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Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*

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Summary

1. Morphological characteristics (snout–vent length, badge area, mass, limb and head measures) and whole-animal performance capacities (sprint speed, acceleration capacity, stamina and bite force) were measured in male lizards, *Gallotia galloti*. These males were also tested in paired staged contests to assess relative fighting capacity and to link these results to morphology and performance.

2. A multivariate analysis of the four performance features revealed a clear difference between the physiological capacities of winners *vs* losers, with bite force being the most important predictor of the outcome of fights.

3. The finding that bite performance is linked to dominance fits in with the high sexual dimorphism in head size in this species, as head size is a predictor of bite force performance.

4. Winners of contests also tended to have larger total areas of blue patches on their sides, suggesting that these badges convey information on the social status of the males. However, since no correlation was found between bite force and badge size, the patches seem to contain information on a component of fighting capacity other than bite force.

Key-words: Behaviour, dominance, intrasexual competition

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Introduction

Because winners of intramale agonistic interactions often get primary access to vital resources (including females), fighting ability is an important determinant of male Darwinian fitness in many animals. Therefore, identifying the characteristics that make up a winner is central to understanding the evolution of the male phenotype. Until recently, most previous studies have focused on individual morphological, behavioural and endocrinological characters relevant to establishing social dominance (e.g. review in Andersson 1994; Berglund, Bisazza & Pilastro 1996; Molina-Borja, Padron-Fumero & Alfonso-Martin 1998; Kemp 2003), while whole-animal performance traits have received far less attention (Perry *et al.* 2004). This is unfortunate, because knowing the performance abilities relevant to the outcome of an interaction should help identify the morphological and physiological attributes that determine fighting ability, and explain why they do so (Arnold 1983; Huey *et al.* 2003a). For instance, a correlation between sprint speed and success in agonistic interactions would aid in understanding the evolution of longer limbs (e.g. in species in which fights involve rapid chases); an association between bite force and dominance would help explain the development of larger heads (e.g. in species that bite each other during combat). Moreover, the behavioural options open to an individual may be constrained by its whole-organism performance (Perry *et al.* 2004; see also Huey, Hertz & Sinervo 2003b).

Thus, several studies on lizards have examined relationships among physiological performance ability and success in agonistic interactions. The results are disparate. Garland, Hankins & Huey (1990) found a positive relationship between dominance and sprint speed in *Sceloporus occidentalis*, but dominance and stamina were unrelated in this species. Robson & Miles (2000) found that dominant *Urosaurus ornatus* males had higher sprint capacities and higher stamina than subordinate males. López & Martín (2002) found a negative relationship between sprint speed and social dominance in male *Lacerta monticola*. Finally, Perry

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et al. (2004) reported a positive correlation between dominance and endurance (but not sprint speed) in male *Anolis cristatellus*. Presently, the number of species studied is insufficient to test whether these seemingly inconsistent outcomes actually reflect interspecific differences in the types of agonistic behaviour displayed.

A possible shortcoming of previous studies is that the measurement of whole-animal performance was limited to two aspects of locomotory capacity, namely sprint speed and endurance. Speed and endurance are routinely used as indices of overall physiological capacity in lizards, and several authors have implied that they may be directly linked to dominance (but see Garland *et al*. 1990). Robson & Miles (2000) suggested that sprint speed is correlated with the frequency of head bobbing and push-up displays in *Urosaurus ornatus*, and Perry *et al*. (2004) linked endurance to the prolonged vigorous interactions in *Anolis cristatellus*. However, we can think of several other performance variables that are (more) likely to be relevant to fighting ability in lizards. One of them is acceleration capacity, the ability to develop speed from standstill, which is not often measured in lizards (Huey & Hertz 1984; Irschick & Jayne 1998). In many lizard species, the opponents in a conflict typically approach each other slowly, and then, as the conflict escalates, start launching short, forceful attacks at one another. In such a situation, acceleration capacity may be a more direct correlate of fighting ability than sprint speed, which is generally measured by chasing lizards over relatively long (> 2 m) race tracks. Moreover, sprint speed and acceleration capacity are not necessarily correlated (B. Vanhooydonck, unpublished data).

Another performance variable that seems particularly relevant is bite force. In many lizard species, escalated conflicts will result in fierce fighting during which opponents will bite each other severely on the head and other parts of the body. Although it has repeatedly been suggested that the sexual dimorphism in head size characteristics of many lizard species results from intrasexual selection for higher bite force, a correlation between bite force and success in agonistic interactions has to our knowledge been described only once (Lailvaux *et al*. 2004): in interactions between the bigger male *Anolis carolinensis*, bite force influences dominance. However, until now, performance capacities and fighting ability were always examined from a univariate perspective, neglecting the possibility of interacting effects of performance.

The goal of the present study is to establish relationships between morphological characteristics, whole-animal performance and success in agonistic interactions in males of the lacertid lizard *Gallotia galloti*. In this paper, four estimates of whole-animal performance are assessed in each individual lizard, and multivariate analyses are used to evaluate the relative influence of the different aspects of performance on the outcome of aggressive interactions.

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Materials and methods

STUDY ANIMALS

Gallotia galloti is a medium-sized diurnal (average snout–vent length, SVL, ♂ = 107 mm, ♀ = 88 mm, Molina-Borja & Rodríguez-Domínguez 2004) omnivorous lizard endemic to the Canary Islands of Tenerife and La Palma (Spain). The species is sexually dimorphic in body size, head dimensions and coloration. Males tend to be larger than females, with relatively robust heads (Molina-Borja, Padron-Fumero & Alfonso-Martin 1997; Herrel *et al*. 1999). Females and immature males are dull and cryptic in colour, while sexually mature males have a series of bright blue spots on the sides of their head and trunk (Thorpe & Richard 2001; Font & Molina-Borja 2004). The mating system is probably polygynous (Molina-Borja *et al*. 1998). Although these lizards do not seem to be strictly territorial, aggressive interactions between males are common in the field (Molina-Borja 1987a). A conflict typically starts with the two males circling each other at a distance of about 30 cm, on raised forelegs, the dewlaps extended and the anterior part of the body laterally compressed (Molina-Borja 1987b). If neither of the opponents retreats, the conflict will escalate into actual fighting, involving extremely rapid movements, turning and fierce biting. This intense phase may last up to several minutes; the total duration of an encounter may take up to 30 min (Molina-Borja *et al*. 1998). At the end, one of the males will flee, usually chased by the other one.

In June 2003, 40 adult males were collected using pitfalls at Punta Prieta (E Tenerife, Canary Islands), and transported to the University of Antwerp, Belgium. Lizards were kept individually in glass cages measuring 40 × 40 × 40 cm^3 which were provided with rocks and bark for hiding, and a light bulb (100 W) for basking (light cycle of 12:12 h light : dark). Lizards were fed twice a week with pieces of banana and tomato and once a week with field crickets, *Gryllus campestris*. Water was always available. One male died after transportation to Belgium, all the other lizards maintained good health during the experiments and were released where captured at the end of the experiment, after a medical check by local (Tenerife) authorities.

MORPHOLOGY

Lizards were weighed on an electronic balance (± 0·01 g; model FX-3200, A & D Instruments, Abingdon, UK). SVL, hindlimb length and head dimensions (length, width and height) were measured using digital callipers (± 0·01 mm; model CD-15DC; Mitutoyo, Telford, UK). Photographs of the left and right sides of each animal were taken using a digital camera (Nikon Coolpix 885, Nikon, Tokyo, Japan). From the images, the blue lateral badges were digitized with tpsDIG32 software (version 1·4, F.J. Rohlf, SUNY, Stony Brook, NY) and the area of each individual badge was calculated. The sum of all badge areas (left + right) was used as an indicator of an individual lizard's badge size.

PERFORMANCE

Prior to each performance measurement, lizards were placed in individual cloth bags and kept for at least 1 h in an incubator set at 34 °C. This procedure ensured that all measures were taken near the selected and optimal body temperatures for this species (K. Huyghe *et al.*, personal observation). Between consecutive measurements of sprint speed, acceleration capacity and bite force, lizards were allowed to rest for at least 1 h. Endurance trials were performed on separate days, with only one trial per day.

Maximal sprint speed was determined by chasing the lizards down a 2-m racetrack with a cork substrate. Along the racetrack, seven pairs of photocells, distributed at 0·25 m intervals, communicated passing times to a personal computer. Each lizard ran five times and the highest velocity over 25 cm was considered the maximal sprint speed for each individual.

Endurance capacity was determined by measuring the time an individual could walk on a treadmill, moving at the constant speed of 0·22 m s^{-1}, until exhaustion, i.e. when there was no more righting response (Vanhooydonck, Van Damme & Aerts 2001). The best performance of three trials was considered an index of an indivual lizard's stamina.

Acceleration capacity was defined as the peak acceleration value (m s^{-2}) of five escape trials. Lizards were encouraged to flee as fast as possible from standstill over a distance of 2 m on a cork substrate, and the first 0·30 m were high-speed video-filmed (250 frames s^{-1}) using a Redlake Motionscope (Redlake, San Diego, CA). On every frame of each sequence, x and y-coordinates of the snout-tip were digitized using Didge software (Image Digitizing Software, version 2·20, A. Cullum, Creighton University, Omaha, NE), and displacements per 0·004 s were calculated. The raw data were filtered with a low-pass Butterworth filter program (courtesy of P. Aerts, University of Antwerp, Belgium) and the first (velocity m s^{-1}) and second derivative (acceleration m s^{-2}) were calculated. The highest acceleration value per individual was used for further analysis.

Bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) connected to a Kistler charge amplifier (type 5058 A, Kistler Inc.). Lizards are encouraged to bite on two metal bite plates and the resulting pull on the force transducer is communicated to a portable computer (see Herrel *et al.* 1999 for details). The hardest bite out of five trials was considered an individual's maximal bite performance.

SOCIAL DOMINANCE

We organized paired staged contests to assess (relative) fighting capacity. Two randomly chosen males were placed in a terrarium (80 × 40 × 40 cm^3) and were allowed to become accustomed to the new environment for 30 min prior to the experiment. During this period, the terrarium was divided by a non-transparent removable wall, with one male on each side. Both males had access to stones for hiding and a light bulb (100 W) for basking, which allowed both males to have an equal access to their heat sources for thermoregulation. After 30 min, the dividing wall was removed, the periphery lights were turned off and a single light bulb (100 W) was switched on, providing heat to the centre of the arena only. This induced the lizards to compete over a single basking spot. The behaviour of the two contestants was filmed from above using a Panasonic camera (colour CCTV, model WV-CP150E, Matsushita Communication Industrial Co., Yokohama, Japan) connected to a time lapse recorder (Panasonic AG 6730, Matsushita Communciation Industrial Co.). Trials were ended after 30 min, or sooner (with a minimum of 15 min) if the outcome was obvious at an earlier stage. The lizards were then put back in their home terraria and left undisturbed for at least 2 days until the next test.

From the video-recordings, we determined the winner and loser of every staged encounter. A contestant was given a score of +1 each time he attacked his opponent and a score of −1 whenever he fled from his opponent. The lizard with the highest score at the end of the observation period was considered the winner, and received a score of 1 (0 for the loser) for this contest. This binomial trait was used in the statistical analyses for an honest comparison between contests and individuals.

STATISTICAL ANALYSES

All morphological and performance variables were log$_{10}$-transformed prior to statistical analysis, because not all had a normal distribution. Relationships among performance variables were assessed using Pearson correlation analyses. Principal component analysis (varimax rotation) was used to collapse the highly intercorrelated head measures into one single 'head size' variable. The contribution of morphological variables (SVL, mass, head size, hindlimb length and badge area) to the variation in performance was assessed through multiple regression analyses (backward stepwise elimination). We report partial regression coefficients (B) and partial correlation coefficients (r_P) if more than one variable was retained in the final model. Testing whether differences in performance between contestants can help explain the outcome of a fight was complicated by the fact that the same individuals were tested with different opponents in consecutive experiments, introducing an element of non-independency. To confront this potential problem, we used the procedure MIXED (SAS, version 8·2) to fit a linear model, with type of performance (sprint speed, acceleration, endurance and bite force), individual number, confrontation number and outcome (win/lose) as independent variables and the (standardized) performance measurements as the dependent variable. The performance data were standardized to remove any effects of differential scaling. In this way every contest is split into eight different data points (two individuals × four performance traits), and the repetition of individuals can be accounted for. This procedure results in an overall F-statistic, portraying general (multivariate) differences in performance between winners and losers, and allows testing of which performance variable contributes most to the chance of winning a fight. The latter tests take into account any correlations that exist between the performance variables. The residuals of the fitted model were normally distributed (Shapiro Wilk's $W = 0·98$). Many previous studies that have used staged contests to detect determinants of dominance have ignored possible effects of repeated testing of the same individuals. To aid in comparison, we therefore also report the results of univariate paired sample t-tests, although in fact, the conclusions appear independent of the statistical approach used.

Results

MORPHOLOGY

A summary of the morphological measurements is given in Table 1. Log_{10}-transformed values of body mass ($r = 0·61$, $P < 0·001$) and hindlimb length ($r = 0·45$, $P = 0·004$) correlated positively with $\log_{10}$[SVL]. The three head variables (head length, head width and head height) were strongly intercorrelated (all $r > 0·65$, all $P < 0·001$). Principal component analysis on $\log_{10}$-transformed head measures yielded one composite variable (hereafter referred to as 'head size'), which accounted for 80% of the total variation and showed high positive loadings for all original variables (all loadings > 0·88). Head size correlated with $\log_{10}$[SVL] ($r = 0·60$, $P < 0·001$). The area of the lateral blue badges was independent of $\log_{10}$[SVL] ($r = 0·17$, $P = 0·30$), but correlated positive with $\log_{10}$[mass] ($r = 0·54$, $P < 0·001$). The total area was not correlated with the number of individual spots ($r = 0·091$, $P = 0·58$).

Table 1. Descriptive statistics for the morphological and performance variables measured on male *Gallotia galloti* lizards used in this study

Variable	Mean	SD	Min	Max	N
Snout–vent length (mm)	110·61	4·84	102·03	121·49	39
Mass (g)	40·91	4·50	32·38	54·12	39
Head length (mm)	28·48	1·17	26·15	30·53	39
Head height (mm)	15·32	0·88	13·33	17·87	39
Head width (mm)	19·83	1·08	17·94	22·04	39
Hindlimb length (mm)	40·52	1·17	37·60	42·80	39
Badge size (mm^2)	332·06	201·95	85·74	1124·03	39
Sprint speed (cm s^{-1})	211·09	47·40	138·89	312·50	38
Acceleration (cm s^{-2})	5611·81	1367·48	2611·30	7891·87	38
Endurance (s)	341·54	85·79	185·70	513·78	37
Bite force (N)	29·82	3·80	23·19	38·83	38

PERFORMANCE

Descriptive statistics for the performance variables are given in Table 1. In general, performance variables tended to vary independently of each other (all $r < |\,0·28\,|$, all $P > 0·10$), but bite force capacity was positively correlated with sprint speed ($r = 0·38$, $P = 0·02$).

In general, interindividual variation in morphology was a poor predictor of differences in performance. For sprint speed, multiple regression with backwards elimination resulted in a marginally significant model ($r^2 = 0·076$, $F_{1,36} = 2·98$, $P = 0·09$) with badge size as the only contributing independent variable. Lizards with larger badge sizes tended to run faster (partial regression coefficient $B \pm \text{SE} = 0·11 \pm 0·07$). No significant model was obtained for acceleration capacity ($F_{1,36} = 1·22$, $P = 0·3$). Endurance capacity was related to SVL only ($r^2 = 0·12$, $F_{1,35} = 4·94$, $P = 0·03$), with smaller lizards running for longer ($B = -2·042 \pm 0·92$). For bite force, three predictor variables were retained in the final model ($r^2 = 0·67$, $F_{3,34} = 31·47$, $P < 0·001$): mass ($B = 0·67 \pm 0·16$, $r_P = 0·59$, $P < 0·001$), hindlimb length ($B = -1·24 \pm 0·42$, $r_P = -0·45$, $P = 0·006$) and head size ($B = 0·024 \pm 0·007$, $r_P = 0·49$, $P = 0·002$), suggesting that heavier lizards with relatively short hindlimbs and more massive heads can bite harder.

SOCIAL DOMINANCE

Some 109 of the 183 encounters staged during this study resulted in clear aggressive interactions. In these trials, males typically approached each other, often in the vicinity of the basking spot, and engaged in threatening behaviour, soon followed by one male attacking (i.e. approaching at high speed) the other. Most of the times the other male fled immediately, but sometimes there were short physical combats during which the lizards rolled over each other, trying to or actually biting their opponent. Such escalated fights lasted for a few seconds only and resulted in one male retreating. In most trials, several of these interactions could be observed. The outcome of these 109 encounters was almost always immediately evident, one of the two males being clearly more 'dominant' and the other more 'submissive'. The other 74 staged encounters did not result in interactions and could not be used in our analyses. This usually happened because one or both males retreated to a refuge and remained there for the full 30 min of the observation period.

After $\log_{10}$-transformation of the data, all variables had a normal distribution (Shapiro Wilk's $W = 0·98$, $P < 0·001$). Winners and losers differed in overall performance ($F_{4,143} = 3·19$, $P = 0·015$). Examination of the results for the individual performance variables (in the multivariate setting) revealed that differences in bite force contributed most to the outcome of a fight ($t_{146} = 2·65$, $P = 0·009$). Winners tend to have higher bite capacities than losers (mean ± SE standardized values of bite force for winners: $0·17 \pm 0·08$; for losers:

Table 2. Mean (and standard error, SE) differences in performance between winners and losers of 109 staged encounters between male *Gallotia galloti* lizards. A positive difference indicates that the winner has a better performance than the loser. The *t*-statistics are for univariate paired *t*-tests ignoring the repeated use of the same individuals and are given for comparative purposes only. See text for more appropriate multivariate tests

	Mean difference	SE	*t*	df	*P*
Velocity (m s^{-1})	–0·0029	0·0065	–0·451	105	0·65
Acceleration (m s^{-2})	–0·79	1·91	–0·345	100	0·73
Endurance (s)	–7·36	14·00	–1·516	95	0·13
Bite force (N)	14·69	0·44	2·582	105	0·01

–0·17 ± 0·10). Including body size as well as bite force capacity in the analysis still retained a model with bite force as a determining factor for the outcome of fights: ($t_{126} = 2{\cdot}53$, $P = 0{\cdot}013$): winners have a higher bite force capacity than losers in spite of a possible size difference. The effects of differences in sprint speed ($t_{150} = 0{\cdot}63$, $P = 0{\cdot}53$) and acceleration capacity ($t_{110} = 0{\cdot}22$, $P = 0{\cdot}82$) were clearly not statistically significant, while the marginally significant effect of differences in endurance ($t_{117} = -1{\cdot}76$, $P = 0{\cdot}08$) suggests that winners had lower stamina (0·11 ± 0·10) than losers (–0·12 ± 0·09). Very similar results were obtained with univariate paired *t*-tests (Table 2).

Although colour badges are often said to signal fighting ability, we found no association between badge size and bite force or endurance, the two performance variables that differed between winners and losers in the experiments. To examine the possibility that badge size signals affects the outcome through an unmeasured factor, we used the same multivariate method as when testing the effect of the performance variables, but this time with badge size and mass as the target variables. Mass was included in the analysis because it was shown earlier that badge size is correlated with mass. Both mass ($t_{142} = 4{\cdot}66$, $P < 0{\cdot}0001$) and badge size ($t_{142} = 3{\cdot}67$, $P = 0{\cdot}0003$) differed between winners and losers. Winners were usually heavier and had larger badge sizes than losers.

Discussion

Our results show that winners of agonistic interactions between male *Gallotia galloti* lizards differ from losers in their physiological performance. Until now, dominance in lizards has been associated with locomotor performance (Garland *et al*. 1990; Robson & Miles 2000; Perry *et al*. 2004; but see López & Martín 2002), but our findings suggest a more prominent role for bite force capacity. As far as we know, only one other study has demonstrated a correlation between bite force and social dominance in lizards (Lailvaux *et al*. 2004).

According to our results, badge size conveys information about a male *Gallotia galloti*'s dominance. This confirms previous findings in other lacertids (Olsson 1992, 1994; Martín & Forsman 1999; López, Martín & Cuadrado 2004) and other lizard families (Cooper & Vitt 1988; Zucker 1994; review in Whiting, Nagy & Bateman 2003). However, since no correlations between badge size and bite force or head size were found, badge size seems to signal a component of fighting capacity other than bite force (e.g. motivation). In an earlier study, Molina-Borja *et al*. (1998) found no relationship between dominance and the number of lateral patches in *Gallotia galloti*. This does not contradict our findings, since there was no necessarily significant correlation between the number of badges and the total badge size in our sample. It should be noted that our results on the effect of badge size must be interpreted with caution, since our measurements concerned spots visible by the human eye only. Ultraviolet photography and spectrophotometry in *Gallotia galloti* have shown that the blue badges reflect UV and are bordered by areas of non-reflective skin (Font & Molina-Borja 2004). The badges may therefore communicate information through other aspects than mere size. Clearly, this is an area that deserves more detailed research in the future.

In our experiments, a substantial part of the intraspecific variation in bite force could be explained by differences in body mass, head size and hindlimb length. The fact that larger individuals and individuals with relatively large heads could bite harder is in line with earler findings (e.g. Herrel, Van Damme & De Vree 1996; Herrel *et al*. 1999; Verwaijen, Van Damme & Herrel 2002). The negative correlation between bite force and hindlimb length is more enigmatic; we know of no studies that have established direct or indirect (e.g. via hormones) relationships between limb length and bite capacity.

Because male *Gallotia galloti* are highly aggressive in the field and will attack and bite other males, it is tempting to link dominance and bite capacity directly. This would concur with the sexual dimorphism in (relative) head size (Bischoff 1971; Molina-Borja *et al*. 1997; Herrel *et al*. 1999), the disproportionately high bite forces in males (Herrel *et al*. 1999), and the importance of head size in dominance in this species (Molina-Borja *et al*. 1998). Previous studies on other lizard species have provided indications of the potential importance of bite force capacity in settling territorial disputes. Intraspecifically, male head size is correlated with dominance in male *Uta palmeri* (Hews 1990), *Iguana iguana* (Pratt *et al*. 1992), *Cyclura nubila* (Alberts *et al*. 2002), *Lacerta monticola* (López, Munoz & Martín 2002) and *Anolis cristatellus* (Perry *et al*. 2004). Interspecifically, head size dimorphism and the occurrence of male combat are associated in the Eublepharidae (Kratochvíl & Frynta 2002) and herbivorous Iguaninae (Carothers 1984). Since head dimensions are directly related to bite force (Herrel *et al*. 1996, 1999; Verwaijen *et al*. 2002), it seems likely that bite force, through its effect on dominance, is a performance trait under sexual selection. However, the design of our experiment does not allow us to rule out the possibility that bite force and thus social dominance are influenced by a third, unmeasured variable. For instance, Garland *et al*. (1990), Robson & Miles (2000) and Perry *et al*. (2004) have already argued that testosterone may affect both dominance and locomotory measures of physiological capacity. Moreover, in *Sceloporus undulatus*, experimentally elevated plasma testosterone levels induced a greater sprint speed ability and burst stamina (Klukowski, Jenkinson & Nelson 1998). Although we are unaware of studies that have investigated the effect of sex hormones on bite force in any species, there are several reasons to expect such a relationship. First, it is well known that sex hormones influence mandibular bone growth in mice (Fujita *et al*. 2004), rats (Verdonck *et al*. 1998; Gebhardt & Pancherz 2003) and humans (Verdonck 1997; Verdonck *et al*. 1999). Second, sex hormones may influence bite performance through their effects on the muscles of mastication. For instance, in adult guinea pigs (Lyons, Kelly & Rubenstein 1986) and mice (Eason *et al*. 2000), androgens alter the composition of masseter muscle fibres and are required for the maintenance of sexual dimorphism in that muscle. On the other hand, it is also possible that these hormones are actually influencing social dominance, through their effects on bite performance.

Sexual dimorphism in head size is typical of a wide range of animal species (e.g. fish, Reyes Gavilan, Ojanguren & Braña 1997; amphibians, Serra-Cobo, Uiblein & Martinez-Rica 2000; birds, Temeles *et al*. 2000; mammals, Berge & Penin 2004; snakes, Shine 1991) and particularly of lizards (Vitt & Cooper 1985; Braña 1996; Herrel *et al*. 1999; Butler & Losos 2002; Kratochvíl & Frynta 2002). In addition there is growing evidence for a concurrent dimorphism in bite force (e.g. Herrel *et al*. 1996; Julien *et al*. 1996; Verwaijen *et al*. 2002; but see Erickson, Lappin & Vliet 2003). Unraveling the evolutionary and mechanistic relations between dominance, bite force and hormone levels therefore seems a fruitful avenue for future studies.

Our results seem to stand in contrast with earlier findings that dominance in lizards is correlated with locomotor performance (Garland *et al*. 1990; Robson & Miles 2000; Perry *et al*. 2004). At this time, it is hard to assess whether and why lizard species differ in the performance variables that determine their dominance status. Differences in social and sexual behaviour may select for different performance variables: in species in which disputes are decided in fast agonistic interactions (such as in *Sceloporus occidentalis* and *Urosaurus ornatus*), sprint speed or acceleration might be important; in species in which conflicts involve lengthy sequences of display behaviour (such as in *Anolis cristatellus*), endurance may be more relevant; in species that readily engage in physical combat, bite force might be decisive. Of course, interspecific variation in performance variables is likely to be subject to differences in other selective pressures (e.g. predation intensity) as well. In any case, the paucity of species studied, discrepancies in the methodology used by different authors (e.g. in the measurement of endurance) and the fact that bite force has not often been measured before, currently prevent tests of this idea. Our finding that some of the performance variables may be intercorrelated further stresses the need to measure different, potentially important variables simultaneously. In addition, inferences based on experiments in the laboratory need to be verified with observations made in (more) natural settings (as in Perry *et al*. 2004).

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