



Boldness, Dominance, and Territoriality in the Color Polymorphic Tree Lizard, *Urosaurus ornatus*

Julie N. Taylor & Matthew S. Lattanzio

Department of Organismal and Environmental Biology, Christopher Newport University, Newport News, VA 23606, USA

Correspondence

Matthew S. Lattanzio, Department of Organismal and Environmental Biology, Christopher Newport University, Newport News, VA 23606, USA.
E-mail: matthew.lattanzio@cnu.edu

Received: April 28, 2016

Initial acceptance: June 2, 2016

Final acceptance: August 14, 2016

(W. Koenig)

doi: 10.1111/eth.12534

Keywords: alternative mating tactics, escape behavior, flight-initiation distance, resource defense

Abstract

Social dynamics in territorial species often reflect underlying variation in aggression and other aspects of social dominance among individuals. In ornate tree lizards (*Urosaurus ornatus*), males differing in dewlap color differ in social dominance: while blue males are the dominant, aggressive morph and always territorial, yellow males tend to exhibit a less-aggressive satellite behavioral tactic. However, in habitats with fewer available territorial resources, yellow males defend territories and increase in relative abundance. These observations suggest that consideration of social dominance alone may be insufficient to explain *U. ornatus*' territorial dynamics in the wild. Here, we tested how both dominance and another important behavioral trait, boldness, contribute to the outcome of territorial disputes in tree lizards. We recorded the territorial behavior of blue and yellow male tree lizards (entered in pairs) in an experimental arena. At the end of each trial, we then approached each male and recorded whether it fled (shy) or not (bold) in response to our approach. As expected, dominant blue males exploited the higher quality perch more often than yellow males. However, when approached by a simulated predator, blue males were more likely to flee than yellow males. Thus, while blue males are more dominant, yellow is likely the bolder morph. As a result, this morph may be better equipped to defend territories in riskier environments. We conclude that although dominance asymmetries may predictably drive initial territorial interactions among competing males, variation in other behaviors (like boldness) may perturb the long-term outcome of these interactions across variable environments.

Introduction

In many territorial species, individual variation in dominance shapes the outcome of social interactions (Carpenter 1995; Pryke & Griffith 2006; Dijkstra et al. 2009a,b) and may also act as a driver of ecological diversification (Lattanzio & Miles 2016). However, variation in other behaviors should also contribute to that process and, in certain contexts, may override the expected ecological products of social dominance asymmetries. For example, imagine a polygynous species of animal exploiting an open habitat characterized by low vegetation as well as rock piles (hereafter perches) that vary in size and structural and thermal complexity (and thus quality). Males of the focal

species can use these perches for territory patrol, mate searching, and foraging. However, differences in social dominance among males would generate competitive interactions whereby only the most-dominant individuals would be capable of defending access to the highest quality perches. In this context, variation in individual behavior drives microhabitat exploitation patterns, promoting ecological diversification.

Now imagine the introduction of predation risk into the system. Although fleeing a predator is important, initiating escape increases mortality risk, and thus, it is more beneficial to only initiate escape when mortality risk is imminent (Broom & Ruxton 2005). Here, individual variation in antipredator behavior will influence resource-holding patterns: only individuals

that resist fleeing from a predator—for example, those that are bolder, will be able to maintain hold on their territories in a risky habitat. In contrast, less-bold individuals are more likely to flee from an approaching predator, abandoning their territory. If boldness and dominance behavior are not positively related, then this territorial abandonment might allow subordinate individuals to access high-quality microhabitat resources that would otherwise be inaccessible to them. The nature of these intra- and interspecific interactions should have important consequences for their realized territorial dynamics in the wild.

In other words, whereas variation in dominance affects an individual's ability to monopolize access to preferred ecological resources relative to conspecifics (Calsbeek & Sinervo 2002; Lailvaux et al. 2012), sustained defense of those resources may also require expression of other traits, such as boldness, to cope with other, heterospecific threats, such as predators (Bell & Stamps 2004). Here, dominance refers to an individual's ability to obtain and retain possession of a territory resource using aggression and other behavioral displays (Lincoln et al. 1986). Variation in dominance affects the nature and extent of social interactions within a population. The effects of variable social dominance on resource partitioning have been studied extensively in laboratory and field experiments (Watt et al. 1984; Garland et al. 1990; Pryke & Griffith 2006; Lattanzio & Miles 2016). For example, in lizards, aggressive displays include head bobs and push-ups that show off the throat in an attempt to intimidate the rival male. In some cases, individuals may even result to biting to establish their dominance. Among those studies where males are paired and competing for access to one-two resources, the male exhibiting greater frequencies of aggressive displays outcompetes the other male and wins access to the resource (Garland et al. 1990; Healey et al. 2007). In the wild, variation in these phenotypic traits among males should interact with variation in the quality and availability of defendable resources to affect patterns of niche partitioning. Specifically, asymmetries in dominance behavior may lead to despotic territorial dynamics (Fretwell 1972), whereby only dominant individuals exploit better-quality resources, like higher trophic level prey (Lattanzio & Miles 2016).

Another important phenotypic trait, boldness, has received growing attention over the past decade because of its broad implications for the nature of social interactions, ecology, and behavior (López et al. 2005; Réale et al. 2007), as well as the ecological dynamics of entire populations (Pike et al. 2008; Croft

et al. 2009). Boldness can be defined as an individual's tendency to resist escape under a perceived threat of predation (Cooper 2009; Petelle et al. 2013), which, justifiably, should have important life-history consequences. In other words, whereas bold individuals typically have greater access to life-history resources, they typically face heightened predation risk as a result. In contrast, shy (non-bold) individuals experience reduced predation risk but sacrifice their access to crucial resources. Several studies have shown that greater boldness is also associated with fewer social interactions. For example, in fish, boldness is associated with reduced shoaling behavior (Ward et al. 2004), fewer interactions with other fish in the population (Croft et al. 2009), and greater aggression (Bell & Stamps 2004). In birds, boldness has been shown to influence spatial positioning in foraging flocks (Aplin et al. 2014), cooperation among breeding adults (Öst et al. 2015), and even nest site selection (Selmann et al. 2014).

Because boldness is partly shaped by environmental conditions, including resource availability and predator density (Riesch et al. 2009; Chapman et al. 2010), its consequences are likely to be situation-dependent. For example, although high boldness levels in areas of high predator density are expected to increase mortality risk, this may not always be the case (Carlson & Langkilde 2014). Moreover, bolder individuals have also been shown to exhibit higher levels of resource acquisition, growth rates, and mass in lieu of any predation pressures (Fraser & Gilliam 1987; Ward et al. 2004; Brown et al. 2007). In this manner, boldness 1) impacts both individual- and population-level ecology, but 2) its relative impact on those processes may depend on local environmental conditions (Bell & Sih 2007).

Dominance and boldness should both contribute to species' socio-ecological dynamics in the wild (Croft et al. 2009). Specifically, greater dominance should allow an individual to initially usurp a preferred microhabitat resource and defend it from conspecifics. However, behavioral tactics exhibited during territorial defense should also increase an individual's exposure to predators (Díaz-Uriarte 2001). Because boldness facilitates successful exploitation of predator-rich environments, it may also enhance an individual's ability to sustain defense of their territory despite risk of predation. In this scenario, we would predict that for a given habitat resource under dispute, an individual with greater dominance should win the territorial contest and monopolize initial access to the resource (Calsbeek & Sinervo 2002), driving less-dominant individuals to use poorer quality

microhabitats (Lattanzio & Miles 2016). However, the risk of predation might favor only bolder individuals to sustain exploitation of preferred territories over time (Bell & Sih 2007). The nature of the interaction between boldness and dominance is unclear: Whereas some studies find support for a positive correlation between boldness and social dominance (Bell & Stamps 2004; Pintor et al. 2008; Barnett et al. 2012), others fail to support any interaction or a negative interaction between these two traits (Bell 2005; Niemelä et al. 2012). Knowledge of the nature of the interactions between dominance and boldness behavior should therefore provide important insights into our understanding of the ecological dynamics of territorial species.

Here, we evaluate the contribution of social dominance and boldness to staged territorial interactions between pairs of adult male tree lizards (*Urosaurus ornatus*) in an outdoor arena. *U. ornatus* is an ideal system for this study because males exhibit a fixed polymorphism in throat coloration that reflects variation in suites of physiological and behavioral traits linked with asymmetries in relative dominance among morphs (Hover 1985; Thompson & Moore 1991). Specifically, blue males are dominant, aggressive, and defend territories, yellow males are less aggressive and exhibit a satellite tactic, exploiting habitats directly adjacent to and surrounding blue male territories (Lattanzio & Miles 2016), and orange males are non-aggressive (Thompson & Moore 1991; Moore et al. 1998). Males communicate their dominance status via head-bob and push-up behaviors that display their throat coloration to other males (McElroy et al. 2007). The same behaviors are also used to communicate territory boundaries, which typically remain stable throughout the breeding season (Lattanzio, unpubl. data). These morph relationships afford us the unique opportunity to use male throat color as an indicator of social dominance.

Although the social dynamics of *U. ornatus* are well studied, scant attention has been paid to characterizing how morphs differ in other behaviors, including boldness. If morphs also diverge in boldness attributes, the degree that variation in boldness also coincides with their throat color polymorphism is also of interest as it may have strong implications for *U. ornatus* territorial dynamics in the wild. Our study will therefore provide information on the nature of boldness interactions with their dominance hierarchy to generate variation in territory use.

Males in our experiment were observed in the arena as they competed for access to perches differing in thermal and structural quality. Thus, we predicted

that dominant blue males would utilize the higher quality perch more often than subordinate yellow males. In terms of boldness differences among the morphs, there seems to be no consistent relationship between boldness and dominance across other taxa (Pintor et al. 2008; Barnett et al. 2012; Niemelä et al. 2012). Data from a 2012 field study indicate that in a more open (canopy and ground cover), frequently burned grassland region, yellow males were more abundant and able to sustain access to higher quality ecological resources like trees and higher trophic level prey (Lattanzio & Miles 2014, 2016). Habitats with more open canopy and therefore more exposure should be associated with a higher risk of predation to small-bodied lizards like *U. ornatus*. Thus, the dynamics observed by Lattanzio & Miles (2014) may reflect the outcome of an interaction between environmental variation (in terms of resource availability and predation risk) and the patterns of social dominance and boldness expressed within a population. Given these considerations, we also predict that yellow males are bolder than blue males and thus should be less likely to flee an approaching predator.

Methods

Study System

We captured 76 adult male *U. ornatus* by noose-pole at the Appleton-Whittell Research Ranch near Elgin, Arizona during June 2015 (31°33'23"N, 110°29'43"W). We restricted our sampling to only blue ($n = 35$) and yellow ($n = 41$) morph males because orange males are rare at our study site (<10% of the population, see Lattanzio & Miles 2014) and do not defend territories.

Throughout our experiment, individual males were housed in separate enclosures (17.4 L \times 17.4 W \times 7.9 H, in cm) at an on-site laboratory. Lights suspended above their terraria were connected to a timer to mimic the local photoperiod (15-h light, 9-h dark). We provided water *ad libitum* and food in the form of two 12 mm (total length) mealworms every other day. Upon capture, we measured snout-vent length (SVL, in mm) using calipers, mass (in g) using a spring scale, and recorded the color morph of each male. All males were released following our experiment within 72 h of initial capture.

Experimental Design

We first determined the experimental dyad (each consisting of one blue and one yellow male) for each trial

using a random number generator. We staged territory contests between males in each dyad within a small, circular arena (114 cm D \times 25 cm H) with 1 cm layer of sand substrate placed outdoors to facilitate natural lighting and temperature conditions. We constructed two artificial perches: a high- and low-quality perch (hereafter HQ and LQ, respectively), within the arena. High-quality microhabitat resources for male *U. ornatus* in the wild include rocks, living trees, and canyon walls in our study region that are heterogeneous in structure and thermal properties (Lattanzio, personal observ.). Our HQ perch was ~15 cm in height and included three shaded retreat sites. In contrast, the LQ perch was smaller in size (fewer rocks and ~8 cm height) with only one shaded retreat site. We quantified differences in perch quality by estimating relevant surface temperatures over a two-day period using a handheld Raytek infrared thermometer (Fluke Corporation, Everett, WA, USA). Specifically, we obtained 10 estimates each for the following environmental parameters: T_{sun} (temperature at the top of the perch for HQ or LQ, or in center of arena for G), and T_{refuge} (temperature within a refuge, or along the edge of the arena for G). Temperatures were recorded between 0700 and 1100 h, which matches the time frame of our experimental trials. All non-perch areas in the arena were considered bare ground (G). The HQ and LQ were spaced 80 cm apart to ensure that they could be perceived as independent perches, but far enough from the edge to prevent escape from the arena.

We conducted all trials between 0700 and 1100 h. For a given trial, we first simultaneously introduced the two focal males into the arena by placing them on opposite sides of the arena, faced toward the center, and equidistant from the HQ and LQ perches. We then allowed the males to explore the arena for a five-minute acclimation period prior to the start of data collection. After this period, one observer (JNT) recorded the position of each male in the arena on a data check-sheet: on the ground (G), on the HQ perch, or on the LQ perch at five-minute intervals for a total of 25 min. Observations were made ~10 m from the arena to avoid disturbing the lizards. At the conclusion of a trial, we tested male boldness by approaching the arena and recording 1) each males' escape response (flee, hide, or no response) and, for those males that fled, 2) their flight-initiation distance (in cm, using a tape measure) (Cooper 2003; Martín et al. 2005), following Lattanzio (2014). The approach always began from the observation area (~10 m from arena) at a practiced, consistent pace (~80 m/min) and aimed directly at the center of the arena. Here,

flight-initiation distance refers to the distance between the lizard and the simulated predator (JNT) at the initiation of an escape response (Cooper 2003). We used each male at least twice overall in our experiment in non-consecutive trials. Males were also never used more than once on the same day or paired to the same opponent.

Statistical Analysis

Prior to analyzing our temperature data, we calculated the available surface temperature range (T_{range}) for the HQ, LQ, and G at each time point as $T_{\text{sun}} - T_{\text{refuge}}$. We then used separate Analyses of variance (ANOVAs) to compare variation in T_{sun} , T_{refuge} , and T_{range} by perch type (HQ, LQ, or G). We compared SVL and body condition (residuals from a mass-SVL regression, Schulte-Hostedde et al. 2005) between the two morphs using separate unpaired t-tests.

Overall, we ran a total of 71 trials in our experiment. There were 76 males total, but more yellow males ($n = 41$) than blue males ($n = 35$). To compensate for the inconsistency in numbers, six yellow males and one blue male were used three times on different days and never with the same opponent. Five of the trials had no clear winner, so these were omitted from our analysis. We scored male behavior during each trial based on his position in the arena at each observation time: We assigned two points for HQ, one point for LQ, and zero points for G. The total of these points for each lizard at the end of a trial comprised his behavioral score. Based on our experimental design (5 observations per trial), a male's behavioral score ranged from 0 to 10, with higher behavioral scores indicating greater use of the HQ perch over other locations in the arena. The arena we designed for this experiment is small enough to force interactions between the males in each trial. The initial acclimation period served as an exploratory period for the individuals to explore the arena and establish preliminary interactions with each other. The behavioral score technique that we employed used each individual's position as an estimate of their relative dominance, under the likely assumption that males would engage in display behaviors and compete for access to the perches in the arena. An alternative to this approach would involve direct observations of male-male interactions throughout the trial; however, this might impose unnecessary stress on the animals. Given that male lizards readily interact with one another and compete for perches in both laboratory and field settings, the fact that these contests are often settled in under 30 min, and only more-dominant

individuals secure access to the experimental resource (s) (Thompson & Moore 1991; Carpenter 1995; Lattanzio & Miles 2014), we feel our use of behavioral scores (and thus animal positions/perch use in the arena) is a valid estimate of their relative dominance. In addition, a status was subjectively assigned to each male by the observer (JNT) based on each male's position in the arena at the end of a trial: The male occupying the HQ perch was deemed the winning male, following protocol modified from Garland et al. (1990). It was not possible to assign a clear winner in 5 of our 71 trials because both males were either never observed on either perch or never used the HQ perch. We omitted these trials prior to analysis in order to focus on cases where status assignment was unambiguous ($n = 66$ trials). We used generalized linear mixed-effects models with morph and male status (win or lose) as fixed effects, SVL as a covariate, and individual identity as a random effect to analyze variation in these behavioral scores. We did not include body condition in these models because preliminary analyses indicated that this trait does not correlate with behavioral score (Spearman's ρ , $r = -0.09$, $p = 0.24$). A Poisson error distribution with a logit-link function was used in these models. We evaluated model fit using sample size-corrected Akaike information criteria (AICc) (Burnham & Anderson 2002) and Akaike weights and calculated ΔAICc as $\Delta\text{AICc} = \text{AICc}_i - \min(\text{AICc})$. Akaike weights $w_i(\text{AICc})$ were calculated via the Weights function in the MuMIn package in R (Bartoń 2013).

We used a binomial generalized linear model (GLM) with a logit-link function to test for differences in escape response (flee or not flee) by morph, status, and their interaction. For males that fled on approach, we used an analysis of covariance (ANCOVA) to test for effects of morph, status, and their interaction on their flight-initiation distance. Flight-initiation distance was log-transformed to satisfy assumptions of

normality. The sample size for this ANCOVA ($n = 41$) included five males that were repeated once; however, exclusion of repeats does not change the interpretation of the results of this analysis (Table S1). We thus report the ANCOVA that includes the repeated males in Results. Both SVL and body condition were included in our ANCOVA and GLM models as covariates. All analyses were conducted within the R software environment (R Development Core Team 2012), and all means are presented ± 1 standard error (SE). Relevant assumptions of normality for the ANCOVA, and predictor independence for all models (including covariates), were verified prior to running each model described above. To assess pairwise effects underlying significance of terms in models with >2 levels, we employed a *post hoc* pairwise t-test with Bonferroni-corrected p-values.

Ethical Note

This work was conducted with permission by the Arizona Department of Game and Fish (#SP715013) and was approved by the Christopher Newport University Institutional Animal Care and Use Committee (#2015-8). All lizards were released alive at their point of initial capture following completion of the study.

Results

Quality of Perches within the Arena

The HQ perch was higher quality than the other options available to lizards in the arena (Table 1). Specifically, the perches differed in T_{refuge} ($F_{2,27} = 8.7$, $p = 0.001$) and T_{range} ($F_{2,27} = 3.5$, $p = 0.046$). The HQ perch had cooler refuge temperatures than G ($p_{\text{adj}} = 0.05$), as well as a greater range of temperatures than either the LQ perch or G ($p_{\text{adj}} = 0.001$ and

Table 1: Variation in structural (number of rocks and shaded refuges) and thermal (T_{sun} , T_{refuge} , T_{range} , see Methods) characteristics of the three perch options included in our study: a high-quality (HQ) or low-quality (LQ) perch, or the ground (G). The final column provides the percent of all temperature measurements (T_{sun} and T_{refuge} , $n = 20$ per perch) that fall below our estimate of CT_{max} for adult male *U. ornatus* (43.2°C , Lattanzio, unpubl. data). Values for T_{sun} and T_{refuge} are mean [min, max], and values for T_{range} are mean [SE]

Perch	Number of rocks	Number of refuges	T_{sun} ($^\circ\text{C}$)	T_{refuge} ($^\circ\text{C}$)	T_{range} ($^\circ\text{C}$)	Below CT_{max} (%)
G	0	0	47.9 [36.2, 55.4]	40.5 [28.2, 49.2]	7.1 [1.6]	40
LQ	4	1	46.2 [40.8, 52.4]	38.6 [32.8, 44.4]	7.6 [1.4]	55
HQ	10	3	45.4 [38.4, 52.6]	32.9 [29.4, 35.6]	12.4 [1.8]	65

0.027, respectively) (Table 1). We detected no differences among the HQ, LQ, and G in T_{sun} ($F_{2,27} = 0.6$, $p = 0.58$). Finally, the HQ perch was the only microhabitat in the arena where the majority of recorded temperatures fell below *U. ornatus*' CT_{max} (Table 1).

Morphology and Territorial Behavior

B and Y morphs overlapped in body size (B, 46.8 ± 0.5 mm; Y, 47.4 ± 0.5 mm; $t = -0.55$, $df = 71.963$, $p = 0.58$) and body condition (B, -0.02 ± 0.1 ; Y, 0.02 ± 0.1 ; $t = -0.4$, $df = 73.3$, $p = 0.69$). B males tended to have higher behavioral scores than Y males (B males, 4.1 ± 0.5 ; Y males, 3.6 ± 0.4). In addition, winning lizards (regardless of morph) had higher behavioral scores than losers (winners, 5.9 ± 0.4 ; losers, 1.8 ± 0.3). Our null model (Model T0) incorporated variation in all individuals (intercept only) in behavioral score (AICc: 703.92, Table 2). While including status alone as a fixed effect improved overall model fit, inclusion of morph and SVL separately as well as within the same model lead to a reduced model fit (Models TM, TSVL, and TMSVL; see Table 2).

Inclusion of all three effects generally improved model fit to varying degrees relative to the null model (Table 2). The model including the effect of morph, status, and their interaction on behavioral score in our experimental contests had the highest support of all candidate models (Model TSMi in Table 2) (Fig. 1). Our best-fit model supports data trends described above for the effects of morph and for status. In addition, the morph \times status interaction supports that losing B and Y males had lower behavioral scores than either winning morph (all $p_{\text{adj}} < 0.001$), and that losing Y males had higher behavioral scores than losing

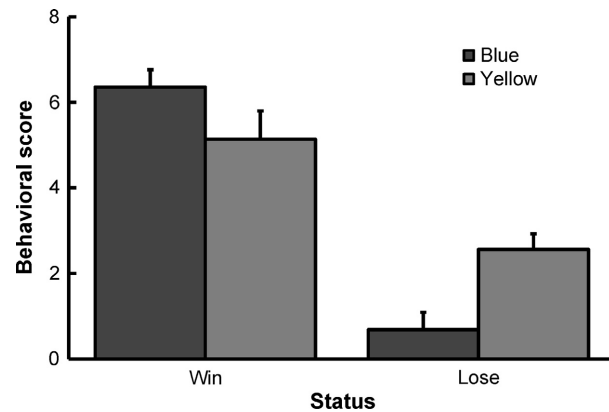


Fig. 1: Behavioral scores of winning and losing male *U. ornatus* ($n = 76$) in our experiment, by throat color: blue (dark gray) or yellow (light gray). See Methods for variable definitions and details on the calculation of behavioral scores. Bars are mean + 1 standard error.

B males ($p_{\text{adj}} = 0.019$) (Fig. 1). The next best model included SVL as a covariate, but this model was a poor fit relative to Model TSMi ($w_i[\text{AICc}] = 0.28$ vs. 0.68 in model excluding SVL; see Table 2).

Boldness

In terms of boldness, morph and status were the only significant predictors of male flight responses in our GLM model. Winning males were more likely to stay rather than flee from the approaching observer than losing males (status, $\chi^2 = 5.57$, $df = 1$, $p = 0.018$). Yellow males were also bolder than blue males (morph, $\chi^2 = 4.7$, $df = 1$, $p = 0.03$). We detected no interaction between morph and status or effect of morphology on the escape response (morph \times status, $\chi^2 = 0.15$, $df = 1$, $p = 0.7$; SVL, $\chi^2 = 0.1$, $df = 1$, $p = 0.75$; body condition, $\chi^2 = 0.15$, $df = 1$, $p = 0.07$). For the subset of males that fled (B males, $n = 26$; Y males $n = 15$), only morph had a significant effect on a male's flight-initiation distance: B males fled sooner than Y males (flight-initiation distance, B males: 67.7 ± 6.1 cm, Y males: 44.7 ± 3.4 cm; morph, $F_{1,35} = 6.38$, $p = 0.016$; status, $F_{1,35} = 0.004$, $p = 0.95$; morph \times status, $F_{1,35} = 0.02$, $p = 0.88$; SVL, $F_{1,35} = 0.49$, $p = 0.49$; body condition, $F_{1,35} = 0.24$, $p = 0.63$).

Discussion

Our findings are concordant with previous studies on asymmetries in male *U. ornatus* dominance behavior coincident with their color polymorphism. In the wild, blue males are aggressive and hold territories

Table 2: Results of generalized linear mixed-effects models describing the relationship of behavioral score to color morph (blue or yellow), status (win or lose), and body size (snout-vent length, SVL) of male *U. ornatus* lizards. See Methods for details on the calculation of behavioral scores and evaluation of model fit. Only AICc weights >0 are shown

Model	Syntax	AICc	ΔAICc	$w_i(\text{AICc})$
TSMi	~status \times morph	601.6	0	0.68
TSMiSVL	~status \times morph + SVL	603.4	1.8	0.28
TS	~status	608.8	7.2	0.02
TSSVL	~morph + SVL	610	8.4	0.01
TSM	~status + morph	610.7	9.2	0.01
TMSVL	~status + morph + SVL	611.8	10.2	
T0	~1	703.9	102.3	
TSVL	~SVL	703.9	102.3	
TM	~morph	705.7	104.1	
TMSVL	~status + SVL	705.9	104.3	

and yellow males usually exhibit a satellite tactic around blue male territories (Thompson & Moore 1991; Lattanzio & Miles 2016). Yellow males do however defend territories in one population (Lattanzio & Miles 2014). In this study, these two morphs partitioned the available perches in the arena and overall, blue males used the higher quality perch more often than yellow males (resulting in higher behavioral scores for this morph, see Results). In terms of boldness however, our findings add some interesting complexity to the behavioral nature of this polymorphic system. Specifically, yellow males were considered bolder than blue males because they exhibited 1) a decreased likelihood to flee the approaching observer and, for those that fled, 2) a shorter flight-initiation distance compared to blue males. Winning lizards behaved similarly to yellow males in both respects. In contrast, losers were equally as likely to flee or not flee from an approaching predator.

Studies of boldness and, more generally, escape behavior in vertebrates rely on human proxies for potential predators because many species have been shown to respond to an approaching human as they would a natural predator (Cooper 2003; Martín et al. 2005; Cooper 2009; Lattanzio 2014). Our results support that *U. ornatus* lizards are no exception to this general rule. Given the patterns of responses described above, it appears that although blue males are the dominant morph in *U. ornatus* (Thompson & Moore 1991; Thompson et al. 1993), yellow males may be bolder in terms of their antipredator response. Overall, the interaction between these behavioral tactics may help to explain geographic variation in the social and ecological dynamics of *U. ornatus* throughout its range.

Dominance is an aspect of behavior that is important for shaping social and ecological hierarchies within many species (Healey et al. 2007; Dijkstra et al. 2009b; Vercken et al. 2010; Brazill-Boast et al. 2013). Within a population, individuals may compete for food, thermal refugia, potential mates, and other environmental resources needed to meet life-history demands. The outcome of these interactions typically falls in favor of dominant over submissive individuals, particularly when resources are limited (Fretwell 1972; Lattanzio & Miles 2014). Many species, like *U. ornatus*, are color polymorphic and morphs exhibit asymmetries in social behavior that may also manifest as variation in ecological tactics (Lattanzio & Miles 2016). For example, adult male white-throated sparrows (*Zonotrichia albicollis*) typically exhibit two forms, a larger, white morph and a smaller tan-striped form (Watt et al. 1984). Captive experiments illustrate that

white morph males frequently supplanted and displaced tan males from small feeding dishes, essentially blocking them from a limiting resource (Watt et al. 1984). Furthermore, in Lake Victoria cichlids (*Pundamilia* sp.), red males are dominant and able to monopolize access to simulated rocky crevices (territories) better than blue males (Dijkstra et al. 2009a). These studies all support despotic resource-use dynamics among color morphs differing in social dominance (Calsbeek & Sinervo 2002; Lattanzio & Miles 2014), with only dominant individuals securing access to higher quality resources.

In our arena, the best perch option was the HQ perch because it was more structurally (number of rocks and refuges) and thermally (greater variation in surface temperature and lower refuge temperatures) heterogeneous than the LQ or G. In addition, more temperatures at the HQ perch were below *U. ornatus*' critical limit (43.2°C, Lattanzio, unpubl. data) than on the LQ perch or G (65% vs. 55% and 40%, respectively, see Table 1). Given what we know about dominance asymmetries in *U. ornatus*, we predicted that blue males would be more likely to exploit the HQ perch, both overall and at the end of a trial, than yellow males. Our findings that blue morphs won more trials and had higher behavioral scores than yellow males are consistent with this prediction.

What is particularly interesting in our findings however is the fact that the morphs also differed in boldness, but not in parallel to their dominance hierarchy (Results). Specifically, the shorter flight-initiation distance exhibited by yellow males supports our prediction that this morph is bolder than blue males (Díaz-Uriarte 2001). Boldness is an important phenotypic trait that has the potential to transcend multiple social and ecological contexts. Typically, shyer individuals are more likely to engage in those behaviors that enhance survival, whereas bolder individuals engage in riskier behavior in both inter- and intraspecific social contexts (Carlson & Langkilde 2014). Bolder behaviors typically emerge in environments where availability of resources is unpredictable (Chapman et al. 2010); these same types of environments also promote despotic, aggression-driven social dynamics (Fretwell 1972). However, boldness has a complex relationship with aggression, at best (Pintor et al. 2008; Barnett et al. 2012; Niemelä et al. 2012).

In *U. ornatus*, greater dominance is not associated with greater boldness, yet both seem to influence male territorial dynamics. Male tree lizards use aggressive behavioral displays to communicate their dominance status and compete with other males for

access to food, potential mates, and territories (Carpenter 1995). This social dominance hierarchy is a common phenomenon in many lizard species and often considered to be the primary driver in determining territorial dynamics in nature. However, boldness can also affect social interactions and spacing patterns in a population that may influence territorial dynamics (Pike et al. 2008; Croft et al. 2009), and as such represents another potential driver of ecological diversification. Shifts toward using higher quality microhabitat and prey resources by yellow male *U. ornatus* in the wild in more open habitats appear to support this claim (Lattanzio & Miles 2014). Aside from ecological opportunity, the relative frequency of yellow male *U. ornatus* in a population also increases as habitats become more open (Lattanzio, personal observ.). If yellow males have higher mating success in open habitats relative to other morphs (which would lead to greater numbers), then perhaps their greater boldness holds underlying reproductive fitness benefits as well. In other taxa, bolder animals appear to exhibit greater reproductive success compared to shier individuals (Réale et al. 2009; Ariyomo & Watt 2012), potentially due to the prioritization of survival by shy individuals over other fitness components (Cole & Quinn 2014). Regardless, more work is needed to elucidate how boldness and dominance interact to shape the social, ecological, and fitness landscapes in *U. ornatus*.

Conclusions

The results of our study support a role for traits important for both competitive (social dominance) and predatory (boldness) interactions in shaping within-population ecological dynamics. Moreover, the types of habitats exploited by widespread color polymorphic species like *U. ornatus* vary in their availability of ecological resources and predator exposure. Thus, the importance of male asymmetries in dominance and/or boldness behavior should also be environment-dependent. Although this latter prediction is not novel (Fretwell 1972), it may partly explain the observed geographic variation in morph frequencies within populations of color polymorphic taxa across their range (Hover 1985; Zucker 1989; Lattanzio & Miles 2014). The incorporation of boldness, dominance, and other important behavioral traits into ecological studies of *U. ornatus* and other color polymorphic taxa will therefore add substantial insight into the factors maintaining ecological and phenotypic diversity within a species.

Acknowledgements

A Christopher Newport University Faculty Development Grant awarded to MSL provided funding for this study. Kylie Krohmaly and Cynthia Morris assisted in the field. Linda Kennedy provided access to our study site and laboratory facility. Finally, we are indebted to Kortney Jaworski, Zachary Martin, Walter Koenig, and two anonymous reviewers for their input on earlier permutations of our manuscript. We have no conflict of interest to declare.

Literature Cited

- Aplin, L. M., Farine, D. R., Mann, R. P. & Sheldon, B. C. 2014: Individual-level personality influences social foraging and collective behaviour in wild birds. *Proc. R. Soc. Lond. B* **281**, 20141016.
- Ariyomo, T. O. & Watt, P. J. 2012: The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Anim. Behav.* **83**, 41–46.
- Barnett, C. A., Thompson, C. F. & Sakaluk, S. K. 2012: Aggressiveness, boldness and parental food provisioning in male house wrens (*Troglodytes aedon*). *Ethology* **118**, 984–993.
- Bartoń, K. 2013: MuMIn: Multi-model Inference. R package version 1.9.13. The Comprehensive R Archive Network (CRAN), Vienna, Austria.
- Bell, A. 2005: Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J. Evol. Biol.* **18**, 464–473.
- Bell, A. M. & Sih, A. 2007: Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.* **10**, 828–834.
- Bell, A. M. & Stamps, J. A. 2004: Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Anim. Behav.* **68**, 1339–1348.
- Brazill-Boast, J., Griffith, S. & Pryke, S. 2013: Morph-dependent resource acquisition and fitness in a polymorphic bird. *Evol. Ecol.* **27**, 1189–1198.
- Broom, M. & Ruxton, G. D. 2005: You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behav. Ecol.* **16**, 534–540.
- Brown, C., Jones, F. & Braithwaite, V. 2007: Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. *J. Fish Biol.* **71**, 1590–1601.
- Burnham, K. P. & Anderson, D. R. 2002: Model Selection and Multimodel Inference: A Practical Information – Theoretic Approach, 2nd edn. Springer-Verlag, New York, USA. 488 p.

- Calsbeek, R. & Sinervo, B. 2002: An experimental test of the ideal despotic distribution. *J. Anim. Ecol.* **71**, 513–523.
- Carlson, B. E. & Langkilde, T. 2014: No evidence of selection by predators on tadpole boldness. *Behaviour* **151**, 23–45.
- 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.
- Chapman, B. B., Morrell, L. J. & Krause, J. 2010: Unpredictability in food supply during early life influences boldness in fish. *Behav. Ecol.* **23**, 501–506.
- Cole, E. F. & Quinn, J. L. 2014: Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. *Biol. Lett.* **10**, 20140178.
- Cooper, W. E. 2003: Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Can. J. Zool.* **81**, 979–984.
- Cooper, W. E. 2009: Variation in escape behavior among individuals of the striped plateau lizard *Sceloporus virgatus* may reflect differences in boldness. *J. Herpetol.* **43**, 495–502.
- Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J. & James, R. 2009: Behavioural trait assortment in a social network: patterns and implications. *Behav. Ecol. Sociobiol.* **63**, 1495–1503.
- Díaz-Uriarte, R. 2001: Territorial intrusion risk and antipredator behaviour: a mathematical model. *Proc. R. Soc. Lond. B* **268**, 1165–1173.
- Dijkstra, P. D., Hemelrijk, C., Seehausen, O. & Groothuis, T. G. G. 2009a: Color polymorphism and intrasexual competition in assemblages of cichlid fish. *Behav. Ecol.* **20**, 138–144.
- Dijkstra, P. D., van Dijk, S., Groothuis, T. G. G., Pierotti, M. E. R. & Seehausen, O. 2009b: Behavioral dominance between female color morphs of a Lake Victoria cichlid fish. *Behav. Ecol.* **20**, 593–600.
- Fraser, D. F. & Gilliam, J. F. 1987: Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behav. Ecol. Sociobiol.* **21**, 203–209.
- Fretwell, S. D. 1972: *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey, USA. 224 p.
- Garland, T., Hankins, E. & Huey, R. 1990: Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* **4**, 243–250.
- Healey, M., Uller, T. & Olsson, M. 2007: Seeing red: morph-specific contest success and survival rates in a colour-polymorphic agamid lizard. *Anim. Behav.* **74**, 337–341.
- Hover, E. L. 1985: Differences in aggressive behavior between two throat color morphs in a lizard, *Urosaurus ornatus*. *Copeia* **1985**, 933–940.
- Lailvaux, S. P., Huyghe, K. & Van Damme, R. 2012: Why can't we all just get along? Interspecific aggression in resident and non-resident *Podarcis melisellensis* lizards. *J. Zool.* **288**, 207–213.
- Lattanzio, M. S. 2014: Temporal and ontogenetic variation in the escape response of *Ameiva festiva* (Squamata: Teiidae). *Phyllomedusa* **13**, 17–27.
- Lattanzio, M. S. & Miles, D. B. 2014: Ecological divergence among colour morphs mediated by changes in spatial network structure associated with disturbance. *J. Anim. Ecol.* **83**, 1490–1500.
- Lattanzio, M. S. & Miles, D. B. 2016: Trophic niche divergence among colour morphs that exhibit alternative mating tactics. *R. Soc. Open Sci.* **3**, 150531.
- Lincoln, R. J., Boxshall, G. A. & Clark, P. F. 1986: *A Dictionary of Ecology, Evolution, and Systematics*, 2nd edn. Cambridge University Press, New York, USA. 361 p.
- López, P., Hawlena, D., Polo, V., Amo, L. & Martín, J. 2005: Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. *Anim. Behav.* **69**, 1–9.
- Martín, J., Luque-Larena, J. J. & López, P. 2005: Factors affecting escape behavior of Iberian green frogs (*Rana perezi*). *Can. J. Zool.* **83**, 1189–1194.
- McElroy, E. J., Marien, C., Meyers, J. J. & Irschick, D. J. 2007: Do displays send information about ornament structure and male quality in the ornate tree lizard, *Urosaurus ornatus*? *Ethology* **113**, 1113–1122.
- 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.
- Niemelä, P. T., DiRienzo, N. & Hedrick, A. V. 2012: Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. *Anim. Behav.* **84**, 129–135.
- Öst, M., Seltmann, M. W. & Jaatinen, K. 2015: Personality, body condition and breeding experience drive sociality in a facultatively social bird. *Anim. Behav.* **100**, 166–173.
- Petelle, M. B., McCoy, D. E., Alejandro, V., Martín, J. G. & Blumstein, D. T. 2013: Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* **86**, 1147–1154.
- Pike, T. W., Samanta, M., Lindström, J. & Royle, N. J. 2008: Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. Lond. B* **275**, 2515–2520.
- Pintor, L. M., Sih, A. & Bauer, M. L. 2008: Differences in aggression, activity and boldness between native and

- introduced populations of an invasive crayfish. *Oikos* **117**, 1629–1636.
- Pryke, S. R. & Griffith, S. C. 2006: Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc. R. Soc. Lond. B* **273**, 949–957.
- R Development Core Team. 2012: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007: Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318.
- Réale, D., Martin, J., Coltman, D. W., Poissant, J. & Festa-Bianchet, M. 2009: Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.* **22**, 1599–1607.
- Riesch, R., Duwe, V., Herrmann, N., Padur, L., Ramm, A., Scharnweber, K., Schulte, M., Schulz-Mirbach, T., Ziege, M. & Plath, M. 2009: Variation along the shy–bold continuum in extremophile fishes (*Poecilia mexicana*, *Poecilia sulphuraria*). *Behav. Ecol. Sociobiol.* **63**, 1515–1526.
- Schulte-Hostedde, A. I., Zinner, B., Millar, J. S. & Hickling, G. J. 2005: Restitution of mass-size residuals: validating body condition indices. *Ecology* **86**, 155–163.
- Selmann, M. W., Jaatinen, K., Steele, B. B. & Öst, M. 2014: Boldness and stress responsiveness as drivers of nest-site selection in a ground-nesting bird. *Ethology* **120**, 77–89.
- Thompson, C. W. & Moore, M. C. 1991: Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Anim. Behav.* **42**, 745–753.
- Thompson, C. W., Moore, I. T. & Moore, M. C. 1993: Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. *Behav. Ecol. Sociobiol.* **33**, 137–146.
- Vercken, E., Clobert, J. & Sinervo, B. 2010: Frequency-dependent reproductive success in female common lizards: a real-life hawk-dove-bully game? *Oecologia* **162**, 49–58.
- Ward, A. J., Thomas, P., Hart, P. J. & Krause, J. 2004: Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* **55**, 561–568.
- Watt, D. J., Ralph, C. J. & Atkinson, C. T. 1984: The role of plumage polymorphism in dominance relationships of the white-throated sparrow. *Auk* **101**, 110–120.
- Zucker, N. 1989: Dorsal darkening and territoriality in a wild population of the tree lizard, *Urosaurus ornatus*. *J. Herpetol.* **23**, 389–398.

Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Table S1. Results of an analysis of covariance (ANCOVA) of male tree lizard (*Urosaurus ornatus*) flight-initiation distance (cm) relative to color morph (blue or yellow), status, and the interaction between these two traits. Body size (snout-vent length, SVL) and body condition (residual mass) were included as covariates in this model. Unlike the model presented in Results, this ANCOVA is a reduced model that excludes repeated estimates of FID on the same male ($n = 5$ males were repeated). Exclusion of those repeated males does not change our interpretation of the model results.