

It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard

KATLEEN HUYGHE^{1*}, ANTHONY HERREL^{1,2}, DOMINIQUE ADRIAENS³, ZORAN TADIĆ⁴ and RAOUL VAN DAMME¹

¹Laboratory for Functional Morphology, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium

²Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

³Evolutionary Morphology of Vertebrates, Ghent University, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium

⁴Department of Animal Physiology, University of Zagreb, Rooseveltov trg 6, 10000 Zagreb, Croatia

Received 31 December 2007; accepted for publication 21 April 2008

Males of the lizard *Podarcis melisellensis* occur in three distinct colours that differ in bite performance, with orange males biting harder than white or yellow ones. Differences in bite force among colour morphs are best explained by differences in head height, suggesting underlying variation in cranial shape and/or the size of the jaw adductors. To explore this issue further, we examined variation in cranial shape, using geometric morphometric techniques. Additionally, we quantified differences in jaw adductor muscle mass. No significant differences in size corrected head shape were found, although some shape trends could be detected between the colour morphs. Orange males have relatively larger jaw adductors than yellow males. Not only the mass of the external jaw adductors, but also that of the internal jaw adductors was greater for the orange morph. Data for other cranial muscles not related to biting suggest that this is not the consequence of an overall increase in robustness in orange individuals. These results suggest that differences in bite performance among morphs are caused specifically by an increase in the mass of the jaw adductor, which may be induced by differences in circulating hormone levels. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **96**, 13–22.

ADDITIONAL KEYWORDS: geometric morphometrics – muscle mass – performance – *Podarcis* – shape.

INTRODUCTION

The coexistence of alternative phenotypes (polymorphism) in a population has been described in many taxa, with morphs primarily differing in external morphology, colour, and/or behaviour. Polymorphism implies a selective balance between the morphs, resulting in similar fitness advantages for each. The mechanisms underlying the origin and maintenance of polymorphisms can be two-fold. Divergent selection can cause a differentiation in habitat use (*Hyla*:

Wente & Phillips, 2003), foraging mode (cichlids: Hori, 1993), diet (*Tyto alba*, Roulin), or thermal niche (salamanders: Petrucci, Niewiarowski & Moore, 2006). Sexual selection, on the other hand, not only promotes sexual dimorphisms (differences between males and females), but can also give rise to sex-limited divergence. In damselflies, female limited morphs may represent different strategies of mating behaviour (Forbes, 1991). Alternative reproductive behaviours are, however, more typical in male limited morphs, often resulting in one dominant and one satellite or sneaker strategy. For example, in the lek-breeding ruff (*Philomachus pugnax*), plumage

*Corresponding author. E-mail: katleen.huyghe@ua.ac.be

colour polymorphism is associated with dominance behaviour, with males of both the dominant and satellite strategy having an equal lifetime reproductive success but differing in plumage colour (Widemo, 1998). Similarly, in the side-blotched lizard (*Uta stansburiana*), males exhibit one of three alternative colour morphs, reflecting one of three mating strategies (Sinervo & Lively, 1996): one morph is ultra dominant, defending large territories; a second defends a small territory, but also mate guards; and a third morph comprises the sneaker males, which do not defend territories. The continued existence of polymorphism in a population is guaranteed through frequency-dependent selection, providing a greater fitness pay-off for the rarer morph, thus preventing one morph from out-competing the other(s) (Sinervo & Lively, 1996).

Not only can variation in phenotype (e.g. colour, size of sexual structures, etc.) be associated with reproductive fitness, but also variation in performance. Surprisingly, few studies have addressed the question of whether morphs that differ in their appearance and lifestyle also differ in performance traits, which can play a significant role in behaviours associated with reproduction, and thus fitness. Male swordtails (*Xiphophorus nigrensis*) occur in three discrete morphs, which differ in body size and in endurance capacity (Ryan, 1988). Another study showed that blue, territorial male pupfish (*Cyprinodon pecosensis*) can swim longer and at higher speeds than pale, nonterritorial males (Kodric-Brown & Nicoletto, 1993). By contrast, in the colour polymorphic lizard *Urosaurus ornatus*, males of the different morphs do not differ in residual bite force or sprint speed capacity (Meyers *et al.*, 2006). However, in the side blotched lizard (*Uta stansburiana*), colour morphs do differ in endurance capacity (Sinervo *et al.*, 2000). In a population of the medium ground finch (*Geospiza fortis*), beak size distribution is bimodal, with large beak males producing songs of different frequencies compared to small beak males (Huber & Podos, 2006). This appears to be a consequence of ecological selection for bigger beaks and sexual selection on vocal mating signals. Bigger, more robust beaks are limited in opening and closing rates, they are slower, and, consequently, produce songs with lower trill rates and narrower frequency band widths than birds with smaller, more gracile beaks (Podos, 2001). This latter example aside, the underlying functional causes for the differences in performance between morphs often remain unclear. In some cases, sexual performance dimorphisms have been explained through dimorphisms in body shape and muscle mass allocation (e.g. male *Anolis carolinensis* lizards differ from females in bite force as a consequence of differences in skull shape and jaw adductor

mass; Herrel, McBrayer & Larson, 2007). These sexual dimorphisms in muscle mass can be induced by androgen hormones (Regnier & Herrera, 1993; Eason *et al.*, 2000). The mechanistic reasons for performance polymorphisms (i.e. differences in performance capacity among morphs of the same sex), however, are generally not known.

In the lizard *Podarcis melisellensis*, males occur in three different colours. Orange males have larger heads and bite harder than white ones. White males bite harder than yellow ones (Huyghe, Vanhooydonck & Tadić Van Damme, 2007). The present study aimed to investigate the underlying functional morphological basis for the differences in bite force between morphs. First, we compared external head measures and bite force in one set of lizards to determine whether, and how, these external measurement(s) determine the observed variation in bite force. Second, we tested the hypothesis that differences in bite performance are related to differences in head shape, excluding size effects, using geometric morphometric techniques. Finally, we compared jaw muscle masses to investigate whether differences in muscle mass and/or allocation between morphs exist.

MATERIAL AND METHODS

HEAD SIZE AND BITE PERFORMANCE

A first set of adult male lizards ($N = 42$) was caught by noose on the island Lastovo (Croatia) and transported to the laboratory in Belgium. Only males with a body size greater than 55 mm were kept, to ensure that each individual was sexually mature (K. Huyghe, pers. observ.). They were housed individually in glass vivaria ($30 \times 30 \times 50$ cm), and provided with food (crickets, dusted with calcium powder) and water *ad libitum*. Using digital calipers (Mitutoyo, with a precision of 0.01 mm), the following measurements were taken: head length (from tip of the snout to the posterior edge of the parietal bone), head width (at the widest part of the head), head height (at the highest part of the head just posterior to the orbit), lower jaw length, distance from quadrate to the tip of the jaw (jaw out-lever), and the distance from the coronoid to the tip of the lower jaw. The in-lever for jaw closing was estimated by subtracting the latter distance from the jaw out-lever length.

Bite forces were recorded by inducing lizards to bite onto two metal plates connected to an isometric force transducer (type 9203; Kistler Inc.), mounted on a purpose-built holder and connected to a charge amplifier (type 5995A; for a more detailed description of the set-up, see Herrel *et al.*, 1999). Lizards were allowed to thermoregulate to obtain their preferred body temperature (32 ± 1 °C) before and inbetween trials. Recordings were repeated five times, and only the

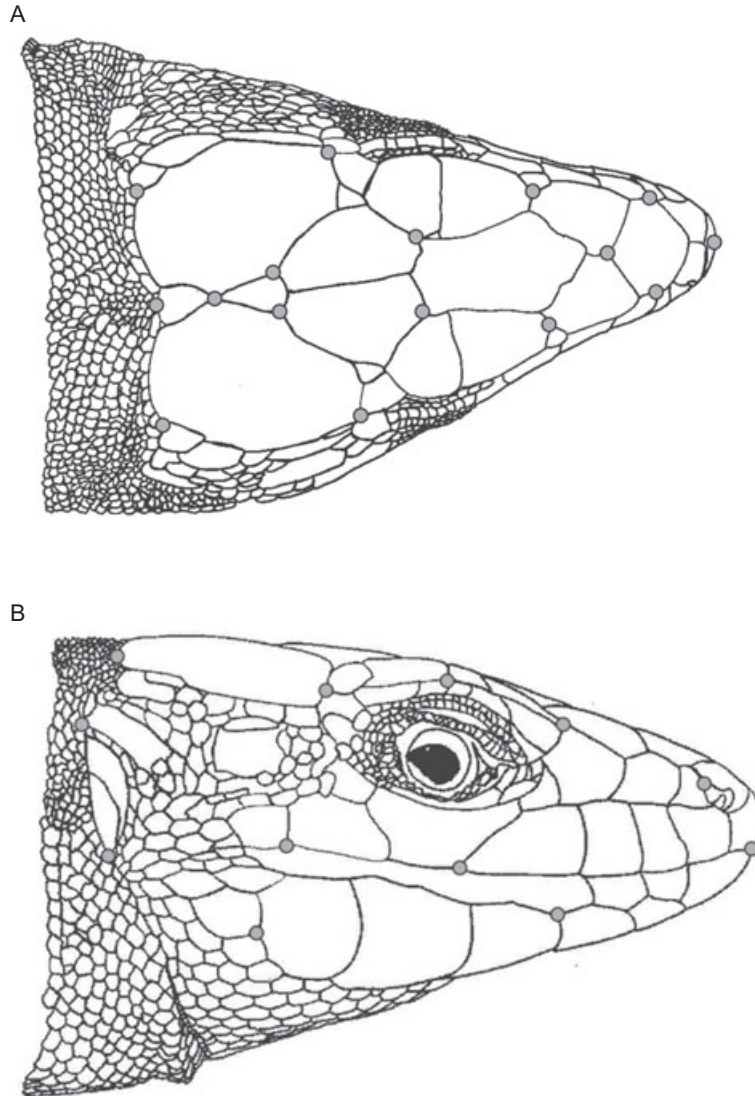


Figure 1. Landmarks used in the geometric morphometric analyses in the dorsal (A) and lateral (B) view.

highest bite force was retained, and was considered to be the maximal bite performance for each individual.

HEAD SHAPE ANALYSIS

Dorsal and lateral head shape was quantified using landmark-based geometric morphometric methods (Rohlf, 1993, 1995; Rohlf & Marcus, 1993), standardizing for size by performing generalized procrustes analysis. Two high resolution photos of all individuals were taken with a digital camera (Nikon D70), one in dorsal and one in lateral view. Photos were made with a grid as a background for scaling, and lizards were held such that the anterior–posterior body axis was identically oriented for all individuals. From each image, landmarks were recorded using TpsDig (Rohlf,

2001a; available at: <http://life.bio.sunysb.edu/morph/>): 16 in the dorsal and 12 in the lateral view (Fig. 1). Landmarks were chosen based on their reliability of identification in all specimens in addition to their coverage of regions that could be functionally related to biting. Moreover, these landmarks were tested in previous studies on *Podarcis* lizards (Bruner & Constantini, 2007; Kallantzopoulou, Carretero & Llorente, 2007). The thin plate spline approach was used and the distribution of shape configurations into the Euclidean tangent space was checked using tpsSmall (Rohlf, 1998). TpsRelw (Rohlf, 2001b) was used to calculate the consensus configuration of each of the colour morphs (lateral and dorsal view), and to perform a principal component analysis on the weight matrix (including scores of both uniform and

non-uniform partial warps). The centroid size of all specimens was calculated, and used for regressing shape variables versus size using tpsRegr (Rohlf, 2000).

MUSCLE MASSES

A second set of 11 lizards ($N_{\text{white}} = 4$; $N_{\text{yellow}} = 3$; $N_{\text{orange}} = 4$) was used for quantifying muscle masses. These were road-killed specimens, with intact heads, of the same population of lizards used for the morphometric and performance measures. Specimens used for dissection were chosen on the basis of their head lengths, such that the difference in head length between the smallest and biggest individual is minimized (i.e. no more than 1.10 mm). Specimens were preserved in 10% aqueous formaldehyde solution for 24 h, rinsed, and transferred to a 70% aqueous ethanol solution. All jaw closers (i.e. adductor externus, adductor internus and adductor posterior groups *sensu* Lakjer, 1926) and jaw openers (musculus cervicomandibularis and musculus depressor mandibulae) were removed on one side in each individual. Muscles were blotted dry and weighed using a Mettler MT5 microbalance (with a precision of 0.01 mg).

STATISTICAL ANALYSIS

All data were \log_{10} -transformed to fulfill assumptions of normality. A principal component analysis was used to reduce the number of external head measures. Subsequently, an analysis of covariance (ANCOVA) was used to determine differences in bite force capacity between colour morphs, using the newly-generated principal component as covariate. Nonsignificant interaction effects ($P > 0.05$) are not reported. A model including all six head measures as independents and bite force as dependent variable was tested in a multiple regression analysis.

To examine variation in head shape (geometric morphometrics), a canonical variate analysis was performed on the weight matrix to test for differences between colour morphs using STATISTICA, version 6.0 (Statsoft Inc.). Additionally, to exclude nonsignificance levels due to non-normality and heterogeneity of variance, a nonparametric multivariate analysis of variance was performed (Bonferroni corrected) using Euclidean distance measures (with 10 000 permutations) with PAST (Ryan, Harper & Whalley, 1995). For both centroid size and the canonical root scores, the Goodall test for goodness of fit was performed, combined with a permutation test of a 1000 replicas. Differences in shape between the consensus of each morph were visualized by deformation grids generated by tpsSpline (Rohlf, 2002).

Univariate ANCOVAs and post-hoc pairwise comparisons were used (with head length as covariate) to compare muscle masses between colour morphs.

RESULTS

HEAD SIZE AND BITE PERFORMANCE

A principal component analysis on all six external head measurements yielded one principal component, with positive factor loadings for all included variables, and describing 72.25% of the variation (eigenvalue 4.34). This new variable was called overall head size.

Morphs differed in bite force capacity in absolute terms ($F_{2,39} = 7.51$, $P = 0.002$). Furthermore, when correcting for head size, morphs still differed in bite force capacity (ANCOVA, covariate = overall head size, interaction effect colour X head size nonsignificant, $F_{2,38} = 3.89$, $P = 0.029$; Fig. 2). Keeping overall head size equal, orange males can bite relatively harder than white males, and white males can bite relatively harder than yellow males. This means that the variation in bite force capacity between morphs cannot be fully explained by differences in overall head size. To investigate which of these six external dimensions individually best predicted bite force, we performed a multiple regression analysis with bite force as the dependent variable and all the external head measurements as independents. This model was significant ($F_{6,35} = 2.67$, $P = 0.031$) and showed that head height was the best predictor for bite performance ($\beta = 0.53$). When keeping all other measures equal, lizards having higher heads can bite harder.

HEAD SHAPE ANALYSIS

Both the dorsal and lateral datasets indicated that very little of the shape variation for the combined dataset of all three colour morphs could be explained by size-related allometry (5.4% for the dorsal dataset, $P = 0.05$; 2.3% for the lateral dataset, $P < 0.05$). There was no significant difference in shape between the colour morphs for both the dorsal and lateral datasets (for results of the canonical variate analysis, see Table 1). However, a plot of canonical root 1 versus root 2 shows a different pattern for the two datasets: (1) for the dorsal view, the yellow morphs are separated from the orange ones along root 2, with the white morph being separated along root 1 and taking an intermediate position along root 2 (Fig. 3A) and (2) in lateral view, the yellow morph is separated from the other two groups by root 1, but taking an intermediate position along root 2 (Fig. 3B). In the plot of the canonical scores based on the dorsal view, the specimens of all three groups lie well clustered and

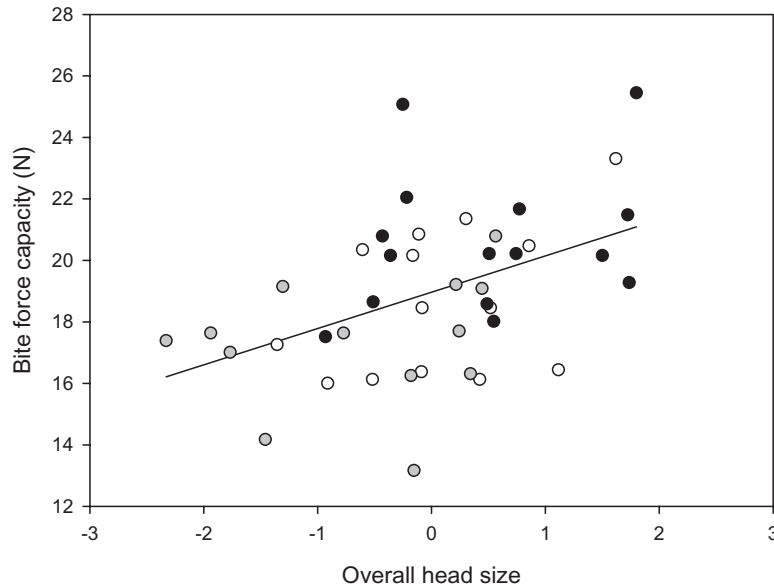


Figure 2. Scatter plot showing the regression of the newly-generated head size variable in the x -axis versus bite force capacity (N) in the y -axis. White symbols, white males; grey symbols, yellow males; black symbols, orange males. Note that the residuals of bite force capacity still differ between morphs.

Table 1. Statistics of the canonical variate analyses (F , parametric and nonparametric P -values) using the partial warp scores for the dorsal dataset (below the diagonal of the matrix, italic) and lateral datasets (above the diagonal, roman)

	White	Yellow	Orange
<i>F</i> -values			
White		1.81	1.36
Yellow	<i>1.50</i>		2.01
Orange	<i>1.63</i>	<i>1.06</i>	
Parametric P -values			
White		0.100	0.255
Yellow	<i>0.231</i>		0.067
Orange	<i>0.187</i>	<i>0.481</i>	
Nonparametric P -values			
White		0.261	1
Yellow	<i>1</i>		0.258
Orange	<i>0.349</i>	<i>0.457</i>	

Note that none of the pairwise comparisons were significant.

morphs are separated. However, between-group differences are not significant.

When exploring the subtle shape differences between morphs, some interesting patterns were observed. First, the amount of shape variance that can be explained by the regression with root 2 (dorsal) and 1 (lateral) versus shape (partial warp scores) is quite low (3.9% and 6.5%, respectively) (Fig. 4).

Second, this subtle between-group variance is not correlated to centroid size ($R^2 < 0.2$; Fig. 4), indicating that there is a fair amount of within-morph variance. However, when visualizing the aspect of shape variation that is largest (i.e. between the yellow and the orange morph), the most distinctive feature appears to be situated in the temporal region (Fig. 4). For the dorsal view, this corresponds to a subtle increase in the width of the orbito-temporal region, whereas, for the lateral view, it mainly involves a shorter temporal scale for the orange morphs.

MUSCLE MASSES

For a given head length, there is a tendency for morphs to differ in total adductor muscle mass (ANCOVA: $F_{2,7} = 3.78$, $P = 0.094$). When looking at the graph (Fig. 5), it appears that orange males have a relatively greater muscle mass than yellow males. The white morph can be considered average, having adductor muscle masses in between those of the orange and yellow males. Post-hoc pairwise comparisons show indeed that only the yellow and orange morphs differ significantly from each other ($F_{1,7} = 6.68$, $P = 0.036$). White do not differ from yellow morphs ($F_{1,7} = 1.50$, $P = 0.26$), nor from orange morphs ($F_{1,7} = 2.04$, $P = 0.20$).

When comparing the jaw adductor muscle groups separately, the same trend can be seen for the externus (Fig. 6A) and internus (Fig. 6B) muscle groups: orange individuals tend to have higher muscle masses than yellow ones and white morphs show average

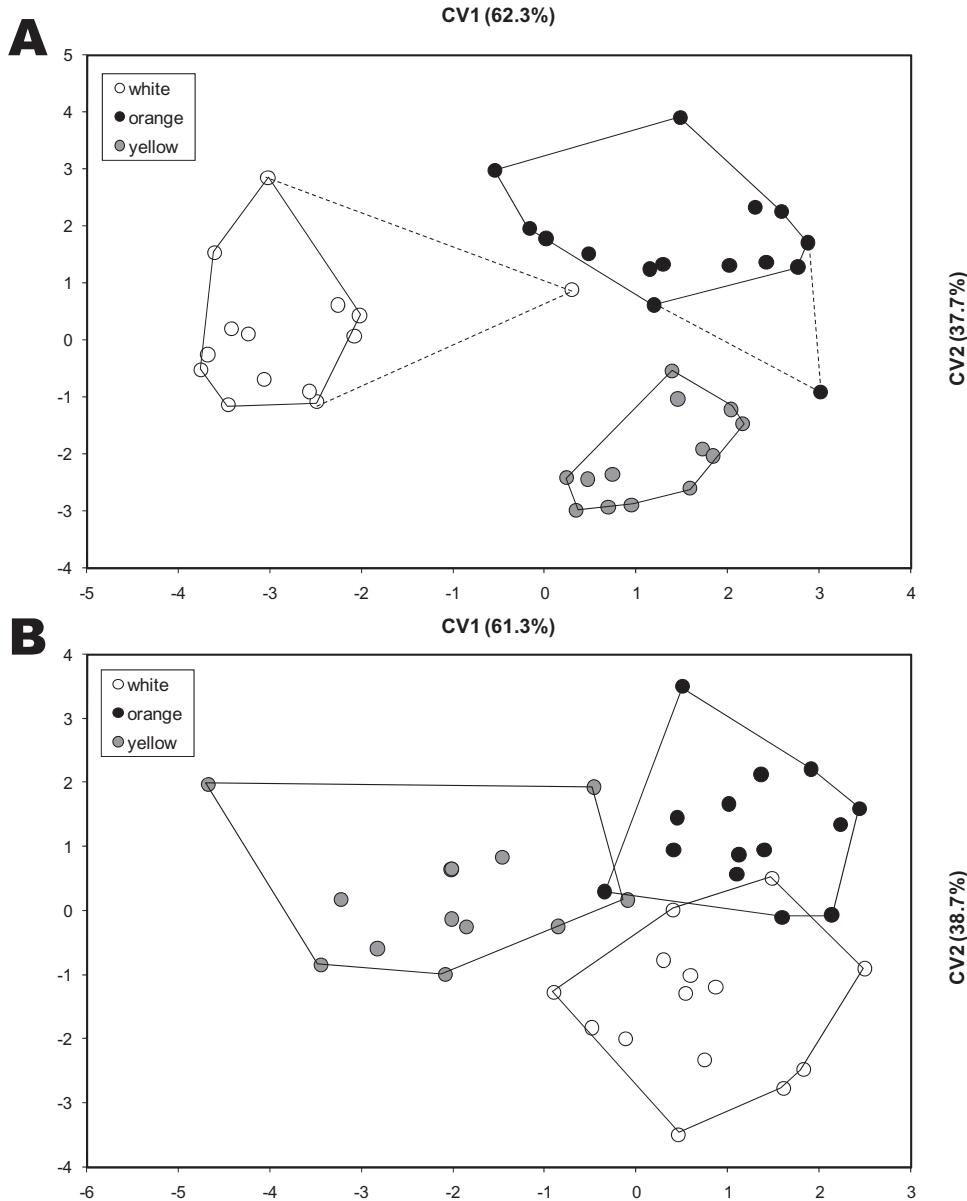


Figure 3. Scatter plot of canonical variate analysis scores based on data from dorsal view (A) and lateral view (B) (percentages given are the amount of between-group variance explained by each root in the morphospace defined by root 1 and 2).

values. For the adductor posterior group (Fig. 6C), all three morphs have similar muscle masses.

The total mass of the jaw opener muscles did not differ between morphs (ANCOVA: $F_{2,7} = 1.06$, $P = 0.40$).

DISCUSSION

In accordance with previous studies (Huyghe *et al.*, 2007) colour morphs of *P. melisellensis* differ in bite force capacity in both absolute and relative terms: orange males bite harder than white and yellow ones,

and white males bite harder than yellow ones. The increase in bite force is larger than would be predicted by the differences in external head dimensions between the morphs. When correcting for head size, males of the orange morphs still have greater bite forces than yellow males, indicating differences in internal head morphology and musculature. The results obtained in the present study also showed that head height predicted bite force best of all the external head measurements. An increase in head height may increase the available space for jaw

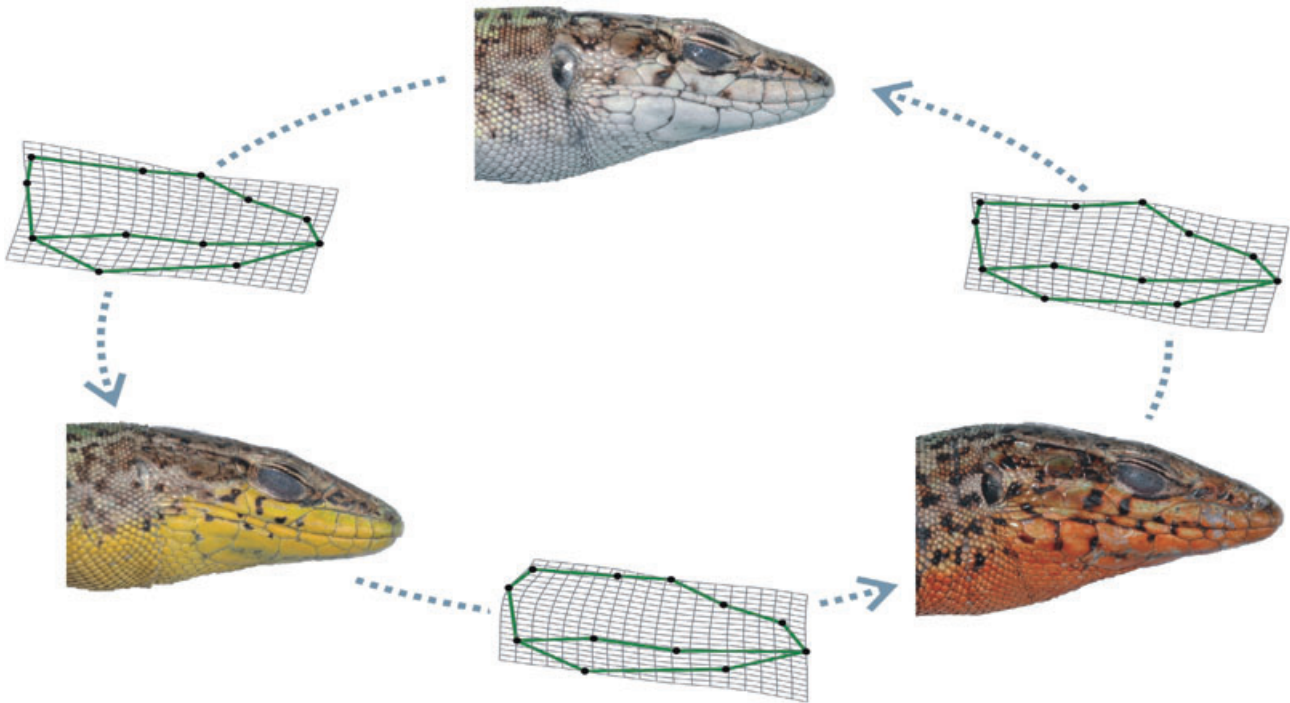


Figure 4. Colour morphs with deformation grids, showing the shape differences between the mean shape of each morph. Each grid represents pairwise shape difference, by deforming a rectangular grid fitting one morph until it fits another morph (shape differences magnified three times).

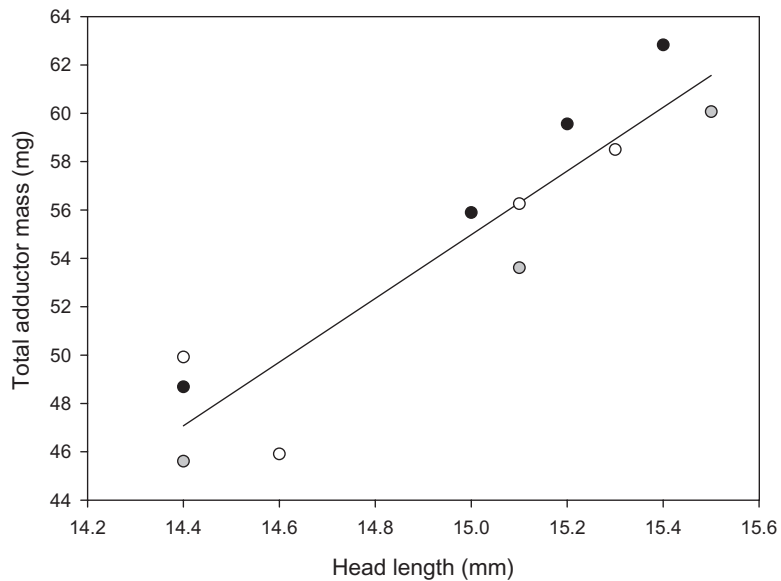


Figure 5. Scatterplot illustrating that orange coloured males (black symbols) have a greater residual jaw adductor muscle mass than do yellow males (grey symbols). White males are the average (white symbols).

adductor muscles resulting in a higher physiological cross-section, and thus bite force (Herrel *et al.*, 1999; Herrel, Grauw & Lemos-Espinal, 2001). Alternatively, a taller head may allow for a more vertical orientation of the jaw adductors, providing them with

an increased moment arm around the quadrato-mandibular joint (Herrel, Aerts & Vree, 1998). However, because we were restricted to using road killed animals for the dissections, we do not have muscle mass and bite force data available from the

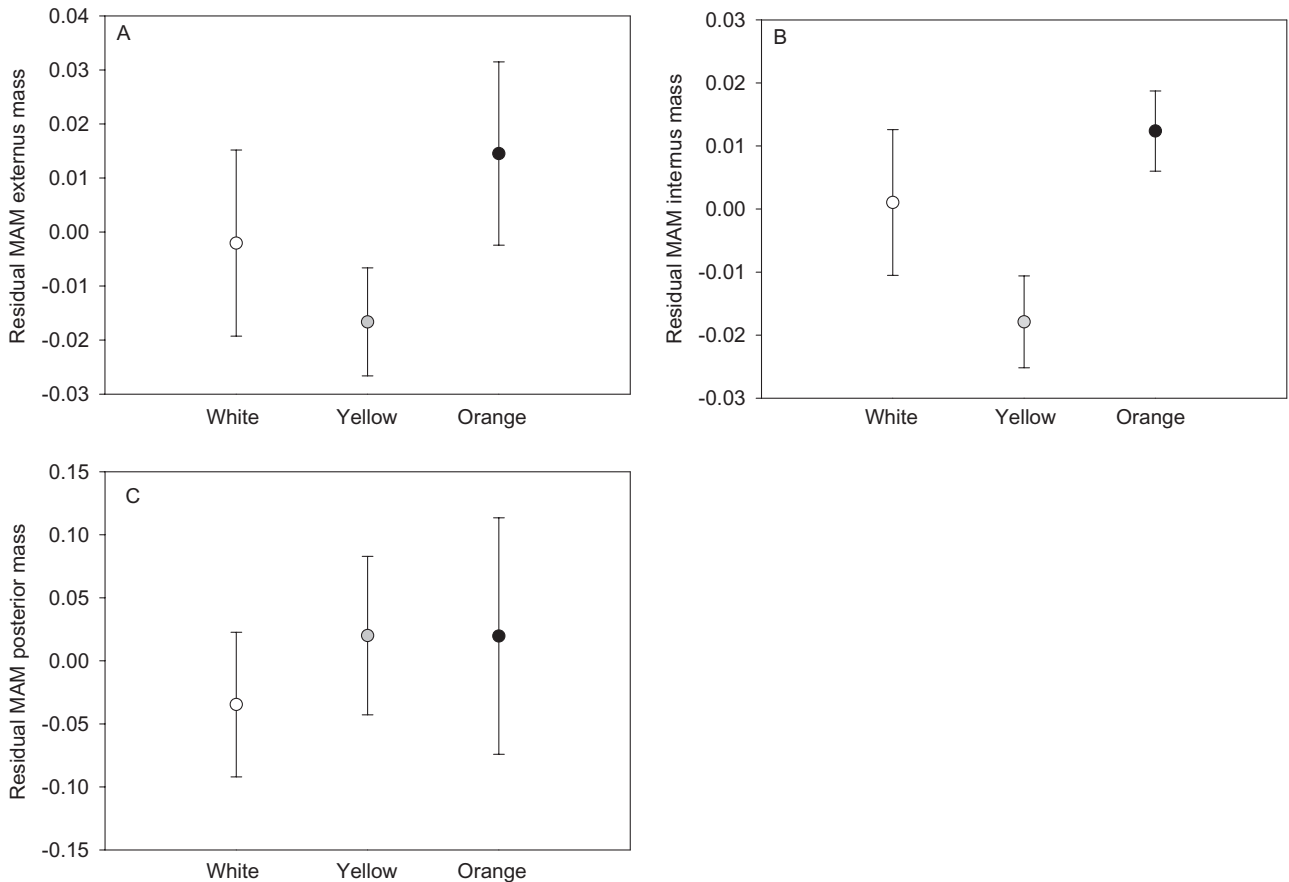


Figure 6. Means \pm SE of the residuals of the different jaw closer muscle groups for the three morphs (white symbols, white; grey symbols, yellow; black symbols, orange). A, musculus adductor mandibularis externus. B, musculus adductor mandibularis internus. C, musculus adductor mandibularis posterior. MAM, musculus adductor mandibularis.

same individuals. Consequently, we have to assume that a positive correlation exists between jaw muscle mass and bite force on the individual level. Previous data comparing *in vivo* bite forces to bite forces calculated based on the morphological properties of the muscles and the jaw system in bats suggest that this is a reasonable assumption (Herrel *et al.*, 2008).

Interestingly, although geometric morphometric analyses did not reveal any significant head shape differences between morphs, we did find a subtle trend that could be related to differences in mass of the jaw adductor muscles: the width of the orbito-temporal region is slightly larger in orange individuals than in yellow individuals. Moreover, orange males have a higher relative muscle mass than yellow males despite the near-identical head size (no more than 1 mm difference). The observed subtle but higher relative width of the orbito-temporal region in orange males may thus provide a slightly expanded space for the jaw muscles. Yet, additional space for muscles still can be available (e.g. orange males may have a medially enlarged adductor chamber). As we

were restricted to using non-invasive techniques, no skulls were available for geometric morphometric analyses to test this hypothesis. Alternatively, higher muscle mass could also be achieved by a higher degree of pennation, allowing for a more optimal packing of muscle fibres and thus a higher mass and force output (Gans & De Vree, 1987). A different orientation of the muscles themselves might also allow for more optimal packing and thus a higher muscle mass. In short, differences in muscle architecture between yellow and orange males may exist that could explain the observed difference in adductor muscle mass without changes in external head shape. Additionally, even though landmark-based geometrics are considered to efficiently grasp subtle changes in shape, a suitable selection of landmarks is no guarantee that all relevant shape variation are included.

Proximate mechanisms possibly explaining this difference in muscle masses between morphs involve testosterone levels. Skeletal muscle is a major site of testosterone action (Bardin & Catterall, 1981) not only early in development through permanent orga-

nizational effects on cells and tissues, but also past sexual maturity (Emerson, 2000). An increase in testosterone can activate the recruitment of quiescent satellite cells in muscles and, consequently, cause muscle fibre hypertrophy in males (Joubert & Tobin, 1995). This anabolic effect in males versus females also occurs within males: the cross-sectional areas of a frog's forelimb muscles enlarge after testosterone treatment (Dorlöchter, Astrow & Herrera, 2004). In a previous study, we found that morphs of *P. melisellensis* differ in circulating testosterone levels: orange males have higher levels than yellow ones (K. Huyghe, J.F. Husak & A. Herrel, unpubl. data). Moreover, testosterone levels appeared to be positively correlated with bite force capacity on the individual level. Combining these results with what those obtained in the present study, testosterone might be a probable proximate factor causing differences in muscle masses between the morphs. Testosterone implant or castration experiments are needed to confirm this hypothesis.

The finding that only the external and internal jaw adductor muscle groups differed between morphs, and not the posterior group or the jaw openers, means that there is no overall increase in muscle mass. Only the first two functional muscle groups (external and internal) contribute significantly to the generation of force through biting, whereas the adductor posterior group is attached to the quadrate and lower jaw and has predominantly a joint stabilizing function during the biting process (Herrel *et al.*, 1999). This result indicates that selection for biting harder is occurring, resulting in muscle hypertrophy in the orange morph, and that the presumed action of circulating testosterone is very site specific. Selection on bite force could be ecological, resulting in dietary divergence between morphs, with orange males being able to handle and crush harder prey items. Indeed, orange males had a larger proportion of hard prey items in their stomachs than the other two morphs (Huyghe *et al.*, 2007). However, the hardness of food items available does not appear to restrain any of the morphs from eating all potential food items: all maximal bite forces are higher than the force needed to crush the hardest food item found on the study site. The divergence in diet is thus not limited by performance, but is at least partly related to differential foraging behaviour.

Alternatively, a second type of selection might be occurring. Greater bite forces may be favored through sexual selection either directly or indirectly through selection on some other trait (e.g. aggression). Biting opponents in male–male competitive interaction or territorial defense is common in lizards (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Lappin & Husak, 2005), and males with higher maximal bite forces have a higher probability of dominating such encounters.

Biting is clearly associated with aggressive behaviour. Within a polymorphic species, where morphs have differential bite force capacities, one might expect morphs representing different strategies in male–male interactions, with the most aggressive morph biting hardest. In general, in *P. melisellensis*, males were frequently observed attacking each other using fast chases and biting. In particular, the orange males clearly behave more aggressively than the other morphs (K. Huyghe, B. Vanhooydonck & A. Herrel, unpubl. data), suggesting that their higher bite forces are a reflection of this behaviour. The other morphs might be using other behavioral strategies, resulting in an equal net lifetime reproductive success. Mate guarding after copulation, defending small or no territories, or displaying a sneaker strategy are a few possibilities, but further intensive behavioral observations should shed light on this issue. In conclusion, we find that selection can have an effect on performance (bite force), either directly or indirectly, through underlying lower-level mechanisms, such as morphology (head size), muscle mass and architecture, and possibly hormone levels (testosterone). Ultimately, behaviour (competitive ability, aggression, feeding behaviour) might be the target of selection, and performance, morphology, muscles and hormone levels are consequently affected.

ACKNOWLEDGEMENTS

The authors would like to thank the Croatian Ministry of Culture for providing permits to collect these data (permit no. 532-08-01-01/3-07-02). We also thank Patricija Oković, Duje Lisičića, and Bieke Vanhooydonck for their impressive field assistance and lizard catching skills. Lateral and dorsal images for shape analyses were made by Filip van Boven.

REFERENCES

- Bardin CW, Catterall JF. 1981.** Testosterone: a major determinant of extragenital sexual dimorphism. *Science* **211**: 1285–1294.
- Bruner E, Constantini D. 2007.** Head morphological variation in *Podarcis muralis* and *Podarcis sicula*: a landmark-based approach. *Amphibia-Reptilia* **28**: 566–573.
- Dorlöchter M, Astrow SH, Herrera AA. 2004.** Effects of testosterone on a sexually dimorphic frog muscle: repeated *in vivo* observations and androgen receptor distribution. *Journal of Neurobiology* **25**: 897–916.
- Eason JM, Schwartz GA, Pavlath GK, English AW. 2000.** Sexually dimorphic expression of myosin heavy chains in the adult mouse masseter. *Journal of Applied Physiology* **89**: 251–258.
- Emerson SB. 2000.** Vertebrate secondary sexual characteristics – physiological mechanisms and evolutionary patterns. *American Naturalist* **156**: 84–91.
- Forbes MR. 1991.** Female morphs of the damselfly

- Enallagma boreale* Selys (Odonata: Coenagrionidae): a benefit for androchromatypes. *Canadian Journal of Zoology* **69**: 1969–1970.
- Gans C, De Vree F. 1987.** Functional bases of fiber length and angulation in muscle. *Journal of Morphology* **192**: 63–85.
- Herrel A, Aerts P, De Vree F. 1998.** Ecomorphology of the lizard feeding apparatus: a modelling approach. *Netherlands Journal of Zoology* **48**: 1–25.
- Herrel A, De Grauw E, Lemos-Espinal JA. 2001.** Head shape and bite performance in xenosaurid lizards. *Journal of Experimental Zoology* **290**: 101–107.
- Herrel A, De Smet A, Aguirre LF, Aerts P. 2008.** Morphological and mechanical determinants of bite force in bats: do muscles matter? *Journal of Experimental Biology* **211**: 86–91.
- Herrel A, McBrayer LD, Larson PM. 2007.** Functional basis for intersexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society* **91**: 111–119.
- Herrel A, Spithoven L, Van Damme R, De Vree F. 1999.** Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**: 289–297.
- Hori M. 1993.** Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **5105**: 216–219.
- Huber SK, Podos J. 2006.** Beak morphology and song features covary in a population of Darwin's finches (*Geospiza fortis*). *Biological Journal of the Linnean Society* **88**: 489–498.
- Huyghe K, Vanhooydonck B, Herrel A, Tadić Z, Van Damme R. 2007.** Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Integrative and Comparative Biology* **47**: 211–220.
- Huyghe K, Vanhooydonck B, Scheers H, Molina-Borja M, Van Damme R. 2005.** Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology* **19**: 800–807.
- Joubert Y, Tobin C. 1995.** Testosterone treatment results in quiescent satellite cells being activated and recruited into cell cycle in rat levator ani muscle. *Developmental Biology* **169**: 236–294.
- Kaliantzopoulou A, Carretero MA, Llorente GA. 2007.** Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology* **268**: 152–165.
- Kodric-Brown A, Nicoletto PF. 1993.** The relationship between physical condition and social status in pupfish *Cyprinodon pecosensis*. *Animal Behaviour* **46**: 1234–1236.
- Lailvaux SP, Herrel A, Vanhooydonck B, Meyers JJ, Irschick DJ. 2004.** Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London Series B, Biological Sciences* **271**: 2501–2508.
- Lakjer T. 1926.** *Studien über die Trigemini-versorgte Kaumuskelatur der Sauropsiden*. Carlsbergstiftung. Copenhagen: CA Rietzel.
- Lappin AK, Husak JF. 2005.** Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist* **166**: 426–436.
- Meyers JJ, Irschick DJ, Vanhooydonck B, Herrel A. 2006.** Divergent roles for multiple sexual signals in a polygynous lizard. *Functional Ecology* **20**: 709–716.
- Petrucci EE, Niewiarowski PH, Moore FB-G. 2006.** The role of thermal niche selection in maintenance of a colour polymorphism in redback salamanders (*Plethodon cinereus*). *Frontiers in Zoology* **5**: 3–10.
- Podos J. 2001.** Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**: 185–188.
- Regnier M, Herrera AA. 1993.** Changes in contractile properties by androgen hormones in sexually dimorphic muscles of male frogs (*Xenopus laevis*). *Journal of Physiology* **461**: 565–581.
- Rohlf FJ. 1993.** Relative warp analysis and an example of its application to mosquito wings. In: Marcus LF, Bello E, García-Valdecasas A, eds. *Contributions to morphometrics*. Madrid: CSIC, 131–159.
- Rohlf FJ. 1995.** Multivariate analysis of shape using partial-warp scores. In: Mardia KV, Gill CA, eds. *Proceedings in current issues in statistical shape analysis*. Leeds: University of Leeds, 154–158.
- Rohlf FJ. 1998.** *tpsSmall: thin plate spline small variation analysis*, Version 1.20. Stony Brook, NY: State University of New York at Stony Brook.
- Rohlf FJ. 2000.** *tpsRegr: thin plate spline shape regression*, Version 1.31. Stony Brook, NY: State University of New York at Stony Brook.
- Rohlf FJ. 2001a.** *tpsDig: thin plate spline digitise*, Version 1.40. Stony Brook, NY: State University of New York at Stony Brook.
- Rohlf FJ. 2001b.** *Tpsrelw: thin plate spline relative warp analysis*, Version 1.42. Stony Brook, NY: State University of New York at Stony Brook.
- Rohlf FJ. 2002.** *tpsSpline: thin plate spline*, Version 1.20. Stony Brook, NY: State University of New York at Stony Brook.
- Rohlf FJ, Marcus LF. 1993.** A revolution in morphometrics. *Trends in Ecology and Evolution* **8**: 129–132.
- Ryan MJ. 1988.** Coevolution of sender and receiver: effect on local mate preferences in cricket frogs. *Science* **240**: 1786.
- Ryan PD, Harper DAT, Whalley JS. 1995.** *PALSTAT, statistics for palaeontologists*. London: Chapman & Hall.
- Sinervo B, Lively CM. 1996.** The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380**: 240–243.
- Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF. 2000.** Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior* **38**: 222–233.
- Wente W, Phillips JB. 2003.** Fixed green and brown color morphs and a novel color-changing morph of the Pacific tree frog *Hyla regilla*. *American Naturalist* **162**: 461–473.
- Widemo F. 1998.** Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? *Animal Behaviour* **56**: 329–336.