0.12
JW	JL	0.66	0.0011*	0.24	0.30
JW	HW	0.73	0.0002*	0.39	0.08

Male–male contests

A total of 51 contests was observed, 29 before and 22 trials during mating period. The total number of interactions and bites per trial was higher during the mating period than before (interactions: VGLZ one-way ANOVA, $\chi^2 = 62.80$, d.f. = 1, $P < 0.001$; bites: $\chi^2 = 72.07$, d.f. = 1, $P < 0.001$), indicating a higher level of activity and aggressiveness of sexually receptive males. Because of the low number of interactions observed during trials outside the mating period, these observations were removed from further analyses. Winners of contests had significantly longer HL, JL and HW than losers (paired *t*-test, HL: $t = 2.51$, d.f. = 21, $P = 0.02$, $1\text{-}\beta = 0.74$; JL: $t = 2.30$, $P = 0.03$, $1\text{-}\beta = 0.73$; HW: $t = 2.86$, $P = 0.01$, $1\text{-}\beta = 0.89$), though only the comparison of HW had acceptable statistical power to correctly reject the null hypothesis. Differences in JW and BL were non-significant (JW: $t = 1.03$, $P = 0.31$; BL: $t = 1.90$, $P = 0.07$). Comparisons of relative head sizes (i.e. after removing the effect of overall body size) between winners and losers revealed similar results as those of absolute sizes, except of JL (HL: $t = 2.41$, $P = 0.03$; JL: $t = 1.62$, $P = 0.12$; HW: $t = 3.10$, $P = 0.005$; JW: $t = 0.21$, $P = 0.83$; Fig. 2).

Within trials, repeated encounters between the males involved generally resulted in the same outcome, i.e. the lizard that won the first skirmish also won all subsequent ones. In only one of the 22 trials, an initial winner later became a loser. This suggests that a dominance relationship was established after the first encounter during a trial. Among trials, the winner–loser status of males changed in eight of the 18 males that were tested with different opponents χ^2 test, $\chi^2 = 0.11$, d.f. = 1, $P = 0.74$) suggesting a minor winner–loser effect (Pusey & Packer, 1997).

Copulatory behaviour

A total of 18 uninterrupted copulatory behaviours was observed. The duration of particular intervals was highly variable but capture and handling time was substantially shorter than copula duration (capture: 2.82 ± 0.43 min;

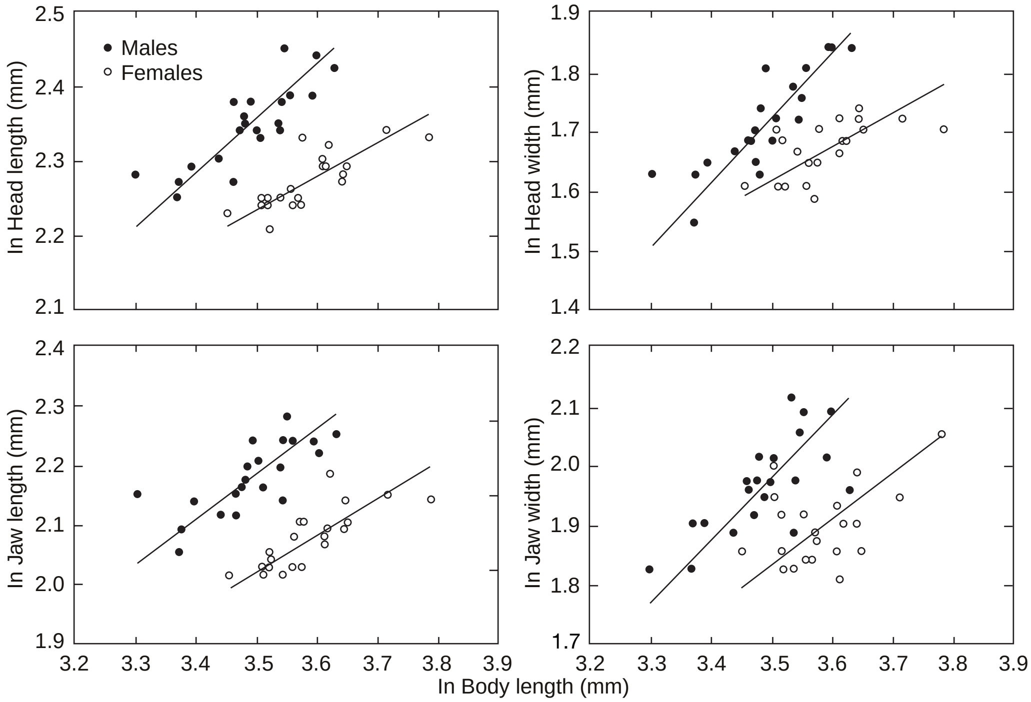

Fig. 1. Scaling of head size measurements on body length in males and females of *Zootoca vivipara*. See Table 2 for statistical details.

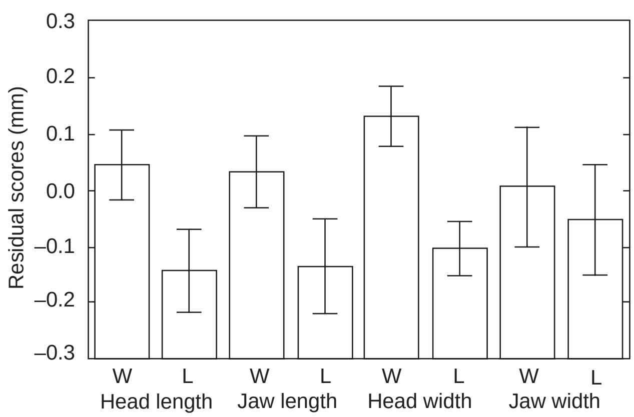

Fig. 2. Residual scores (mean ± SE) from a log–log regression of head size measurements on body length between winners (W) and losers (L) in male–male contests of *Zootoca vivipara*.

handling: 2.19 ± 0.21 min; copulation: 28.27 ± 2.42 min). Because relative head measurements were intercorrelated in males (Table 3), the level of multicollinearity among them was assessed before testing their effect on the duration of mating behaviour. Tolerance values for JL and HW (0.20 and 0.17, respectively) indicate that these variables were from 80% to 83% predicted by other variables. Because they could decrease the predictive power of the remaining variables, they were omitted from multiple regression analysis. Subsequently, the effect of collinearity decreased between the remaining predictors (tolerance: HL = 0.62, JW = 0.72). Males with longer heads relative to BL, captured females faster then those with shorter heads (multiple regression, $F_{1,15} = 5.19$, $P = 0.04$, 1-β = 0.57). This was probably a consequence of a positive relationship between capture time and number of bite hold attempts on a female (Spearman rank correlation, $r_S = 0.58$, d.f. = 16, $P = 0.01$). The effect of relative HL and JW on handling, copulation and total time (capture + handling + copulation) was non-significant (multiple regression, handling, HL: $F_{1,15} = 2.37$, $P = 0.14$; JW: $F_{1,15} = 3.42$, $P = 0.08$; copulation, HL: $F_{1,15} < 0.01$, $P = 0.99$; JW: $F_{1,15} = 0.14$, $P = 0.71$; total time, HL: $F_{1,15} = 0.20$, $P = 0.67$; JW: $F_{1,15} = 0.02$, $P = 0.89$).

DISCUSSION

Sexual head-size dimorphism

Consistently with previous studies (Wermuth, 1955; Dély, 1981; Šmajda & Majláth, 1999), we found a clear sexual dimorphism in head size in *Z. vivipara*. The similarity of our findings with those from other populations suggests that proximate environmental factors (Shine, 1990; Stamps, 1993) can be less important determinants of sexual dimorphism in head size than ultimate ones (natural selection, phylogenetic history) in this species. Growth of HW and HL, relative to growth in BL, was faster in males than in females (Fig. 1), but this trend was not significant for jaw measurements (JL and JW). The sexual dimorphism in head size in adult *Z. vivipara* therefore seems primarily to arise from a differential growth of the postorbital head regions. Winners of male–male contests had wider heads than losers, whereas differences in other head and jaws measurements were less prominent. Also, total HL explained more of the variation in capture time than the other head measures. The whole head size, therefore, seems to be more important for contest and copulatory success than the size of jaws alone. Bite force of lacertids depends on the mass of jaw adductor muscles that are attached on the postorbital regions of the skull (Herrel, Van Damme *et al.*, 1996; Herrel, Spithoven *et al.*, 1999). The larger this area, the bigger the muscles that may be attached, and the higher the bite forces that can be expected. We therefore hypothesize that the extent of sexual dimorphism in head size is determined mainly by an increase of the postorbital regions of the head in males that is brought about by the selective advantage of a stronger bite force during male–male contests and grasping a female for copulation.

Sexual differences in head size are common within the clade of lacertid lizards (e.g. Castilla *et al.*, 1989; Braña, 1996; Molina-Borja, Padron-Funero & Alfonso-Martin, 1997; Gvoždík & Boukal, 1998; Huang, 1998); this has two implications. First, it is likely that sexual dimorphism in head size was also present in a common ancestor of lacertids. Thus, we think that sexual dimorphism in head size did not evolve *de novo* in *Z. vivipara* but more probably is a result of its phylogenetic history (see Perry, 1996 for a general discussion). However, as demonstrated here, the actual extent of the dimorphism may be maintained through competition over mates (sexual selection). Second, because of the general similarity of contest and mating behaviour (e.g. Kitzler, 1941; Verbeek, 1972; Olsson, 1992; Molina-Borja *et al.*, 1998), males of other lacertids should use their jaws for the same purposes. It is, therefore, probable that sexual dimorphism in the head size of other species is maintained by similar mechanisms as in *Z. vivipara*. Only a few data support this assumption (Olsson, 1992; Molina-Borja *et al.*, 1998). Nevertheless, minor sexual differences in consumed food types despite sex differences in trophic structures in several species (Braña, 1996; Gvoždík & Boukal, 1998) suggest that an alternative hypothesis, i.e. intersexual dietary divergence, is less important for the extent of sexual dimorphism in head size than sexual selection in lacertids.

Contest behaviour

The importance of head size as a weapon in male–male contests has been demonstrated several times in lizards (Carothers, 1984; Vitt & Cooper, 1985; Anderson & Vitt, 1990; Hews, 1990; Molina-Borja *et al.*, 1998). In territorial lizards, winners of male–male contests have better access to females (Stamps, 1983) and so males with larger heads have a selective advantage over those with smaller heads (Hews, 1990). Although males in *Z. vivipara* are non-territorial (Buschinger & Verbeek, 1970), the outcome of fights during the breeding season may also affect reproductive success. Our results show that a dominance relationship was established after the first skirmish, which is supported by preliminary observations of dominance hierarchy among males in semi-natural enclosures (Heulin, 1988). If losers continuously escape then meet with winners again, their access to females can be seriously restricted. Moreover, because in *Z. vivipara*, female receptiveness is not completely synchronized, the operational sex ratio (the ratio of fertilizable females to sexually active males at any given time; Emlen & Oring, 1977) is highly male-biased. This gives rise to more intense male–male competition and the opportunity for sexual selection increases (Anderson, 1994).

Copulatory behaviour

The possible advantage of a larger head in copulatory behaviour has been discussed several times (Hews, 1990; Braña, 1996; Herrel, Van Damme *et al.*, 1996; Herrel, Spithoven *et al.*, 1999). Our results not only support this suggestion but also specify it further because head size affected the duration of the first component of copulatory behaviour, i.e. capture. The difficulties that small males may have grasping females has also been observed in another lacertid, *Lacerta agilis* (Olsson, 1993). Comparing among all three components of copulatory behaviour, the time necessary to find and grasp a female seems to be the most important component for mating success, especially when the operational sex ratio is male-biased and competition over mates is strong (see Discussion). The positive correlation of mating scar size with female body size (Braña, 1996) may also confirm the supposed mating advantage of males with larger heads in the field.

Even though males bite the female throughout the entire copulation-event (lasting on average 28 min), head size had no significant effect on the duration of this behaviour. Consistent with a previous study (Bauwens, Nuijten *et al.*, 1987), we observed that the end of copulation was initiated by the female in all trials. From a female's perspective, it may be advantageous to mate with several males, because this may increase offspring viability (Madsen *et al.*, 1992; Olsson *et al.*, 1994). Females of *Z. vivipara* mate with two to three males in the field (Bauwens & Verheyen, 1985). On the other hand, the behaviour of males indicated attempts to continue with copulation. From a male's perspective, it might be advantageous to copulate with a female as long as possible to transfer relatively more spermatozoa, and to prevent sperm leakage or rival matings (Olsson & Madsen, 1998). We therefore suggest that the duration of copulation in *Z. vivipara* results from a conflict between the costs and benefits of copulation for both sexes.

CONCLUSIONS

Our results show that *Z. vivipara* males with larger heads have a more likely to win male–male contests and to grasp females for copulation. The effect of head size on the outcome of male–male contests has been demonstrated in several species of lizards (Carothers, 1984; Vitt & Cooper, 1985; Anderson & Vitt, 1990; Hews, 1990; Molina-Borja *et al.*, 1998). In this study, head size is also shown to be important for males of a non-territorial species with the lowest levels of aggressiveness among lacertids (Verbeek, 1972). Our observations also suggest that having a large head may help males to grasp females during copula, a possible benefit that seems to have been overlooked in the literature. Since our results were obtained under artificial conditions they provide no direct evidence for the selective advantage of head size in the wild. However, available field data (Braña, 1996) corroborate our findings and thus we conclude that sexual dimorphism in head size in this species is probably maintained through intra- and intersexual selection.

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