Folia Zool. - 47(3): 189–195 (1998)

Sexual dimorphism and intersexual food niche overlap in the sand lizard, *Lacerta agilis* (Squamata: Lacertidae)

Lumír GVOŽDÍK[1] and Milan BOUKAL[2]

Department of Zoology, Palacký University, tř. Svobody 26, CZ-771 46 Olomouc, Czech Republic;
[2]e-mail: boukal@risc.upol.cz

Received 18 November 1997; Accepted 23 July 1998

Abstract. Sexual dimorphism and food niche competition were studied between sexes of the sand lizard *Lacerta agilis* living in Moravia, Czech Republic. Significant sexual differences were found in morphometric traits, with the males being smaller and lighter than females but still having larger head and legs. However, there were no differences in diet composition between the sexes, resulting in a high food niche overlap. These results do not support the hypothesis that food is a factor forcing the evolution of sexual dimorphism in the sand lizard.

Key words: intersexual differences, niche breadth, morphometry

Introduction

Males and females may differentially allocate resources to reproduction and growth, and these allocations can result in differences in morphological traits or body size between sexes (Darwin 1871, Trivers 1972). To explain the evolution of sexual dimorphism, three major hypotheses have been advanced, based upon mechanisms of sexual selection, intersexual food competition and reproductive role division (see Hedrick & Temeles 1989 for a review). As the primary explanation of how sexual dimorphism evolved, the sexual selection hypothesis was proposed (Darwin 1871). The hypothesis is based on the premise that sexual dimorphism evolves when characters that confer an advantage in either competition for mates or mate choice are selected for within one sex. Dimorphic niche hypothesis (Hedrick & Temeles 1989) or female fecundity hypothesis (Shine 1989, Jensen et al. 1995) focus upon selection acting only on females, i.e. females are larger than males because large body size is associated with increased number or size of eggs. The third hypothesis, intersexual food competition (Schoener 1967, Slatkin 1984, Shine 1989), may also be a selective force leading to sexual dimorphism, especially in trophic structures e.g. jaw (head) length or width. Potentially, sexual dimorphism may evolve in response to any of these factors alone, or through a combination of these selective forces acting together or sequentially. Each of these factors may amplify or constrain the degree of sexual dimorphism favoured by the action of the other factors (Shine 1989).

The sand lizard *Lacerta agilis* is one of the most common reptiles in the Czech Republic (Opatrný 1992). The nominotypic subspecies occurring in this territory is characterized by considerable sexual dimorphism (Nöllert 1988). Larger males have higher contest success (Olsson 1992) as well as mating success (Gullberg et al. 1997), which is

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[1] To whom correspondence should be addresed. Present address: *Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Studenec 122, CZ-675 02 Koněšín, Czech Republic; e-mail: gvozdik@brno.cas.cz*

consistent with sexual selection hypothesis. Reproductive success (litter size) of females also correlates with body size (Olsson & Shine 1996), but no information exists about ecological causes of sexual dimorphism in *L. agilis* such as food competition. Ecological differences between the sexes may be seen as (1) sources of selective forces for sexual dimorphism, (2) passive consequences of sexual dimorphism that has evolved for other reasons (sexual selection or fecundity selection), (3) adaptations that have evolved to allow a reduction in sexual dimorphism, by minimizing intraspecific competition, or (4) the expression of constraints preventing the evolution of more extreme sexual dimorphism (Shine 1989). Thus, a study of intersexual food competition may be important for the understanding of the evolution of sexual dimorphism. The main aims of the present study are: 1) to determine the level of sexual dimorphism in population studied, and 2) to compare food composition and to evaluate food niche overlap between males and females.

Material and Methods

The study area was situated on the left side of a 600 m-long river embankment along the River Opava in the town of Opava (Czech Republic: Opava Distr.; 17°54'E 49°56'N; alt. 250 m). The river embankment was formed of 4 m-high slopes with SW exposition covered by grassy vegetation (*Bromus* sp., *Festuca* sp. *Poa* sp.) with scattered trees (*Fraxinus* sp., *Tilia* sp.).

Thirty-five specimens of *L. agilis* were captured during July and August 1994. Sex was determined by the presence of secondary sexual characters (Bischoff 1984). Males and females were collected at the same time and in the same microhabitats. The size distributions in the sample were assumed to reflect the size distributions typical for this habitat. Every specimen was individually marked by toe clipping (Waichman 1992), weighted using a Pesola scale (to 0.1 g) and the following morphometric characters were measured with plastic calipers (to 0.1 mm): snout-vent length (SVL), head length (HL), head width (HW), axilla-groin distance (AGD), fore limb length (FLL) and hind limb length (HLL). Tail length was excluded due to the high rate of regenerated tails (62.9 %) in the population.

Stomach contents were obtained by stomach flushing (James 1990) and stored in 10 % formalin. For each lizard, prey items were counted and identified at least to the family if possible (Buchar et al. 1995). Further relative abundance (percentage of particular prey categories in stomachs) and constancy of prey (percentage of stomachs containing a determined category of prey) were measured (Gadsen Palacios-Orona 1997). Food niche breadth *B* was calculated for each sex using the reciprocal Simpson's measure (Pianka 1973, 1986):

$$B = 1/\sum_{i=1}^{n} p_i^2$$

where *p* is the proportion of resource category, *i* and *n* is the total number of categories. Niche breadths may vary from 1 (exclusive use of one category or uneven use of many categories) to *n* (even use of all categories). To standardize niche breadths for comparison between sexes, we divided them by the number of resource categories, *n*. Standardized niche breadths vary from 1/*n* to 1 (Pianka 1986). To compare the diets of males and females, we used the symmetric niche overlap formula:

$$Q_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}$$

where the symbols are the same as above, but with *j* and *k* representing different sexes (Pianka 1973, 1986). Overlap values range from 0 (no overlap) to 1 (complete overlap).

Diet composition was compared using the G-test (Zar 1996) and differences between sexes in morphometric characters were tested by the Student t-test. To remove the effect of different body size on remaining morphometric traits (Borcea 1979, Nöllert 1988), analysis of covariance (ANCOVA) was used with SVL as the covariate (Sokal & Rohlf 1981), using STATGRAPHICS 5.0.

Results

Statistical analysis of morphometric characters showed that females had larger SVL ($t = 2.78$, $P < 0.01$) and AGD ($t = 3.9$, $P < 0.001$) than males (Table 1). However, males had longer HL (ANCOVA, $F_{1,32} = 190.0$, $P < 0.001$), HW ($F_{1,32} = 27.3$, $P < 0.001$), FLL ($F_{1,32} = 12.2$, $P < 0.01$), HLL ($F_{1,31} = 19.3$, $P < 0.001$), and weight ($F_{1,32} = 15.5$, $P < 0.001$) than females. Absolute values (without removing the effect of SVL) revealed no differences in HW, FLL, and HLL ($P > 0.05$) between sexes. Marginal differences were found only in HL ($t = 2.1$, $P = 0.04$).

Table 1. Mean ($\bar{x}$), standard error (SE), minimum and maximum (min-max) for lengths (mm) and weight (g) of morphometric characteristics in male and female (n = no. of specimen) *L. agilis* from Opava.

	Males (n = 17)		Females (n = 18)	
Character	$\bar{x}$±SE	min - max	$\bar{x}$±SE	min - max
Snout-vent length	64.3±1.8	47.5 - 81.6	70.7±1.4	61.3 - 79.8
Head length	15.7±0.4	12.5 - 19.7	14.7±0.3	13.2 - 16.4
Head width	7.1±0.2	6.2 - 9.2	6.8±0.1	5.6 - 7.5
Axilla-groin distance	39.8±1.0	30.6 - 47.5	45.3±0.9	38.8 - 52.5
Front leg length	19.9±0.4	16.3 - 24.4	19.9±0.3	17.8 - 22.3
Hind leg length	29.6±0.8	22.1 - 35.9	29.1±0.4	26.8 - 32.4
Mass	8.3±0.8	2.7 - 17.4	9.0±0.4	5.7 - 12.9

The diet analysis of 35 stomachs revealed 163 food items of various insects, arachnids, crustaceans and molluscs were arranged in 26 food categories (Tables 2 and 3). Differences in proportions of particular food categories between sexes were not significant (G-test, $G = 32.1$, $df = 25$, $P > 0.1$) similarly as for differences in constancy of prey ($G = 19.3$, $df = 25$, $P > 0.8$). The average number of consumed prey items per stomach in males (5.1 ± 0.6) was not significantly different from that in females (4.3 ± 0.5) (Mann Whitney U-test, $Z = 1.0$, $P = 0.3$). The standardized food niche breadth was calculated as 0.21 for males and 0.19 for females, with high niche overlap of 0.78.

Discussion

We have demonstrated apparent sexual dimorphism in all measured characters in *L. agilis*. Females are larger than males but males have longer HL, HW, FLL and HLL relative to SVL. These findings are consistent with data measured in age-known population of *L. agilis* (Olson & Shine 1996) as well as in other papers (Rahmel & Meyer 1987, Nöllert 1988), which suggests that our results were not biased by non-random sampling (e.g. Gibbons & Lovich 1990, Shine 1990, Stamps 1993).

Despite significant sexual dimorphism, numerical diet composition, constancy of prey, standardized food niche breadths and average number of prey eaten were not different

Table 2. Niche breadth and abundance of prey in stomachs of males and females *L. agilis.* (undet. = undetermined).

	Males (n = 17)		Females (n = 18)	
Prey type	No.	%	No.	%
Mollusca	1	1.2	-	-
Isopoda	6	7.0	2	2.6
Araneida	6	7.0	10	13.0
Opilionida	2	2.3	3	3.9
Dermaptera	1	1.2	1	1.3
Orthoptera[1]-undet.	-	-	1	1.3
Acrididae	6	7.0	4	5.2
Heteroptera-undet.	4	4.7	2	2.6
Miridae	-	-	2	2.6
Auchenorhyncha	2	2.3	1	1.3
Neuroptera-larvae	1	1.2	-	-
Coleoptera-larvae	5	5.8	4	5.2
Carabidae	4	4.7	4	5.2
Chrysomelidae	8	9.3	3	3.9
Coccinellidae	10	11.6	1	1.3
Elateridae	1	1.2	1	1.3
Curculionidae	3	3.5	7	9.1
Hymenoptera-undet.	3	3.5	2	2.6
Formicidae	10	11.6	12	15.6
Vespidae	-	-	1	1.3
Apidae	1	1.2	-	-
Lepidoptera-larvae	1	1.2	3	3.9
Diptera	3	3.5	2	2.6
Shed skin	1	1.2	-	-
Plants	3	3.5	8	10.4
Unidentified prey items	4	4.7	3	3.9
Niche breadths		5.04		4.63
Adjusted niche breadths		0.21		0.19

[1] Ensifera and Caelifera

between the sexes. These results correspond with the data by Lukina (1976). Unfortunately, no additional information on the degree of sexual dimorphism was given in this paper. However, niche overlap was relatively low when compared to interspecific values for *L. agilis* and *L. vivipara* (Strijbosch 1986, 1992) or *L. agilis* and *L. viridis* (Korsós 1984). But this parameter should be accepted with caution because it could be affected by sample size (Ricklefs & Lau 1980) and the number of resource categories (Smith & Zaret 1982). For example, if we recalculated food niche overlap for 15 categories (orders only as in Korsós 1984, Strijbosch 1986, 1992), then it increased to 0.93.

Different diet composition between males and gravid females was found in several populations from the territory of the former USSR (see Lukina 1976 for a review) and Transcarpathian Ukraine (Shcherbak & Shcherban' 1980). Generally, such differences could be caused by: 1) higher nutrient requirements of females during egg development (Shine 1989), 2) reduced food intake (see Shine 1980 for review), and 3) reduced speed and mobility (e.g. Van Damme et al. 1989, Sinervo et al. 1991). Therefore, the observed causes were more likely consequences of pregnancy rather than causes forcing the evolution of sexual dimorphism or the effect of sexual dimorphism in *L. agilis.*

Table 3. Constancy of prey in stomachs (number of stomachs containing a determined category of prey) of males and females *L. agilis* (undet. = undetermined).

Prey type	Males (n = 17)		Females (n = 18)	
	No.	%	No.	%
Mollusca	1	5.9	-	-
Isopoda	4	23.5	2	11.1
Araneida	6	35.3	10	55.6
Opilionida	2	11.8	3	16.7
Dermaptera	1	5.9	1	5.6
Orthoptera[1]-undet.	-	-	1	5.6
Acrididae	5	29.4	3	16.7
Heteroptera-undet.	2	11.8	2	11.1
Miridae	-	-	2	11.1
Auchenorhyncha	2	11.8	1	5.6
Neuroptera-larvae	1	5.9	-	-
Coleoptera-larvae	3	17.7	3	16.7
Carabidae	4	23.5	3	16.7
Chrysomelidae	4	23.5	3	16.7
Coccinellidae	1	5.9	1	5.6
Elateridae	1	5.9	1	5.6
Curculionidae	2	11.8	5	27.8
Hymenoptera-undet.	3	17.7	2	11.1
Formicidae	4	23.5	2	11.1
Vespidae	-	-	1	5.6
Apidae	1	5.9	-	-
Lepidoptera-larvae	1	5.9	3	16.7
Diptera	2	11.8	2	11.1
Shed skin	1	5.9	-	-
Plants	2	11.8	6	33.3
Unidentified prey items	3	17.7	3	16.7

[1] Ensifera and Caelifera

There could be several reasons why we did not find differences in diet composition between the sexes. First, habitat diversity at the study area did not vary enough to generate differences. Second, even if sexual dimorphism in the relative size of head to body length was highly significant, absolute values were only slightly significant in HL ($P = 0.04$) and even insignificant in HW ($P = 0.17$). These findings suggest there may be a trend to an optimal size for adults living in the given environment independent of body-size differences or of sex (Cooper & Vitt 1989). This is contradictory to the idea that sexual differences in the size of trophic apparatus might have evolved to reduce competition for food between the sexes (see e.g. Schoener 1967). Third, adjusted niche breadths of males and females were almost identical and their low values indicated uneven use of many prey categories (Table 2). Small differences in absolute head measurements coupled with food generalization in *L. agilis* are consistent with Selander's (1966) observations in birds, where small sexual dimorphism in bill size may indicate that food supplies are sufficiently abundant to permit extensive sexual overlap in utilization.

In conclusion, the results of our study do not support the hypothesis that food niche divergence is a critical factor for the evolution of sexual dimorphism in *L. agilis* nor the passive consequence of sexual dimorphism that has evolved for other reasons (sexual selection or fecundity selection). However, the degree of sexual dimorphism varied considerably within the species range (Darevsky et al. 1976), suggesting that selection pressures amplify or constrain sexual dimorphism at different rates within particular populations. Therefore, for the final judgment more data on the degree of sexual dimorphism as well as its possible causes is needed.

Acknowledgements

We wish to thank J. Piálek and E. Tkadlec (Academy of Sciences of the Czech Republic, Brno) for useful comments and corrections on the earlier version of MS. We also thank D. Bowman (Silesian University, Opava) for improving our English.

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