

Divergent roles for multiple sexual signals in a polygynous lizard

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Summary

1. An unresolved issue in sexual selection concerns the utility of multiple sexual signals that are used simultaneously during displays. We examined male lizards (*Urosaurus ornatus*) that exhibit two colourful ornaments (throat patch and belly patch) during territorial displays. Populations of *Urosaurus ornatus* can be polymorphic in throat coloration, and previous studies have shown that the morphs differ in behavioural aggression. We assume that throat coloration correlates with behavioural aggression in our population, as for other populations of *U. ornatus*.

2. We show that these different morphs do not differ significantly in morphological shape or bite force, a key aspect of fighting capacity. However, by contrast, the size of the belly patch is a significant predictor of maximum bite force, which is a predictor of dominance in other lizards.

3. We suggest that belly patch size and throat patch coloration are largely exclusive in that dominant individuals can exhibit small belly patches and low bite forces, whereas subordinate individuals can have large belly patches and high bite forces. Thus, embedded within the same male lizard display are divergent sexual structures that signal different traits, implying that the possession of multiple sexual signals within animals may be favoured by selection.

Key-words: sexual selection, performance, lizards, signals, evolution

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Introduction

Sexual structures represent some of the most colourful and elaborate structures in the animal kingdom (Andersson 1994; Berglund, Bisazz & Pilastro 1996; Whiting, Nagy & Bateman 2003). Males of many animal species possess colourful and elaborate sexual structures that are used for several purposes, including signalling to rival males and potential predators (Whiting *et al.* 2003). The exact role of male sexual signals is a topic of hot debate within the evolutionary community. Some studies have focused on understanding whether males with particularly large and/or colourful signals tend to acquire high-quality territories and relatively more matings (Andersson 1994). Other studies have examined whether the relative size of male sexual structures are correlated with whole-organism performance capacities (Vanhooydonck *et al.* 2005). Although valuable, these studies have largely focused on the role of a single prominent sexual structure within a particular taxon. Signalling is

an inherently complex process, and many animals not only exhibit a behavioural repertoire of stereotyped displays, but also possess multiple sexual signals that are used simultaneously when signalling to rival males, females and predators (Leal & Rodriguez-Robles 1997).

Within species that possess multiple signals, little is understood concerning whether they provide the same information on male quality, and an ongoing debate concerns whether the relative size, colour and/or intensity of male sexual signals are 'honest' indicators of male quality (Zahavi 1975; Berglund *et al.* 1996; Vanhooydonck *et al.* 2005). For example, some studies have shown that the relative size of the prominent dewlaps of male *Anolis* lizards are honest indicators of maximum bite force (Vanhooydonck *et al.* 2005), which is a key determinant of dominance in male lizards (Lailvaux *et al.* 2004; Perry *et al.* 2004). However, these studies have focused primarily on single sexual ornaments, and many animals possess multiple sexual ornaments (Andersson 1994).

There are three likely possibilities regarding the roles of multiple sexual signals within a species (Moller & Pomiankowski 1993). One is that differing sexual signals

will reinforce one another by transmitting the same information to the receiver. A second is that different sexual signals will transmit differing information; in this case, one signal might transmit information on male behaviour (i.e. level of aggressive behaviour), whereas another signal might transmit information on other aspects of male quality, such as male performance capacity. A final possibility is that male sexual signals are not currently used as indicators of male quality or have arisen for reasons unassociated with female mate choice (Moller & Pomiankowski 1993).

Previous studies have shown that two key non-exclusive factors are strong predictors of male fighting success, namely behavioural aggression and high functional capacities that bear directly on fighting (e.g. Barlow, Rogers & Fraley 1986; Whiting *et al.* 2003). Some studies have shown that particularly aggressive invasive species, for example, can push out equally sized, or sometimes even larger (and hence probably stronger) competing species (e.g. Losos & Spiller 1999; Dame & Petren *in press*; see also Jenssen, Decourcy & Congdon 2005 on size/aggression). Recent studies have also shown that whole-organism performance capacities represent one useful measure of male quality, particularly in polygynous lizards (Garland, Hankins & Huey 1990; Robson & Miles 2000; Sinervo *et al.* 2000; Perry *et al.* 2004; Huyghe *et al.* 2005). For example, maximum bite force is a predictor of male territory size in Collared Lizards (*Crotaphytus collaris*, Lappin & Husak 2005; see also Hews 1990) and male dominance in Green Anole Lizards (*Anolis carolinensis*, Lailvaux *et al.* 2004). Additionally, the link between these whole-organism performance measures and the relative size of male sexual structures has been noted in several species of lizards (Vanhooydonck *et al.* 2005).

We examined the polymorphic lizard *Urosaurus ornatus* as a model system for testing the information content of multiple sexual signals. Prior studies have shown that in some populations of *U. ornatus*, variation in throat patch coloration reflects behavioural aggression, which has been shown to be a significant predictor of dominance among male morphs (Thompson & Moore 1991b; Carpenter 1995; Hews *et al.* 1997). Prior studies indicate that populations of *U. ornatus* may have up to five male morphs that are distinguished by throat coloration (defined by a combination of background and dewlap coloration; Fig. 1). These morphs may include animals with blue, orange or yellow background colours and two bicoloured morphs that have blue dewlaps on top of yellow or orange background (Hover 1985; Thompson & Moore 1991a,b; Hews *et al.* 1997). Prior work has also shown that the organizational effects of hormones are crucial in the development of these morphs (Moore, Hews & Knapp 1998). In some populations, male morphs with a blue dewlap (regardless of background colour) are behaviourally dominant over other morphs (Hover 1985), as evidenced by their tendency to bite other morphs (e.g. orange-dewlapped morph) more often (Moore *et al.* 1998). However, no

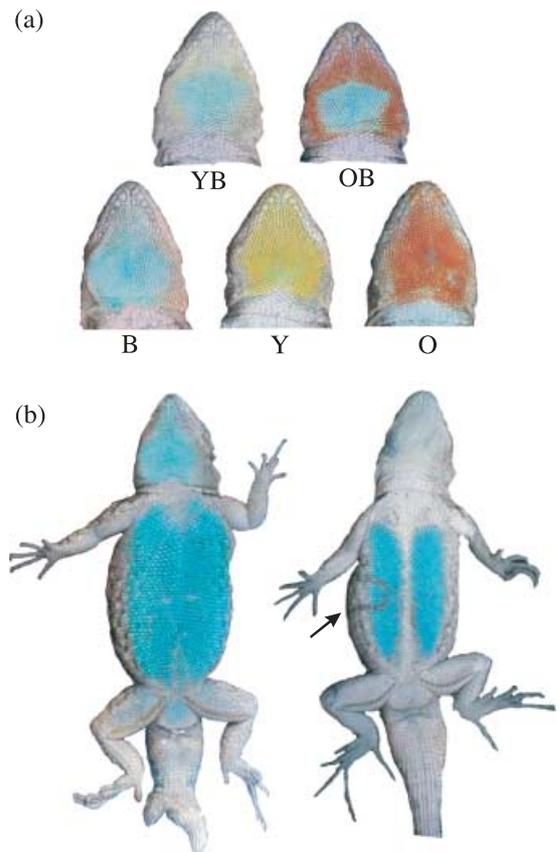


Fig. 1. (a) Throat coloration consists of two colours, the base background colour and the more localized dewlap colour. The five morphs identified in our population are the yellow-blue (YB), orange-blue (OB), blue (B), yellow (Y) and orange (O). The dewlap area is most visible in the bicoloured morphs as a blue patch, in the bottom three morphs the background and dewlap coloration are identical. (b) Ventral view of two individuals of *U. ornatus* displaying the variation in the size of the bright blue belly patches that are displayed during agonistic interactions. The arrow indicates a bite mark incurred during fighting.

studies have examined whether the coloration or size of these throat patches are significant predictors of male performance capacity, predictors which might in turn explain differential dominance among some morphs. We examined these predictors as well as the relative size of a more widespread sexual signal within lizards (colourful belly patches) to determine whether they are also correlated with male performance capacity. Belly patches are widespread in the males of many lizard species, and are displayed in conjunction with the dewlap in *Urosaurus* lizards during displays to rival males and females (Fig. 2).

We gathered a large sample of male *Urosaurus ornatus* lizards during the peak of the breeding season (May–July) in the South-western United States, and quantified throat coloration and size, belly patch size, morphology and two key aspects of male performance capacity (maximum bite force and maximum sprint speed). We then tested whether these two sexual signals (throat coloration/size and belly patch size) transmit the same information on



Fig. 2. A male *Urosaurus ornatus* displaying the dewlap and belly patches used for signalling during intraspecific interactions. Signals are accentuated by ventral extension of the hyoid to expose the dewlap and lateral compression of the body to expose the blue belly patches characteristic of many phrynosomatid lizards.

male performance capacity and morphological shape, or alternatively, provided either different information or no information at all.

Materials and methods

Animals were captured during the months of May, June and July 2005 at Wet Beaver creek in north-central Arizona, which is a mid elevation (1100 m) site characterized by a perennial stream dominated by a boulder creek bed and large cottonwood trees. A total of 159 adult male *Urosaurus ornatus* were captured. After capture, we measured morphology, throat and belly patch size, and two kinds of performance: bite force and sprint speed. Bite force and sprint speed were measured on separate days to avoid animal fatigue. Because temperature can have an effect on patch colour, bite force and sprint speed, all of these measurements were taken at field ambient temperatures of 28–32 °C, which is similar to the animals' preferred field temperatures (Lowe & Vance 1955; Pianka 1986) at this elevation. Animals were released within 48 h of capture at the initial site of capture.

DEWLAPS AND BELLY PATCHES

Animals were pressed against a piece of glass to expose the animals' undersides and produce a clear view of the belly and throat patches. A digital photograph was then

taken using a Canon EOS Digital Rebel (Canon U.S.A. Inc., One Canon Plaza, Lake Success, NY 11042) with a scale bar in view. Digital photographs were imported into Image J (W. S. Rasband, ImageJ, US NIH, Bethesda, MD, <http://rsb.info.nih.gov/ij/>, 1997–2006) and the belly and throat patches were digitized to calculate the total area covered by each patch. While the belly patches are generally visible as two discrete patches in most *Urosaurus ornatus*, in some individuals the belly patches are continuous; therefore, we present belly patch area as the sum of total patch area. We found five colour morphs, defined by throat coloration (the combination of a background and dewlap colour), at our field site: yellow (Y), orange (O), blue (B), yellow-blue (YB) and orange-blue (OB) (Fig. 1). The dewlap colour in the first three morphs is identical to the background colour, whereas the latter two morph colours represent the background and dewlap coloration, respectively. While background colour was easily determined, the considerable variation in size and colour of the dewlap required use of the methodology described by Thompson & Moore (1991a) to categorize its coloration. Using their criteria, if the dewlap contained more than 10% blue in a concentrated spot, then it was considered to be a blue dewlapped morph; if it contained less than 10%, then the colour was recorded as the same as the background coloration. In our study site, the most common morphs were the blue 35% (56) and yellow-blue morphs 31% (50), with the yellow 15% (24) and orange-blue 14% (22) being less common and the orange morphs 4% (7) extremely rare.

MORPHOLOGY

To examine whether morphs differ morphologically, we measured morphological characters of the head and limbs that have been found to be predictors of performance (bite force and sprint speed) in other species of lizards. We measured body mass to the nearest 0.01 g using a pesola scale. Additionally, the following morphological measurements were made using digital callipers (Mitutoyo CD-15 DC (Mitutoyo Corporation, 965 Corporation Blvd., Aurora, ILL 60502); precision 0.01 mm): snout to vent length (svl), head length (hl), head width (hw), head height (hh), mandible length (ml), body width (bw), body height (bh), tail length (tl), femur length (fl), tibia length (tbl), metatarsus length (mtl) and longest toe (lt).

PERFORMANCE MEASURES

Bite forces were measured using a Kistler piezoelectric force transducer (type 9203, Kistler Inc., Kistler Instrument Corp., 75 John Glenn Drive, Amherst, NY 14228) mounted in a custom holder (see Herrel *et al.* 1999) and connected to a portable Kistler charge amplifier (type 5995A). Animals were persuaded to bite on the bite plates connected to the transducer, and the maximum value of five trials was taken as each

individual's maximum bite force. To measure maximal sprint speeds, we used an electronic racetrack with infrared photocells placed every 25 cm. The track surface was a $3 \times 0.20 \text{ m}^2$ wide board covered with cork to facilitate traction. Maximal sprint speeds were elicited by chasing the lizard down the runway of the track. Each lizard was run three times, with intervals of 30–45 min separating each trial. The fastest 25-cm interval recorded was used as an estimate of an individual's maximum sprint speed. Prior studies on other lizard species using this methodology have found sprint speed measurements to be highly repeatable (Huey & Dunham 1987).

DATA ANALYSES

Statistical analyses were performed using SPSS v.12 (SPSS inc., Chicago, IL) on logarithmically (\log_{10}) transformed variables. Because performance differences among morphs may solely be determined by differences in body size, we first performed an analysis of variance comparing the masses and snout–vent lengths of the five morphs. Although snout–vent length did not differ ($F_{4,154} = 2.111$, $P = 0.082$), body masses did ($F_{4,154} = 5.252$, $P = 0.001$), and a Bonferroni post-hoc test revealed that it was primarily orange-blue morphs that were lighter than blue ($P = 0.009$) and yellow morphs ($P = 0.040$). Because differences in both absolute and relative size of morphological traits may influence interactions among males, we examined differences in morphology and performance using both absolute and size-corrected data. Size-corrected data were derived by calculating the residuals from regressions of snout–vent length regressed against each of the morphological and performance variables.

To compare both the morphology and performance of *Urosaurus ornatus* morphs, we performed both ANOVAS (performance) and MANOVAS (morphology) with morph type (throat and also dewlap coloration) as the independent variable and morphology and performance as the dependent variables. We then examined the relationships among background, dewlap and belly patch size and our performance measures. Separate regression analyses were performed with either background or dewlap patch size as the independent variable, regressed against bite force and sprint speed as dependent variables. Because there are several studies indicating that animals with any blue in their throat patch (whether blue, yellow-blue or orange-blue) are often dominant over yellow and orange throated morphs, we also performed the above analyses comparing blue throated individuals (blue, yellow-blue, or orange-blue) to the yellow and orange throated morphs.

Results

SIZE-CORRECTED ANALYSES

A MANOVA using all morphological variables did not reveal significant differences in head or limb dimen-

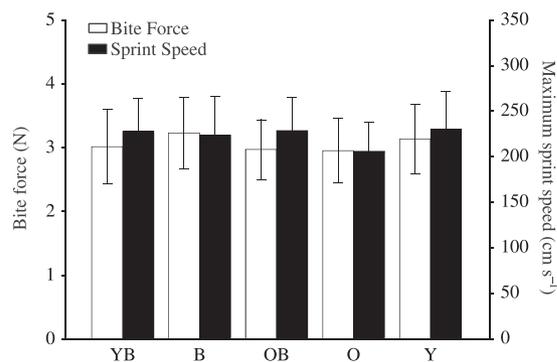


Fig. 3. Bar graphs displaying mean and standard deviation of bite force and sprint speeds for all five *Urosaurus ornatus* morphs in our population. There were no differences between morphs in either measure of performance, suggesting that throat coloration does not provide information about either of these measures of male performance capacity.

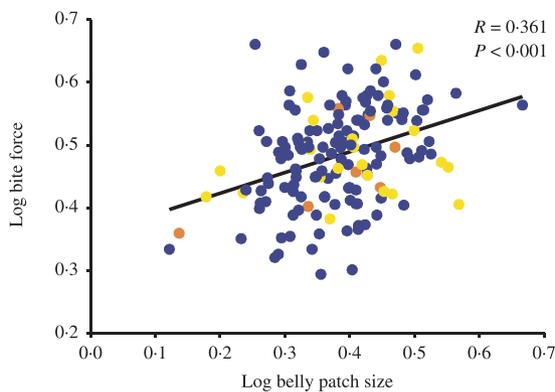
sions among the morphs (Wilks' lambda $F = 0.977$, $P = 0.532$). We performed separate ANOVAS to determine if residual bite force or residual sprint speed was associated with throat coloration. The morphs did not differ significantly in residual sprint speed ($F = 0.590$, $P = 0.670$; Fig. 3) or residual bite force ($F = 0.626$, $P = 0.645$; Fig. 3). Previous studies have shown that, in some populations, animals having blue dewlaps (regardless of background colour) tend to be dominant males, in part because of increased aggressive behaviour (Moore *et al.* 1998). As these studies have indicated that orange-blue and yellow-blue throated are behaviourally equivalent to blue throated morphs, we compared all blue dewlapped individuals (orange-blue, yellow-blue and blue) against the yellow and orange dewlapped morphs using the contrasts from the above ANOVA. These contrasts showed that the blue dewlapped morphs did not differ significantly in morphology, residual sprint speed or residual bite force when compared with yellow or orange dewlapped morphs (all P -values > 0.25 , Table 1).

While neither morphology nor performance differed significantly among morphs, it is possible that the size of the background and/or dewlap patch, regardless of colour, may be used to indicate morph differences in performance and/or morphology. However, regressions of residual background size against residual bite force ($r = 0.041$, $F_{1,105} = 0.181$, $P = 0.672$) and residual sprint speed ($r = 0.050$, $F_{1,105} = 0.264$, $P = 0.608$) revealed that these performance measures were not significantly correlated with patch size. Additionally, the size of the dewlap is not significantly correlated with either residual bite force ($r = 0.101$, $F_{1,135} = 1.399$, $P = 0.239$) or residual sprint speed ($r = 0.092$, $F_{1,134} = 1.145$, $P = 0.286$).

To examine whether information could be transmitted by belly patch size, we regressed residual belly patch size against both residual sprint speed and residual bite force. Residual sprint speed showed no significant correlations with residual belly patch size ($r = 0.029$, $F_{1,156} = 0.135$, $P = 0.714$), but residual belly patch size was a significant predictor of residual bite force

Table 1. Mean and standard deviation of morphological variables, signal size and performance measurements for the five throat colour morphs

	Blue	Orange	Orange-blue	Yellow	Yellow-blue
Mass (g)	0.461 ± 0.061	0.393 ± 0.020	0.401 ± 0.079	0.462 ± 0.076	0.426 ± 0.062
Snout-vent length (cm)	5.157 ± 0.262	5.035 ± 0.171	4.991 ± 0.264	5.135 ± 0.265	5.064 ± 0.223
Tail length (cm)	6.320 ± 2.316	6.753 ± 1.347	6.229 ± 2.789	5.910 ± 2.419	6.470 ± 2.644
Body width (cm)	1.380 ± 0.114	1.317 ± 0.143	1.368 ± 0.114	1.418 ± 0.121	1.349 ± 0.111
Body height (cm)	0.787 ± 0.076	0.736 ± 0.052	0.737 ± 0.057	0.777 ± 0.060	0.753 ± 0.070
Head length (cm)	1.185 ± 0.061	1.158 ± 0.041	1.155 ± 0.049	1.190 ± 0.058	1.156 ± 0.048
Head height (cm)	0.627 ± 0.033	0.620 ± 0.029	0.610 ± 0.032	0.622 ± 0.026	0.619 ± 0.041
Head width (cm)	0.960 ± 0.048	0.930 ± 0.023	0.940 ± 0.050	0.967 ± 0.046	0.943 ± 0.048
Femur length (cm)	1.248 ± 0.084	1.175 ± 0.091	1.213 ± 0.092	1.239 ± 0.080	1.218 ± 0.068
Tibia length (cm)	1.056 ± 0.067	1.014 ± 0.065	1.031 ± 0.064	1.036 ± 0.054	1.027 ± 0.057
Metatarsus length (cm)	0.565 ± 0.045	0.549 ± 0.038	0.559 ± 0.043	0.561 ± 0.045	0.571 ± 0.039
Longest toe length (cm)	0.785 ± 0.058	0.746 ± 0.036	0.786 ± 0.060	0.805 ± 0.074	0.784 ± 0.046
Total belly patch area (cm ²)	2.582 ± 0.538	2.423 ± 0.276	2.262 ± 0.450	2.599 ± 0.533	2.373 ± 0.390
Background area (cm ²)	0.806 ± 0.223	1.061 ± 0.108	0.883 ± 0.180	0.941 ± 0.187	0.835 ± 0.165
Dewlap area (cm ²)	0.375 ± 0.089	0.355 ± 0.075	0.313 ± 0.063	0.397 ± 0.089	0.328 ± 0.095
Sprint speed (m s ⁻¹)	2.235 ± 0.412	2.057 ± 0.414	2.276 ± 0.311	2.302 ± 0.416	2.274 ± 0.351
Bite force (N)	3.236 ± 0.568	2.952 ± 0.478	2.965 ± 0.627	3.133 ± 0.465	3.008 ± 0.557

**Fig. 4.** Linear regression of the log of belly patch size plotted against the log of bite forces. Coloured data points denote the dewlap coloration of the different morphs; yellow (yellow morph), orange (orange morph), blue (blue, orange-blue and yellow-blue morphs).

($r = 0.182$, $F_{1,156} = 5.363$, $P = 0.022$), with animals with relatively larger belly patches having higher bite forces (Fig. 4). Thus, it appears that whereas the throat coloration or size does not reveal any information about the performance measures we examined, the size of the belly patch is a significant predictor of an individual's bite force capacity.

NON-SIZE-CORRECTED ANALYSES

Because the absolute size of ornaments and morphology may also be important in signalling, we also performed the above analyses without correcting for body size. A MANOVA comparing the morphology and performance of the morphs revealed that morphs significantly differ morphologically in body height ($F = 2.971$, $P = 0.021$) and head length ($F = 3.128$, $P = 0.017$), but post-hoc tests failed to reveal significant differences between specific morphs. Neither maximum sprint speed ($F =$

0.615 , $P = 0.652$) nor bite force capacity ($F = 1.530$, $P = 0.196$) differed between morphs. As in the size-corrected analysis, we also compared blue dewlapped animals (OB, YB, B morphs; see above) with the orange and yellow morphs, and the ANOVAs revealed no significant differences in either morphology ($F = 0.884$, $P = 0.415$), sprint speed or bite force ($F = 0.290$, $P = 0.749$) between the different morphs.

Regression analyses of both background and dewlap patch size regressed against maximum sprint speed revealed that the absolute size of these badges does not provide information about locomotor ability. However, in contrast to the size-corrected data, bite force is significantly correlated with the absolute size of both the background throat coloration ($r = 0.235$, $F_{1,105} = 6.136$, $P = 0.015$) and the absolute size of the dewlap coloration ($r = 0.256$, $F_{1,105} = 9.507$, $P = 0.002$). This result is not surprising in that both the size of the background coloration and the size of the dewlap coloration increase with body size, and bite force also increases with body size. Regression analysis of belly patch size regressed against maximum sprint speed indicate that the two variables are not correlated ($r = 0.016$, $F_{1,156} = 0.038$, $P = 0.846$). However, as with the size-corrected data, bite force is significantly correlated with belly patch size ($r = 0.361$, $F_{1,105} = 23.583$, $P > 0.001$).

Discussion

The role of sexual signals in conveying information on male quality has been a controversial topic for researchers interested in sexual selection, especially in instances in which animals exhibit multiple sexual structures that are used simultaneously during displays. Our study provides a fresh insight by showing that, embedded within the same male display, are two sexual structures that independently act as indicators of functional capacity (belly patch size) and possibly behavioural aggression

(dewlap colour). Specifically, we showed that different male morphs of the lizard *Urosaurus ornatus* do not differ significantly in performance (bite force and sprint speed) or in morphological shape, once the effects of body size are removed. However, the relative size of the belly patch was a significant predictor of relative maximum bite force.

Although we have not directly investigated whether sexual signals display information about aggressive behaviour within our population, several lines of evidence provide strong support for this hypothesis. First, in two other populations of *U. ornatus* (Hover 1985; Moore *et al.* 1998), dominance trials revealed that blue throated morphs tend to dominate other morphs because of increased aggressive behaviour. Second, a preliminary investigation of undisturbed behaviour in our Wet Beaver Creek population suggests that blue throated morphs invest a larger percentage of their time involved in territorial behaviours (displaying, fights with neighbours) compared to other morphs, and that blue throated morphs more often defeat other morphs during territorial interactions (E. McElroy, D.J. Irschick & J. Meyers, personal communication). Thus, while we assume that blue throated morphs in our population are the dominant morphs, as has been well documented in other studies (Moore *et al.* 1998), more research is needed to test this assumption.

Because polygynous species spend a large portion of their time vying for resources (food, access to females, habitat), the ability to win male–male interactions is critical. In *U. ornatus*, both the dewlap and belly patch are displayed to rival males during dominance interactions, and the ability to use these signals to display multiple aspects of fighting ability (aggressiveness and bite force) may allow quick assessment of dominant individuals, thereby reducing the duration of confrontations. Dominance interactions often involve a progression of display behaviours that are used to assess the dominant individual (Parker 1974). Yet, not only is the progression of the display important, but the intensity of aggressive behaviours (displays and agonistic behaviours such as biting) can influence the outcome of dominance interactions. For instance, during male–male interactions, the dominant morphs of *Uta stansburiana* display more frequently and vigorously (Sinervo *et al.* 2000), and those of *U. ornatus* more readily bite opponents (Thompson & Moore 1992). Additionally, in cichlids (Barlow *et al.* 1986) and Flat Lizards (Whiting *et al.* 2003), the more aggressive individuals that instigate interactions are able to dominate size-matched opponents. Thus, it appears that overt aggression can outweigh other potential factors (e.g. functional capacity) in the early stages of a conflict, at least among size-matched opponents. However, at later stages of a conflict, agonistic interactions may escalate to physical confrontation, at which point the ability to bite more forcefully and inflict injury upon an opponent may be the ultimate determinant of fight success (see Fig. 1b). The fact that harder-biting individuals of *Anolis carolinensis* (Lailvaux *et al.* 2004) and *Gallotia galloti*

(Huyghe *et al.* 2005) win more often in dominance trials emphasizes the importance of bite force in determining the outcome of male–male interactions (see also Lappin & Husak 2005).

Comparison of the two ornaments examined here and the information they signal reveals that whereas dewlap coloration appears to present morph-specific information (behavioural aggression), belly patches are a widespread sexually dimorphic structure in phrynosomatid lizards, and hence span the different morphs. For *Urosaurus*, the simultaneous expression of multiple aspects of male quality indicates that individuals with both blue throats and large belly patches should be especially dominant males. However, it also indicates that the less aggressive orange morphs with large belly patches can bite harder than dominant blue morphs with small belly patches. Thus, dominant blue morphs may at times be pitted against less behaviourally dominant but functionally superior adversaries. We are not aware of any studies that have simultaneously examined both aggressiveness and functional capacity in relation to dominance, but examination of these traits may provide insight into why the most aggressive or hardest biting individuals do not always win male–male contests. This finding generally suggests that different sexual signals have not coevolved in the sense that they do not necessarily reflect the same level of ‘quality’ in the same male.

Because belly patches arose early in the evolution of Phrynosomatid lizards and are present in most species (Wiens 1999), belly patches may be viewed as a conserved sexual ornament that acts as an indicator of functional capacity. The belly patches in *Urosaurus* may be considered functionally analogous to the extendable throat-fans (dewlaps) of *Anolis* lizards, which are also plesiomorphic ornaments that display information about bite force (Vanhooydonck *et al.* 2005). While throat patches are also an ancestral character of Phrynosomatid lizards, unlike belly patches, they are more often polymorphic and may represent an ornament that can be tailored to species-specific contexts. The most notable examples are *Uta stansburiana* (Sinervo & Lively 1996) and the current study species (*Urosaurus ornatus*), both of which boast multiple male phenotypes that are differentiated by throat coloration. In these two species, throat patches act as social badges that denote the level of territoriality and aggressiveness of the different morphs. Our identification of the divergent roles of belly and throat patches sets forth the prediction that the relative size of generalized sexually dimorphic structures (e.g. belly patches) generally acts as an indicator of male functional capacity, whereas species-specific signals (e.g. throat colour polymorphisms) relay information on behavioural aggression that dictates dominance within specific social systems.

Considering the importance of locomotion during a wide variety of crucial behaviours (foraging, predator escape, fighting) and the fact that sexual ornaments have been found to be indicators of functional capacity (Sinervo *et al.* 2000; Vanhooydonck *et al.* 2005), it is

surprising that neither throat coloration nor belly patch size is associated with locomotor capacity in our study. Whereas several studies have revealed that maximum sprint speed and endurance may be determinants of social dominance in lizards (*Sceloporus*, Garland *et al.* 1990; *Anolis*, Perry *et al.* 2004; *Urosaurus*, Robson & Miles 2000), conflicting evidence suggests that this is not always the case (Lopez & Martín 2002; Huyghe *et al.* 2005). While no direct relationship between ornament size and performance was found in the lizard *Gallotia galloti* (Huyghe *et al.* 2005), the dominant morphs of *Uta stansburiana* have a higher endurance capacity than the less dominant orange and blue morphs (Sinervo *et al.* 2000). These conflicting results may result from the fact that *Uta stansburiana* is a territorial, polygynous lizard, whereas *Gallotia galloti* is a more wide-foraging, herbivorous and less territorial lizard (Molina-Borja 1987). As the *Urosaurus ornatus* system is more similar to *U. stansburiana* than to *G. galloti*, in that territorial males maintain constant vigil of their home range to ward off intruders, it may be that endurance and not sprint speed is important in agonistic interactions of dominant morphs. If this is the case, then higher endurance capacity may be a costly (Brandt 2003) but necessary attribute that will be reflected in the signalling ornaments of the different morphs. Finally, one cannot ignore the potential utility of male sexual structures for female choice, although support for female choice in lizards has been equivocal (Tokarz 1995). A recent study with *U. ornatus* (Hamilton & Sullivan 2005) showed that females preferred males that possessed key combinations of morphology and large belly patch size, and thus we cannot rule out the possibility that characters such as the belly patch and throat colour/size could have also evolved under the influence of female choice.

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