

# Resource variability and the collapse of a dominance hierarchy in a colour polymorphic species

Dawson M. Brown and Matthew S. Lattanzio \*

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

\*Corresponding author's e-mail address: matthew.lattanzio@cnu.edu

Received 14 January 2018; initial decision 16 February 2018; revised 6 May 2018;  
accepted 8 May 2018; published online 22 May 2018

---

## Abstract

Intraspecific social dominance hierarchies should be influenced by environmental variation; however, in colour polymorphic species, dominance hierarchies are often assumed fixed, and thus insensitive to environmental variability. We ran a series of experiments using the colour polymorphic long-tailed brush lizard (*Urosaurus graciosus*) to challenge this assumption. We staged contests between orange and yellow morph males over a single heated perch, two perches at the same temperature, or two perches differing in temperature. Our first experiment revealed that orange-throated males are socially dominant. However, this hierarchy collapsed in our other experiments as yellow males became more aggressive. Interestingly, both males only ever secured their own perch where the perches differed in temperature. These findings mirror observations of morph behavioural flexibility in nature and studies of behaviour–environment interactions in non-polymorphic taxa. We conclude that colour morphs may have an underappreciated ability to assess resource-level changes and respond with concomitant flexibility in behaviour.

## Keywords

aggression, alternative mating tactics, environmental variation, lizard, social behaviour, *Urosaurus graciosus*.

## 1. Introduction

Social dominance hierarchies reflect outcomes of intraspecific asymmetries in agonistic behaviour and can therefore have a substantial influence on access to resources including food, microhabitats, and mates in numerous taxa (Vessey, 1984; Vogel & Janson, 2007; Bastiaans et al., 2013; Cristaldo et al., 2016). In general, access to the preferred or highest-quality resources may be

limited to socially-dominant members of a population (Fretwell, 1972). For example, in rhesus monkeys (*Macaca mulatta*), individuals assert dominance through direct stares, open-mouth threats, and vertical tail-pointing; in contrast, submission is conveyed via fleeing, grimacing, and/or dropping their tail (Vessey, 1984). These aggressive/submissive behaviours allow for a dominance hierarchy to be established without repetitive, energy-expensive and harmful conflict. Similarly, dyadic encounters in the white-throated sparrow lead to a linear dominance hierarchy, in which only the winning, dominant birds maintain access to food (Schneider, 1984). These studies highlight the effect of social behaviour on resource utilization within a shared habitat. However, this interaction is not one-sided, as characteristics of the habitat itself, such as its overall resource availability and quality, should influence social behaviour as well. Evidence of this phenomenon has been documented in a variety of taxa, including mammals (Moritz et al., 2008; Liford & Cechala, 2016), reptiles (Gvoždík, 2002), and amphibians (Maerz & Madison, 2000).

Despite this consideration, species characterized by colour polymorphisms are rarely studied in the context of how environmental conditions and social dominance hierarchies interact (but see Bastiaans et al., 2013; Lattanzio & Miles, 2014). In many polymorphic species, discrete morphs diverge in suites of physiological, morphological, and ecological traits that are inferred to reflect alternative mating strategies (Thompson & Moore, 1991; Sinervo & Lively, 1996; Sinervo et al., 2000a). Aside from these traits, colour morphs also diverge in social dominance and aggression behaviour. For example, in the side-blotched lizard (*Uta stansburiana*), males with orange throats are dominant to blue-throated males, which themselves outcompete yellow-throated sneaker males (Sinervo & Lively, 1996). A similar hierarchy exists in the closely-related *Urosaurus ornatus* (although morph roles differ, see Thompson & Moore, 1991; Moore et al., 1998) and Gouldian finches (*Erythrura gouldiae*, Pryke & Griffith, 2006). In these systems, evidence supports that morph colour expression has a genetic basis (e.g., Thompson et al., 1993; Sinervo et al., 2000b), and sexual selection is the primary process maintaining the polymorphism and underlying morph differences in male social behaviour (e.g., Sinervo et al., 2000a). Given the genetic basis of morph colour expression and the association of their behaviours with mating tactics, a common yet often unstated assumption in these systems is that morph social roles are fixed throughout the species range (e.g., Foster, 1999). In other

words, for *U. stansburiana*, orange males are the dominant morph across all populations, regardless of any environmental variation between habitats. Recent indirect evidence drawing from studies on two other polymorphic species challenges this assumption, showing that morph behaviour may vary among populations (i.e., *Sceloporus grammicus*, see Bastiaans et al., 2013), including across an environmental gradient (i.e., *U. ornatus*, see Lattanzio & Miles, 2014). On a broader level, possible flexibility in morph behaviour may coincide with shifts in the morph composition of distinct populations across the species' range (reviewed by McLean & Stuart-Fox, 2014; see also Lotter & Scott, 1977; Corl et al., 2010). Hence, the impact of local environmental conditions on morph behaviour, as well as the ecological outcomes of the social interactions between morphs, may be stronger than expected.

In this study we capitalize on manipulations of a common experimental design used to characterize social dominance hierarchies to provide insight into the influence of environmental variation on morph behaviour and the social dominance hierarchy of the long-tailed brush lizard, *Urosaurus graciosus*. In their sister taxon, *U. ornatus*, the results of previous studies have shown that male throat colour signals variation in social dominance and other ecological and physiological traits (Thompson & Moore, 1991; Moore et al., 1998; Lattanzio & Miles, 2016; Taylor & Lattanzio, 2016). However, the hierarchy among *U. graciosus* colour morphs is unknown, as past research efforts have addressed their habitat use, diet, and reproductive effort at the individual, sex, or population level (Carpenter, 1962; Vitt & Ohmart, 1975; Vitt, 1977; Vitt et al., 1978; Congdon et al., 1982). At our field site, males exhibit one of two discrete throat colours (hereafter colour morphs): orange or yellow (see Figure A1 in the Appendix). We first established the baseline dominance hierarchy between these two morphs using dyadic contests over a single, heated perch, following standard methods (Garland et al., 1990; Thompson & Moore, 1991; Robson & Miles, 2000; Lattanzio & Miles, 2014). Then, we ran two additional experiments that manipulated (1) resource availability (perch number) and (2) resource quality (perch temperature), and explored the effects of those environmental shifts on male behaviour and the outcomes of their dyadic interactions. Specifically, if morph behavioural (dominance) roles are fixed, then environmental variability should not influence morph behaviour or the outcomes of male interactions.

## 2. Material and methods

### 2.1. Capture, housing and morphology

We captured 40 adult male *U. graciosus* via noose-pole along the Santa Cruz River, approximately 0.5 km west of Gladden Farms in Marana, AZ, USA in June 2017. The habitat was flat and open-canopied, with dominant vegetation types including desert broom (*Baccharis sarothroides*), mesquite (*Prosopis* sp.), and palo verde (*Parkinsonia* sp.). We visually classified the colour morph of each male based on his throat colouration (orange or yellow). Throat colouration is fixed at adulthood in other *Urosaurus* species and in their sister group (*Uta*) and is likely fixed in *U. graciosus* as well. Mark-recapture data from our population supports this claim, as recaptured lizards exhibited the same throat colour in 2016 and 2017 (Fisher's Exact Test,  $p = 1$ ;  $N = 3$  (orange) and  $N = 4$  (yellow)). In addition, colour expression differs significantly by morph ( $p < 0.001$ ; see Appendix) and does not overlap among individuals belonging to different morph classifications (Figure A1 in the Appendix). These data support classification of *U. graciosus* males into discrete colour morphs (e.g., Vercken et al., 2007). Our sample for the current study included  $N = 15$  orange and  $N = 25$  yellow males. We transported lizards in a cooler (to prevent overheating) back to a laboratory near Elgin, AZ, USA. We housed each lizard in opaque-walled individual enclosures ( $21.6 \times 15.2 \times 5.1$  cm, L  $\times$  W  $\times$  H). We provided food to each lizard in the form of one mealworm (*Tenebrio* sp.) every other day during the afternoon hours (after experiment trials were completed), and water was provided ad libitum. Suspended lamps were used to maintain temperatures  $\sim 32^\circ\text{C}$  during the day and were set to a timer to mimic the typical diel cycle (15 h light, 9 h dark) experienced by the lizards during this time of year. We measured the body size (snout-vent length (SVL)) of each male on the day of capture to the nearest 0.1 mm using dial calipers.

### 2.2. Social contests

We staged all social contests in a small plastic circular arena ( $0.2 \times 1.2$  m, depth  $\times$  diameter). We used 2 cm of sand as a substrate because sand is the primary substrate at our capture site. In Experiment 1, we sought to describe the colour morph hierarchy in *U. graciosus*. For this experiment, we added a single, centralized perch (raised branch) to the arena beneath a central heat source (100-W bulb suspended 0.4 m above the centre of the arena)

(Figure 1a). This heat source generated a gradient in the arena ranging 22–39°C from edges to perch (centre), which encourages focal lizards to move towards the central perch, encounter one another, and engage in social competition for sole access to the perch (Garland et al., 1990). Use of this arena design (and other procedures described below for each experiment) force lizards to engage in visual displays over other modes of communication (e.g., via chemical cues), enabling us to limit our focus to male behavioural displays during a trial. We selected this perch temperature based on data on field (measured at capture) and preferred (estimated in a laboratory gradient) body temperatures of male *U. graciosus*, which we determined as part of another study (field body temperature:  $40 \pm 2.8^\circ\text{C}$ ,  $N = 40$ ; preferred body temperature:  $37 \pm 1.1^\circ\text{C}$ ,  $N = 16$ ; both mean  $\pm 1$  standard deviation; Lattanzio, unpublished data). Our perch temperature in this experiment falls within the range of preferred and realized body temperatures for male *U. graciosus*, and thus should represent an ecologically-relevant, high-quality perch to males. All trials for all experiments were conducted during the morning hours (ca. 0800–1200 h). All orange males, and some yellow males, were used twice in each experiment, but never paired against the same individual opponent.

For each trial (in all three experiments), we selected a pair of males (one of each colour morph) from our sample at random (without replacement) to compete for the central perch. We placed each male at opposite ends of the arena facing perpendicular to the perch and covered them with opaque plastic cups. Focal males were held under these cups for a 2-min acclimation period prior to initiating a trial. At the start of a trial, these cups were simultaneously lifted out of the arena, and the behaviour of the two males was observed for a period of 20 min from behind a blind (dark, opaque solid-coloured sheet). This blind was set in place during the 2-min acclimation period to avoid effects of lowering it on male behaviour (i.e., males never saw it move). The frequencies of aggressive (head-bob, lateral, fullshow, chase and bite) and submissive (hide and flee) behaviours were tallied for each male during this 20-min period (behaviours are described in detail by Carpenter & Grubitz, 1961; Martins, 1993). Following previous work (Garland et al., 1990), we considered the male that occupied the perch at the end of a trial as the winner.

Next, we conducted two additional experiments that capitalized on manipulations to this base experimental design. Specifically, these design manipulations allowed us to evaluate how changes in resource (perch) availability

and quality (temperature) perturb the baseline morph hierarchy identified from the results of Experiment 1. Aside from these manipulations, we ran all trials for the same duration, recorded frequencies of the same male behaviours, and used orange males twice in each experiment. In Experiment 2, we manipulated perch availability: the two focal males (one of each colour morph) competed for access to two high-quality perches (39°C each) placed 0.5 m apart from one another in the centre of the arena (Figure 1b). In Experiment 3, we manipulated perch quality: the two focal males competed for access to two perches differing in thermal profile: one high-quality perch (39°C, approximately 1°C above their upper preferred body temperature for *U. graciosus*) and one low-quality perch (35°C) (Figure 1c). Our definition of status for winners and losers remained unchanged in these latter two experiments in cases where only one of the two males occupied a perch at the end of a trial. However, we also included draw as an option in Experiments 2 and 3 to describe when both males occupied their own perch. In total, each experiment consisted of 30 trials, resulting in 90 total trials overall.

After a trial, focal males were returned to their respective enclosures to rest for at least 24 h; no males were used twice in a single day to prevent exhaustion. After each experimental day we removed any faecal pellets that had been deposited and mixed the sand in the arena. In addition, no males were observed with any waxy femoral pore secretions (which are used for chemical communication in lizards; e.g., Pellitteri-Rosa et al., 2014) post-capture or during the experimental period. After all experimentation was concluded (lizards were held for a total of 12 days), we released all lizards back to their original capture points.

### 2.3. Statistical analysis

All analyses were conducted within the R 3.4.1 software environment (R Core Development Team, 2013). Unless otherwise noted, all statistical procedures were conducted using functions included in the base R software environment. We calculated dominance scores for each male at the end of each trial as the sum of all aggressive behaviours minus the sum of all submissive behaviours exhibited by that male (Garland et al., 1990). As a result, these dominance scores may be positive, zero, or negative, depending on the male's behavioural repertoire during a trial (see above). This variation prevented analysis of dominance score data using typical methods for scores (i.e., Poisson regression, which requires all values to be positive). These raw

scores also failed Shapiro–Wilk’s normality tests (Experiment 1:  $W = 0.9$ ,  $p < 0.001$ ; Experiment 2:  $W = 0.8$ ,  $p < 0.001$ ; Experiment 3:  $W = 0.7$ ,  $p < 0.001$ ). Thus, we rankit-transformed dominance scores for each experiment prior to analysis, using the following equation (Bliss, 1967):

$$\Phi^{-1}((\text{Rank}_i - 0.5)/n).$$

Here,  $\Phi^{-1}$  is the inverse normal cumulative distribution function,  $\text{Rank}_i$  is the rank of value  $i$ , and  $n$  is the sample size. We chose this transformation because recent work has demonstrated its utility for approximating a normal distribution from non-normal data (Solomon & Sawilowsky, 2009), as well as its ability to preserve statistical power and avoid inflating type-I error rates (Bishara & Hittner, 2012), thus overcoming our concerns as well as making it a preferred transformation method for non-parametric data like dominance scores.

Although yellow morph males were slightly larger than orange males in SVL (orange males:  $49.2 \pm 0.6$ ; yellow males:  $49.9 \pm 0.6$ ), these differences were non-significant (independent-samples  $t$ -test,  $t = -0.53$ ,  $df = 29.298$ ,  $p = 0.6$ ). Because we did not size-match males in our trials (males were assigned at random), relative differences in male SVL in each trial were variable (Experiment 1:  $3.3 \pm 0.6$  mm; Experiment 2:  $4.5 \pm 0.7$  mm; Experiment 3:  $4.5 \pm 0.6$  mm). However, one-sample  $t$ -tests on raw SVL differences between morphs indicated no morph-specific size bias in any experiment (Experiment 1,  $t = 0.86$ ,  $df = 29$ ,  $p = 0.4$ ; Experiment 2,  $t = -1.23$ ,  $df = 29$ ,  $p = 0.23$ ; Experiment 3,  $t = -1.07$ ,  $df = 29$ ,  $p = 0.29$ ). We also detected no association between these morph differences in SVL and their behavioural scores (Spearman’s correlation tests: Experiment 1,  $r = 0.19$ ,  $p = 0.31$ ; Experiment 2,  $r = 0.25$ ,  $p = 0.18$ ; Experiment 3,  $r = -0.08$ ,  $p = 0.66$ ). Given these considerations, we omitted contestant SVL differences from further consideration. However, we retained male raw SVL as a covariate in all models to control for any effects of absolute male size on contest outcomes. Models were implemented using the function ‘lmer’ in the lme4 package in R (Bates et al., 2015). Each model included trial and individual identity as random effects.

We ran a set of overall linear mixed-effect models to provide a formal test of whether patterns of morph behaviour (dominance scores) differed among experiments. These models explored all possible combinations of the effects of morph (orange or yellow) and experiment (1, 2, or 3) on male

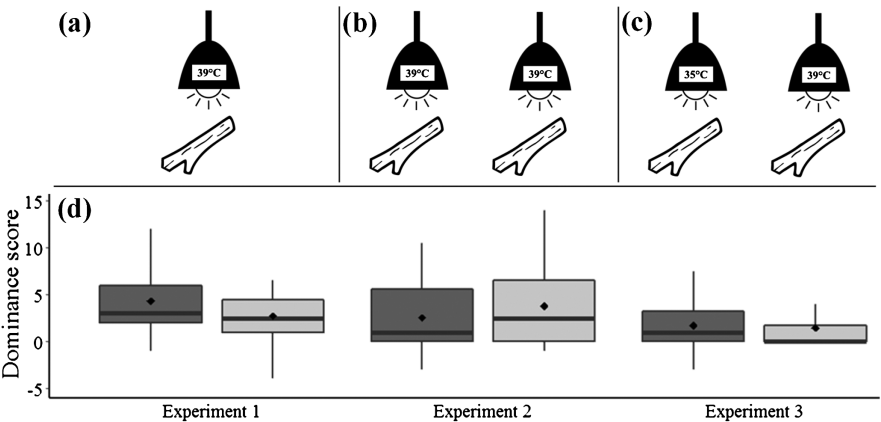
dominance scores. In these analyses, a significant morph  $\times$  experiment interaction would support a role for experimental manipulations in perturbing the morph social hierarchy in *U. graciosus*. For these models, our high pooled sample sizes ( $N = 180$  dominance scores) enabled us to evaluate fit among the candidate models via the Akaike Information Criterion (AIC) (Burnham & Anderson, 2003; Burnham et al., 2011). We also include likelihood ratio tests as an additional test of model significance (Bolker et al., 2009).

For our experiment-specific models, given their small sample sizes, we evaluated fit among candidate models using the sample size-corrected AIC (AICc) and Akaike weights ( $w_i[\text{AICc}]$ ) (Bolker et al., 2009), calculated using the functions ‘AICc’ and ‘Weights’, respectively, in the MuMIn package in R (Bartoń, 2013). Experiment-specific linear mixed-effects models explored the effects of morph (orange or yellow), status (winner or loser), their combination, or their absence (intercept-only null model) on rankit-transformed dominance scores. Finally, for Experiment 3 (the only experiment where we had contests end in a draw, see Results) we also tested for differences in frequency of contests with a clearly identifiable winner (and loser) and those that ended in a draw using a Chi-Square test. Key assumptions of linear mixed-effects models (i.e., residual normality, within-group errors centred at zero and constant variance, independence of residuals and random effects, and lack of influential data points; see Pinheiro & Bates, 2000) were verified prior to model interpretation using Shapiro–Wilk’s tests of model residuals (all  $p > 0.1$ ) as well as examination of quantile-quantile plots, plots of residuals versus fitted values, correlations of residuals and random effects, and partial leverage plots. Assumption evaluation procedures relied in part on plots produced via the function ‘ggplot’ in the ggplot2 package in R (Wickham, 2009). All means are presented as  $\pm 1$  standard error.

### 3. Results

We formally tested whether the *U. graciosus* colour morph behavioural hierarchy (i.e., differences in dominance scores) differed among our experiments via AIC values and likelihood-ratio tests comparing a set of candidate mixed-effect models (Table 1). Our analyses supported a significant interaction between morph and experiment (likelihood-ratio tests, all  $p \leq 0.05$ ). Thus, male morph behaviours (and thus dominance scores) were affected by our manipulations, and thus contest outcomes differed across the three experiments (Table 1).





**Figure 1.** (a)–(c) Arena designs for the three social contest experiments implemented in our study. We included a single high-quality perch for Experiment 1, two high-quality perches for Experiment 2, and a low- and high-quality perch available for male *Urosaurus graciosus* to compete for access to in Experiment 3. (d) Variation in orange (dark grey boxes) and yellow (light grey boxes) morph *U. graciosus* dominance scores across our three experiments. Boxes reflect the middle 50% of the data distribution, including median (heavy-bold line) and mean (diamond) values. End caps of the whiskers correspond to the first and third quartiles (25th and 75th percentiles, respectively) of the data distribution. Details on arena design for each experiment and calculations of dominance scores are provided in Material and Methods.

3.1. Experiment 1

Orange males had higher scores than yellow males ( $6.4 \pm 0.7$  versus  $2.3 \pm 0.5$ , respectively), and winning lizards had higher scores than losers

**Table 1.**  
*U. graciosus* morph behaviour varied among our social dominance experiments.

Model	Syntax	AIC	$w_i$ (AIC)	$\chi^2$	$p$
<i>BEMi</i>	<i>~morph × experiment</i>	490.8	0.92		
BE	~experiment	497.8	0.03	10.98	0.004
BEM	~morph + experiment	498.8	0.02	10	0.002
B0	~1	498.9	0.02	16.15	0.003
BM	~morph	499.1	0.01	14.26	0.003

We ran a series of linear mixed-effects models and tested for model significance via likelihood-ratio tests and AIC weights (see Methods). All models included SVL as a covariate to control for effects of male body size on his behaviour. Our best-supported model (lowest AIC, highest  $w_i$ [AIC]), which supported an interaction between morph and experiment, is italicised.

( $7 \pm 0.7$  versus  $1.7 \pm 0.5$ , respectively). Our best-fit model explaining variation in dominance scores in Experiment 1 supported these patterns and included effects of colour morph and status (AICc = 156.4,  $w_i$ [AICc] = 0.82; Table 2). This model had a significantly better fit to the data than all other models (likelihood-ratio tests, all  $p < 0.05$ ; see Table 2). Specifically, orange morph males had significantly higher dominance scores than yellow males (Figure 1d), and winning males had significantly higher scores than losers. Orange males were more likely to win social contests in this experiment ( $N = 20$  contests won by orange males; Chi-Square test,  $\chi^2 = 5.4$ ,  $df = 1$ ,  $p = 0.02$ ).

### 3.2. Experiment 2

Morph behavioural changes were evident in Experiment 2, with yellow males exhibiting similar dominance scores compared to orange males (Figure 1d). However, only the effect of status was retained in our best-fit model (AICc = 163.6,  $w_i$ [AICc] = 0.77; Table 2). Winning males had higher dominance scores than losing males (winners:  $7 \pm 0.8$ ; losers:  $1.6 \pm 0.4$ ). The lack of morph effect supports that yellow males exhibited similar (but higher) dominance scores to orange morph males in this experiment (yellow males,  $4.6 \pm 0.5$ ; orange males,  $2.5 \pm 0.9$ ). The increased aggressive behaviour frequencies of yellow males also led to a significant shift in winning frequency for this morph ( $N = 21$  contests won by yellow males; Chi-Square test,  $\chi^2 = 8.1$ ,  $df = 1$ ,  $p = 0.005$ ).

### 3.3. Experiment 3

In this experiment, the number of contests ending in a draw (i.e., both males occupying a perch) occurred as frequently as contests with a clearly identifiable winner (12 versus 18 trials; Chi-Square test,  $\chi^2 = 1.2$ ,  $df = 1$ ,  $p = 0.27$ ). In contrast, all contests in either previous experiment had clear winners. Our best-fit model for this experiment only retained status as a predictor (AICc = 139.6,  $w_i$ [AICc] = 0.78; Table 2), with winning males exhibiting higher dominance scores than losing males or males in contests that ended in a draw (winners:  $11.7 \pm 1.7$ ; losers:  $1.9 \pm 0.4$ ; draw:  $0.3 \pm 0.1$ ). Yellow males had higher dominance scores than orange males in this experiment (yellow males,  $5.1 \pm 1.8$ ; orange males,  $3.4 \pm 1.3$ ; Figure 1d), although differences were non-significant (Table 2). Of contests ending in a clear winner, yellow males won more contests than orange males, but this

**Table 2.**

Evaluation of candidate mixed-effects models for each experiment.

Model	Syntax	AICc	$\Delta$ AICc	$w_i$ (AICc)
Experiment 1				
<i>E1-MS</i>	<i>~morph + status</i>	<i>156.4</i>	<i>0</i>	<i>0.82</i>
E1-S	~status	158.8	2.4	0.18
E1-M	~morph	169.4	13	0
E1-Null	~1	176.8	20.4	0
Experiment 2				
<i>E2-S</i>	<i>~status</i>	<i>165.2</i>	<i>0</i>	<i>0.77</i>
E2-MS	~morph + status	167.7	2.5	0.17
E2-Null	~1	171.2	6	0.04
E2-M	~morph	172.3	7.1	0.02
Experiment 3				
<i>E3-S</i>	<i>~status</i>	<i>139.6</i>	<i>0</i>	<i>0.78</i>
E3-MS	~morph + status	142.1	2.5	0.22
E3-Null	~1	169.2	29.6	0
E3-M	~morph	171.4	31.8	0

Candidate linear mixed-effects models for each experiment evaluated the effect of male *U. graciosus* colour morph (orange or yellow), status, or their combination on male dominance scores. Status in our experiments was a subjective designation for each male in trials where only one male occupied a perch (winner) and the other did not (loser) at the end of a trial. In Experiments 2 and 3, if both males occupied their own perch at the end of a trial, the contest was considered a draw. Instances of a draw only occurred in Experiment 3 (see Results). All models included SVL as a covariate to control for effects of male body size on his behaviour. Due to lower sample sizes than those in our pooled dataset (see Table 1), we follow recommendations by Bolker et al. (2009) and evaluated fit among candidate models for each experiment via sample-size corrected AIC scores (AICc) and AICc weights only (see Material and Methods). Our best-supported model for each experiment is italicised.

trend was non-significant ( $N = 12$  versus 6 contests won by yellow and orange males, respectively; Chi-Square test,  $\chi^2 = 2.8$ ,  $df = 1$ ,  $p = 0.1$ ).

#### 4. Discussion

Orange and yellow morph male *U. graciosus* differ in social dominance; however, the outcomes of their social interactions varied depending on the number and quality of available territorial resources. Our results from Experiment 1 provide the first insights into the nature of this hierarchy: orange males are dominant to yellow males. Field studies on male *U. graciosus*' behavioural interactions are thus an important next step to evaluate how

this hierarchy manifests in the wild. Interestingly, examples of dominance by orange or reddish-coloured morphs are widespread in lizards (e.g., *U. stansburiana*, Sinervo & Lively, 1996; *Pseudomoia entrecasteauxii*, Stapley, 2006; *Ctenophorus pictus*, Healey et al., 2007; *Podarcis melisellensis*, Huyghe et al., 2007; *Liolaemus sarmientoi*, Fernández et al., 2018), and often assumed to be fixed. However, for our study species, this hierarchy dissolved in Experiment 2 (two high-quality perches), with yellow males becoming much more aggressive towards their orange counterparts, resulting in an even behavioural match between the morphs. We observed similar outcomes in Experiment 3 (two perches of uneven quality), although both males could also occupy their own perch in this context. Overall, our findings suggest that morph behaviour, and consequently, the ecological outcomes of social dominance hierarchies in colour polymorphic species may be more plastic than previously appreciated.

The difference in social dominance behaviour observed between Experiments 1 and 2 emphasizes a key ecological concept: namely, that resource availability influences natural social behaviour in animals (e.g., Boccia et al., 1988; Gabor & Jaeger, 1995; Grover et al., 2007; Vogel & Janson, 2007; Cristaldo et al., 2016). For example, in neotropical termites, areas of intermediate resource availability encourage increased agonistic behaviour, but exposure to low and high resource availability tend to yield less aggressive behaviour overall (Cristaldo et al., 2016). In other species, like the bonnet macaque (*Macaca radiata*), low resource availability and scarcity leads to more agonistic behaviour within a social group (Boccia et al., 1988). Such flexibility in social behaviour has gone underappreciated in studies of colour polymorphic species like *U. graciosus*. In general, morph colouration is fixed by maturity in these species, and behavioural roles reflect the outcome of physiological and developmental differences among the morphs during ontogeny (e.g., Sinervo et al., 2000a). However, a few studies conducted over the past few decades have identified links between shifts in testosterone levels (*U. stansburiana*, Sinervo et al., 2000a) and resource availability (*U. ornatus*, Lattanzio & Miles, 2014) with changes in aggressive behaviour. Another study further suggested evolutionary lability in the morph colour-behaviour association between populations (Bastiaans et al., 2013). Our data reveal flexibility in yellow morph *U. graciosus* agonistic behaviour: yellow morph male aggressive behaviour increased almost two-fold in the presence

of two resources of equal quality. Because of this behavioural plasticity, yellow and orange males exhibited similar dominance scores, collapsing the morph dominance hierarchy identified in Experiment 1. Yellow males were also the subjective winner more often than orange males in Experiment 2.

Jointly, these outcomes suggest that shifts in yellow male behaviour may occur in response to changes in resource availability, and they have the potential to influence the ecological consequences of social contests. Flexibility in yellow morph behaviour in a colour polymorphic species is not novel and has been associated with shifts in microhabitat use and prey acquisition in a resource-limited environment (for *U. ornatus*, see Lattanzio & Miles, 2014), as well as shifts in circulating hormones that promote increases in territoriality and endurance capacity (for *U. stansburiana*, Sinervo et al., 2000a). In terms of our data, in Experiment 1, the presence of only one perch likely meant that only one lizard could occupy it at a time, and so orange males may have simply gone undisputed in most trials. In our other experiments, the presence of a second perch may therefore have encouraged all males to behave more aggressively and increased the frequency of agonistic encounters. However, only yellow males shifted behaviour across experiments. Given similar findings flexibility in yellow male behaviour in other related species, this plasticity may simply be a universal characteristic of yellow morphs. To that end, field-based studies are a critical next step to evaluate the fitness benefits of these behavioural shifts by yellow morph *U. graciosus*, including whether they enable territory defence and/or provide access higher-quality ecological resources as observed in other taxa.

In Experiment 3, we mimicked an environmental context that may very well be the most relevant to conditions *U. graciosus* and other species experience in the wild: whereas population densities may covary with overall resource availability, environmental resources likely vary in quality (Fretwell, 1972). When colour morphs vary in social dominance, only the most-aggressive phenotypes may exploit the highest-quality resources (e.g., Calsbeek & Sinervo, 2002). This context also serves as a direct contrast to Experiment 2 (two high-quality perches), and findings across these experiments provide some insight into the effect of varying resource quality on the social hierarchy in *U. graciosus*. Specifically, we only ever observed instances of both males occupying a perch in Experiment 3 (classified as a draw, see Methods). These draw outcomes were common (12 of 30 trials) and marked

by a sharp decline in aggressive behaviour by both males compared to trials ending with a clear winner and loser (see Results). In the simplest sense, environmental heterogeneity favoured a more peaceful coexistence between competing males. In contrast, when both resources are high quality, the 'winning' male always prevented the other male from occupying the other perch.

Because we allowed males sufficient time to rest in between trials and matched males at random in all experiments, our contrasting findings between Experiments 2 and 3 should not be a consequence of male fatigue. Alternatively, it may be that the two perches in Experiment 2 were perceived as a single, higher-quality resource by the males, possibly due to the proximity of the perches in the arena, their overlapping thermal traits, or both. Experiment 3 negates perch proximity as a driver of those findings (i.e., same perch distance), and so the relative heterogeneity in perch thermal quality between those two experiments may have driven these contrasting outcomes. For example, in *Liolaemus sarmientoi* (a Patagonian lizard species), red morphs exhibit more aggressive dominant behaviours and attain higher body temperatures in the wild than other male colour morphs (Fernández et al., 2018). As a result, only the body temperatures of red males overlapped with the species' preferred temperature range (Fernández et al., 2018), suggesting that morphs differing in aggressive behaviour partition available microhabitats in thermally heterogeneous environments (e.g., Calsbeek & Sinervo, 2007). We may also draw relevant parallels between our current findings and those of studies on behaviour-environment interactions in non-colour polymorphic species. For example, in a study of the effects of manipulations to the visual environment on spacing and aggressive behaviour in benthic-zone arctic charr (*Salvelinus alpinus*), fish housed over a uniform black substrate exhibited increased spatial clustering and fighting frequency compared to fish housed over a heterogeneous substrate (i.e., a black-and-white striped pattern; see Mikheev et al., 1996). Similarly, in the desert grass spider (*Agelenopsis aperta*), populations exploiting riparian habitats are less aggressive and specialize on divergent prey resources compared to conspecifics in arid grasslands (Riechert, 1999). One of the primary drivers for this behavioural shift is the thermal buffer provided by structurally-heterogeneous woodland vegetation, which are only present in riparian areas (Riechert, 1999).

Collectively, these studies support a negative relationship between resource heterogeneity and intraspecific aggression (Mikheev et al., 1996; Riechert, 1999). Comparisons between Experiments 2 and 3 suggest that

*U. graciosus* morphs adhere to this paradigm as well. Thus, male *U. graciosus* appear to be capable of dynamic resource assessment in terms of availability and quality (e.g., Riechert, 1979). This tactic, coupled with the observed shifts in behaviour of yellow males across our lab experiments, support that morph roles may be flexible, thus enabling *U. graciosus* populations to respond differently to divergent environmental conditions throughout their geographic distribution. Comparisons of yellow morph social behaviour among contrasting habitat types would be particularly fruitful for addressing this prediction.

#### 4.1. Conclusions

Staged, dyadic contests over a central resource are a useful method for revealing the form of social dominance hierarchies in lizards (e.g., Garland et al., 1990; Thompson & Moore, 1991), and our study provides the first insight into the social hierarchy in *U. graciosus*. The genetic and physiological architecture driving morph differences in behaviour and colouration in colour polymorphic species, coupled with the ties between morph behaviour and their mating tactics, underlie a common assumption that morph dominance hierarchies should remain stable throughout the species' distribution. In the case of *U. graciosus*, one might therefore reasonably expect orange males to remain dominant across all environmental contexts. However, our findings and the results of a few other studies challenge this assumption by supporting flexibility in the behavioural role of (some) male morphs (Sinervo et al., 2000a; Bastiaans et al., 2013; Lattanzio & Miles, 2014). Behavioural flexibility in response to changes in environmental conditions may have an important impact on the social and ecological outcomes of male-male competition in the wild. One prediction drawing from this conclusion is that the ecological outcomes of morph dominance interactions should differ among habitats. To-date, few studies have explicitly tested this prediction (but see Calsbeek & Sinervo, 2002; Lattanzio & Miles, 2014). In a broader context, these behaviour-environment interactions might also help to explain geographic variation in colour morph diversity and relative frequency (McLean & Stuart-Fox, 2014). Consequently, flexibility in morph behaviour across environmental contexts may influence the maintenance of a colour polymorphism across a species' range, as well as rates of adaptive divergence among populations (Foster, 1999). Our appreciation of the evolutionary significance of the behavioural component of a colour polymorphism would be enhanced by further inquiry into the degree of flexibility in morph roles in other taxa.

## Acknowledgements

This work was supported by a National Audubon Society Apacheria Fellowship and Honor's Summer Research Stipend (both to D.M.B.), and a Christopher Newport University Faculty Development Grant (to M.S.L.). All work conducted in this study was approved by the CNU Institutional Animal Care and Use Committee (No. 2015-8) and done under an Arizona Department of Game and Fish permit (No. SP510761). We thank Macy Friend for assistance in the field. Linda Kennedy provided access to the lab facilities. Kortney Jaworski, Julie Taylor, William Ternes, and Madison McCann provided helpful comments on earlier permutations of this manuscript.

## References

- Bartoń, K. (2013). MuMIn: multi-model inference. R package version 1.9.13. — The Comprehensive R Archive Network (CRAN), Vienna.
- Bastiaans, E., Morinaga, G., Castañeda Gaytán, J.G., Marshall, J.C. & Sinervo, B. (2013). Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. — *Behav. Ecol.* 24: 968-981.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. — arXiv preprint. arXiv:1406.5823.
- Bishara, A.J. & Hittner, J.B. (2012). Testing the significance of a correlation with nonnormal data: comparison of Pearson, Spearman, transformation, and resampling approaches. — *Psychol. Methods* 17: 399-417.
- Bliss, C.I. (1967). *Statistics in biology*. — McGraw Hill, New York, NY.
- Boccia, M.L., Laudenslager, M. & Reite, M. (1988). Food distribution, dominance, and aggressive behaviors in bonnet macaques. — *Am. J. Primatol.* 16: 123-130.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H. & White, J.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. — *Trends Ecol. Evol.* 24: 127-135.
- Burnham, K.P. & Anderson, D.R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*. — Springer, New York, NY.
- Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). AIC model selection and multi-model inference in behavioral ecology: some background, observations, and comparisons. — *Behav. Ecol. Sociobiol.* 65: 23-35.
- Calsbeek, R. & Sinervo, B. (2002). An experimental test of the ideal despotic distribution. — *J. Anim. Ecol.* 71: 513-523.
- Calsbeek, R. & Sinervo, B. (2007). Correlational selection on lay date and life-history traits: experimental manipulations of territory and nest site quality. — *Evolution* 61: 1071-1083.



- Carpenter, C.C. (1962). A comparison of the patterns of display of *Urosaurus*, *Uta*, and *Streptosaurus*. — *Herpetologica* 18: 145–152.
- Carpenter, C.C. & Grubitz, G. (1961). Time-motion study of a lizard. — *Ecology* 42: 199–200.
- Congdon, J.D., Vitt, L.J., van Loben Sels, R.C. & Ohmart, R.D. (1982). The ecological significance of water flux rates in arboreal desert lizards of the genus *Urosaurus*. — *Physiol. Zool.* 55: 317–322.
- Corl, A., Davis, A.R., Kuchta, S.R., Comendant, T. & Sinervo, B. (2010). Alternative mating strategies and the evolution of sexual size dimorphism in the side-blotched lizard, *Uta stansburiana*: a population-level comparative analysis. — *Evolution* 64: 79–96.
- Cristaldo, P.F., Araújo, A.P., Almeida, C.S., Cruz, N.G., Ribeiro, E.J., Rocha, M.L., Santana, A.S., Santos, A.A., Passos, A., de Souza, O. & Florencio, D.F. (2016). Resource availability influences aggression and response to chemical cues in the Neotropical termite *Nasutitermes*. — *Behav. Ecol. Sociobiol.* 70: 1257–1265.
- Fernández, J.B., Bastiaans, E., Medina, M., De la Cruz, F.R., Sinervo, B.R. & Ibargüengoytía, N.R. (2018). Behavioral and physiological polymorphism in males of the austral lizard *Liolaemus sarmientoi*. — *J. Comp. Physiol. A.* 204: 219–230.
- Foster, S.A. (1999). The geography of behaviour: an evolutionary perspective. — *Trends Ecol. Evol.* 14: 190–195.
- Fretwell, S.D. (1972). *Populations in a seasonal environment*. — Princeton University Press, Princeton, NJ.
- Gabor, C.R. & Jaeger, R.G. (1995). Resource quality affects the agonistic behaviour of territorial salamanders. — *Anim. Behav.* 49: 71–79.
- Garland, T., Hankins, E. & Huey, R.B. (1990). Locomotor capacity and social dominance in male lizards. — *Funct. Ecol.* 4: 243–250.
- Grover, C.D., Kay, A.D., Monson, J.A., Marsh, T.C. & Holway, D.A. (2007). Linking nutrition and behavioural dominance: carbohydrate scarcity limits aggression and activity in Argentine ants. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 274: 2951–2957.
- Gvoždík, L. (2002). To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. — *Can. J. Zool.* 80: 479–492.
- 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.
- Huyghe, K., Vanhooydonck, B., Herrel, A., Tadić, Z. & Van Damme, R. (2007). Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. — *Integr. Comp. Zool.* 47: 211–220.
- 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. — *Roy. Soc. Open Sci.* 3: 150531.
- Liford, A.N. & Cechala, K.K. (2016). Does riparian disturbance alter stream amphibian antipredator behaviors? — *Can. J. Zool.* 95: 75–79.

- Lotter, F. & Scott, N.J. (1977). Correlation between climate and distribution of the color morphs of the salamander *Plethodon cinereus*. — *Copeia* 1977: 681-690.
- Maerz, J.C. & Madison, D.M. (2000). Environmental variation and territorial behavior in a terrestrial salamander. — In: The biology of plethodontid salamanders (Bruce, R.C., Jaeger, R.G. & Houck, L.D., eds). Springer, New York, NY, p. 395-406.
- Martins, E.P. (1993). Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. — *Anim. Behav.* 45: 25-36.
- McLean, C.A. & Stuart-Fox, D. (2014). Geographic variation in animal colour polymorphisms and its role in speciation. — *Biol. Rev.* 89: 860-873.
- Mikhееv, V.N., Adams, C.E., Huntingford, F.A. & Thorpe, J.E. (1996). Behavioural responses of benthic and pelagic Arctic charr to substratum heterogeneity. — *J. Fish Biol.* 49: 494-500.
- 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.
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. — *Science* 322: 261-264.
- Pellitteri-Rosa, D., Martín, J., López, P., Bellati, A., Sacchi, R., Fasola, M. & Galeotti, P. (2014). Chemical polymorphism in male femoral gland secretions matches polymorphic coloration in common wall lizards (*Podarcis muralis*). — *Chemoecology* 24: 67-78.
- Pinheiro, J. & Bates, D. (2000). Mixed-effects models in S and S-PLUS. — Springer, New York, NY.
- Pyke, S.R. & Griffith, S.C. (2006). Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 273: 949-957.
- R Core Development Team (2013). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna.
- Riechert, S.E. (1979). Games spiders play: II. Resource assessment strategies. — *Behav. Ecol. Sociobiol.* 6: 121-128.
- Riechert, S.E. (1999). The use of behavioral ecotypes in the study of evolutionary processes. — In: Geographic variation in behavior: perspectives on evolutionary mechanisms (Foster, S.A. & Endler, J.A., eds). Oxford University Press, Oxford, p. 3-32.
- Robson, M.A. & Miles, D.B. (2000). Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. — *Funct. Ecol.* 14: 338-344.
- Schneider, K.J. (1984). Dominance, predation, and optimal foraging in white-throated sparrow flocks. — *Ecology* 65: 1820-1827.
- Sinervo, B. & Lively, C.M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. — *Nature* 380: 240-243.
- Sinervo, B., Miles, D.B., Frankino, W.A., Klukowski, M. & DeNardo, D.F. (2000a). Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. — *Horm. Behav.* 38: 222-233.

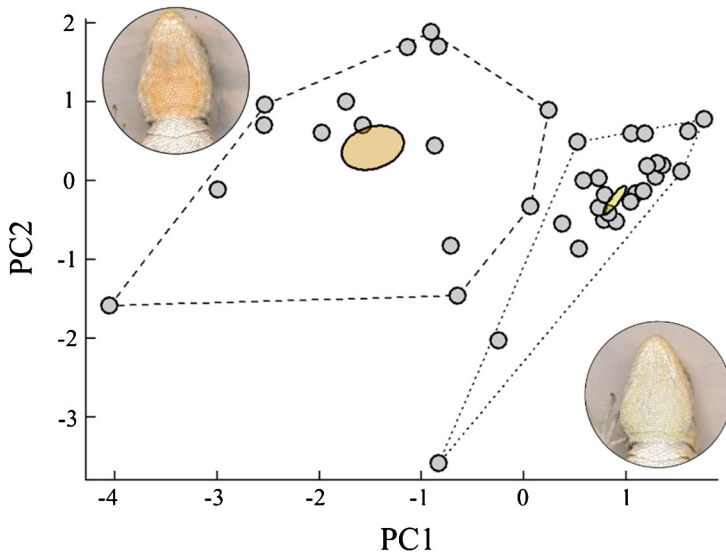
- Sinervo, B., Svensson, E. & Comendant, T. (2000b). Density cycles and an offspring quality versus quantity game driven by natural selection. — *Nature* 406: 985–988.
- Solomon, S.R. & Sawilowsky, S.S. (2009). Impact of rank-based normalizing transformations on the accuracy of test scores. — *J. Mod. Appl. Stat. Methods* 8: 448–462.
- Stapley, J. (2006). Individual variation in preferred body temperature covaries with social behaviours and colour in male lizards. — *J. Therm. Biol.* 31: 362–369.
- Taylor, J.N. & Lattanzio, M.S. (2016). Boldness, dominance, and territoriality in the color polymorphic tree lizard, *Urosaurus ornatus*. — *Ethology* 122: 892–901.
- 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., Massot, M., Sinervo, B. & Clobert, J. (2007). Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. — *J. Evol. Biol.* 20: 221–232.
- Vessey, S.H. (1984). Dominance among rhesus monkeys. — *Polit. Psychol.* 5: 623–628.
- Vitt, L.J. (1977). Observations on clutch and egg size and evidence for multiple clutches in some lizards of southwestern United States. — *Herpetologica* 33: 333–338.
- Vitt, L.J. & Ohmart, R.D. (1975). Ecology, reproduction, and reproductive effort of the iguanid lizard *Urosaurus graciosus* on the lower Colorado river. — *Herpetologica* 31: 56–65.
- Vitt, L.J., Sels, R.C. & Ohmart, R.D. (1978). Lizard reproduction: annual variation and environmental correlates in the iguanid lizard *Urosaurus graciosus*. — *Herpetologica* 34: 241–253.
- Vogel, E.R. & Janson, C.H. (2007). Predicting the frequency of food-related agonism in white-faced capuchin monkeys (*Cebus capucinus*), using a novel focal-tree method. — *Am. J. Primatol.* 69: 533–550.
- Wickham, H. (2009). *ggplot2: elegant graphics for data analysis*. — Springer, New York, NY.

## Appendix

In colour polymorphic species, morphs should exhibit discrete and non-overlapping variation in colour expression (e.g., Vercken et al., 2007; Lattanzio et al., 2014). We explicitly tested whether the *U. graciosus* morphs differ in throat colour expression using the following procedure. First, ventral images were obtained of each male using a high-resolution Canon flatbed scanner (CanoScan 9000F Mark II, Canon USA). A ruler placed on the platen facilitated conversion of pixels to mm<sup>2</sup> for these measurements. This

method produces images of lizard features at a fixed distance and lighting conditions, and the scanned images were saved in uncompressed Tag Image File Format (TIFF). These methods were employed to guarantee consistency in how images were taken for analysis purposes, as well as to prevent loss of colour information problematic of other image formats (reviewed by Stevens et al., 2007). We extracted mean red, green and blue colour channel data over a  $11.1 \pm 0.13 \text{ mm}^2$  square polygon area on the centre of the throat of each male captured for this study ( $N = 40$  (15 orange males, 25 yellow males)). Colour data were extracted using the histogram tool in the program ImageJ version 1.46r (Abràmoff et al., 2004). We explicitly tested for differences in colour expression (red, green and blue channel data) by morph using a multivariate analysis of variance, and evaluated the contribution of each colour channel to those findings via post-hoc univariate ANOVAs with Bonferroni-adjusted  $P$ -values to account for multiple comparisons.

On average, orange morphs had higher loadings on red, but lower loadings for both green and blue channels compared to yellow males (orange morphs: red =  $226.62 \pm 2.47$ , green =  $176.78 \pm 4.83$ , blue =  $132.8 \pm 7.75$ ; yellow morphs: red =  $222.88 \pm 1.64$ , green =  $213.48 \pm 1.72$ , blue =  $199.16 \pm 2.37$  (mean  $\pm 1$  SE)). The two morphs significantly differ in throat colouration (Pillai's trace = 0.77,  $F_{1,38} = 39.74$ ,  $P < 0.001$ ). In addition, individual lizard throat colour expression did not overlap between the two morphs (see Figure A1). These patterns were primarily driven by morph differences in green and blue channel loadings (red:  $F_{1,38} = 1.71$ ,  $P_{\text{adj}} > 0.2$ ; green:  $F_{1,38} = 71.94$ ,  $P_{\text{adj}} < 0.001$ ; blue:  $F_{1,38} = 98.15$ ,  $P_{\text{adj}} < 0.001$ ).



**Figure A1.** Results of a Principal Component Analysis (PCA) of throat colour expression (red, green and blue channel loadings; see Appendix text) of  $N = 40$  male long-tailed brush lizards (*Urosaurus graciosus*). Points are component axis values. For each colour morph, dashed lines represent outer (= convex) hulls describing total variation in colour expression, and shaded ellipses describe the 95% confidence limit of the centroid. Sample sizes for each morph are  $N = 15$  (orange) and  $N = 25$  (yellow). Insets are images of representative throats of each morph. Overall, morph colour expression does not overlap in *U. graciosus*.

## References

- Abràmoff, M.D., Magalhães, P.J. & Ram, S.J. (2004). Image processing with ImageJ. — *Biophoton. Int.* 11: 36–42.
- Lattanzio, M.S., Metro, K.J. & Miles, D.B. (2014). Preference for male traits differ in two female morphs of the tree lizard, *Urosaurus ornatus*. — *PloS One* 9: e101515.
- Stevens, M., Parraga, C.A., Cuthill, I.C., Partridge, J.C. & Troschianko, T.S. (2007). Using digital photography to study animal coloration. — *Biol. J. Linn. Soc.* 90: 211–237.
- Vercken, E., Massot, M., Sinervo, B. & Clobert, J. (2007). Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. — *J. Evol. Biol.* 20: 221–232.

Copyright of Behaviour is the property of Brill Academic Publishers and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.