THE ROYAL SOCIETY

Received 9 March 2004
Accepted 2 August 2004

Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*)

Simon P. Lailvaux[1*], **Anthony Herrel**[2], **Bieke VanHooydonck**[2], **Jay J. Meyers**[3] **and Duncan J. Irschick**[1]

[1]*Department of Ecology and Evolutionary Biology, 310 Dinwiddie Hall, Tulane University, New Orleans, LA 70118, USA*
[2]*Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Antwerpen, Belgium*
[3]*Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA*

The evolution of alternative male phenotypes is probably driven by male–male competition for access to reproductive females, but few studies have examined whether whole-organism performance capacities differ between male morphs, and if so whether any such differences affect fighting ability. We show how ontogenetic changes in performance and morphology have given rise to two distinct life-stage male morphs exhibiting different fighting tactics within the green anole lizard (*Anolis carolinensis*). Field studies show a bimodal distribution of adult males within a single population: larger 'heavyweight' males have relatively large heads and high bite forces for their size, whereas smaller 'lightweight' males have smaller heads and lower bite forces. In staged fights between size-matched heavyweight males, males with greater biting ability won more frequently, whereas in lightweight fights, males with greater jumping velocity and acceleration won more often. Because growth in reptiles is indeterminate, and the anole males examined are sexually mature, we propose that the heavyweight morph arose through selection against males with small heads and poor bite forces at the lightweight–heavyweight size transition. Our findings imply that one may not be able to predict male fighting success (and hence potential mating success) by examining aspects of male 'quality' at only one life stage.

Keywords: *Anolis*; plastic alternative phenotype; performance; male combat

1. INTRODUCTION

Intraspecific polymorphism is an intriguing feature of biological systems that has been implicated as a key factor in adaptation and speciation (West-Eberhard 2003). Within this broad concept, the evolution of alternative male phenotypes within animal populations appears to be driven largely by male–male competition for access to reproductive females (Andersson 1994; Gross 1996; Shuster & Wade 2003; Zamudio & Sinervo 2003). These alternative male phenotypes may be genetically based, as in swordtail fish (Ryan *et al.* 1992) and in some lizards (Sinervo & Lively 1996), or male morph status can be phenotypically induced by factors such as food quality, or the amount of food obtained during the juvenile and/or larval stages (Emlen 2000). For invertebrates, males usually remain a particular morph for their entire adult lives. For example, some dung beetles emerge as 'sneaker' males, and remain as such until they die; they do not grow to become larger 'guarder' males, as their size is fixed at pupation (Emlen 2000). In vertebrates, however, male status and morphology can change with age (and hence size) (Moore 1991; Andersson 1994). Furthermore, species with indeterminate or asymptotic growth patterns (Stamps *et al.* 1998) may experience dramatic shifts in morphology as a result of differential partitioning of resources across ontogeny (Huxley 1931).

Any such changes in morphology and status across ontogeny would be expected to result in differences in whole-organism performance capacities, such as sprinting ability or endurance (Huey & Hertz 1982, 1984; Arnold 1983; Garland & Losos 1994; Irschick 2000). Thus, whole-organism performance capacities could be an important factor in the evolution of alternative male mating strategies (see Sinervo *et al.* 2000), a point that has thus far been largely neglected. For example, several recent studies have shown that male dominance in some lizard species is influenced by locomotor performance, with better performers holding territories over weaker performers (Garland *et al.* 1990; Robson & Miles 2000; Perry *et al.* 2004). Furthermore, because many lizard species bite one another during territorial disputes, one might also expect that biting ability could play an important role in mediating male–male encounters (Herrel *et al.* 1999; see also Hews 1990). Because both locomotor performance and biting ability typically increase with size within lizard species (Garland & Losos 1994; Meyers *et al.* 2002), one might expect that males of different sizes would adopt different strategies for how these performance capacities are used during male–male territorial encounters. However, despite the extensive literature on both whole-organism performance capacities (i.e. Huey & Stevenson 1979; Huey & Hertz 1982, 1984; Bennett & Huey 1990; Losos 1990; Garland & Losos 1994; Wainwright 1994; Irschick & Garland 2001, and references therein) and alternative mating strategies (see Gross 1996; Shuster & Wade 2003; Zamudio & Sinervo

---

[*] Author for correspondence (slailvau@tulane.edu).

doi:10.1098/rspb.2004.2891

2003 for reviews), few studies have empirically addressed whether alternative male phenotypes are associated with different performance abilities. An exception to this generalization is work by Sinervo *et al.* (2000), who showed that male morphs of the lizard *Uta stansburiana* differ in locomotor endurance capacity, and that high levels of testosterone may have contributed to the high endurance capacity. We extend this approach by showing more directly how ontogenetic changes in morphological shape and whole-organism performance capacities have resulted in distinct fighting tactics in the green anole lizard (*Anolis carolinensis*).

The green anole is an ideal species in which to examine how changes in performance with size influence the evolution of male morphs and alternative fighting strategies. First, previous work has shown that green anole males will acquire breeding territories based, in large part, on the location of females, and fight intensely to exclude other males from those territories (McMann 1993; Perry 1996; Jenssen *et al.* 2000, 2001; see Stamps 1983; Stamps & Krishnan 1997, 1998 for a general overview of lizard territoriality). Second, such fights will sometimes escalate into biting and jaw locking (Greenberg & Noble 1944; McMann 1993; figure 1), suggesting that bite performance could be important for determining the outcome of male–male fights. Finally, this species makes extensive use of its locomotor abilities in nature (Irschick & Losos 1998), implying that locomotor performance could also be important for acquiring and defending territories (Garland *et al.* 1990; Robson & Miles 2000; Perry *et al.* 2004).

We performed field studies and laboratory experiments to document the presence of two distinct male life-stage 'morphs' within green anole lizards. The two green anole male morphs differ substantially in head morphology, size-adjusted bite performance and in their behavioural tactics for winning male–male fights. We show that the smaller life-stage morph ('lightweight' males) has a relatively small head, low bite forces, displays frequently and appears to use locomotor ability (jumping ability) to gain dominance during male–male fights. By contrast, the larger life-stage morph ('heavyweight' males) has a relatively large head, high bite forces, displays infrequently and appears to use biting ability to win male–male fights. We show that the green anoles sampled follow a simple model of indeterminate growth, strongly suggesting that the two morphs differ in age. Consequently, we suggest that lightweight males should mature into heavyweight males unless they are eliminated from the population, thus fitting the pattern of 'plastic' alternative phenotypes described by Moore (1991).

We documented the presence of these life-stage morphs in two steps. First, we conducted an extensive survey of all age and sex classes of the green anole in a natural lowland swamp habitat ('field data'). For all animals captured during this survey, we measured bite force and head morphology to understand how both variables change with size across sexually mature males, and to compare males with juveniles and females. Second, we conducted laboratory studies of male–male dominance ('male–male dominance data') for 'heavyweight' trials (e.g. heavyweight males versus heavyweight males), and for 'lightweight' trials. For each lizard used in these dominance trials, we then measured head morphology, maximum bite force and maximum jumping capacity on a force platform (acceleration and velocity), and determined which aspect of performance (if any) was the predictor for winning heavyweight and lightweight bouts. In addition to documenting the presence of these two morphs, we also discuss the evolutionary and ecological factors that may have led to their origin.

Figure 1. Male *Anolis carolinensis* lizards engaging in a territorial dispute. Note that the lizards are biting one another. Photograph by Jitnapa Suthikant.

2. MATERIAL AND METHODS

(a) *Field data*

During autumn 2002 (15 September–30 October), we daily surveyed a 760 m transect in Good Hope Field (St Charles Parish, LA), which consists of a 3 m wide road with narrow (3–4 m) strips of vegetation on either side (Irschick *et al.* 2004). The vegetation at the site consists of a mixture of large trees and dense bushes adjacent to a freshwater swamp. A total of 403 lizards were captured (81 females, 102 juveniles and 220 adult males) by walking through the habitat during normal activity hours (09.00–17.00), and capturing any lizard present. Lizards were captured either by hand or with a noose attached to a pole. Lizards were then transported to Tulane University to measure both maximum bite force and morphology. We measured bite forces (see § 2b below), as well as snout–vent length (SVL), mass, head height and head depth for all individuals using Mitutoyo digital callipers (±0.01 mm), and a Denver Instruments M-220 electronic balance (±0.01 mg). We defined adult males (size range: 48–74 mm SVL) by the presence of mature sexual characters (enlarged dewlap, enlarged tail base). After performance and morphology were measured on each lizard, each lizard was marked permanently to prevent resampling and released at the point of capture, typically within 48 h of capture.

(b) *Measurement of bite force*

We measured biting force by using an isometric Kistler force transducer (type 9023, Kistler Inc., Wintherthur, Switzerland) connected to a Kistler charge amplifier (type 5058a, Kistler Inc.). We induced lizards to bite forcefully on the free ends of the bite force device (see Herrel *et al.* 1999). We measured bite forces five times for each animal with a 30 min rest period between measures. The largest bite force obtained from each session was taken as the maximal bite force for that individual. All individuals were placed inside an incubator at 32 °C for at least 30 min before bite force measurement, and in between measures (similar temperatures as used in Toro *et al.* (2003)).

(c) *Male–male dominance data*

We performed male–male contests following established methodologies (Garland *et al.* 1990; Robson & Miles 2000; Perry *et al.* 2004) to enable comparison with these previous studies. In

June 2003, we collected a large sample of adult male *A. carolinensis* lizards from the same population in which the above field studies were conducted. Immediately after capture, and at least 24 h before contests, we measured SVL, mass, head dimensions (length, height and width) and performance (bite force (see § 2b above) and jumping (see § 2d below)) in all individuals. Next, two male *A. carolinensis* were introduced simultaneously into opposite ends of a 38 l terrarium containing one perching site beneath a suspended heat lamp. Males were size-matched (no greater than 3 mm SVL difference; Perry *et al.* 2004) as body size is an important determinant of dominance in lizards, with large lizards being dominant over smaller individuals (Perry *et al.* 2004; Leuck 1995 and references therein).

Following these introductions, a 30 min 'acclimation' period was allowed, during which no observations were made (cf. Perry *et al.* 2004). Although it is possible that males interacted during this acclimation period, this should not bias the results, as all trials had equal acclimation times. After this period, each cage was observed for 5 min at 20 min intervals over a period of 2 h (30 min observation time in total per cage). As in Perry *et al.* (2004), aggressive behaviours received a positive score and submissive behaviours a negative score (see McMann (1993) and Leal & Rodríguez-Robles (1995, 1997) for further details on identification of aggressive and submissive behaviours in anoles). Push-ups and dewlap displays were assigned a weight of 0.5, whereas lateral displays, chasing and biting an opponent each received a score of 1 (Leal & Rodríguez-Robles 1995, 1997). We also noted which male was present on the perch and for how long.

At the end of the 2 h period, we gave each male an overall score by summing the above measurements. Each cage was also examined 3 h after a trial was completed (thus lizards were not inspected for 1 h prior), and we noted where the lizards were positioned in the cage (i.e. which male was on the perch, etc.) to verify the results of the scored bouts. In all cases, except those where the winner could not be determined, the male that held the perch 3 h after the conclusion of the scored trial was also the male with the highest 'score'. Trials in which males earned equal scores or did not interact during the observation period, were excluded from analyses (lightweights, $n = 3$; heavyweights, $n = 4$). Each male was tested in two contests, each on different days, and paired against different individuals, and results from the two rounds were pooled.

(d) *Jumping*

We measured jumping performance only in lizards used in dominance trials because we were primarily interested in how jumping influenced male–male dominance. We placed lizards on a custom-built force platform, and induced them to jump onto a horizontal board positioned at the level of the platform and placed just out of reach of the individual (as in Toro *et al.* 2003). The three-dimensional ground reaction forces were recorded by using Superscope software on an Apple Macintosh G4 computer. Force traces were smoothed using a low-pass filter before further analysis. We motivated lizards to jump by startling them, for example, by hand-clap. Only jumps that began with all four feet square on the platform were included in the analyses. Each individual was jumped five times, and the best jump (based on overall jump dynamics such as distance and take-off velocity) was used in the final analyses. Before, and in between performance measurements, lizards were placed inside an incubator at 32 °C for at least 1 h.

(e) *Statistical analyses*

To compare the morphology and performance of lightweight and heavyweight males collected from the 'field data', we used one-way ANOVAs to compare residual values of head width, head depth and bite force. Residual values for lightweight and heavyweight males were obtained by regressing (least-squares linear regression) each of the above log-transformed variables (dependent variable) versus log-transformed SVL (independent variable) for all 403 lizards from the 'field data'. We used this approach because although figure 2*b* shows a nonlinear relationship between bite force and SVL, the plot of log-transformed data was linear (figure 2*c*). In addition, relationships between log-transformed head measures (width, depth) and log-transformed SVL were also linear for all 403 lizards. Thus, scaling the residuals to all individuals, rather than just males, allowed a more robust estimate of size-adjusted bite force and head dimensions in lightweight and heavyweight males. Also, we used a residual, rather than an ANCOVA approach (see Garcia-Berthou 2001) because the two male classes do not overlap in the independent variable (SVL), and thus results from the ANCOVA are likely to be less robust.

To test whether age and size are correlated in our population, we fitted a generalized growth model for *Anolis* lizards (Stamps *et al.* 1994) to anoles captured in the field ($n = 403$ lizards):

$$\text{mass (grams)} = \text{mass (grams)} = \left(\frac{L}{35}\right)^{2.94}, \tag{2.1}$$

where L is the SVL in millimetres. A close fit of the model to our data would suggest that our sample represents a reasonable approximation of the growth trajectory of *A. carolinensis*, and that larger individuals can be expected to be older than smaller individuals (Stamps *et al.* 1994).

Performance variables for winners and losers of male–male dominance bouts ('male–male dominance data') were compared using two-way paired *t*-tests. We did not account for the effects of size in these latter comparisons because lizards were size-matched in dominance trials. We used χ^2-tests with Yates's correction to compare the number of headbob displays exhibited by the lightweight and heavyweight males. We focused on headbob displays because previous studies (Leal 1999; Brandt 2003) have shown that the intensity of these displays is closely tied to locomotor ability.

3. RESULTS

(a) *Field data*

Demographic field studies in a lowland freshwater swamp population of *A. carolinensis* in southern Louisiana revealed the presence of two distinct male morphs. The size distribution of adult males ($n = 220$ males), ranging in SVL from 48 to 74 mm, is bimodal (figure 2*a*), with a distinct 'gap' in the size distributions (figure 2*a*,*b*). Based on the presence of this 'gap' in figure 2*a*,*b*, we estimated the threshold between the two morphs (see Kotiaho & Tomkins 2001) to be between 64 and 65 mm SVL (figure 2*b*), but for analytical purposes, we divided the male population into 'lightweight' males (less than 64 mm SVL), and 'heavyweight' males (more than 64 mm SVL) males (figure 2*a*). We defined different size thresholds (e.g. 63 mm SVL) but only at 64 mm SVL did the below behavioural and performance differences between the morphs become apparent. Lightweight males outnumber heavyweight males by a ratio of 1.9 : 1 (144 lightweight males : 76 heavyweight males; figure 2*a*). Heavyweight males have significantly wider and deeper heads than lightweight males (figure 3*a*),

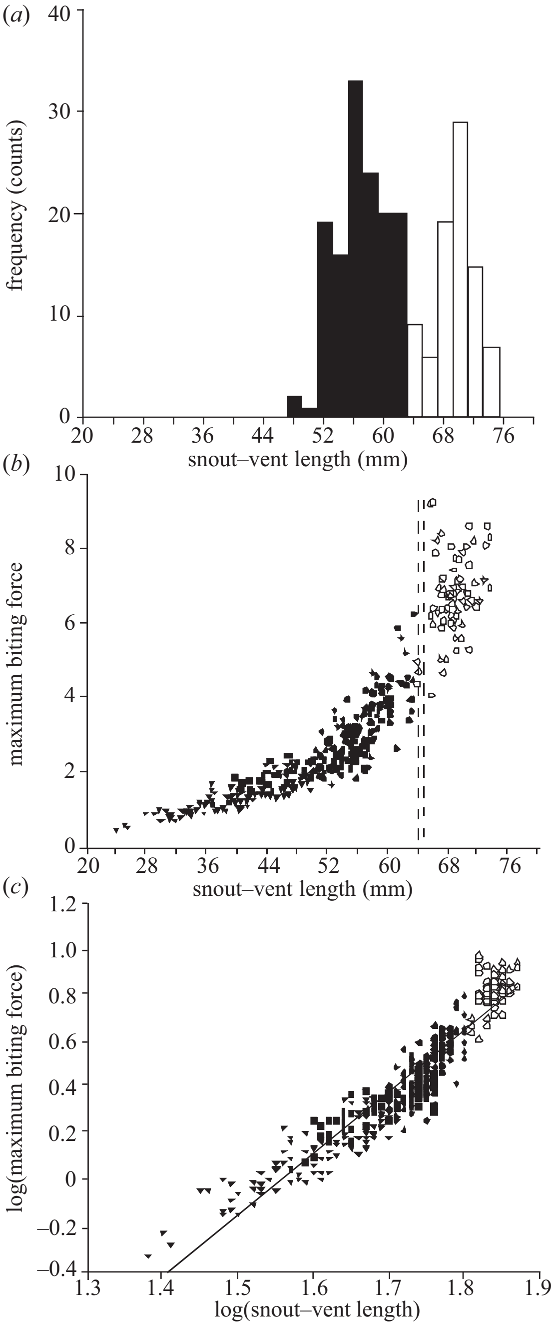

Figure 2. (*a*) A histogram of body sizes for 220 male green anoles from Good Hope Field, LA, showing the presence of lightweight (filled bars) and heavyweight (open bars) males. (*b*) A scatter-plot showing the relationship between SVL (*x*-axis) and maximum bite force (*y*-axis) for 403 green anoles. The dashed lines indicate the approximate threshold between the two morphs, estimated between 64 and 65 mm SVL (see text for how we defined the two size classes). Note that bite force increases linearly within juveniles and females, and then increases approximately exponentially with size in adult males, resulting in heavyweight males having very high bite forces (heavyweight males, open circles; lightweight males, filled circles; females, filled squares; juveniles, filled inverted triangles). (*c*) A scatter-plot showing the relationship between log-transformed SVL (*x*-axis) and log-transformed bite force (*y*-axis). Note that the overall relationship now becomes linear, thus allowing residual analysis (figure 3*b*). Also note that heavyweight males are clearly above the regression line. The *x*-axes are similar in (*a*) and (*b*), but do not match with (*c*), because of the log–log scale.

and the two morphs can be readily identified in the field. Based on biomechanical considerations, relatively wider and deeper heads are predicted to increase bite force in lizards (Herrel *et al.* 1999, 2001*a*,*b*; Verwaijen *et al.* 2002). Examination of a plot comparing bite force versus SVL for an extensive survey of 403 green anoles (pooling juveniles, females, lightweight and heavyweight males) shows that bite force (non-log-transformed) increases linearly within juveniles, females and lightweight males, but increases approximately exponentially with size in large males, resulting in heavyweight males having very high bite forces relative to their size (figures 2*b* and 3*b*). Once bite force and SVL are log-transformed, the overall relationship becomes more linear overall, but heavyweight males clearly fall above the regression line (figures 2*c* and 3*b*).

The anoles from the Good Hope Field population show a close fit to the generalized anole growth model ($y = (x/35.91)^{2.91}$, where y is mass in grams, x is SVL in millimetres; s.e.m. $= 0.32$, $r = 0.99$). Thus, lightweight and heavyweight males appear to fall along the same growth curve, suggesting that heavyweights are likely to be older than lightweights, and that the largest heavyweights represent the asymptotic size (Stamps *et al.* 1998) in this population.

(b) *Male–male dominance data*

For analytical purposes, we separated male bouts into those occurring between lightweight males less than 64 mm SVL ($n = 29$ fights), and those between heavyweight males greater than 64 mm SVL ($n = 19$ fights). In 'lightweight' fights, winners had significantly greater maximum jumping velocities ($t_{28} = 2.39$, $p = 0.024$) and maximum accelerations ($t_{28} = 3.22$, $p = 0.003$) than losers, but did not differ significantly in bite force ($t_{28} = -1.30$, $p = 0.21$; figure 4*a*). In 'heavyweight' fights, no significant differences existed between winners and losers for any aspect of jumping performance; however, winners had significantly greater bite forces than losers ($t_{18} = 2.35$, $p = 0.03$; figure 4*b*).

In addition to these differences, observational data also suggest two different behavioural tactics for winning fights (although a detailed analysis of male fighting strategies is needed to verify this trend). In 60.9% of the lightweight bouts, the first male on the perch was the winner, as opposed to only 40.2% of heavyweight bouts, suggesting that locomotor quickness enables lightweight males to first acquire, and subsequently retain, a perch. By contrast, acquiring a perch first appears to be unimportant for heavyweight males. Further, out of the eight trials in which actual biting occurred, seven of those cases (88%) occurred in males 62 mm SVL or greater, suggesting that large, not small males, more often use biting as a tactic to win male–male fights, and also that the use of this tactic begins near the lightweight–heavyweight size threshold (64–65 mm SVL). Finally, males in lightweight fights headbobbed significantly more than males in heavyweight fights ($\chi^2 = 139.49$, $p < 0.001$); indeed, both lightweight winners and losers headbobbed approximately 2.5 times more than heavyweight winners and losers.

4. DISCUSSION

Our findings provide evidence for two morphologically and functionally distinct adult male morphs within *A. carolinensis* lizards that differ both in age and their tactics

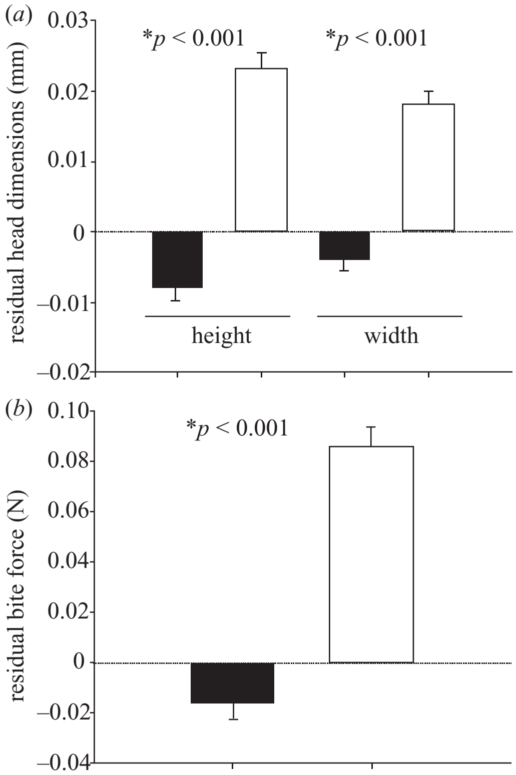

Figure 3. Mean residual values of head shape (*a*) and bite force (*b*) comparing lightweight (filled bars) and heavyweight (open bars) males. Note that heavyweight males have much wider and deeper heads, and greater bite forces, compared with lightweight males. One-way ANOVAs comparing residuals of lightweight versus heavyweight males from regressions of log-transformed head shape and bite force variables versus log-transformed SVL for all 403 lizards (juveniles, females, and males) in figure 2*b*; head width, $F_{1,218} = 80.7, p < 0.001$; head depth, $F_{1,218} = 105.2$, $p < 0.001$; bite force, $F_{1,218} = 96.1$, $p < 0.001$). Graphs are means ± s.e.m.

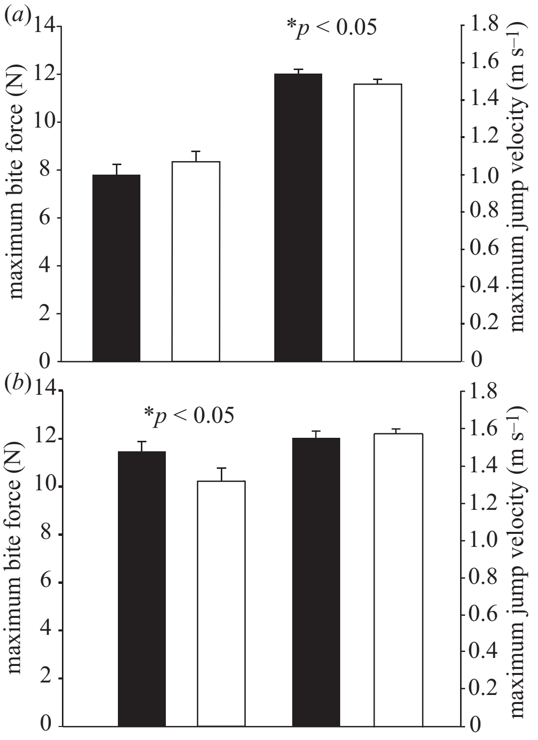

Figure 4. Mean values of maximum bite force and jumping velocity for (*a*) lightweight and (*b*) heavyweight winners (filled bars) and losers (open bars) from male–male dominance laboratory experiments. Note that for lightweight males, winners have significantly higher jump velocities than losers, whereas for heavyweight males, winners have significantly higher bite forces than losers. Graphs are means ± s.e.m.

for winning male–male fights. Lightweight males have smaller heads, lower bite forces, higher display rates and appear to use locomotor quickness for winning male–male fights. By contrast, heavyweight males have larger heads, higher bite forces, lower display rates and appear to use biting ability to win male–male fights. Our results are consistent with previous studies showing that both locomotor performance (Garland *et al.* 1990; Robson & Miles 2000; Perry *et al.* 2004) and head size (Hews 1990; Pratt *et al.* 1992; Perry *et al.* 2004) are key determinants of male dominance status in lizards (see also Leal 1999), with the twist that whichever aspect of performance (locomotion versus bite force) dictates winning versus losing changes with size. In addition to these morphological and performance differences between lightweight and heavyweight males, our data also show a distinct bimodal distribution of these two morphs in nature (*ca.* 64–65 mm SVL; figure 2*a*,*b*), suggesting that this dichotomy is real, and not an artificial division (see Caro & Bateson 1986; Kotiaho & Tomkins 2001).

Previous authors have extensively discussed the evolution and causes of alternative male morphs within a variety of animal species (Gross 1996; Shuster & Wade 2003; Zamudio & Sinervo 2003). Although previous studies have shown that male morphs differ in behaviour and performance capacity (e.g. *Uta stansburiana* morphs; Sinervo & Lively 1996; Sinervo *et al.* 2000), our data are among the first to show how differences among morphs in performance capacity also affect how morphs fight. The broad evolutionary implication of this result is that one may not be able to predict male fighting success (and hence potentially mating success) by examining any aspect of male ‘quality’ at only one life stage. In this regard, it is important to emphasize that these green anole male life-stage morphs are all sexually mature males, and hence one cannot explain our results as a consequence of morphological changes occurring as a result of sexual maturation. These findings underscore the importance of accounting for life-history information to understand the evolution of reproductive fitness (Kokko 1998, 2001; Badyaev & Qvarnström 2002; Huey *et al.* 2003; Kokko *et al.* 2003; West-Eberhard 2003).

The size distribution of the Good Hope Field *A. carolinensis* closely fits the distribution we would predict from the generalized growth model for *Anolis* lizards. Although not conclusive (see Andrews 1982; Halliday & Verrell 1988), this analysis strongly suggests that age and size are highly correlated in this population, meaning that each smaller lightweight male will eventually grow to become a heavyweight male, provided it survives (ongoing field studies are investigating this possibility; D. J. Irschick, unpublished data). This scenario is consistent with discussions of ‘plastic’ alternative phenotypes described by

Moore (1991), in which males change (in this case irreversibly) from one phenotype to another during their adult lives. Thus, although we follow Moore (1991) in our use of the term 'morph' to describe the two classes, we include the qualifier 'life-stage morph' to remind the reader that the two morphologically distinct male types arise at different stages of the *A. carolinensis* life history.

There are two possible explanations for the presence of these green anole life-stage male morphs. First, the two life-stage morphs have arisen via different developmental pathways whereby the heavyweight morph undergoes accelerated growth in head dimensions, whereas the lightweight males do not. Such a difference implies that the two morphs either experience different environmental conditions (e.g. food quality or quantity; Emlen 2000) early in development, or differ genetically (Sinervo & Lively 1996; see also Shuster & Wade 2003), or both. Further, if this scenario were correct, the underlying mechanisms may involve differential expression of hormones during development (Crews & Gans 1992). We view this possibility as unlikely for the reason that the 'threshold' size between the morphs (64–65 mm SVL) occurs long after the onset of sexual maturity in green anoles (*ca.* 45 mm SVL) (D. J. Irschick, A. Herrel, B. Vanhooydonck and J. J. Meyers, unpublished data). Thus, to provide evidence for this possibility, one would have to show that differential head growth in each morph likewise occurs long after the onset of sexual maturity in *A. carolinensis*. This phenomenon has so far not been documented.

A second, more likely possibility is that the two morphs have arisen through a process of intense male mortality through selection at the lightweight–heavyweight male size threshold (see Stamps 1983). For example, as lightweights enter the size transition between the two morphs, they may attempt to gain access to prime territorial sites (e.g. large trees) held by heavyweight males. Our data indicate that unless the lightweight males have large heads and powerful bites for their size, they will probably lose ensuing fights with established heavyweight males. The resulting injuries inflicted by the high bite forces of the heavyweight males may lead to death either directly (bite forces of heavyweights approach those needed to crush lightweight skulls), or through increased susceptibility of injured males to predation (Stamps 1983). Indeed, we have observed severe scars on heavyweight males; many probably resulting from male–male fights (S. P. Lailvaux, personal observation), and mortality in younger males is extremely high (more than 90%) in some green anole populations (D. J. Irschick, A. Herrel, B. Vanhooydonck and J. J. Meyers, unpublished data). If the above inferences are correct, then this would also underscore why the criteria for winning male–male fights shifts from quickness (during jumping) in small males to biting ability in large males, as the increase in absolute bite force with size means that bites by larger males have a greater chance of injuring an opponent compared with a bite from a smaller male. However, although this hypothesis of severe male mortality at the lightweight–heavyweight size threshold would explain both the 2 : 1 ratio of lightweight : heavyweight males and the bimodal size distribution, other factors, such as intense predation on heavyweight males, may also be important. Further, one must consider the possibility that lightweight males could avoid confrontations with 'dominant' heavyweight males by 'sneaking' matings. Indeed, Orrell & Jenssen (2003) suggest that *A. carolinensis* populations may harbour small 'covert' males that mimic females, suggesting a 'sneaking' strategy for lightweight males. This finding is consistent with previous studies showing that larger lizards are dominant over smaller lizards (Leuck 1995 and references therein), further suggesting that lightweights are unable to gain victory in fights with heavyweights.

Although selection resulting from male combat may ultimately be responsible for the current distribution of the two morphs, proximate mechanisms, such as differing hormone levels in the two morphs, may also be important in generating the variation for selection to act upon. For example, Sinervo *et al.* (2000) showed that the dominant orange-throated male morph of the lizard *U. stansburiana* had higher testosterone levels, and hence higher endurance capacities, than the two other male morphs (blue-throated, yellow-throated). Similarly, within lightweight green anole males there may be variation in testosterone levels among individuals, which in turn could be linked to variation in both maximum jumping ability and maximum bite force. Thus, it is possible that selection could be eliminating lightweight males with low testosterone levels, and hence small heads and low performance capacities, thus resulting in older heavyweight males having large heads and high bite forces. This explanation would be consistent with the relative plasticity hypothesis of Moore (1991), which predicts that adult morphs of plastic alternative phenotypes will differ in hormone profiles.

However, our findings differ from those of Sinervo *et al.* (2000) in two important ways. First, our life-stage morphs appear to differ in age, whereas the *U. stansburiana* morphs do not. Consequently, we argue that the lightweight and heavyweight morphs probably do not differ genetically, as has been shown for *U. stansburiana*. Second, although the documented differences in endurance capacity among *U. stansburiana* morphs probably contribute to different generalized male strategies, our work links performance and fighting tactics more directly. For example, whereas enhanced endurance capacity may enable the orange-throated male morphs to have larger home ranges (Sinervo *et al.* 2000), it is not clear why enhanced endurance would enable the orange-throated morph to defeat the blue-throated mate guarder morph, for example.

By contrast, our data provide strong evidence for two alternative bases for conflict resolution in lightweight and heavyweight anole life-stage morphs. Heavyweight males rely upon their potentially destructive biting ability to resolve male fights, whereas locomotor capacity appears more important for smaller lightweight males. The difference between lightweights and heavyweights in display behaviour is particularly interesting, as bobbing-type displays are known to be related to locomotor endurance in both the closely related *Anolis cristatellus* (Leal 1999), and the more distantly related *U. stansburiana* (Brandt 2003), further underscoring that lightweight males are more dependent on locomotor capacity compared with heavyweight males.

However, exactly why lightweight males with high jumping capacities tend to win contests over lightweight males with low jumping capacities remains unclear. Our observation that winning lightweight males were more often the first on the perch compared with losers suggests that locomotor ability may enable males to achieve 'resident male advantage', but proving this conclusively is difficult. It is worth noting that, to our knowledge, no studies that have documented positive relationships between locomotor capacity (endurance, maximum speed) and dominance in lizards (Garland *et al.* 1990; Robson & Miles 2000; Perry *et al.* 2004) have conclusively demonstrated a mechanism by which locomotor performance translates into victory in male bouts. Indeed, reports of such mechanisms are also scarce in other taxa; many studies have shown links between dominance and some intrinsic male trait (Andersson 1994, and references therein; Pryke & Andersson 2003; Whiting *et al.* 2003), but few have shown that such traits offer a mechanistic benefit to males in fights. In this regard, it is possible that enhanced locomotor performance is simply an indicator of general male vigour, and does not directly benefit lightweight males during contests. Further research that investigates this possibility would be useful. Specifically, detailed behavioural observations of lightweight and heavyweight male contests, especially under field conditions, are necessary to demonstrate conclusively whether the two morphs use different behavioural tactics that may interface with their differing performance capacities.

In conclusion, we have shown the presence of two male life-stage morphs within a species that differ significantly in head morphology, biting performance and fighting tactics, one based on locomotor ability, the other based on destructive biting ability, to win male–male contests. The possible fitness consequences of this type of age-dependent alternative phenotype lend support to current ideas about the importance of life-history approaches to individual mating success (Kokko 1998, 2001; Badyaev & Qvarnström 2002; Huey *et al.* 2003; Kokko *et al.* 2003; West-Eberhard 2003). However, an understanding of fitness functions, in addition to behaviour, is required to properly interpret patterns of selection acting on alternative male tactics (Moore 1991; Hunt & Simmons 2001; Shuster & Wade 2003).

The authors thank Martin Whiting and Simon Elwen for advice and suggestions, and Rob Knell and the Irschick Functional Morphology laboratory group for commenting on a previous draft of this paper. This work was supported by two NSF grants to D.J.I. (IBN 9983003 and 042917) and funding from the Coypu foundation. A.H. and B.V.H. are postdoctoral researchers of the Fund for Scientific Research, Flanders (FWO-Vl). All experiments were carried out in accordance with an approved animal use protocol (IACUC 0189-2-16-0301).

REFERENCES

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Andrews, R. M. 1982 Patterns of growth in reptiles. In *Biology of the Reptilia*, vol. 13 (ed. D. Crews & C. Gans), pp. 273–335. The University of Chicago Press.

Arnold, S. J. 1983 Morphology, performance, and fitness. *Am. Zool.* **23**, 347–361.

Badyaev, A. V. & Qvarnström, A. 2002 Putting sexual traits into the context of an organism: life-history perspective in studies of sexual selection. *Auk* **119**, 301–310.

Bennett, A. F. & Huey, R. B. 1990 Studying the evolution of physiological performance. In *Oxford surveys of evolutionary biology*, vol. 7 (ed. D. Futuyma & J. Antonovics), pp. 251–284. New York: Oxford University Press.

Brandt, Y. 2003 Lizard threat display handicaps endurance. *Proc. R. Soc. Lond.* B **270**, 1061–1068. (doi:10.1098/rspb.2003.2343)

Caro, T. M. & Bateson, P. 1986 Organization and ontogeny of alternative tactics. *Anim. Behav.* **34**, 1483–1499.

Crews, D. & Gans, C. 1992 The interaction of hormones, brain, and behavior: an emerging discipline in herpetology. In *Biology of the Reptilia* (ed. D. Crews & C. Gans), vol. 18, pp. 1–24. The University of Chicago Press.

Emlen, D. J. 2000 Integrating development with evolution: a case study with beetle horns. *BioScience* **50**, 403–418.

Garcia-Berthou, E. 2001 On the misuse of residuals in ecology: testing regression residuals versus analysis of covariance. *Funct. Ecol.* **70**, 708–711.

Garland Jr, T. & Losos, J. B. 1994 Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology: integrative organismal biology* (ed. P. C. Wainwright & S. Reilly), pp. 240–302. University of Chicago Press.

Garland Jr, T., Hankins, E. & Huey, R. B. 1990 Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* **4**, 243–250.

Greenberg, B. & Noble, G. K. 1944 Social behavior of the American chameleon (*Anolis carolinensis* Voigt). *Physiol. Zool.* **17**, 392–439.

Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within the sexes. *Trends Ecol. Evol.* **11**, 92–98.

Halliday, T. R. & Verrell, P. A. 1988 Body size and age in amphibians and reptiles. *J. Herpetol.* **22**, 253–265.

Herrel, A., Spithoven, L., Van Damme, R. & De Free, F. 1999 Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**, 289–297.

Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. 2001*a* The implications of bite force for diet in two species of lacertid lizards. *Can. J. Zool.* **79**, 662–670. (doi:10.1139/cjz-79-4-662)

Herrel, A., De Grauw, E. & Lemos-Espinal, J. A. 2001*b* Head shape and bite force in xenosaurid lizards. *J. Exp. Zool.* **290**, 101–107.

Hews, D. 1990 Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. *Evolution* **44**, 1956–1966.

Huey, R. B. & Hertz, P. E. 1982 Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *J. Exp. Biol.* **97**, 401–409.

Huey, R. B. & Hertz, P. E. 1984 Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.* **110**, 113–123.

Huey, R. B. & Stevenson, R. D. 1979 Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**, 357–366.

Huey, R. B., Hertz, P. E. & Sinervo, B. 2003 Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)

Hunt, J. & Simmons, L. W. 2001 Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. *Proc. R. Soc. Lond.* B **268**, 2409–2414. (doi:10.1098/rspb.2001.1758)

Huxley, J. S. 1931 *Problems of relative growth*. London: Methuen and Company Ltd.

Irschick, D. J. 2000 Effects of behavior and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. *Funct. Ecol.* **14**, 438–444.

Irschick Jr, D. J. & Garland Jr, T. 2001 Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *A. Rev. Ecol. Syst.* **32**, 367–396. (doi:10.1146/annurev.ecolsys.32.081501.114048)

Irschick, D. J. & Losos, J. B. 1998 A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219–226.

Irschick, D. J., Vanhooydonck, B, Meyers, J. & Herrel, A. 2004 Intraspecific correlations among morphology, performance, and habitat use within a green anole lizard (*Anolis carolinensis*) population. *Biol. J. Linn. Soc.* (In the press.)

Jenssen, T. A., Orrell, K. S. & Lovern, M. B. 2000 Sexual dimorphism in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia* **2000**, 140–149.

Jenssen, T. A., Lovern, M. B. & Congdon, J. D. 2001 Field-testing the polyandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model? *Behav. Ecol. Sociobiol.* **50**, 162–172.

Kokko, H. 1998 Good genes, old age, and life-history trade-offs. *Evol. Ecol.* **12**, 739–750. (doi:10.1023/A:1006541701002)

Kokko, H. 2001 Fisherian and 'good genes' benefits of mate choice: how (not) to distinguish between them. *Ecol. Lett.* **4**, 322–326.

Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. 2003 The evolution of mate choice and mating biases. *Proc. R. Soc. Lond.* B **270**, 653–664. (doi:10.1098/rspb.2002.2235)

Kotiaho, J. S. & Tomkins, J. L. 2001 The discrimination of alternative male morphologies. *Behav. Ecol.* **12**, 553–557.

Leal, M. 1999 Honest signalling during prey–predator interactions in the lizard. *Anolis cristatellus*. *Anim. Behav.* **58**, 521–526. (doi:anbe.1999.1181)

Leal, M. & Rodríguez-Robles, J. A. 1995 Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia* **1995**, 155–161.

Leal, M. & Rodríguez-Robles, J. A. 1997 Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Anim. Behav.* **54**, 1147–1154.

Leuck, B. E. 1995 Territorial defense by male green anoles: an experimental test of the roles of residency and male quality. *Herpetol. Monogr.* **9**, 63–74.

Losos, J. B. 1990 Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* **60**, 369–388.

McMann, S. 1993 Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. *Anim. Behav.* **46**, 657–668.

Meyers, J. J., Herrel, A. & Birch, J. 2002 Scaling of morphology, bite force, and feeding kinematics in an iguanian and a scleroglossan lizard. In *Topics in functional and ecological vertebrate morphology* (ed. P. Aerts, K. D'aout, A. Herrel & R. Van Damme), pp. 47–62. Maastricht: Shaker Publishing.

Moore, M. C. 1991 Application of organization-activation theory to alternative male reproductive strategies: a review. *Horm. Behav.* **25**, 154–179.

Orrell, K. S. & Jenssen, T. A. 2003 Heterosexual signaling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour* **140**, 603–634. (doi:10.1163/156853903322149469)

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

Perry, G., Levering, K., Girard, I. & Garland Jr, T. 2004 Locomotor performance and dominance in male *Anolis cristatellus*. *Anim. Behav.* **67**, 37–47. (doi:10.1016/j.anbehav.2003.02.003)

Pratt, N. C., Alberts, A. C., Fulton-Medler, K. G. & Phillips, J. A. 1992 Behavioral, physiological, and morphological components of dominance and mate attraction in male green iguanas. *Zool. Biol.* **11**, 153–163.

Pryke, S. R. & Andersson, S. 2003 Carotenoid-based status signaling in red-shouldered widowbirds (*Euplectes axillaries*): epaulet size and redness affect captive and territorial competition. *Behav. Ecol. Sociobiol.* **53**, 393–401. (doi:10.1007/s00265-003-0587-2)

Robson, M. A. & Miles, D. B. 2000 Locomotor performance and dominance in tree lizards, *Urosaurus ornatus*. *Funct. Ecol.* **14**, 338–344.

Ryan, M. J., Pease, C. M. & Morris, M. R. 1992 A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the predictions of equal fitness. *Am. Nat.* **139**, 21–31.

Shuster, S. M. & Wade, M. J. 2003 *Mating systems and strategies*. Princeton University Press.

Sinervo, B. & Lively, C. M. 1996 The rock–scissors–paper game and the evolution of alternative male strategies. *Nature* **340**, 240–246.

Sinervo, B., Miles, D. N., Frankino, A. W., Klukowski, M. & DeNardo, D. F. 2000 Testosterone, endurance and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards *Horm. Behav.* **38**, 222–233. (doi:10.1006/hbeh.2000.1622)

Stamps, J. A. 1983 Sexual selection, sexual dimorphism, and territoriality. In *Lizard ecology: studies of a model organism* (ed. R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 169–204. Baltimore, MD: John Hopkins University Press.

Stamps, J. A. & Krishnan, V. V. 1997 Functions of fights in territory establishment. *Am. Nat.* **150**, 393–405.

Stamps, J. A. & Krishnan, V. V. 1998 Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. *Anim. Behav.* **55**, 461–472. (doi:0003-3472/98/020461+12$25.00/ar970612)

Stamps, J. A., Krishnan, V. V. & Andrews, R. M. 1994 Analyses of sexual size dimorphism using null growth-based models. *Copeia* **1994**, 598–613.

Stamps, J. A., Mangel, M. A. & Phillips, J. A. 1998 A new look at relationships between size at maturity and asymptotic size. *Am. Nat.* **152**, 470–479.

Toro, E., Herrel, A., Vanhooydonck, B. & Irschick, D. J. 2003 A biomechanical analysis of intra- and interspecific scaling of jumping biomechanics and morphology in Caribbean *Anolis* lizards *J. Exp. Biol.* **206**, 2641–2652. (doi:10.1242/jeb.00473)

Verwaijen, D., Van Damme, R. & Herrel, A. 2002 Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Funct. Ecol.* **16**, 842–850.

Wainwright, P. C. 1994 Functional morphology as a tool in ecological research. In *Ecological morphology: integrative organismal biology* (ed. P. C. Wainwright & S. M. Reilly), pp. 42–59. University of Chicago Press.

West-Eberhard, M. J. 2003 *Developmental plasticity and evolution*. Oxford University Press.

Whiting, M. J., Nagy, K. A. & Bateman, P. W. 2003 Evolution and maintenance of status-signalling badges: experimental manipulations in lizards. In *Lizard social behavior* (ed. S. F. Fox, J. K. McCoy & T. A. Baird), pp. 47–82. Baltimore, MD: Johns Hopkins University Press.

Zamudio, K. & Sinervo, B. 2003 Ecological and social contexts for the evolution of alternative mating strategies. In *Lizard social behavior* (ed. S. Fox, J. McCoy & T. Baird), pp. 83–106. Baltimore, MD: Johns Hopkins University Press.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.