SEXUAL DIMORPHISM OF HEAD SIZE IN *PODARCIS HISPANICA ATRATA*: TESTING THE DIETARY DIVERGENCE HYPOTHESIS BY BITE FORCE ANALYSIS

by

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ABSTRACT

Sexual dimorphism of relative head size is a widespread phenomenon in lizards, males having larger head/trunk ratios than females. In an attempt to explain this sexual dimorphism several hypotheses have been formulated. The two most frequently cited ones are: 1) sexual selection acting on those structures important in intrasexual competition and 2) natural selection for reduction of food competition between the sexes.

In the insular subspecies of *Podarcis hispanica* (*P. h. atrata*) males tend to have significantly larger heads than similarly sized females. We here test an implicit assumption of the dietary divergence hypothesis, namely that an increase in head size results in an increase in gape width and/or bite force, thereby allowing the larger headed sex to exploit larger prey classes. Using a static bite force model, we calculated the magnitude of bite forces for given directions at given positions on the jaws and for different head sizes. We experimentally determined the hardness of three different prey items and compared the data to the maximal bite force produced by both sexes.

Our results suggest an important difference in male and female bite capacity, which may bear significant ecological relevance, and are in agreement with the implicit assumption of the dietary divergence theory.

KEY WORDS: sexual dimorphism, food niche separation, bite force modelling, *Podarcis hispanica atrata*.

INTRODUCTION

In many lizard species, males tend to have larger heads than similarly sized females. Two evolutionary mechanisms have been invoked to explain this sexual dimorphism in head shape: 1) intrasexual selection, acting on features important in combat (*e.g.*, TRIVERS, 1976; STAMPS, 1977; FITCH, 1981; ANDERSON & VITT, 1990) and 2) natural selection, acting on features that reduce food competition between the sexes (*e.g.*, SCHOENER, 1967, 1977; STAMPS, 1977; PREEST, 1994).

In the insular subspecies of the Spanish wall lizard, *Podarcis hispanica atrata*, the sexual dimorphism in relative head size is well developed; males

having markedly larger heads than females (*cf.* CASTILLA & BAUWENS, 1991). The hypothesis of intrasexual selection, leading to enlarged heads in males, does not seem likely in this species, since both males and females engage in territorial fights. The scarcity of food on the islands inhabited by *P. h. atrata*, makes the alternative hypothesis (dietary divergence for food competition reduction) more attractive. Although these lizards will occasionally eat plant material, stomach content analyses showed a preference for beetles and butterflies (CASTILLA *et al.*, 1987). In accordance with the dietary divergence theory, lizards with larger heads (*i.e.*, males) are expected to eat larger prey items.

In this contribution, we test two implicit assumptions of the dietary divergence hypothesis, namely 1) that the increase in relative head size comes with a increase in gape width and/or bite force (CAROTHERS, 1984) and 2) that these morphological changes allow males to capture larger prey.

MATERIALS AND METHODS

We dissected the head of one male (snout-vent length: 66.6 mm, mass: 7 g) and one female (SVL: 63.2 mm, mass: 5.5 g) preserved specimen of *P. h. atrata* from Columbrete Grande (province of Castellon, Spain). Drawings were made of all stages of the dissection using a dissecting microscope (Wild M3Z — Wild Inc., Switzerland) equiped with a camera lucida. One additional specimen of each sex was used to prepare the skull. For each muscle we determined the position, the three dimensional coordinates of origin and insertion and the mass. Fibre lengths were obtained experimentally by submerging the muscles in a 30% nitric acid (HNO_3 30%) solution for 24 hours to dissolve all connective tissue. Muscle fibres were then immersed in a 50% glycerol solution and the average fibre length of each muscle or muscle bundle was determined by drawing approximately 20 fibres for every muscle (using a dissecting microscope with camera lucida). The individual fibers were then digitised and the average length calculated. The physiological cross section of the muscles was calculated as the mass divided by the fibre length (assuming a muscle density of 1 g/cm^3). Forces were scaled to the physiological cross section of the muscles (250 Kpa; HERZOG, 1994).

The physiological cross section of the jaw muscles and their 3D coordinates of origin and insertion were used as input for the bite model. The position of the point of application of bite forces on the lower jaw (halfway across the tooth row) was chosen based on observations of feeding sequences under semi-natural conditions.

The orientation of the food reaction forces (FRF) was set to vary between -150 and -30 degrees (*cf.* CLEUREN *et al.*, 1995) and the gape angle was set at 10°. Bite forces (BFs) must be regarded as rough estimates of the forces exerted, and are calculated for one side only. BFs have to be multiplied by two to obtain the overall bite force on the prey; note that in lizards jaw closers of both sides are always simultaneously active (GANS *et al.*, 1985; HERREL *et al.*, 1995). To allow comparison between the lizards, we simulated a theoretical situation in which all jaw closers are maximally active. A more detailed description of the bite model is presented in CLEUREN *et al.*, 1995.

We also calculated differences in gape width (vertical distance between the most anterior tip of lower and upper jaw) for the two lizards examined. Assuming a fixed gape angle for both lizards (*e.g.*, 30°) the difference in gape width was calculated using the rectilinear distances

between the most anterior point of the jaws to the rotation axis (= the line interconnecting the right and left articulation facets between quadrate and lower jaw).

To our knowledge no data on insect prey hardness are available in literature. Therefore, to be able to assess the ecological relevance of the results of the bite model, prey hardness was estimated experimentally. For this purpose the lower jaw of one specimen of *P. h. atrata* was removed and partially embedded in resin, leaving the toothrows free. The hardened resin was then mounted onto a Kistler force transducer (type 9203 — Kistler Inc., Switzerland) connected to a charge amplifier (model 463A — PCB piezotronics Inc., NY) and chart recorder (Brush 481 recorder — Gould Inc., OH). Prey items were subsequently crushed by pushing the jaw onto the insect until failure of the chitinous exoskeleton occurred. For all prey items tested, the strength of the hardest part was recorded (usually the head and prothorax). For three prey items (crickets: *Acheta domesticus*, grasshoppers: *Locusta migratoria* and mealworms: *Tenebrio melior*) the relationship between the size (length and/or mass) and the hardness of the prey was investigated.

RESULTS

Morphology

The skull of *P. h. atrata* shows a thick osteodermal layer, small nasal openings, a complex fronto-parietal suture and a distinct quadratojugal process; all characteristic for primitive lacertids (*cf.* ARNOLD, 1989).

Jaw muscles in *P. h. atrata* show the basic lacertid pattern and consist of three jaw openers, a number of jaw closers and the constrictor dorsalis group (Fig. 1). Jaw openers consist for the m. depressor mandibulae, the m. cervicomandibularis and the m. para-occipitomandibularis. The jaw closers can be subdivided into the external adductor (superficial, medial and deep parts), the posterior adductor, the pseudotemporal group (superficial and deep parts) and the pterygoid group (lateral and medial parts). The constrictor dorsalis group consists of a well developed m. protractor and m. levator pterygoidei (for a more elaborate description of lacertid musculature, see HAAS, 1973; GOMES, 1974).

We found few differences between sexes in the presence and position of muscles as well as the relative position of origin and insertion. The m. levator anguli oris is the only muscle that is present in male (although rather poorly developed) but not in female lizards. However, as this muscle does not contribute to the bite force (it inserts on the connective tissue at the angle of the mouth) it will not be considered further. The relative distribution of muscle mass (mass of individual muscles relative to the total adductor mass) is also very similar in male and female lizards (Fig. 2A). However, the total adductor mass is much higher in male lizards, even after
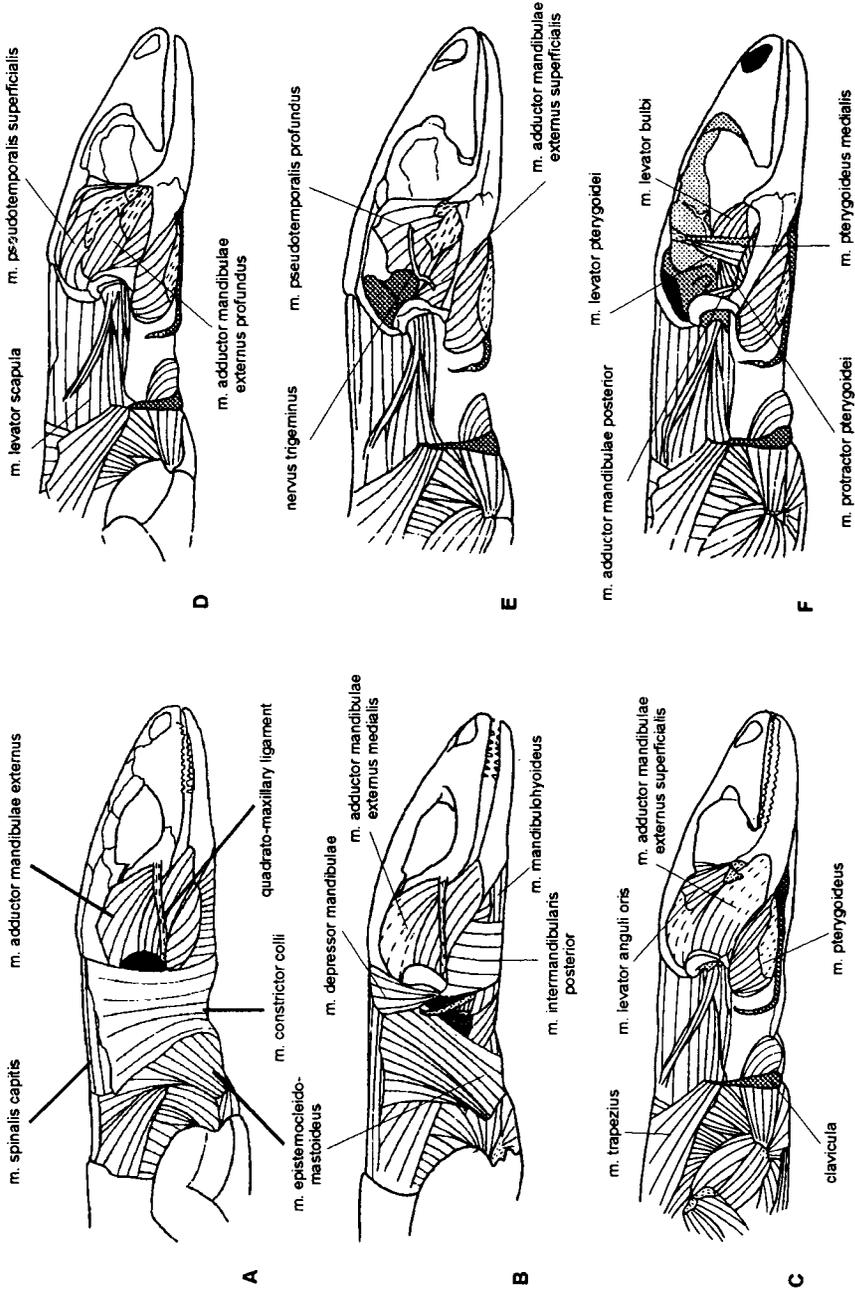
TABLE I

P. hispanica atrata — Morphological data. Mass and fibre length are averaged (right and left side).

Muscle	Mass (g)		Fibre length (mm)	
	male	female	male	female
MDM	0.00355	0.00145	3.32	2.67
MPOM	0.00020	0.00015	2.29	1.46
MCM	0.00480	0.00270	5.76	5.13
MAMES	0.01315	0.00400	2.14	1.85
MAMEM	0.01955	0.0087	1.77	2.55
MAMEP	0.0076	0.0021	2.00	2.36
MPsTS	0.0091	0.0087	2.86	2.51
MPsTP	0.01775	0.0021	1.95	2.30
MAMP	0.00135	0.0005	1.44	1.05
MPtlat	0.0265	0.00885	2.00	1.46
MPtmed	0.0096	0.003	1.11	0.97
MPPt	0.002	0.0008	1.50	1.36
MLPt	0.00075	0.00005	1.47	1.36

correcting for head size differences (Fig. 2B). Fibre lengths are similar for male and female lizards (Fig. 2C, Table I).

Bite force modelling

Bite forces are lowest for food reaction forces oriented perpendicular to the occlusal plane and increase both with an increase and decrease of the angle of the food reaction forces. The male lizard examined here has BFs of 1.41 N for FRFs perpendicular to the occlusal plane at a bite point posterior on the tooth row. In contrast, the female lizard has BFs of 0.58 N in similar conditions. For orientations of the FRFs of $-138°$ and $-42°$ the male specimen can produce BFs of 1.98 N and 2.24 N, respectively. The female lizard reaches BFs of 0.82 N (AFRF: $-138°$) and 0.92 N (AFRF: $-42°$; see Table II, Fig. 3). In summary, the female lizard examined had less than half ($\pm$ 46 %) of the potential bite force of the male lizard when both lizards are scaled to the same snout-vent length.

Fig. 1. *P. hispanica atrata* — Male. A. Lateral view on the head-neck region, after removal of the skin. B. Next level of dissection, after removal of the m. constrictor colli. C. Next level, after removal of the m. episternocleidomastoideus, the m. depressor mandibulae, the intermandibularis group and the quadrato-maxillary ligament. D. Next level, after removal of the m. levator anguli oris, a part of the m. adductor mandibulae externus superficialis and the m. adductor mandibulae externus medialis. E. Next level, after removal of the m. adductor mandibulae externus profundus and the m. pseudotemporalis superficialis. F. Deepest level of dissection, after removal of the remaining part of the m. adductor mandibulae externus superficialis and the m. pseudotemporalis profundus.
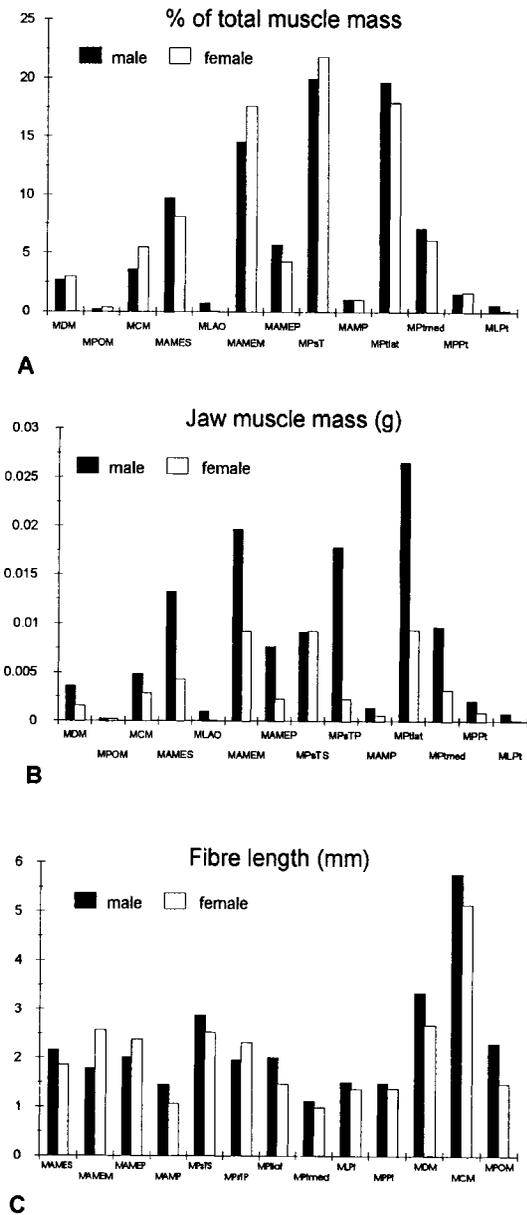
Fig. 2. *P. hispanica atrata* — Morphological data. A. Bar diagram illustrating similarities in relative jaw muscle mass distribution in male and female lizards. B. Bar diagram illustrating differences in jaw muscle mass between male and female lizards. C. Bar diagram illustrating similarities in fibre lengths of jaw muscles in male and female lizards.

TABLE II

Bite forces. AFRF = angle of the food reaction forces; BF = bite force; SBF = bite force for female lizard scaled to same snout-vent length.

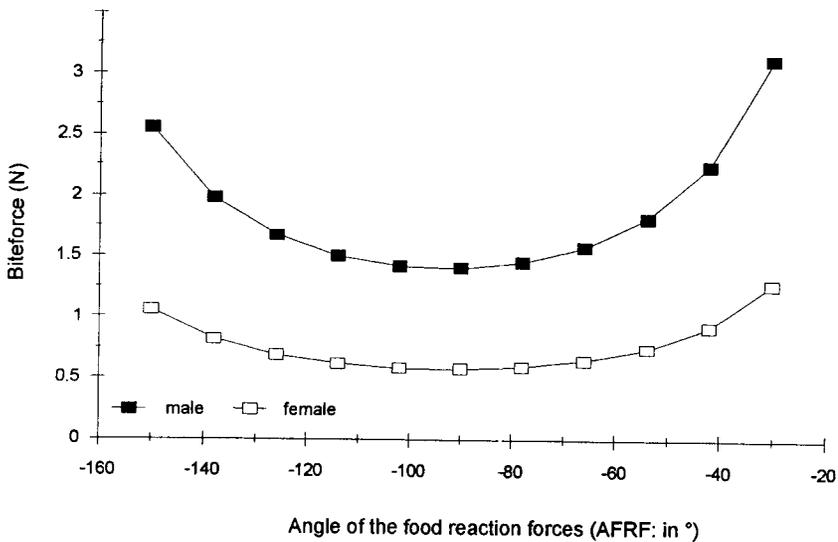| AFRF	BF male (N)	BF female (N)	SBF (female)
−138	1.98	0.82	0.91
−126	1.67	0.69	0.76
−114	1.50	0.62	0.69
−102	1.42	0.59	0.65
−90	1.41	0.58	0.64
−78	1.46	0.60	0.66
−66	1.58	0.65	0.72
−54	1.81	0.75	0.83
−42	2.24	0.92	1.02

Fig. 3. *P. hispanica atrata* — Bite model. Graph illustrating differences in bite force between male and female lizards for given orientations of the food reaction forces at a gape angle of 10°.

Not only do male lizards have higher bite forces, but calculations also show that having a larger head results in a larger gape width for animals having skulls with similar constructional features. In *P. h. atrata*, males have a potential gape width that is ± 20% larger than that of similarly sized females (increase in head length of 3.15 mm results in an increase in gape width of ± 2.4 mm).
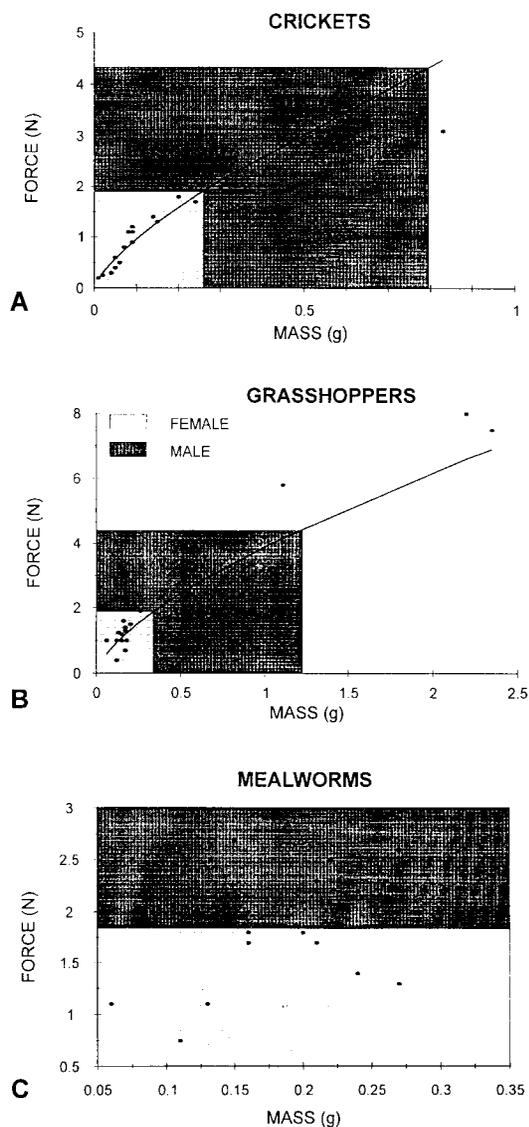
Fig. 4. Prey characteristics. A. Graph illustrating the relation between prey mass and the hardness of the exoskeleton in crickets. B. Graph illustrating the relation between prey mass and the hardness of the exoskeleton in grasshoppers. C. Graph illustrating the relation between prey mass and the hardness of the exoskeleton in mealworms. Dark shading indicates the range of bite forces for the male lizard; lighter shaded area that of the female lizard.

Prey characteristics

The relationship between mass and hardness is highly significant for both crickets and grasshoppers (cricket: $\log F = 0.71 + 0.73 \log M$; grasshopper $\log F = 0.59 + 0.67 \log M$). No relation was apparent for mealworms (Fig. 4A-C). However, the size range of mealworms used was rather small thus increasing the effect of measurement error. Whereas the critical size of crickets (*i.e.*, that size corresponding to a hardness approximating the maximal bite force of the lizard) for female lizards lies at $\pm$ 0.26 g, the critical prey size for males is about 0.50 g (Fig. 4A). A similar difference is present for grasshoppers (female cs: 0.37 g; male cs: 0.68 g; Fig. 4B).

However, not only the prey hardness, but also the prey size can become a limiting factor. As during transport the prey is oriented parallel to the long axis of the head, the most important size variable is probably the prey diameter. Prey transport is preceded by a reduction stage and the diameter of the prey will depend highly on the number of preceding reduction bites. Maximal prey size will thus be the result of the relationship between bite force and gape width on the one hand (BF decreases with increasing gape width) and of the relation between prey diameter and prey hardness on the other hand.

DISCUSSION

Our data suggest that in *P. h. atrata*, males do not only have relatively larger heads, they also show a distinct hypertrophy of the jaw muscles. The bite model outcomes imply that this sexual dimorphism in morphology results in a marked divergence in bite performance capacity. The preliminary data on prey hardness (limited number of prey types) show that the difference in male and female bite capacity may have ecological relevance: critical sizes of prey are well within the species' array of potential prey items. The logical next step will be to look at prey selection in both sexes in the field.

Although our results suggest that the conditions for the dietary divergence theory are fulfilled, this does not prove the validity of the theory. Nor does it refute the alternative (but not mutually exclusive) hypothesis of intrasexual selection. We would also like to coin a third possible explanation, that of intersexual selection. Copulation in these lizards typically involves a struggle, the female trying to escape from the male. Only when the male can maintain a secure grip by biting the female's side, it will succeed to copulate with her. Males with high biting force might therefore be favoured.

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REFERENCES

ANDERSON, R. A. & L. J. VITT, 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. Oecologia **84**: 145-157.

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**(2): 209-257.

CAROTHERS, J. H., 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. Am. Nat. **124**: 244-254.

CLEUREN, J., P. AERTS & F. DE VREE, 1995. Bite and joint force analysis in *Caiman crocodilus*. Belg. J. Zool. **125**: 79-94.

CASTILLA, A. M., J. JIMENEZ & I. LACOMBA, 1987. Los reptiles de Columbretes. In: L. A. ALONSO MATILLA, J. L. CARRETERO & A. M. GARCIA-CARRASCOSA (Eds.): *Islas Columbretes*: 181-194. Generalitat Valenciana, Valencia.

CASTILLA, A. M. & D. BAUWENS, 1991. Observations on the natural history, present status and conservation of the insular lizard *Podarcis hispanica atrata* on the Columbretes Archipelago, Spain. Biol. Cons. **58**: 69-84.

FITCH, H. S., 1981. Sexual size differences in reptiles. Misc. Publ. Mus. Nat. Hist. Univ. Kans. **70**: 1-72.

GANS, C., F. DE VREE & D. CARRIER, 1985. Usage pattern of the complex masticatory muscles in the shingleback lizard, *Trachydosaurus rugosus*: A model for muscle placement. Am. J. Anat. **173**: 219-240.

GOMES, N. M. B., 1974. Anatomie comparee de la musculature trigeminale des lacertiliens. Mem. Mus. Natl. Hist. Nat., Ser. A (Zool.) **90**: 1-107.

HERREL, A., J. CLEUREN & F. DE VREE, 1995. Prey capture in the lizard *Agama stellio*. J. Morphol. **224**: 313-329.

HERZOG, W., 1994. Muscle. In: B. M. NIGG & W. HERZOG (Eds.): *Biomechanics of the musculoskeletal system*: 154-187. John Wiley & Sons, Chichester.

HAAS, G., 1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In: C. GANS & T. PARSONS (Eds.): *Biology of the Reptilia*, Vol. 4: 285-490. London Academic Press, London.

PREEST, M. R., 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: Why do females take smaller prey than males? J. Herpetol. **28**(3): 292-298.

SCHOENER, T. W., 1967. The ecological significance of sexual size dimorphism in the lizard *Anolis conspersus*. Science **155**: 474-477.

SCHOENER, T. W., 1977. Competition and the niche. In: C. GANS & D. W. TINKLE (Eds.): *Biology of the Reptilia*, Vol. 7: 35-136. London Academic Press, London.

STAMPS, J. A., 1977. The relationship between resource competition, risk and aggression in a tropical territorial lizard. Ecology **57**: 1317-1320.

TRIVERS, R. L., 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution **30**: 253-269.