Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses

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Summary

1. Two often cited hypotheses explaining sexual head size dimorphism in lizards are: sexual selection acting on structures important in intrasexual competition, and reduction of intersexual competition through food niche separation.

2. In this study some implicit assumptions of the latter hypothesis were tested, namely that an increase in gape distance and bite force should accompany the observed increase in head size. These assumptions are tested by recording bite forces, *in vivo*, for lizards of the species *Gallotia galloti*. In this species, male lizards have significantly larger heads than female conspecifics of similar snout–vent length.

3. Additionally, the average force needed to crush several potential prey species was determined experimentally and compared with the bite force data. This comparison clearly illustrates that animals of both sexes can bite much harder than required for most insect food items, which does not support the niche divergence hypothesis. The apparent 'excess' bite force in both sexes might be related to the partially herbivorous diet of the animals.

4. To unravel the origin of differences between sexes in bite capacity, the crushing phase of biting was modelled. The results of this model show different strategies in allocation of muscle tissue between both sexes. The origin of this difference is discussed and a possible evolutionary pathway of the development of the sexual dimorphism in the species is provided.

Key-words: Bite forces, bite modelling, prey toughness

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Introduction

Although it has long been recognized that both natural and sexual selection can shape the features of sexually dimorphic organisms, the differential contribution of these selective drives is often hard to determine (e.g. Anderson & Vitt 1990; Hews 1990; Shine 1991, 1993; Stamps 1993; Cordes, Mouton & Van Wijk 1995; Perry 1996; Wikelski & Trillmich 1997) and may vary for different traits within an organism (Gittleman & Van Valkenburgh 1997). Especially susceptible to both evolutionary mechanisms are sexually dimorphic features associated with the trophic apparatus. An often cited example is that of the sexual head size dimorphism in lizards, where an increased male head size may simultaneously be important in intrasexual interactions (e.g. male–male combat, territorial contests; Trivers 1976; Fitch 1981; Anderson & Vitt 1990; Mouton & Van Wijk 1993; Bull & Pamula 1996; Censky 1996), intersexual interactions (copulatory bites; Herrel, Van Damme & de Vree 1996), and aid in resource partitioning (e.g. males being able to eat larger prey than female conspecifics; Schoener 1967, 1977; Stamps 1977; Best & Pfaffenberger 1987; Preest 1994). Although it is often hard to unravel the precise contribution of each selective pressure, at least one of these hypotheses (natural selection resulting in a reduction in food competition between the sexes) can be refuted by testing some of its implicit critical assumptions (see Carothers 1984). To allow for niche differentiation between the sexes, the difference in head size should result in at least a difference in gape or bite performance (or both), allowing males to capture prey not accessible to females (e.g. larger or tougher prey items). The present study tests this last assumption by recording bite forces, *in vivo,* for a large sample of lizards.

Gallotia galloti (Duméril et Bibron, 1839), the Canary Island Lizard, is especially suited to test these predictions as (1) it is sexually dimorphic in head dimensions (both head length, head width and head height; see Bischoff 1971; Molina Borja, Padron-Fumero & Alfonso-Martin 1997), (2) male lizards do not defend territories and have overlapping home

ranges (Molina Borja 1987; Molina Borja, Padron-Fumero & Alfonso-Martin 1998), (3) the diet of the animals is relatively well known and includes large amounts of plants (Diaz 1980; Molina Borja 1991; Valido & Nogales 1994) and (4) *G. galloti* are fairly large lizards (average snout–vent length for males is 135 mm, for females 126 mm; Salvador 1985) which allows bite forces to be recorded from both adult and juvenile lizards. To be able to determine where and when selection for a larger head size takes place, lizards at several ontogenetic stadia were tested (see Shea 1986; Ravosa & Gomez 1992; Watkins 1996; Masterson 1997 for why ontogenetic patterns should be studied). Additionally, in order to assess the ecological relevance of the expected differences in bite performance, the toughness of several potential natural prey items was measured. The goals of this study are thus to test the assumptions of the food niche partitioning hypothesis as an explanation for the observed intersexual difference in head size in lizards of the species *Gallotia galloti*.

Materials and methods

MORPHOMETRICS

Morphometrics (snout–vent length, SVL; mass, M; head width, HW; head length, HL; head height, HH; lower jaw length, LJL) were determined for 56 adult male, 83 adult female and 97 juvenile specimens of the species *Gallotia galloti* using digital callipers (± 0·01 mm; model CD-15DC; Mitutoyo, UK) and an electronic balance (± 0·01 g; model FX-3200; AND, Japan). Specimens were measured either in the field (Tenerife) or in the Institute of Nature Conservation (Br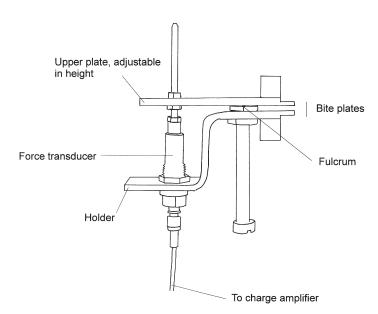ussels). Relationships of morphometric variables were examined by regression analysis, and dimorphism of head dimensions between sexes was estimated by analyses of covariance (all variables were log_{10}-transformed because of the non-normality of the data).

BITE FORCE RECORDINGS

In vivo bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Switzerland) mounted on a purpose-built holder (Fig. 1) and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc.). Biting causes the upper plate to pivot around the fulcrum, and thus pull is exerted on the transducer. Bite forces were registered using a portable computer equipped with an A/D converter (PC-Scope T512, IMTEC GmbH, Germany).

Bite forces were measured for 16 adult male, 24 adult female and 83 juvenile lizards kept at the Institute of Nature Conservation (Brussels, Belgium). Animals were placed in an incubator at 35 °C (approximating the average preferred body temperature for several species of *Gallotia*, Marquez, Cejudo & Prez-Mellado *et al.* 1997) for 60 min before testing. After 1 h animals were hand held which readily resulted in a very characteristic threat response where the jaws are opened maximally. The free end of the holder (= bite plates, see Fig. 1) was then placed between the jaws of the animal which immediately resulted in fierce and prolonged biting. The place of application of bite forces is standardized by mounting acrylic stops on the free end of the holder (see Fig. 1). Measurements were repeated five times for each animal with an inter-trial interval of at least 1 h. The maximum value recorded during such a recording session was considered to be the maximal bite force for that animal. All animals were weighed on the same day, and for juveniles all morphometric values were determined within 2 days of testing. Bite forces were regressed against SVL and head measures for male, female and juvenile lizards separately. The influence of body size on the variables was removed by using analyses of covariance with SVL as covariate.

MORPHOLOGY

The heads of two male (SVL 115 ± 5 mm; mass 55 ± 5 g) and two female (SVL 85 ± 2 mm; mass 30 ± 3 g) preserved specimens of *G. galloti* from Tenerife (Canary Islands, Spain) were dissected. Drawings were made of all stages of the dissection using a dissecting microscope (Wild M3Z, Wild Inc., Switzerland) equipped with camera lucida. One additional specimen of each sex was used to prepare the skull. For each muscle the position, three-dimensional coordinates of origin and insertion and the mass were determined. Fibre lengths were obtained experimentally by submerging the muscles in a 30% nitric acid (HNO_3 30%) solution for 24 h to dissolve all connective tissue. Muscle fibres were then put in a 50%

Fig. 1. Experimental setup used to register bite forces *in vivo*. The animals bite on the bite plates which causes the upper plate to rotate, thus exerting pull on the piezo-electric force transducer. The distance between bite plates is adjustable.

Labels in figure:
Upper plate, adjustable in height
Force transducer
Holder
Bite plates
Fulcrum
To charge amplifier

glycerol solution and the average fibre length of each muscle or muscle bundle was determined by drawing at least 20 fibres for every muscle (using a dissecting microscope with camera lucida). The individual fibres were then digitized 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}, see Herrel *et al.* 1996). Forces were scaled to the physiological cross-section of the muscles (250 kPa; Herzog 1994).

BITE MODELLING

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; see Fig. 2) 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° (see Fig. 2; Herrel, Aerts & De Vree 1998a,b) 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 2 to obtain the overall bite force on the prey; note that in lizards jaw closers of both sides are generally simultaneously active, see Herrel, Cleuren & De Vree 1997). To allow comparison between the lizards, a theoretical situation was simulated in which all jaw closers are maximally active. A more detailed description of the bite model is presented in Herrel *et al.* (1998a).

ESTIMATION OF PREY TOUGHNESS

The only available data on insect prey hardness are those presented in Herrel *et al.* (1996) and Andrews & Bertram (1997). Still, these data are limited to three prey categories. As such data are important to assess the ecological relevance of the results of the bite model and the *in vivo* bite force recordings, prey hardness
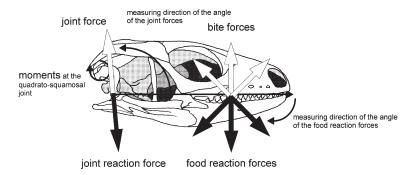
was estimated experimentally for a number of other prey items of prey categories that were untested up to now. For this purpose the lower jaw of one specimen of *G. galloti* was removed and partially embedded in resin, leaving the toothrows free. The hardened resin was then mounted on a Kistler force transducer (type 9203, Kistler Inc.) connected to a charge amplifier (model 463 A, 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 with the insect oriented transversely to the toothrow (as observed during feeding in *Gallotia*) until failure of the chitinous exoskeleton occurred. For all prey items tested, the toughness of the hardest part was recorded (usually the head and prothorax). For two co-occurring potential prey items from Tenerife: *Pimelia radula* (size range 17·26–23·03 mm, $N = 28$) and one hemipteran bug species (Miridae; size range 6·99–11·52 mm, $N = 7$) the toughness of the exoskeleton was determined. Additionally, for crickets (*Gryllus campestris*; size ranging from 4·47 to 30·00 mm, $N = 147$) and one undetermined beetle from Tenerife (Tenebrionidae; size ranging from 5·13 to 9·60 mm, $N = 20$), the relationship between the size (length) and the toughness was investigated by regressing the log$_{10}$-transformed data against one another. These prey are especially interesting as they include the tougher prey categories for which intersexual food niche separation is most likely to occur.

Results

MORPHOLOGY

The skull of *G. galloti* shows a thick osteodermal layer, characteristic for primitive lacertids (Fig. 3). Consequently, no, or only very limited, movements are possible at the mesokinetic axis. The skull is solid, rather high and about twice as long as the width at the level of the quadratojugal process, which is only weakly developed. The teeth are pleurodont, and both the maxillary and dentary ones are somewhat laterally flattened and tricuspid (one large central and two small ex-centric cusps). The premaxillary and pterygoidal teeth on the other hand are simple and conical.

The jaw musculature of *G. galloti* is similar to that described for other lacertids (see Haas 1973; Gomes 1974; Herrel *et al.* 1996) and is composed of three distinct jaw openers and three well-defined jaw closer groups (Fig. 3). The jaw openers consist of the well-developed m. cervicomandibularis and m. depressor mandibulae, and the very small m. paraoccipito-mandibularis (Fig. 3a). Jaw closers consist of the m. adductor mandibulae externus (superficial, medial and deep parts) originating on the posterior dorsal side of the temporal region and inserting on the coronoid process by means of a complex aponeurotic complex (Fig. 3a, b), the m. adductor mandibulae posterior running from the quadrate to the medial side of the

Fig. 2. Graphical representation of action and reaction forces at the jaw joint and the bite point. The direction of the joint force is measured relative to the line interconnecting the jaw joint and the anterior tip of the lower jaw. Bite forces are measured relative to the lower jaw.

lower jaw, posterior to the coronoid (Fig. 3b), and the m. adductor mandibulae internus. This last muscle group consists of the m. pseudotemporalis (superficial and deep parts) running from the parietal and occipital bones to the medial side of the coronoid (Fig. 3b), and the m. pterygoideus (lateral, medial and dorsal parts) originating on the pterygoid and ectopterygoid bones and inserting on the posterior medial and lateral sides of the lower jaw (Fig. 3a).
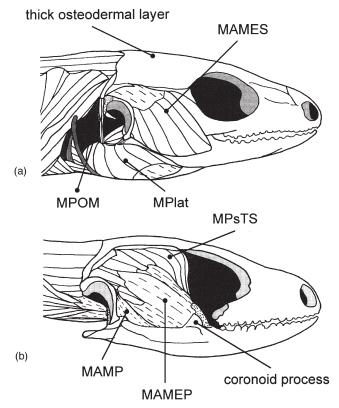

Fig. 3. *Gallotia galloti*, male. (a) Superficial lateral view on the head-neck region after removal of the skin. (b) Deeper view after removal of the superficial and medial parts of the external adductor, and the pterygoid muscle. MAMES, m. adductor mandibulae externus superficialis; MAMEP, m. adductor mandibulae externus profundus; MAMP, m. adductor mandibulae posterior; MPlat, m. pterygoideus pars lateralis; MPOM, m. para-occipitomandibularis; MPsTS, m. pseudotemporalis superficialis.

Table 1. Output of the static bite model based on the data for a male *G. galloti* specimen with a gape angle of 10° (forces are given for one side only)

Orientation of FRF (°)	FRF (N)	JF (N)	Orientation of JF (°)
−150	9·89	25·73	142·32
−138	7·36	23·05	138·69
−126	6·07	21·45	136·01
−114	5·36	20·32	133·80
−102	5·00	19·42	131·79
−90	4·88	18·62	129·80
−78	4·98	17·85	127·63
−66	5·33	17·03	125·05
−54	6·00	16·11	121·60
−42	7·23	14·96	116·26
−30	9·64	13·44	105·93

FRF, food reaction forces; JF, joint forces.

Although the m. pterygoideus is by far the largest muscle in both male and female lizards, some noticeable differences in muscle mass distribution exist (Table 2). Whereas male lizards seem to invest relatively more in the lateral pterygoid, female lizards seem to invest more in the external adductor musculature.

BITE MODELLING

As for other lizard species examined (Herrel *et al.* 1996, 1998a,b) bite forces are lowest for food reaction forces perpendicular to the occlusal plane, and increase with deviations of the angle of the food reaction forces to either side (Table 1). Joint forces may be large and the orientation is largely dependent on the orientation of the food reaction forces. The relative contribution of the different jaw muscles to the moments generated at the jaw joint is represented in Table 2.

MORPHOMETRICS

The results of the morphometric analysis clearly indicate a sexual dimorphism in head size; adult male lizards are significantly larger and have a larger head than females (Tables 3 and 4). The data for the juveniles seem to indicate that heads of male lizards show a disproportionately fast growth (see Fig. 4). Apart from the general size difference, male lizards of a given length have longer (ANCOVA, difference in slope: $F = 11·29$; $N = 1, 135$; $P = 0·001$), wider (ANCOVA, no difference in slope, but significant difference in intercept: $F = 41,02$; $N = 1, 136$; $P < 0·001$) and higher (ANCOVA, difference in slope: $F = 13·35$; $N = 1, 135$; $P < 0·001$) heads than female lizards. There thus seems to be a clear sexual dimorphism in head size and shape.

IN VIVO BITE FORCES

For all groups studied (adult males, adult females and juveniles) a clear and significant relation was observed between bite force and body size, larger lizards being able to bite harder than smaller ones (Fig. 4; Tables 3 and 4). Additionally, a clear sexual dimorphism in bite force could be demonstrated (ANCOVA: slopes $F = 0·31$; df $= 1,34$; $P = 0·58$; intercepts $F = 30·98$; df $= 1,35$; $P < 0·001$); for a given body size, males bite harder than female lizards (see Fig. 4). Even when taking head dimensions into account males are able to bite significantly harder than females (ANCOVA: slopes df $= 1,34$; HL $− F = 3·55$, $P = 0·06$; HW $− F = 0·03$, $P = 0·86$; HH $− F = 0·38$, $P = 0·54$; intercepts df $= 1,35$; HL $− F = 19·56$, $P < 0·001$; HW $− F = 12·87$, $P < 0·001$; HH $− F = 23·52$, $P < 0·001$).

PREY CHARACTERISTICS

Both for crickets and the tenebroid beetles tested, a clear positive relationship (crickets $P < 0·001$; beetles $P = 0·02$) between size and exoskeleton toughness

Table 2. Relative contribution of the jaw closers to the moments delivered at the jaw joint

Muscle	Male			Female		
	phys xs (cm^2)	rmass (%)	rcontr (%)	phys xs (cm^2)	rmass (%)	rcontr (%)
MAMES1	0·14	5·19	5·52	0·011	4·03	3·76
MAMES2	0·18	8·07	21·43	0·025	11·03	25·76
MAMEM1	0·085	3·85	4·41	0·015	6·96	7·01
MAMEM2	0·15	8·25	12·40	0·02	11·91	15·73
MAMEP	0·13	5·16	8·50	0·017	6·87	9·97
MAMP	0·07	2·43	3·13	0·0096	3·24	3·67
MPsTS	0·15	9·04	18·42	0·01	6·04	10·82
MPsTP	0·15	9·85	17·27	0·017	11·03	17·03
MPtlat	0·60	38·47	6·16	0·044	28·50	4·01
MPtmed	0·15	5·23	2·68	0·013	4·82	2·17
MPtdors	0·14	3·22	0·09	0·014	3·33	0·07

Mass and contribution (rmass and rcontr) are expressed relative to the total jaw adductor mass and the total jaw closing moment delivered at the jaw joint, respectively; the physiological cross-section (phys xs) is given in absolute values.
MAMEM1, m. adductor mandibulae externus medialis 1; MAMEM2, m. adductor mandibulae externus medialis 2; MAMEP, m. adductor mandibulae externus profundus; MAMES1, m. adductor mandibulae externus superficialis 1; MAMES2, m. adductor mandibulae externus 2; MAMP, m. adductor mandibulae posterior; MPsTP, m. pseudotemporalis profundus; MPsTS, m. pseudotemporalis superficialis; MPtdors, m. pterygoideus dorsalis; MPtlat, m. pterygoideus lateralis; MPtmed, m. pterygoideus medialis.

could be demonstrated (Fig. 5). Whereas the average force needed to crush a cricket was only 2·15 N (± 1·60 N; $N = 114$), much more force is needed on average to crush the tenebroid beetles (7·00 ± 4·03 N; $N = 20$). As the size range of the *Pimelia* specimens tested was limited, only an average toughness is reported (20·07 ± 2·6 N; $N = 28$). Similarly, for the hemipteran species tested only an average value is reported (3·41 ± 2·04 N; $N = 7$) here.

Discussion

The data gathered in this study clearly indicate a sexual dimorphism in bite performance that can be linked to the dimorphism in head size between male and female lizards. Head dimensions isometrically increase with body size in both females and juveniles (Table 4, Fig. 4), but show a disproportionate growth relative to the body in male lizards after maturation. Based on simple geometrical rules (see Herrel *et al*. 1996), an increase in head size (mainly length) leads

Table 3. Morphometrics and *in vivo* bite forces (averages ± standard deviations)

Variable	Juvenile	Female	Male
N	97	83	56
SVL (mm)	58·88 ± 1·25	93·33 ± 1·09	109·65 ± 1·11
Head length (mm)	14·79 ± 1·20	22·13 ± 1·09	28·18 ± 1·16
Head width (mm)	8·91 ± 1·25	14·13 ± 1·11	18·62 ± 1·17
Head height (mm)	6·76 ± 1·25	11·22 ± 1·13	14·79 ± 1·21
N	64	22	16
Bite force (N)	2·38 ± 1·01	33·51 ± 14·20	108·57 ± 40·21

N, sample size; SVL, snout–vent length.

Table 4. Allometries (reduced major axis regressions)

Variable	Juvenile			Female			Male		
	a	b	r	a	b	r	a	b	r
Allometries of head dimensions and bite force *vs* SVL									
N	97	83	56						
Head length	−0·28	0·82	0·99	−0·73	1·05	0·78	−1·54	1·47	0·86
Head width	−0·78	0·97	0·98	−1·44	1·31	0·82	−1·89	1·55	0·83
Head height	−0·93	0·99	0·97	−1·75	1·42	0·78	−2·67	1·89	0·90
N	64	24	16						
Bite force	−8·22	4·99	0·79	−2·25	3·42	0·40	−4·27	3·07	0·73
Allometries of head dimensions *vs* bite force									
N	64	24	16						
Head length	−6·39	5·99	0·77	5·88	5·43	0·42	−0·89	1·96	0·68
Head width	−4·33	5·25	0·75	−2·95	3·86	0·20	−1·44	2·66	0·65
Head height	−3·01	4·32	0·78	−2·43	3·69	0·11	−0·08	1·73	0·88

All regressions are based on log$_{10}$-transformed data.
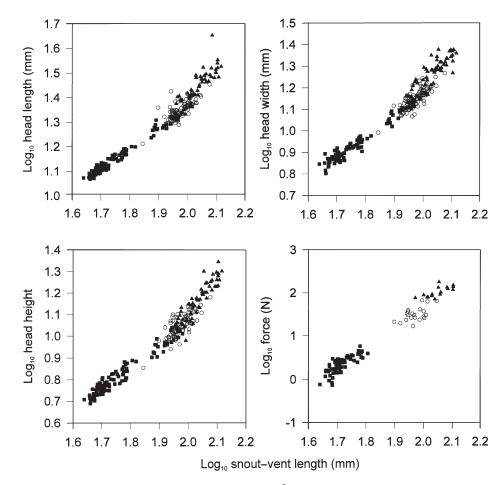
Fig. 4. Allometry of head dimensions and bite force for ▲, male, ○, female and ■, juvenile *G. galloti*. All data are $\log_{10}$-transformed.

to an increase in gape distance too. Given the increase in both bite force and gape distance with increasing head size, and the fact that *Gallotia galloti* crushes prey before swallowing (A. Herrell *et al.*, personal observation), the assumptions of the niche divergence hypothesis seem to be fulfilled.

Without further questioning, one might argue in favour of strong natural selection leading to a food niche partitioning between male and female lizards. However, the prey toughness measurements show that this is probably not the case as both adult male and adult female lizards are able to crush the whole array of prey sizes tested (except for the smallest females that were unable to crush the largest beetles; see Fig. 5). The prey items tested include the very large *Pimelia* beetles, which are presumably among the toughest prey items available in the natural habitat of *G. galloti*. Thus, the sexual dimorphism in bite capacity observed in laboratory conditions probably will not contribute to diet divergence in the field.

It should be noted, however, that the toughness measurements were restricted to arthropod prey items. The diet of *G. galloti* includes substantial amounts of plant material (Valido & Nogales 1994). As plants (at least the vegetative structures) are considered to be very tough and fibrous (Lucas & Luke 1984;

Hiiemae & Crompton 1985; Sibbing 1991), it is generally assumed that higher bite forces are required in order to reduce them adequately. This assertion holds for several strictly herbivorous lizards (Herrel *et al.* 1998a,b) but needs to be verified by assessing plant toughness for the dental configuration of the species considered. If indeed higher bite forces are required to consume plant material, and if these would allow adult male *G. galloti* to consume more, or a wider range of, plant material than females and juveniles, the niche divergence hypothesis may as yet hold. However, preliminary field data (based on the analysis of faeces from 39 male and 60 female lizards) do not indicate differences in the amount of plants eaten by both sexes.

As the data indicate that niche divergence between the sexes presumably does not contribute to the maintenance of a dimorphism in head size, the intersexual difference in bite force is most probably due to, and maintained by, sexual selection. Both intrasexual (male–male combat) and/or intersexual (mating bites) interactions, may lie at the origin of this sexual selective pressure.

Usually, male–male combat in lizards is associated with the defence of a specific territory or critical resources such as food or thermoregulatory sites. However, as *G. galloti* males do not defend such
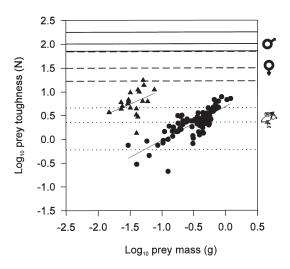
Fig. 5. Allometry of prey toughness for tenebroid beetles ($a = -2.25$, $b = 3.42$, $r = 0.45$, $N = 20$; ▲) and crickets ($a = -2.67$, $b = 2.39$, $r = 0.91$, $N = 114$; ●). The horizontal lines indicate from top to bottom the maximum, the average, and the minimum bite force recorded for male (solid lines), female (dashed lines) and juvenile (stippled lines) *G. galloti*. All data are $\log_{10}$-transformed.

specific territories (Molina Borja 1985, 1987; Molina Borja *et al.* 1998) and resources such as food and heating places are abundant (see Molina Borja 1987) this seems unlikely in the present case. The only potentially limited resource for males might be the access to female conspecifics as observed for some other lizard species (e.g. Smith 1985; see Molina Borja 1987).

Although the morphometric and bite force data clearly indicate that animals with larger heads indeed bite harder, the mechanical basis of this difference can only be assessed by studying the internal morphology of the jaw apparatus. Examination of the jaw muscle mass distribution for both male and female lizards revealed some striking differences. Apparently, male lizards invest a relatively high amount of the total jaw closer mass in the pterygoid muscle (relative to the total jaw muscle mass), whereas female lizards invest more in the external adductor. From a biomechanical point of view this seems very strange. Owing to its position relative to the jaw joint, the mechanical advantage of the pterygoid muscle is low, and its contribution to the overall jaw closing moment (and thus bite force) is minimal, as indicated by the bite modelling (Table 2). Now why might male lizards invest in a muscle with low mechanical advantage? There are a number of possible explanations.

Firstly, males simply might 'want' to increase the bite force even further. In that case, space and packing constraints will limit the increase in muscle mass (Rieppel & Gronowski 1981; Gans & De Vree 1985, 1987). Basically, this means that the space available for muscle in the postorbital head region is limited. To increase the bite force further several options are possible: (1) make a larger head (which may have repercussions on other functions such as locomotor

performance); (2) use highly pennate muscles to increase the physiological cross-section of the jaw closers for the same muscle volume (which is already the case in *Gallotia*); and (3) use the space available outside of the temporal fossa, i.e. increase the size of the pterygoid muscle which lies at the external side of the lower jaw.

Secondly, the pterygoid muscle could play a very important role in stabilizing the jaw joint. Given its position and orientation, a contraction of the m. pterygoideus will tend to generate fairly large forces at the jaw joint. This function may become important during male–male combat and mating bites where female lizards struggle vigorously when grabbed by a male. During such struggles the orientation of the joint forces at the jaw joint will become highly unpredictable, and joint forces may be high owing to extra rotational components.

Finally, sexual selection on the pterygoid muscle might have played an important role too. As this muscle is situated at the side of the head, and the skin surrounding it is coloured dark black with a bright blue spot during the breeding season (Molina Borja 1987; Molina Borja *et al.* 1997), this may have become a visual character used in the assessment of lizards by conspecifics.

Given all of the previous statements, a possible sequence of events leading to the current head size dimorphism in *G. galloti* can be reconstructed. As both sexes can apparently bite harder than required for all but a few insect food items available, an initial selection for increased bite force in both sexes simultaneously, enabling the exploitation of new food resources (i.e. plants), does not seem unlikely. In a next phase an extra selective pressure presumably arose on males, pushing them to develop larger heads, advantageous during both male–male interactions (strongest male will win such a contest) and mating (where female lizards can express a choice by physically resisting copulations). In a last step, a selective pressure on a large pterygoid muscle as a pure visual characteristic may have occurred. This would then allow males to judge the quality of other males (see Molina Borja *et al.* 1998) and allow females to judge the quality of a male lizard in advance (see possible evidence in Molina Borja 1985). Although rarely documented in lizards (see Olsson & Madsen 1999 for an overview on female choice in lizards), female choice may play an important role here. As females have larger home ranges overlapping those of several males (Molina Borja 1985) and males generally do not show aggression towards females (except during mating), females might contribute actively by choosing the stronger males (as judged by the head dimensions) to mate with. However, this hypothesis remains to be tested.

An unexpected result of our analysis was the apparent 'excess' bite force in adult (male and female) lizards. Most adults were able to crush items that were

much tougher than the toughest arthropod prey item in their natural habitat. Obviously the increased bite force capacity in the animals implies a serious, and costly, attribution of resources (i.e. bone and muscle) to the feeding apparatus. What could explain this apparent superfluous investment in bite force and thus feeding machinery?

One possible explanation, which holds for both male and female lizards, is that the high bite forces are a correlative response to the evolution of a larger body size as observed for some lizards and other animals in island situations (e.g. Schoener 1969; Yoccoz, Ims & Steen 1993; but see Case 1978). Still, direct selection for a large body size might also be possible as this would allow the animals to exploit a new food source: plants (e.g. Valido & Nogales 1994; Van Damme in press). For animals living in island situations where insect food resources may be temporally fluctuating and scarce, the ability occasionally to add substantial amounts of plants to the diet may be crucial for long-term survival and fitness. A large body volume is considered to be advantageous for herbivores as this provides a fermenting chamber, and higher thermal inertia which assures an ideal micro habitat for the commensals responsible for the digestion of cellulose. One possibility of testing this hypothesis is by investigating the relationship between body size, and insularity on the one hand (see Van Damme in press), and between body size and bite force on the other hand for a number of lacertid lizards.

As mentioned earlier, selection for high bite forces in relation to a herbivorous diet, independent of selection for a larger body size, might have occurred too. This might be tested by comparing allometries of bite forces for herbivorous and insectivorous lacertids. A third reason for the development of such high bite forces might be the use of defensive bites as an antipredation tactic (e.g. see Hertz, Huey & Nevo 1982; Greene 1988). Unfortunately, little is known about the predators of *G. galloti*. However, as no snakes occur on Tenerife, and as biting is presumably only useful against terrestrial predators, this does not seem likely. Still, this should be verified by observations on anti-predator behaviour of *G. galloti* in natural circumstances.

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References

Anderson, R.A. & Vitt, L.J. (1990) Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* **84,** 145–157.

Andrews, C. & Bertram, J.E.A. (1997) Mechanical work as a determinant of prey-handling behavior in the Tokay Gecko (*Gekko gecko*). *Physiological Zoology* **70** (2)**,** 193–201.

Best, T.L. & Pfaffenberger, G.S. (1987) Age and sexual variation in diet of collared lizards (*Crotaphytus collaris*). *Southwestern Naturalist* **32** (4)**,** 415–426.

Bischoff, W. (1971) *Lacerta galloti galloti*, Duméril et Bibron, 1839, die Eidechse von Teneriffa. *Aquarium Terrarium* **18,** 308–311.

Bull, C.M. & Pamula, Y. (1996) Sexually dimorphic head sizes and reproductive success in the sleepy lizard *Tiliqua rugosa*. *Journal of Zoology, London* **240,** 511–521.

Carothers, J.H. (1984) Sexual selection and sexual dimorphism in some herbivorous lizards. *American Naturalist* **124,** 244–254.

Case, T.J. (1978) A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* **59** (1)**,** 1–18.

Censky, E.J. (1996) The evolution of sexual size dimorphism in the teiid lizard *Ameiva plei*: a test of alternative hypotheses. *Contributions to West Indian Herpetology: a Tribute to Albert Schwartz* (eds R. Powell & R. W. Henderson), pp. 277–289. SSAR, Ithaca, New York.

Cordes, I.G., le Mouton, P., F.N. & Van Wijk, J.H. (1995) Sexual dimorphism in two girdled lizard species, *Cordylus niger* and *Cordylus cordylus*. *South African Journal of Zoology* **30** (4)**,** 187–196.

Diaz, E. (1980) Notas sobre el lagarto tizón (*Lacerta galloti*). *Doñana Acta Vertebrata* **7,** 95–96.

Fitch, H.S. (1981) Sexual size differences in reptiles. *Miscellaneous Publications of the Museum of Natural History University Kansas* **70,** 1–72.

Gans, C. & De Vree, F. (1985) Usage pattern of the complex masticatory muscles in the shingleback lizard, *Trachydosaurus rugosus*: a model for muscle placement. *American Journal of Anatomy* **173,** 219–240.

Gans, C. & De Vree, F. (1987) Functional bases of fibre length and angulation in muscle. *Journal of Morphology* **192,** 63–85.

Gittleman, J.L. & Van Valkenburgh, B. (1997) Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology, London* **242,** 97–117.

Gomes, N.M.B. (1974) Anatomie comparée de la musculature trigeminale des lacertiliens. *Memoires du Musée de la Nature et Histoire naturelle, Série A (Zool.)* **90,** 1–107.

Greene, H.W. (1988) Antipredator mechanisms in reptiles. *Biology of Reptilia* (eds C. Gans & R. B. Huey), pp. 1–152. Alan R. Liss, New York.

Haas, G. (1973) Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. *Biology of the Reptilia* (eds C. Gans & T. Parsons), pp. 285–490. Academic Press, London.

Herrel, A., Van Damme, R. & De Vree, F. (1996) Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. *Netherlands Journal of Zoology* **46** (3–4)**,** 253–262.

Herrel, A., Cleuren, J. & De Vree, F. (1997) Quantitative analysis of jaw and hyolingual muscle activity during feeding in the lizard *Agama stellio*. *Journal of Experimental Biology* **200,** 101–115.

Herrel, A., Aerts, P. & De Vree, F. (1998a) Static biting in lizards with a primitive skull: functional morphology of the temporal ligaments. *Journal of Zoology, London* **244,** 135–143.

Herrel, A., Aerts, P. & De Vree, F. (1998b) Ecomorphology of the lizard feeding apparatus: a modelling approach. *Netherlands Journal of Zoology* **45** (1), 1–25.

Hertz, P.E., Huey, R.B. & Nevo, E. (1982) Fight versus flight: body temperature influences defensive responses of lizards. *Animal Behaviour* **30,** 676–679.

Herzog, W. (1994) Muscle. *Biomechanics of the Musculoskeletal System* (eds B. M. Nigg & W. Herzog), pp. 154–187. John Wiley & Sons, Chichester.

Hews, D.K. (1990) Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri. Evolution*, **44,** 1956–66.

Hiiemae, K.M. & Crompton, A.W. (1985) Mastication, food transport and swallowing. *Functional Vertebrate Morphology* (eds M. Hildebrand, D. Bramble, K. Liem & D. Wake), pp. 230–261. Harvard University Press, Cambridge, MA.

Lucas, P.W. & Luke, D.A. (1984) Basic principles of food break down. *Food Acquisition and Processing in Primates* (eds D. A. Chivers, B. A. Woods & A. Bilsborough), pp. 283–301. Plenum Press, New York.

Marquez, R., Cejudo, D. & Perez-Mellado, V. (1997) Selected body temperatures of four lacertid lizards from the Canary Islands. *Herpetological Journal* **7,** 122–124.

Masterson, T.J. (1997) Sexual dimorphism and interspecific cranial form in two capuchin species: *Cebus albifrons* and *C. apella. American Journal of Physical Anthropology* **104,** 487–511.

Molina Borja, M. (1985) Spatial and temporal behaviour of *Galloti galloti* in a natural population of Tenerife. *Bonner Zoologischer Beitrage* **36** (3/4), 541–552.

Molina Borja, M. (1987) Spatio-temporal distribution of aggressive and courting behaviors in the lizard *Gallotia galloti* from Tenerife, the Canary Islands. *Journal of Ethology* **5,** 11–15.

Molina Borja, M. (1991) Notes on alimentary habits and spatial-temporal distribution of eating patterns in a natural population of lizards (*Gallotia galloti*). *Vieraea* **20,** 1–9.

Molina Borja, M., Padron-Fumero, M. & Alfonso-Martin, M.T. (1997) Intrapopulation variability in morphology, coloration and body size in two races of the Tenerife lizard, *Gallotia galloti. Journal of Herpetology* **31,** 499–507.

Molina Borja, M., Padron-Fumero, M. & Alfonso-Martin, M.T. (1998) Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). *Ethology* **104,** 314–322.

Mouton, P. le F.N. & Van Wijk, J.H. (1993) Sexual dimorphism in cordylid lizards: a case study of the Drakensberg crag lizard, *Pseudocordylus melanotus. Canadian Journal of Zoology* **71,** 1715–1723.

Olsson, M. & Madsen, T. (1999) Sexual selection and sperm competition in reptiles. *Sperm Competition and Sexual Selection*, pp. 503–610. Academic Press, London.

Perry, G. (1996) The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology* **74,** 1238–1245.

Preest, M.R. (1994) Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology* **28** (3), 292–298.

Ravosa, M.J. & Gomez, A.M. (1992) *Ontogenetic Perspectives on Primate Evolutionary Biology*. Academic Press, London.

Rieppel, O. & Gronowski, R.W. (1981) The loss of the lower temporal arcade in diapsid reptiles. *Zoological Journal of Linnean Society of* **72,** 203–217.

Salvador, A. (1985) Guía de campo de los Anfibios y Reptiles de la Península Ibérica, Islas Baleares y Canarias. Léon.

Schoener, T.W. (1967) The ecological significance of sexual size dimorphism in the lizard *Anolis conspersus. Science* **155,** 474–477.

Schoener, T.W. (1969) Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. *Systematic Zoology* **18,** 386–402.

Schoener, T.W. (1977) Competition and the niche. *Biology of the Reptilia* (eds C. Gans & D. W. Tinkle), pp. 35–136. Academic Press, London.

Shea, B.T. (1986) Ontogenetic approaches to sexual dimorphism in anthropoids. *Human Evolution* **1,** 97–110.

Shine, R. (1991) Why do larger snakes eat larger prey items? *Functional Ecology* **5,** 493–502.

Shine, R. (1993) Sexual dimorphism in snakes. *Snakes: Ecology and Behavior* (eds R. A. Seigel & J. T. Collins), pp. 49–86. McGraw-Hill, New York.

Sibbing, F.A. (1991) Food processing by mastication in cyprinid fish. *Symposia of the Society of for Experimental Biology* **43,** 57–92.

Smith, D.C. (1985) Home range and territory in the striped plateau lizard (*Sceloporus virgatus*). *Animal Behaviour* **33** (2), 417–427.

Stamps, J.A. (1977) The relationship between resource competition, risk and aggression in a tropical territorial lizard. *Ecology* **57,** 1317–1320.

Stamps, J.A. (1993) Sexual size dimorphism in species with asymptotic growth after maturity. *Biological Journal of the Linnean Society* **50,** 123–145.

Trivers, R.L. (1976) Sexual selection and resource-accruing abilities in *Anolis garmani. Evolution* **30,** 253–269.

Valido, A. & Nogales, M. (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* **70,** 403–411.

Van Damme, R. (in press) Tendency towards herbivory in insular populations of lacertid lizards. *Journal of Herpetology* in press.

Watkins, G.G. (1996) Proximate causes of sexual size dimorphism in the iguanid lizard *Microlophus occipitalis. Ecology* **77** (5), 1473–1482.

Wikelski, M. & Trillmich, F. (1997) Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* **51** (3), 922–936.

Yoccoz, N.G., Ims, R.A. & Steen, H. (1993) Growth and reproduction in island mainland populations of the vole *Microtus epiroticus. Canadian Journal of Zoology* **71,** 2518–2527.