

Do Displays Send Information about Ornament Structure and Male Quality in the Ornate Tree Lizard, *Urosaurus ornatus*?

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Abstract

Displays can transmit information about ornament or male quality; however, few studies have simultaneously explored the relationship between displays, ornament and male quality within a single species. We quantified ornament morphology (five throat color morphs, throat area, and belly area), male quality (bite force, sprint speed, body condition, and body mass), display behavior [percent time displaying (PTD), number of pushups per display, and display duration], and movement behavior among males in a population of the ornate tree lizard, *Urosaurus ornatus*. Previous studies have shown that male *U. ornatus* are polymorphic in throat coloration and that morphs differ in behavioral aggression. Our study shows that blue throat morphs use 1.5 more pushups per display than other male color morphs, which suggests that throat color and display behavior act as backup signals for aggression. However, other data support the multiple messages hypothesis, and overall our data do not provide conclusive evidence for any one hypothesis. In addition, we show that body mass is positively related to both PTD and percent time moving and this relationship is independent of color morph. We also found that throat area, belly area, bite force, sprint speed, and body condition are unrelated to display behavior. This result highlights at least some discordance between display behavior, ornaments, and performance in *U. ornatus* and suggests that these traits may be evolving independently.

Introduction

Many species have ornaments that may function to convey information about individual quality (Fisher 1915; Zahavi 1975; Berglund et al. 1996). Ornaments are often sexually dimorphic with males usually having larger and brighter ornaments than females (Andersson 1994). Among males, ornaments can signal many aspects of male quality such as: whole-organism performance (*Sceloporus occidentalis*, Garland et al. 1990; *Anolis* lizards, Lailvaux et al. 2004; dung beetles, Lailvaux et al. 2005; *Urosaurus ornatus*, Meyers et al. 2006; Vanhooydonck et al.

2005), fighting ability (*Gallotia gallotia*, Huyghe et al. 2005; *Lacerta agilis*, Olson 1994; *Platysaurus broadleyi*, Whiting et al. 2003), aggression (reviewed in Berglund et al. 1996), and social ranking (house sparrow, Møller 1987, Veiga 1993; paper wasp, Tibbetts & Dale 2004). The idea that ornaments signal performance is appealing because performance can play a key role in determining the outcome of social interactions (e.g. greater sprint speed for chasing rival males, Garland et al. 1990; Robson & Miles 2000; Peterson & Husak 2006; larger bite forces for biting rival males, Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006a) and performance is often

correlated with fitness (Lappin & Husak 2005; Husak et al. 2006b).

Display behaviors (and their interaction with ornaments) may also signal male quality (Enquist & Leimar 1983; Kim 1995). There is marked variation in displays in terms of (1) how much time individual males invest in displays (Perry et al. 2004) and (2) the structure (e.g. duration and repetition of components) of each display (Carpenter & Ferguson 1977; DeCourcy & Jenssen 1994; Leal 1999; Brandt 2003; Orrell & Jenssen 2003; Osborne 2005). Variation in displays may signal the potential fitness benefits (positive or negative) of interacting with the signaling individual by attracting females (female mate choice, e.g. Tokarz 1995; Kodric-Brown & Nicoletto 2001) and/or signaling fighting ability to rival males (male–male competition, e.g. Jenssen et al. 2005; Stuart-Fox et al. 2006). In particular, display variation may signal performance capacity (e.g. pushup displays and endurance, Leal 1999; Brandt 2003; Perry et al. 2004). Some research suggests that male displays act as honest indicators of male quality, such as in pushup displays in lizards (Brandt 2003). Other work has shown that male displays pose a cost because of the increased exposure to predators (Farr 1975; Endler 1987; Godin 1995). Displays are also used for signaling to predators (Leal 1999) and for species recognition (Jenssen 1977; Martins 1993b; Ord & Martins 2006).

While previous work has examined the relationship between ornaments and male quality or displays and male quality, few studies have simultaneously examined interrelationships among ornaments, male quality, and display behavior. Several hypotheses have been proposed to explain how multiple ornaments and displays can signal male quality (Møller & Pomiankowski 1993). First, displays and ornaments may be back-up signals, each sending the same information about male quality (Johnstone 1996). Second, displays and ornaments may send information about different aspects of male quality (multiple messages hypothesis, e.g. Jawor and Breitwisch 2004). Third, display behaviors could amplify ornaments (or vice versa) making the ornaments more conspicuous and easier to assess (Hasson 1989). In addition, displays and ornaments could be used for both rival assessment and mate choice (multiple receiver hypothesis, Andersson et al. 2002).

To assess how both ornaments and displays can signal male quality, we studied a population of the ornate tree lizard, *U. ornatus*. This species has been a model for the study of sexual ornaments (Moore et al. 1998). Male *U. ornatus* have three distinct

ornaments (throat patch, belly patch, and dorsal darkening) and have display behaviors consisting of a variable number of pushups with lateral compression and dewlap extension (Purdue & Carpenter 1972). The polymorphic throat patch consists of combinations of two colors, a centralized dewlap color and base background color. Our study population has five male morphs with males having blue, yellow, or orange backgrounds (B, Y, and O morphs, respectively) or a centralized blue dewlap overlying a yellow or orange background (YB and OB morphs, respectively, Meyers et al. 2006) and females having yellow/orange backgrounds. The specific combination of throat coloration is related to alternative male mating tactics (Moore et al. 1998). Individuals with blue on the throat (B, YB, OB morphs) are aggressive and dominant with large territories while individuals with yellow/orange throats (Y, O morphs) are subordinate, non-territorial or have smaller territories (Hover 1985; Thompson & Moore 1991b; Carpenter 1995; Moore et al. 1998). The belly patch is a widespread sexually dimorphic trait in lizards that consists of two oval-shaped patches that extend from the pectoral to pelvic girdle (Cooper & Greenburg 1992; Weins 2000). In male *U. ornatus*, larger belly patches signal larger bite forces (Meyers et al. 2006). In addition, female *U. ornatus* choose males based on multiple cues including a preference for larger belly patches (Hamilton & Sullivan 2005). We did not observe or quantify the use of dorsal darkening (Zucker 1989, 1994). These studies provide compelling evidence that ornaments signal male quality and are used for female choice; however, they provide no evidence of how variation in displays might signal male quality in *U. ornatus*.

We addressed the following questions: (1) Does display behavior (percent time displaying (PTD), number of pushups per display, and display duration) differ among *U. ornatus* male morphs? (2) Is display behavior related to ornament sizes (belly patch area, dewlap area, and throat background area), body size, body condition, and performance (sprint speed and bite force) across all morphs and individuals?

Methods

Study Site

We studied a population of *U. ornatus* at Wet Beaver Creek, a riparian zone that is a mid-elevation site (1100 m) in central Arizona (exact coordinates available upon request; same site as Meyers et al. 2006).

Urosaurus ornatus is abundant at this site, and males were defending territories and mating during the sampling period (May 31, 2006–Jun. 13, 2006). Display behavior, ornament morphology, and male quality were measured in the field.

Display Behavior

We gathered focal videos of 43 adult male *U. ornatus*. We filmed on bright sunny days from 0800 to 1900 when ambient temperatures ranged between 30 and 35°C, which correspond to the period of peak activity. We gathered focal videos as in McElroy et al. (2007). Briefly, we systematically searched all areas of the site and after finding a lizard, used a 5-min-assessment period to discern whether we disturbed the lizard (disturbance defined in McElroy et al. 2007). If the lizard was not disturbed, we used a handheld JVC – GR DVL 9800 Mini DV (Victor Company, Japan) camcorder mounted to a Bogen monopod to film lizards. We followed each individual continuously as it moved throughout the environment, and made every attempt to minimize disturbances to the lizard. E.J.M. filmed all lizards and wore the same sets of clothing throughout the filming period. Other studies using similar techniques have found that lizard behavior is not affected by the careful observer (Leal 1999; Irschick 2000a,b; Mattingly & Jayne 2004; McElroy et al. 2007). We sampled each individual for ~10 min as this is accepted protocol for studies of field display behavior in lizards (e.g. Perry et al. 2004), particularly for species that display often, as *U. ornatus* does. After filming, we captured each lizard via a handheld slip-noose attached to the end of a pole. Individuals were identified by a unique toe-clipping pattern (individuals were clipped in 2005 and 2006) and each individual was filmed only once. After identification, we kept each lizard for a maximum of 24 h to measure ornament morphology and quality. Lizards were released at their exact point of capture.

We estimated three aspects of display behavior that may be related to ornament morphology and quality for each individual: PTD, average number of pushups per display (#PU), and the average duration of each display (Duration). For each individual, we quantified the total number and time of all displays. A display consisted of extension of all four limbs (pushup) with lateral compression (exposing belly patches) and dewlap extension (exposing throat patches). Thus, we defined a single display as a single occurrence of this series of events. Display time was defined as the time from the start of the first

pushup until the end of the final pushup within a single display. This definition of display corresponds to the displays recorded for *Anolis cristatellus* (Perry et al. 2004). The displays we observed consisted of a variable number of pushups each with lateral compression and dewlap extension (Carpenter & Grubitz 1961). Thus, we quantified the number of pushups only because this measure encapsulated both belly and throat patch exposure, and we could always visualize pushups but not always dewlap and belly patch extension during filming. We defined the # PU as the total number of pushups for all displays divided by the number of displays for each individual. Duration was defined as the total time spent displaying divided by the number of displays. We also measured percent time moving (PTM) for each individual. We defined a locomotor movement as any movement preceded and followed by a pause, and thus PTM represented the percent time an individual spent moving independent of displaying and resting. Movement time was the total time a lizard spent moving. PTD and PTM were estimated by dividing the total time spent displaying or moving by the total time the individual was videoed.

Our goal was to understand display behavior of *U. ornatus* lizards in a natural, as opposed to an experimental, setting. We did not standardize (e.g. use an experimental arena) because (1) we were already taking multiple measurements and did not want to 'over-exert' any animals and (2) data from an experimental setting can overlook potentially important natural variation in behavior (e.g. Garland & Losos 1994; McElroy et al. 2007). However, filming animals under non-standardized conditions could be an issue because display behavior can vary by social context (e.g. Martins 1993b; McMann 1993), which may cause systematic errors in our data because of lizards being filmed in different situations (e.g. presence/absence of females). To account for non-standardized conditions, we quantified four factors that can affect display behavior: the presence of other males or females (defined as a male or female within the visual area of the focal individual), the time of day, and the position within the habitat. We used a MANOVA with the presence/absence of other males and/or females, position along the transect (near creek, middle, and near dry edge), and time of day as the main effects and PTD, # PU, and Duration as responses. In no case did we find any evidence of differences in display behavior related to social situation (whole model: Wilks' $\lambda = 0.63$, $F_{15,78} = 0.95$, $p = 0.51$; males: $F_{3,28} = 0.76$, $p = 0.52$; females: $F_{3,28} = 1.62$, $p = 0.21$; position: $F_{6,56} = 0.27$,

$p = 0.95$; time of day: $F_{3,28} = 0.05$, $p = 0.99$). Based on these results, we feel confident that the variation in display behavior we observed between male morphs in *U. ornatus* cannot be attributed to variation in social context.

Dewlaps and Belly Patches

Dewlap and belly patch structure were quantified as in Meyers et al. (2006). Briefly, a digital photograph was taken as animals were pressed against a piece of glass exposing belly and throat patches. Digital photographs were imported into Image J (W. S. Rasband, ImageJ, US NIH, Bethesda, MD, USA, <http://rsb.info.nih.gov/ij/>, 1997–2006) and the belly and throat patches were digitized to calculate the total area of each patch. Belly patches can be discrete or continuous across the midline; therefore we present the sum of total belly patch area. The Wet Beaver Creek population had five male morphs: blue (B), yellow-blue (YB), orange–blue (OB), yellow (Y), and orange (O) (Meyers et al. 2006). Background color was easily determined; we used the same criteria as Thompson & Moore (1991a) to define dewlap color. If the dewlap contained more than 10% blue in a concentrated centralized spot, we considered the individual to have a blue dewlap; if it contained <10%, we considered the individual to have the same color as the background. We sampled a total of 43 individuals with the following frequencies: 13 B (30%), 13 YB (30%), 9 OB (21%), 5 Y (12%), 3 O (7%). We made every attempt to sample equal numbers of morphs (~10); however, some morphs are rare in this population [Y and O make up ~15 and 5% of the population, respectively, Meyers et al. (2006)]. Our study site has ~200 adults (Meyers, unpubl. data), thus we could have sampled a maximum of ~30 Y and ~10 O; however, this would have required filming ~200 individuals or five times our sampling effort. Previous studies have reported few behavioral differences between orange and yellow morphs (Thompson & Moore 1991a; Meyers et al. 2006) and our study supports this view.

Male Quality

Bite forces were measured using a Kistler piezoelectric force transducer (type 9203; Kistler Inc., Kistler Instrument Corp., Amherst, NY, USA) 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 the bite plates connected to the transducer, and the maximum bite

force for five trials was recorded as an individual's maximum bite force. We measured maximal horizontal and vertical sprint speeds using an electronic racetrack with infrared photocells placed every 25 cm. The track surface was a 3 m long \times 0.20 m wide cork-covered board. We induced maximal sprint speeds by chasing each lizard across the track. Each lizard ran three times, with recovery intervals of 30–45 min separating each trial. The fastest 25-cm interval was recorded as an individual's maximum sprint speed. All performance measurements were taken while ambient temperatures were 30–35°C and animals had been given at least 45 min to thermally equilibrate in the shade. For all animals, we recorded bite force first and sprint speed second. We always collected replicated trials from individuals in the same order. We measured body mass to the nearest 0.01 g using a pesola scale and snout-vent length using digital calipers to the nearest 0.1 mm. We calculated a condition index from the residuals of the regression of mass against snout vent length (SVL)³ (Brandt 2003). Endurance is an additional performance-based measure of male quality that is related to display behavior (Brandt 2003; Perry et al. 2004). We elected not to measure endurance because we were already taking multiple measurements (bite force, sprint speed, and morphology) on each individual and were concerned that quantifying endurance might 'over-exert' the animals.

Data Analysis

We used JMP 5.0 (SAS, Cary, NC, USA) for all analyses. All variables were transformed to conform to normality. We tested for differences in each display behavior variable and PTM among morphs using single-factor ANOVAS with planned linear contrasts to test our two specific hypotheses. We adjusted p-values using a sequential Bonferroni procedure (Quinn & Keough 2003). Our hypotheses were that B, YB, OB > O, Y and B > YB, OB, Y, O for display behavior and PTM. The first hypothesis comes stems from previous studies showing that blue dewlaps (B, YB, OB) are behaviorally dominant. We based our second hypothesis on preliminary observations which suggest that B males are behaviorally dominant over all other morphs at Wet Beaver Creek and that both males and females can have yellow or orange throat coloration (these colors may indicate behavioral submissiveness).

Second, we simultaneously tested for differences in display behavior and movement patterns because of ornament morphology and performance using

multiple linear regression. PTD, PTM, # PU, and Duration were response variables whereas dewlap size, background size, belly patch size, bite force, sprint speed, mass, and condition index were predictor variables. We constructed models with absolute and relative (residuals from the regression of each variable against SVL) values for ornament size and performance, but these did not qualitatively alter the results. We present both full regression models and reduced models generated by a stepwise backward variable selection procedure with $p > 0.10$ to remove a variable. We detected no problems with residual plots, outliers (Mahalanobis distances), collinearity (variance inflation factors were <2), or leverage (Cook's D) for any of the regression analyses.

Results

Differences among Male Morphs in Display Behavior and PTM

Univariate ANOVAS with planned linear contrasts and a sequential Bonferroni revealed that B males used significantly more pushups per display than YB, OB, Y, or O males ($F_{1,32} = 10.840$, $p = 0.002$, Table 1, Fig. 1); while B, YB, OB did not differ from Y or O ($F_{1,32} = 0.913$, $p = 0.346$). Morphs did not differ for PTM (B vs. others, $F_{1,38} = 0.063$, $p = 0.803$; B, YB, OB vs. Y,O, $F_{1,38} = 0.004$, $p = 0.950$), PTD (B vs. others, $F_{1,37} = 0.058$, $p = 0.810$; B, YB, OB vs. Y,O, $F_{1,38} = 472$, $p = 0.496$), or Duration (B vs. others, $F_{1,32} = 0.965$, $p = 0.333$; B, YB, OB vs. Y, O, $F_{1,38} = 0.052$, $p = 0.821$).

Relationship between Ornament Size, Body Size, Condition, Performance and Display Behavior/PTM

None of the full models for the four multiple regression analyses testing the effects of ornament size, body size, condition index, and quality on each aspect of display behavior and PTM were significant (PTD: $R^2 = 0.22$, $F_{6,33} = 1.536$, $p = 0.197$, PTM: $R^2 =$

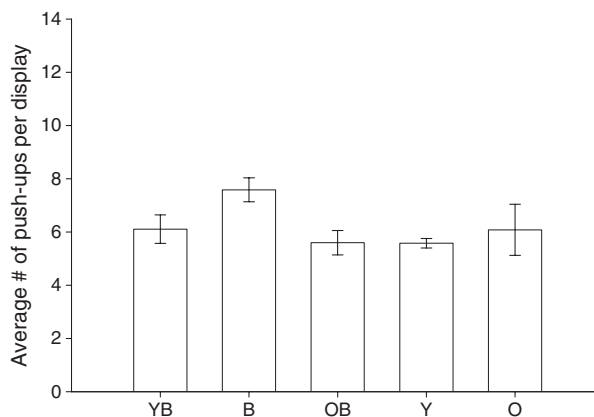


Fig. 1: Bar graphs showing $x \pm SE$ of average number of pushups per display for five male morphs of *Urosaurus ornatus* at the Wet Beaver Creek population. Blue (B) males averaged ~ 7.5 pushups per display which was significantly more than other morphs (OB, YB, O, Y) which did ≤ 6 pushups per display (ANOVA with planned contrasts: $F_{1,32} = 10.840$, $p = 0.002$, Table 1).

0.22 , $F_{6,33} = 1.545$, $p = 0.195$, # PU: $R^2 = 0.20$, $F_{6,33} = 1.421$, $p = 0.236$, Duration: $R^2 = 0.18$, $F_{6,33} = 1.195$, $p = 0.333$). The backward selection procedure concurred with the full models for # PU and Duration, but found that body mass was positively related to both PTD ($r = 0.40$, $F_{1,38} = 7.08$, $p = 0.011$, Fig. 2) and PTM ($r = 0.44$, $F_{1,39} = 9.06$, $p = 0.005$, Fig. 2).

Discussion

Understanding the information content and biological function of animal signals is of central importance to the study of sexual selection and behavioral ecology (Andersson 1994; Hauser 1996; Maynard Smith & Harper 2003). Many studies have focused on relating ornament structure or display behavior to individual quality and/or fitness (Berglund et al. 1996). However, few studies have simultaneously determined how ornaments and display behavior are related to male quality (i.e. whole-organism performance, mass, and condition) and if these

Table 1: $x \pm SE$ for mass, percent time moving (PTM), percent time displaying (PTD), average number pushups per display (#PU), and average duration of each display (duration) among five morphs of *Urosaurus ornatus*

Morph	Blue	Yellow	Orange	Yellow–Blue	Orange–Blue
Mass (g)	4.10 ± 0.17	4.31 ± 0.32	4.15 ± 0.37	4.18 ± 0.18	4.00 ± 0.22
PTM	7.25 ± 1.97	7.64 ± 3.68	10.39 ± 4.25	9.62 ± 2.04	6.67 ± 2.60
PTD	7.04 ± 1.45	7.71 ± 2.61	8.89 ± 3.01	6.67 ± 1.45	5.97 ± 1.84
#PU	7.59 ± 0.50 ^a	5.58 ± 0.90 ^b	6.08 ± 1.04 ^b	5.50 ± 0.57 ^b	5.59 ± 0.68 ^b
Duration (s)	10.80 ± 0.60	8.40 ± 1.32	10.03 ± 1.53	8.16 ± 0.84	7.97 ± 1.00

Superscripts denote significantly different groups for # PU (ANOVA with planned contrasts: $F_{1,32} = 10.840$, $p = 0.002$, Fig. 1).

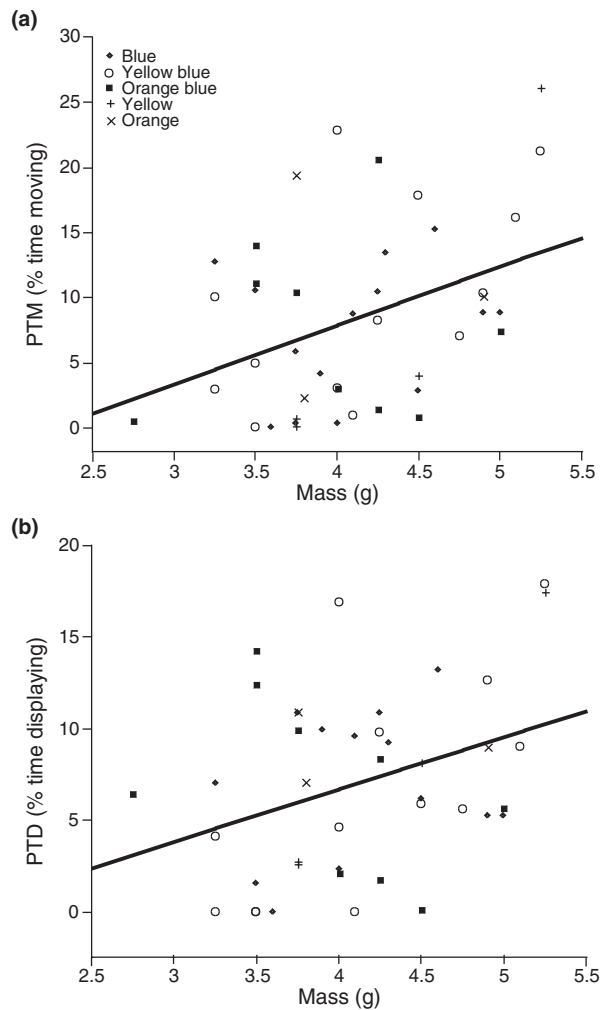


Fig. 2: Relationships between body mass (grams) and percent time moving (PTM, Panel a) and percent time displaying (PTD, Panel b) for 43 adult male *Urosaurus ornatus*. Body mass was significantly positively related to PTM ($r = 0.44$, $F_{1,39} = 9.06$, $p = 0.005$) and PTD ($r = 0.40$, $F_{1,38} = 7.08$, $p = 0.011$). Data are coded in Panel a per male morph.

relationships have any bearing on how ornaments transmit information, particularly in a field setting. *Urosaurus ornatus* blue-throated (B) males use 1.5 more pushups per display than other morphs (Fig. 1, Table 1) and large males spend more time displaying and moving than smaller males (Fig. 2a, b); however, there was generally a lack of significant relationships among displays, ornaments, performance, body size, and condition. Taken overall, our results do not clearly support any one hypothesis, and upon closer inspection, different aspects of our results are concordant with different hypotheses. For example, our results provide some support for both the

backup signaling hypothesis (displays may backup throat coloration) and the multiple messages hypothesis (PTD and # PU send different information); however, we admit that we did not have sufficient data to test the signal amplifier hypothesis.

Blue-throat morphs use more pushups per display than other morphs may suggest that display behavior and throat coloration act as backup signals. The backup signaling hypothesis proposes that multiple signals sending the same information allow receivers to make a more accurate assessment of the signaler's quality (Møller & Pomiankowski 1993). In the Wet Beaver population of *U. ornatus*, B males appear to be the most aggressive morph (they often chase and bite other morphs, McElroy, pers. obs.) and are behaviorally dominant (Meyers et al. 2006). Thus, having a B throat signals aggression and doing more pushups per display signals B throat and presumably aggression. We note that this conclusion awaits quantification of behavioral aggression for the morphs at Wet Beaver Creek. Two additional lines of evidence support our suggestion that displays backup throat color in *U. ornatus*. First, color can be difficult to discern in variable light environments (Endler 1993) and at Wet Beaver Creek *U. ornatus* often display in many different light environments (shade, full sun, filtered sunlight, morning, and evening, E. J. McElroy, pers. obs.). Second, color-based signals are often static whereas display behaviors are more variable and dynamic, yet both are used in female choice (e.g. Hill et al. 1998) and male competition (e.g. Osborne 2005). This difference may afford an individual the opportunity to reinforce information contained within a static signal by using a dynamic display, particularly when the static signal is difficult to assess.

Body size is an important determinant of the outcome of agonistic interactions and dominance rank in a variety of taxa both at the intraspecific level (e.g. *Anolis carolinensis*, Greenberg & Noble 1944; Jenssen et al. 2005; *Uta stansburiana*, Fox 1983; *Anolis sagrei*, Tokarz 1985; elephant seals, Haley et al. 1994; swordtail fish, Moretz 2003; brown antechinus, Fisher & Cockburn 2006) and the interspecific level (e.g. French & Smith 2005; Rychlik & Zwolak 2006). Prior research on *U. ornatus* has revealed that body size is the most important determinant of male-male contest outcome (regardless of morph color or context) with dominant individuals being much heavier (up to 20%, Carpenter 1995) than subordinates (Hover 1985; Deslippe et al. 1990; Carpenter 1995; Zucker & Murray 1996). We found that the heaviest male lizards also spent the most time displaying and

also moved around the most, and this result cut across all throat morphs (Fig. 2).

PTM and PTD were strongly positively correlated (Pearson's product moment correlation, $r = 0.74$, $t = 7.04$, $p < 0.001$) which indicates that males that display more often also move around more often (see also McElroy et al. 2007). Animals that move around more often incur a greater energetic expenditure than those that move around less often (e.g. Nagy et al. 1984), and therefore, large male *U. ornatus* may incur large energetic expenses associated with high levels of field activity (PTD and PTM). In experimental arenas, the largest, dominant male *U. ornatus* spend the largest amount of time displaying and over time, lose body mass, dominance, and territory control (Deslippe et al. 1990). This pattern occurs simultaneously as smaller subordinate males gain body mass and a shift in dominance and territory control to the heaviest subordinate male (Deslippe et al. 1990). Our study implies that the same processes may be occurring in the field and that movement and display may be responsible for the body mass fluctuations.

Meyers et al. (2006) examined the relationship between the same sexual ornaments examined here (e.g. belly patch size and dewlap patch size) and performance capacities in the same population of *U. ornatus* and found that individuals with relatively larger belly patches had larger bite forces. We found no relationship between any aspects of display behavior and bite force or belly patch size. This result was surprising because the body is laterally compressed during displays and this is the only time that the belly patches are exposed. Thus, we expected that individuals that exposed their belly patch more often (greater #PU, Duration, or PTD) would have greater bite forces.

We generally found a lack of concordance among displays and ornaments or performance. Previous studies have demonstrated that display behavior and ornament morphology are not tightly evolutionarily coupled in Phrynosomatid lizards (Martins 1993a; Wiens 2000). The lack of evolutionary coupling of display and ornaments in Phrynosomatids may explain the general lack of correlation between displays and ornaments or performance capacity and this suggests independent evolution of these traits, at least in *U. ornatus*. Future studies could use a phylogenetic comparative approach to further address the apparent lack of relationships between displays, ornaments, and performance.

Our suggestion that display behavior is evolving independently of ornaments and performance is

based on a lack of significant relationships among these traits. We cannot exclude the view that our moderate sample sizes ($n = 43$ individuals) resulted in a lack of statistical significance; however, other studies looking at the relationship between displays and performance have relied on similar samples sizes and have found significant relationships ($n = 38$ Brandt 2003; $n = 21$ Leal 1999; $n = 50$ Perry et al. 2004). In addition, while we focused on natural variation in display behavior, examining these relationships under more controlled laboratory conditions could find different results.

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Literature Cited

- Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton, NJ.
- Andersson, S., Pryke, S. R., Örnborg, J., Lawes, M. J. & Andersson, M. 2002: Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *Am. Nat.* **160**, 683–691.
- Berglund, A., Bisazza, A. & Pilastro, A. 1996: Armaments and ornaments: an evolutionary explanation of trait of dual utility. *Biol. J. Linn. Soc.* **58**, 385–399.
- Brandt, Y. 2003: Lizard threat display handicaps endurance. *Proc. R. Soc. Lond. B* **270**, 1061–1068.
- Carpenter, G. C. 1995: Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetol. Monogr.* **9**, 88–101.
- Carpenter, C. C. & Ferguson, G.W. 1977: Variation and evolution of stereotyped behavior in reptiles. In: *Biology of the Reptilia, Volume 7, Ecology and Behaviour A* (Gans, C. & Tinkle, D.W., eds). Academic Press, New York, pp. 335–454.
- Carpenter, C. C. & Grubitz, G. III 1961: Time-motion study of a lizard. *Ecology* **42**, 199–200.
- Cooper, W. E. & Greenburg, N. 1992: Reptilian coloration and behavior. In: *Biology of the Reptilia* (Gans, C. & Crews, D., eds). Chicago Univ. Press, Chicago, IL, pp. 298–422.

- DeCourcy, K. R. & Jenssen, T. A. 1994: Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim. Behav.* **47**, 251–262.
- Deslippe, R. J., M'Closkey, R. T., Dajczak, S. P. & Szpak, C. P. 1990: A quantitative study of the social behavior of the tree lizards, *Urosaurus ornatus*. *J. Herpetol.* **24**, 337–341.
- Ender, J. A. 1993: The color of light in forest and its implications. *Ecol. Monogr.* **63**, 1–27.
- Endler, J. A. 1987: Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). *Anim. Behav.* **35**, 1376–1385.
- Enquist, M. & Leimar, O. 1983: Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387–410.
- Farr, J. A. 1975: The role of predation in the evolution of social behavior of natural populations of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Evolution* **29**, 151–158.
- Fisher, R. A. 1915: The evolution of sexual preference. *Eugen. Rev.* **7**, 184–192.
- Fisher, D. O. & Cockburn, A. 2006: The large-male advantage in brown antechinuses: female choice, male dominance, and delayed male death. *Behav. Ecol.* **17**, 164–171.
- Fox, S. F. 1983: Fitness, home-range quality, and aggression in *Uta stansburiana*. In: *Lizard Ecology: Studies of a Model Organism* (Huey, R.B., Pianka, E.R. & Schoener, T. W., eds). Harvard Univ. Press, Cambridge, MA, pp. 149–168.
- French, A. R. & Smith, T. B. 2005: Importance of body size in determining dominance hierarchies among diverse tropical frugivores. *Biotropica* **37**, 96–101.
- Garland, T. G. & Losos, J. B. 1994: Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological Morphology: Integrative Organismal Biology* (Wainwright, P. C. & Reilly, S. M., eds). Univ. of Chicago Press, Chicago, IL, pp. 240–302.
- Garland, T. Jr, Hankins, E. & Huey, R. B. 1990: Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* **4**, 243–250.
- Godin, J. G. J. 1995: Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). *Oecologia* **103**, 224–229.
- Greenberg, B. & Noble, G. K. 1944: Social behaviour of the American chameleon (*Anolis carolinensis*, Voight). *Physiol. Zool.* **17**, 392–439.
- Haley, M. P., Deutsch, C. J. & Le Boeuf, B. J. 1994: Size, dominance, and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim. Behav.* **48**, 1249–1260.
- Hamilton, P. S. & Sullivan, B. K. 2005: Female mate attraction in ornate tree lizards, *Urosaurus ornatus*: a multivariate analysis. *Anim. Behav.* **69**, 219–224.
- Hasson, H. I. 1989: Amplifies and the handicap principle in sexual selection: a different emphasis. *Proc. R. Soc. Lond. B* **235**, 383–406.
- Hauser, M. D. 1996: *The Evolution of Communication*. MIT Press, Cambridge, MA.
- Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. 1999: Sexual dimorphism in head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**, 289–297.
- Hill, J. A., Enstrom, D. A., Ketterson, E. D., Nolan, V. Jr & Siegenfus, C. 1998: Mate choice based on static versus dynamic secondary sexual characters in the dark-eyed junco. *Behav. Ecol.* **10**, 91–96.
- Hover, E. L. 1985: Differences in aggressive behavior between two throat color morphs in a lizard, *Urosaurus ornatus*. *Copeia* **1985**, 933–940.
- Husak, J. F., Lappin, A. K., Fox, S. F. & Lemos-Espinal, J.A. 2006a: Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* **2006**, 301–306.
- Husak, J. F., Fox, S. F., Lovorn, M. B. & Van Den Busche, R. A. 2006b: Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* **60**, 2122–2130.
- Huyghe, K., Vanhooydonck, B., Cheers, H., Molina-Borja, M. & Van Damme, R. 2005: Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Funct. Ecol.* **19**, 800–807.
- Irschick, D. J. 2000a: Comparative and behavioural analyses of preferred speeds: *Anolis* lizards as a model system. *Physiol. Biochem. Zool.* **73**, 428–437.
- Irschick, D. J. 2000b: Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. *Funct. Ecol.* **14**, 438–444.
- Jawor, J. M. & Breitwisch, R. 2004: Multiple ornaments in male Northern Cardinals, *Cardinalis cardinalis*, as indicators of condition. *Ethology* **110**, 113–126.
- Jenssen, T. A. 1977: Evolution of anoline lizard display behavior. *Am. Zool.* **17**, 203–215.
- Jenssen, T. A., DeCourcy, K. R. & Congdon, J. D. 2005: Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? *Anim. Behav.* **69**, 1325–1336.
- Johnstone, R. A. 1996: Multiple displays in animal communication: 'backup signals' and 'multiple messages'. *Philos. Trans. R. Soc. Lond. B* **351**, 329–338.
- Kim, Y. G. 1995: Status signaling games in animal contests. *J. Theor. Biol.* **176**, 221–231.
- Kodric-Brown, A. & Nicoletto, P. F. 2001: Female choice in the guppy (*Poecilia reticulata*): the interaction between male color and display. *Behav. Ecol. Sociobiol.* **50**, 346–351.
- Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J. & Irschick, D. J. 2004: Performance capacity, fighting tactics and the evolution of life-stage male morphs in

- the green anole lizards (*Anolis carolinensis*). Proc. R. Soc. Lond. B **271**, 2501—2508.
- Lailvaux, S. P., Hathway, J., Pomfret, J. C. & Knell, R. J. 2005: Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Funct. Ecol.* **19**, 632—639.
- Lappin, A.K. & Husak, J.F. 2005: Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am. Nat.* **166**, 426—436.
- Leal, M. 1999: Honest signaling during prey-predator interactions in the lizard *Anolis cristatellus*. *Anim. Behav.* **58**, 521—526.
- Martins, E. P. 1993a: A comparative study of the evolution of *Sceloporus* push-up displays. *Am. Nat.* **142**, 994—1018.
- Martins, E. P. 1993b: Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Anim. Behav.* **45**, 25—36.
- Mattingly, W. B. & Jayne, B. C. 2004: Resource use in arboreal habitats: structure affects locomotion of four ecomorphs of *Anolis* lizards. *Ecology* **85**, 1111—1124.
- Maynard Smith, J. & Harper, D. 2003: *Animal Signals*. Oxford Univ. Press, Oxford, UK.
- McElroy, E. J., Meyers, J. J., Reilly, S. M. & Irschick, D. J. 2007: Dissecting the effects of behaviour and habitat on locomotion in a lizard, *Urosaurus ornatus*. *Anim. Behav.* **79**, 359—365.
- McMann, S. 1993: Contextual signaling and the structure of dyadic encounters in *Anolis carolinensis*. *Anim. Behav.* **46**, 657—668.
- Meyers, J. J., Irschick, D. J., Vanhooydonck, B. & Herrel, A. 2006: Divergent roles for multiple sexual signals in a polygynous lizard. *Funct. Ecol.* **20**, 709—716.
- Møller, A. P. 1987: Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signaling. *Anim. Behav.* **35**, 1637—1644.
- Møller, A. P. & Pomiankowski, A. 1993: Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167—176.
- Moore, M. C., Hews, D. K. & Knapp, R. 1998: Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. *Am. Zool.* **38**, 133—151.
- Moretz, J. A. 2003: Aggression and RHP in the Northern Swordtail Fish, *Xiphophorus cortezi*: the relationship between size and contest dynamics in male-male competition. *Ethology* **109**, 995—1008.
- Nagy, K. A., Huey, R. B. & Bennett, A. F. 1984: Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology* **65**, 588—596.
- Olson, M. 1994: Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Anim. Behav.* **48**, 607—613.
- Ord, T. J. & Martins, E. P. 2006: Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour. *Anim. Behav.* **71**, 1411—1429.
- Orrell, K. S. & Jenssen, T. A. 2003: Heterosexual signaling by the lizard *Anolis carolinensis* with intersexual comparisons across contexts. *Behaviour* **140**, 603—634.
- Osborne, L. 2005: Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *J. Ethol.* **23**, 189—197.
- Perry, G., Levering, K., Girard, I. & Garland, T. Jr 2004: Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim. Behav.* **67**, 37—47.
- Peterson, C. C. & Husak, J. F. 2006: Locomotor performance and sexual selection: individual variation in sprint speed in collared lizards (*Crotaphytus collaris*). *Copeia* **2006**, 216—224.
- Purdue, J. R. & Carpenter, C. C. 1972: A comparative study of display motion in the iguanid genera *Sceloporus*, *Uta*, and *Urosaurus*. *Herpetologica* **28**, 137—140.
- Quinn, G. P. & Keough, M. J. 2003: *Experimental Design and Data Analysis for Biologists*. Cambridge Univ. Press, New York.
- Robson, M. A. & Miles, D. B. 2000: Locomotor performance and dominance in male Tree Lizards, *Urosaurus ornatus*. *Funct. Ecol.* **14**, 338—344.
- Rychlik, L. & Zwolak, R. 2006: Interspecific aggression and behavioural dominance among four sympatric species of shrews. *Can. J. Zool.* **84**, 434—448.
- Stuart-Fox, D. M., Firth, D., Moussalli, A. & Whiting, M. J. 2006: Multiple signals in chameleon contests: designing and analyzing animal contests as a tournament. *Anim. Behav.* **71**, 1263—1271.
- Thompson, C. W. & Moore, M. C. 1991a: Throat colour reliably signal status in male tree lizards, *Urosaurus ornatus*. *Anim. Behav.* **42**, 745—753.
- Thompson, C. W. & Moore, M. C. 1991b: Syntopic occurrence of multiple dewlap colour morphs in male tree lizards, *Urosaurus ornatus*. *Copeia* **1991**, 493—503.
- Tibbetts, E. A. & Dale, J. 2004: A socially enforced signal of quality in the paper wasp. *Nature* **432**, 218—222.
- Tokarz, R. R. 1985: Body size as a factor determining dominance in staged agnostic encounters between male brown anoles (*Anolis sagrei*). *Anim. Behav.* **33**, 746—753.
- Tokarz, R. R. 1995: Mate choice in lizards: a review. *Herp. Mono.* **9**, 17—40.
- Vanhooydonck, B., Herrel, A. Y., Van Damme, R. & Irschick, D. J. 2005: Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Funct. Ecol.* **19**, 38—42.
- Veiga, J. 1993: Badge size, phenotypic quality, and reproductive success in the house sparrow: a study on honest advertisement. *Evolution* **47**, 1161—1170.

- Whiting, M. J., Nagy, K. A. & Bateman, P. W. 2003: Evolution and maintenance of social status-signaling badges. In: *Lizard Social Behavior* (Fox, S. F., McCoy, K. & Baird, T. A., eds). Johns Hopkins Univ. Press, Baltimore, MD, pp. 47–82.
- Wiens, J. J. 2000: Decoupled evolution of display morphology and display behaviour in phrynosomatid lizards. *Biol. J. Linn. Soc.* **70**, 597–612.
- Zahavi, A. 1975: Mate selection – a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.
- Zucker, N. 1989: Dorsal darkening and territoriality in a wild population of the tree lizard, *Urosaurus ornatus*. *J. Herpetol.* **23**, 389–398.
- Zucker, N. 1994: Social influence of the use of a modifiable status signal. *Anim. Behav.* **48**, 1317–1324.
- Zucker, N. & Murray, L. 1996: Determinants of dominance in the tree lizards *Urosaurus ornatus*: the relative importance of mass, previous experience and coloration. *Ethology* **102**, 812–825.