Behavioural differences across contexts may indicate morph-specific strategies in the lizard *Ctenophorus decresii*

Madeleine St Clair Yewers [a, *], Sarah Pryke [b], Devi Stuart-Fox [a]

[a] *School of BioSciences, The University of Melbourne, Australia*
[b] *Division of Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra, Australia*

Discrete colour polymorphisms are often genetically correlated with other traits under natural and sexual selection, such as behaviour, life history and physiology. Elucidating such correlations is essential to understand the adoption of alternative strategies between morphs and the role they play in the maintenance of colour polymorphisms within a population. Using field experiments, we tested the hypothesis that four visually discrete morphs (orange, yellow, yellow with a central orange patch (orange-yellow) and grey) of the tawny dragon lizard, *Ctenophorus decresii*, display alternative behavioural strategies. Specifically, we compared the response of colour morphs to simulated conspecific territorial intruders and predators in the wild. Although the orange-yellow morph can be objectively classified, it may behaviourally resemble the orange or yellow morph; therefore we compared statistical models in which the orange-yellow morph was considered a separate morph (four-morph model) or grouped with either pure orange or pure yellow individuals (three-morph models). For aggression, a three-morph model with orange-yellow individuals grouped as yellow morphs best fitted the data. The orange morph showed consistently high aggression to all morphs, while the grey morph showed consistently low aggression. Aggression of the yellow morph was conditional on the morph of the intruder. In addition to being the least aggressive, the grey morph was the least bold. Although the orange morph was the most aggressive, it was only the boldest under a three-morph model, which was equally likely compared to a four-morph model. Overall our results support the view that tawny dragon lizard morphs adopt different behavioural strategies, the orange and grey morphs exhibiting more aggressive and cautious strategies, respectively, and the yellow morph changing its aggression depending on its competitor's colour.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Colour-polymorphic species are model biological systems to understand the generation and maintenance of intraspecific phenotypic and genetic diversity (Ford, 1945; Gross, 1991; Hugall & Stuart-Fox, 2012; Huxley, 1955; McKinnon & Pierotti, 2010; Paulson, 1973). Colour polymorphism, defined as the occurrence of two or more discrete, genetically determined colour morphs within age and sex classes within an interbreeding population (Huxley, 1955), is often correlated with differences in other traits such as behaviour, life history and physiology. Such differences between morphs constitute alternative strategies when they combine multiple traits, which affect fitness in combination and are under correlational selection (Miles, Sinervo, Hazard, Svensson, & Costa, 2007; Roulin,

2004; Sinervo & Svensson, 2002). Although many colour-polymorphic species display alternative strategies (Cox & Calsbeek, 2011; Lank, Smith, Hanotte, Burke, & Cooke, 1995; Vercken, Massot, Sinervo, & Clobert, 2007; reviewed in McKinnon & Pierotti, 2010) few studies have specifically examined behaviours in different contexts (e.g. foraging, mating, aggression, antipredator behaviour; but see Da Silva et al., 2013; Mafli, Wakamatsu, & Roulin, 2011; Williams, King, & Mettke-Hofmann, 2012). Such studies are essential to identify alternative strategies of morphs, which is the first step to understanding the evolutionary maintenance of the polymorphism.

Conspecific aggression and antipredator behaviours are frequently assessed in unison and in many species there is a positive correlation between aggression to conspecifics and boldness to predators (Bell & Sih, 2007; Dingemanse et al., 2007; Huntingford, 1976; Kortet & Hedrick, 2007). High individual aggression and

* Correspondence: M. Yewers, School of BioSciences, University of Melbourne, Victoria 3010, Australia.
E-mail address: myewers@gmail.com (M. S. C. Yewers).

boldness are commonly associated with dominance (Dahlbom, Lagman, Lundstedt-Enkel, Sundström, & Winberg, 2011; Ficken, Weise, & Popp, 1990; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004) and reproductive success (Ariyomo & Watt, 2012; Colléter & Brown, 2011; Reaney & Backwell, 2007). However, being more aggressive and bold is associated with costs. Bolder individuals may have a higher predation risk (Bremner-Harrison, Prodohl, & Elwood, 2004; Dugatkin, 1992; Smith & Blumstein, 2008). As such, bolder, more aggressive individuals may differ in their allocation of resources to current versus future reproductive success resulting in different life history strategies (Schuett, Tregenza, & Dall, 2010; Stearns, 1992; Wolf, van Doorn, Leimar, & Weissing, 2007). Despite the importance of aggression and boldness in response to predators for defining potential alternative strategies of colour morphs (Healey, Uller, & Olsson, 2007; Pryke, 2007), bold behaviours and differences between morphs in multiple behavioural traits are not often examined in colour-polymorphic systems (but see Calsbeek & Cox, 2012; Da Silva et al., 2013; Iii, 1992; Mafli et al., 2011; Mettke-Hofmann, 2012; Williams et al., 2012).

Although colour morphs often differ in aggressive behaviours to conspecifics (fish: Barlow, 1976; invertebrates: Brace, Pavey, & Quicke, 1979; birds: Pryke, 2006; reptiles: Thompson & Moore, 1991), the nature of these differences varies between species. In some colour-polymorphic species, morphs can differ in their levels of aggression regardless of the colour of their competitor. For example, the dominant red morph of the Gouldian finch, *Erythrura gouldiae*, is more aggressive than the black morph (Pryke, 2006); however, the red morph experiences increased stress and physiological costs when present in high frequencies within a population, thereby promoting a low and stable frequency of red morphs (Pryke, Astheimer, Buttemer, & Griffith, 2007). Alternatively, a particular colour morph can vary its aggressive response depending on the colour of the competitor. For example, male morphs that mimic female coloration and/or behaviour may be subjected to less aggression from other male morphs (Dominey, 1980; Sinervo & DeNardo, 1996). Under the above scenarios, colour morphs are indicative of alternative behavioural or reproductive strategies that are generally under balancing or frequency-dependent selection, thereby maintaining the polymorphism (Bleay, Comendant, & Sinervo, 2007; Gross, 1991). Additionally, numerous colour-polymorphic systems show like-morph aggression bias (Dijkstra, Seehausen, Pierotti, & Groothuis, 2007; Horton, Hauber, & Maney, 2012; Pauers, Kapfer, Fendos, & Berg, 2008). Morphs show the greatest levels of aggression to individuals of the same colour morph, which could result in a frequency-dependent advantage for the rare morph as it may face lower overall levels of aggression (Seehausen & Schluter, 2004). This promotes negative frequency-dependent selection and polymorphism maintenance if morphs

are behaviourally similar in other ways i.e. they are equally likely to encounter aggressive individuals (Dijkstra et al., 2010; Qvarnström, Vallin, & Rudh, 2012). However, like-morph aggression bias can alternatively indicate divergence between morphs if it is associated with assortative mating (Dijkstra & Groothuis, 2011; Seehausen & Schluter, 2004). Individuals may direct more aggression towards like-morphs if they pose a greater threat to their reproductive resources. This is expected to lead to differentiation between morphs, and potentially speciation (van Doorn, Dieckmann, & Weissing, 2004). Therefore, assessing the nature of colour-biased aggression is important to understand evolutionary processes maintaining the polymorphism or alternatively leading to divergence between morphs.

Here, we used field experiments to test the hypothesis that the visually discrete throat colour morphs of the tawny dragon lizard, *Ctenophorus decresii*, exhibit different behavioural strategies. In polymorphic populations of this species, individual male throat colour falls into one of four discrete colour morphs, which can be reliably classified into orange, yellow, grey and orange-yellow (Teasdale, Stevens, & Stuart-Fox, 2013; Fig. 1). Throat colour develops before sexual maturity, is chromatically conspicuous against native backgrounds and is highly heritable and fixed for life based on long-term studies of captive populations (McLean, Moussalli, & Stuart-Fox, 2014; Osborne, 2004; Rankin, 2014) and 3 years of mark-recapture data from our study population (Yewers & Stuart-Fox, 2013b). Throat colour morph does not vary with body size, such that all morphs are observed in the same age(s) (Teasdale et al. 2013). Thus, like other lizards (Olsson et al., 2007; Sinervo & Zamudio, 2001), the colour polymorphism in this species is likely to have a genetic basis and is not conditionally expressed. Tawny dragon lizards are highly territorial and have discrete territories with an average size of 213 m^2 which they maintain over consecutive years (Yewers & Stuart-Fox, 2012). To defend territories and court females, males engage in complex displays in which individuals extend and lower their throats, laterally compress their bodies and perform head bobs and push-ups on all four legs (Gibbons, 1979; Osborne, 2005a; Stuart-Fox & Johnston, 2005; Umbers, Osborne, & Keogh, 2012). In male–male contests individuals recognize rivals based on their throat colour pattern (Osborne, Umbers, Backwell, & Keogh, 2012) suggesting that colour is used as a social signal. Males adjust their aggressive response to competitors based on prior experience, residency and the proximity and body size of the rival; however, aggressive response to throat colour morph has not been studied (Osborne, Umbers, & Keogh, 2013; Stuart-Fox & Johnston, 2005; Umbers et al., 2012). As territory establishment and the outcome of male contests are arguably the two most critical factors determining male mating success in lizards (Gullberg, Olsson, & Tegelström, 1997; Simon, 2011; Stamps & Krishnan, 1997; Tokarz, 1998), and antipredator

Figure 1. Examples of *Ctenophorus decresii* male throat colour morphs. From left: orange, grey, yellow and orange-yellow.

response is crucial to survival, we performed experiments to quantify aggression to an intruder and boldness towards a potential predator. We tested for differences between morphs in both behaviours to assess whether colour morphs may be employing different behavioural strategies.

Although throat colour in tawny dragon lizards can be reliably classified into four discrete groups based on the presence or absence of yellow and orange (Teasdale et al., 2013), we do not know how these categories correspond to variation in behaviour. For example, in the side-blotched lizard, *Uta stansburiana*, males with composite orange-yellow and orange-blue throats behave similarly to males with solid orange throats and yellow-blue throated males behave as yellow sneaker males (Alonzo & Sinervo, 2001; Sinervo, Svensson, & Comendant, 2000; Sinervo & Zamudio, 2001). In the tawny dragon lizard, it is conceivable that the orange-yellow morph behaves similarly to either the orange or yellow morph. Therefore, we compared statistical support for models in which each of the four morphs was considered separately (four-morph model) and the orange-yellow morph and replica model were grouped with either pure orange or pure yellow individuals (three-morph models).

METHODS

Study Species

The tawny dragon lizard is a small, sexually dimorphic agamid lizard found on rocky outcrops of Kangaroo Island, Mt Lofty Ranges and the southern Flinders Ranges of South Australia (Houston, 1974; McLean, Moussalli, Sass, & Stuart-Fox, 2013). Males exhibit striking throat colour variation both within and between populations (Houston, 1998). In the Flinders Ranges, populations comprise discrete male colour morphs of orange, yellow, grey and orange-yellow coloration (Teasdale et al., 2013) whereas southern populations at Kangaroo Island and Mt Lofty ranges are monomorphic (McLean, Stuart-Fox, & Moussalli, 2015). Orange morphs have an orange throat on a grey or cream background, yellow morphs have a yellow throat with varying amounts of grey, orange-yellow morphs have a yellow throat with varying amounts of orange and grey morphs have either a grey or cream coloured throat with no yellow or orange present. Females have cream coloured throats with a variable yellow wash and/or bib.

The tawny dragon lizard inhabits semiarid rocky terrain where it uses the rocks as basking sites and as vantage points to survey possible competitors, mates or predators (Gibbons, 1977). All four morphs actively defend territories which they maintain over consecutive years and may overlap with the home range of one or more females (Yewers & Stuart-Fox, 2012). The tawny dragon lizard is mainly vulnerable to predation by predatory birds (Nankeen kestrel, *Falco cenchroides*, black-shouldered kite, *Elanus axillaris*, Australian magpie, *Cracticus tibicen*, and grey butcherbird, *Cracticus torquatus*; Gibbons & Lillywhite, 1981; Stuart-Fox, Moussalli, Marshall, & Owens, 2003) but snakes are also predators (e.g. eastern brown snake, *Pseudonaja textilis*, and red-bellied black snake, *Pseudechis porphyriacus*; Gibbons & Lillywhite, 1981; Stuart-Fox et al., 2003; M. S. Yewers, S. Pryke, & D. Stuart-Fox, personal observations). Tawny dragon lizards have been observed to react quickly and flee from predators using rock crevices as refuges, as well as for thermoregulation (Gibbons, 1977).

Study Site and Population

We studied a wild population of tawny dragon lizards at the Yourambulla Caves Historic Reserve in the Flinders Ranges, South Australia, Australia (138°37′E, 31°95′S) during two breeding seasons between October and December in 2011 and 2012. The reserve is located in a semiarid region and lizards are found in rocky areas interspersed with ground cover, casuarinas, cypress pines and low-lying shrubs. We captured 98 male lizards in 2011 and 92 male lizards in 2012 and permanently marked them using elastomer implants (Northwest Marine Technology, Shaw Island, WA, U.S.A.). For visual recognition we wrote a temporary unique number on the back of each lizard using acrylic paint pens.

Male Colour and Morphology

We visually assigned males to 'morphs' previously defined by Teasdale et al. (2013) on the basis of the presence or absence of orange or yellow on the throat (Fig. 1). For each individual we took the following morphometric measurements: mass to the nearest 0.25 g using a spring balance (Pesola, 30 g), snout to vent length (SVL) and vent to tail tip to the nearest mm and head depth (deepest point of the head before the tympanum), width (widest point of the head before the tympanum) and length (angle of the lower jaw to the tip of the snout) to the nearest 0.01 mm using digital callipers. We size-corrected head measurements by taking the residuals of head length, width and depth regressed against SVL. SVL was $\log_{10}$ transformed to meet assumptions of normality.

Aggression

In 2011 and 2012, we tested the response of male colour morphs to replica tawny dragon lizard models (Fig. 2). We made our models out of rigid urethane casting resin from a specimen cast with an SVL of 80 mm which fell within the range of naturally occurring focal male size (average SVL = 83.6, range 78–94). We created models of each of the four throat colour morphs and a 'control' model. Each colour morph replica model was painted with colours matched to previously collected field spectral measures of lizard throat and body colours (Teasdale et al., 2013; Fig. 2). Tawny dragon lizards have tetrachromatic colour vision including UV visual sensitivity (Yewers et al., 2015), similar to other diurnal lizards (Olsson, Stuart-Fox, & Ballen, 2013) and visual models indicate that they can easily detect differences between colour morphs (and indeed much more subtle differences between lizard colours and the background; Teasdale et al., 2013). Each paint colour fell within the range of naturally occurring individuals of that colour morph which have minimal reflectance in the UV range (Appendix 1 and Fig. A1). We gave the four coloured models black chest patches and coloured cheek stripes, both of which are male-specific in tawny dragon lizards. We painted coloured cheek stripes that were the most commonly found on each morph (orange and grey morph: cream cheek stripe; yellow and orange-yellow morph: orange cheek stripe). We also painted dark-grey dorsolateral stripes found on all male tawny dragon lizards, irrespective of throat colour morph (Houston, 1974). The control model was painted a uniform colour that matched the dorsal coloration of male lizards.

Each focal male lizard was presented with a model of each colour morph (grey, orange, yellow and orange-yellow) and a control model. We alternated the order of presentation of the five types of model to each focal individual. We placed a model lizard within the focal male's territory when the focal male was engaged in active behaviour either basking or perched in a prominent position. We knew the territory size of focal males due to repeat sightings (Yewers & Stuart-Fox, 2012). We approached the lizard and placed the model above the rock crevice in which the lizard took refuge (less than 1 m from the lizard) so that when the lizard emerged the throat colour of the model would be clearly visible.

Figure 2. The replica model tawny dragon lizards. From left: control model, orange-yellow model, yellow model, orange model and the grey model. Although the throat colour of the grey and control models is the same, the grey morph had additional male-specific markings: a dark chest patch, coloured cheek stripes and dark-grey dorsolateral stripes.

We filmed each trial using a video camera (Panasonic SDR H85 mini digital video camera) between 6 and 10 m from the lizard for 15 min from when they first saw the model unless the lizard attacked the model at which point filming was stopped. We separated model presentations to the same focal male by at least a day and all were performed in the same year. On average, there were 3.62 days between trials (SEM = 0.42; range 1–29 days). We obtained a complete set of five trials for a total of 34 males: grey ($N = 9$), orange ($N = 9$), orange-yellow ($N = 7$) and yellow ($N = 9$), giving a total of 170 trials. For a subset of trials, we recorded the temperature of the rock on which the lizard had spent most of its time (perch temperature) using a surface temperature laser (Digitech QM-7221, www.digitech.com).

We scored model lizard interactions by reviewing video footage. We used a modified behavioural scale based on previous studies of aggressive encounters between male tawny dragon lizards (Osborne, 2005a; Stuart-Fox & Johnston, 2005; Umbers et al., 2012). We noted the occurrence of the following behaviours, which were given scores reflecting the level of aggression (in parentheses): tail flick (1), distended throat/gular display (2) hind leg push-up (2), lunge (3) and bite (3). For each lizard's interaction with a model, we gave a single score of the most aggressive behaviour observed as not all trials were the same length because we ended trials after the model was attacked. This scoring system provided a conservative index of aggression in each trial.

Flight Distance

We collected data on flight initiation distances (FID) for 59 male adult lizards in total; 30 in 2011 and 29 in 2012. To do this, we simulated an approaching predator to provoke escape behaviour, a method widely used to study antipredator behaviour in lizards (Cooper, 2011; Cooper, Martin, & Lopez, 2003). After sighting, with binoculars, a marked male lizard basking or perched on a prominent lookout the observer moved at a constant walking speed towards it. The observer continued to approach until the lizard began to flee at which point the observer immediately stopped and measured FID to the nearest 0.1 m using a 50 m tape measure. We measured perch temperature using a surface temperature laser (Digitech QM-7221) as surface temperature is known to affect the FID of lizards due to its strong correlation with body temperature which greatly influences the defensive fleeing behaviour of lizards (Cooper, 2000; Hertz, Huey, & Nevo, 1982). For 35 of the FID trials, we also measured the distance to the crevice as FID can also be dependent on the distance to a refuge (Dill & Houtman, 1989). FID was $\log_{10}$ transformed to meet assumptions of normality.

Ethical Note

We caught lizards either by hand or by noosing (using a telescopic pole and noose made of fishing line). After capture, we held

onto either the neck or the pelvis for less than 40 min while we took measurements and photos, inserted elastomer implants and wrote a paint ID number on their back. Lizards were released into a crevice as close to their point of capture as possible. No adverse effects were observed.

For elastomer marking, these small lizards can be held in one hand and do not struggle when restrained in this way. They were injected with three elastomers into the underside of their hind and fore limbs (approximately 10 µl with a 29 gauge needle sterilized with ethanol after each use) to form a 2−3 mm implant under the skin. We used orange, yellow, red and green elastomers that are all visible under UV light. No pain relief was given as the procedure involves minimal pain or distress for the animal. We observed no short-term evidence of distress, pain or skin irritation and no long-term effects (such as infection) in recaptured individuals within or between seasons.

The research was conducted under the following animal ethics permits: South Australia Department of Environment and Natural Resources Permit to Undertake Scientific Research (E25861), South Australian Wildlife Ethics Committee approval (18/2010-M1) and the University of Melbourne Animal Ethics Committee approval (1011760).

Statistical Analysis

We analysed data in GenStat (version 15.2.0.8821, VSN international Ltd., Hemel Hempstead, U.K.). In a relatively large percentage of trials (37.5%) lizards did not show any aggression within the 15 min trial time towards coloured model intruders. Therefore, we used levels of aggression shown towards models (ranging from 0 to 3) and the attack response (attack as lunge or bite only/did not attack) to the models as dependent variables.

For the levels of aggression and FID, we compared statistical models in which morphs were classified into four categories (yellow, grey, orange and orange-yellow) with models in which morphs were classified into three categories (yellow, grey and orange) with orange-yellow individuals classified as either orange or yellow. For levels of aggression we also classified the orange-yellow replica lizard model as either a yellow or orange model when we had done the same for individual lizards. We compared four-morph and three-morph models using second-order Akaike's information criteria (AICc).

To test for differences in levels of aggression, we used a general linear mixed model with lizard ID as a random variable. The fixed factors in these models were focal lizard colour morph, model lizard colour and their interaction. We also included morphometric variables (SVL, weight, head length, head width, head depth), year and order of model lizard presentations in initial models and removed nonsignificant variables using stepwise selection with cutoffs for both initial inclusion and retention in the model set at $P = 0.1$. Based on the best model (three- or four-morph) for aggression levels, and using the same model construct, we tested whether colour morphs differed in their propensity to attack the model intruder (lunge or bite only; see Table 2 in the Results). As attack was a binary variable, we specified a binary distribution and logit link function.

We used analysis of covariance (ANCOVA) to test whether flight distance (dependent variable) was influenced by the focal male's colour morph (independent variable), with perch temperature as the covariate (there was no significant heterogeneity of slopes; interaction between colour morph and perch temperature: four morphs: $F_{3, 51} = 2.58$, $P = 0.06$; three morphs OY as Y: $F_{2, 53} = 2.26$, $P = 0.115$; three morphs OY as O: $F_{2, 53} = 1.19$, $P = 0.311$). For all final models we obtained significance levels of fixed effects using F tests.

RESULTS

Aggression

There was no difference in levels of aggression or attack response between years or due to the order that coloured models were presented (aggression level: year: $F_{1, 28} = 0.06$, $P = 0.801$; order: $F_{4, 115} = 1.30$, $P = 0.274$; attack response: year: $F_{1, 28} = 0.03$, $P = 0.857$; order: $F_{4, 115} = 1.14$, $P = 0.343$). There was no difference in perch temperature during model presentations between morphs (ANOVA: $F_{3, 133} = 1.52$, $P = 0.213$).

After stepwise model selection with aggression levels as the dependent variable, head width was the only covariate retained in the final model (Table A1). When we took head width into account, the three-morph model with orange-yellow individuals grouped as the yellow morph had a substantially smaller AICc than the four-morph model or the three-morph model with orange-yellow individuals grouped as the orange morph (Table 1; and see Tables A2 and A3 for the four-morph model fixed effects and parameter estimates). Based on the three-morph model with orange-yellow individuals grouped as yellow, there was a significant effect of focal male colour morph ($F_{2, 29} = 4.41$, $P = 0.021$), model colour ($F_{3, 126} = 15.58$, $P < 0.001$) and the interaction between them ($F_{6, 126} = 3.10$, $P = 0.007$). Male colour morphs had different aggression levels depending on the colour of the model presented (Fig. 3). Orange males were more aggressive than grey males (t test: $t_{126} = 3.11$, $P = 0.002$; Fig. 3) and yellow males (t test: $t_{126} = 2.462$, $P = 0.015$; Fig. 3). All morphs were more aggressive towards the model of their own morph than the control (t tests: grey-control: $t_{126} = 2.82$, $P = 0.006$; orange-control: $t_{126} = 3.68$, $P < 0.001$; yellow-control: $t_{126} = 4.87$, $P < 0.001$; Fig. 3). Grey males were also more aggressive to the yellow model than the control (t test: $t_{126} = 3.13$, $P = 0.002$), orange males were more aggressive to the yellow and grey models than the control (t tests: yellow-control: $t_{126} = 3.32$, $P = 0.001$; grey-control: $t_{126} = 3.68$, $P < 0.001$) and the yellow morph was also more aggressive to the orange model than the control (t test: $t_{126} = 2.86$, $P = 0.005$). Furthermore, yellow males showed higher aggression to the yellow model and the orange model than the grey model (t tests: yellow-grey: $t_{126} = 4.48$, $P < 0.001$; orange-grey: $t_{126} = 2.39$, $P = 0.018$; Fig. 3).

Under a three-morph model with orange-yellow individuals classified as yellow and head width as a covariate, the morphs differed significantly in their propensity to attack the model intruder (chi-square test: $\chi^2_2 = 6.17$, $P = 0.049$). The orange morph was more likely to attack the model intruder than the grey morph (orange versus grey: t test: $t_{155} = 2.67$, $P = 0.008$; Table 2), as was the yellow morph (yellow versus grey t test: $t_{155} = 2.20$, $P = 0.029$;

Table 1
Candidate models, second-order Akaike's information criterion and Akaike weights for conspecific aggression and flight initiation distance (FID)

Behaviour	Model	AICc	ΔAICi	Akaike weight (wi)
Aggression levels	Three morphs OY=orange	223.55	9.78	0.006
	Three morphs OY=yellow	213.77	0.00	0.837
	Four morphs	217.12	3.35	0.157
FID	Three morphs OY=orange	17.1	0.30	0.380
	Three morphs OY=yellow	16.7	0.00	0.441
	Four morphs	18.6	1.80	0.179

Morphs are categorized as four morphs or three morphs with orange-yellow (OY) individuals grouped as either the orange morph or the yellow morph. The best model is indicated by the smallest AICc and the smallest ΔAICi with ΔAICi <2 considered equally as good a fit (Richards, 2005). Akaike weight is the probability that the associated model is the best in the set.
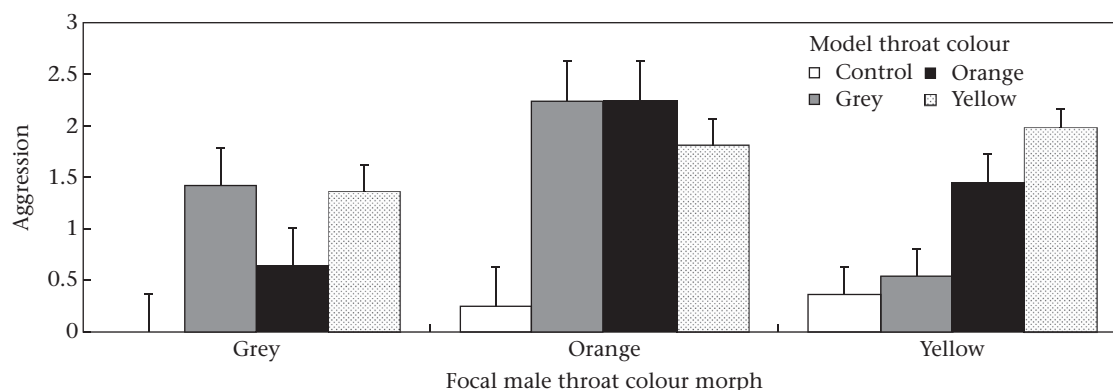
Figure 3. Aggression levels (mean ± SE) of focal male throat colour morphs, grey (N = 9), orange (N = 9) and yellow (N = 16), to each of five different replica model lizard colours.

Table 2
The proportion of trials (percentage) in which the focal male attacked the model intruder

Morph	Model				
	Control	Grey	Yellow	Orange	Total
Grey	0/9	1/9	4/18	1/9	6/45
	(0)	(66.7)	(22.2)	(11.1)	13.3
Orange	0/8	4/8	5/16	4/8	13/40
	(0)	(50)	(31.3)	(50)	(32.5)
Yellow	0/17	0/17	15/34	7/17	22/85
	(0)	(0)	(44.1)	(41.2)	(25.9)
Total	0/34	5/17	24/68	12/34	
	(0)	(14.7)	(34.3)	(35.3)	

Orange-yellow individuals are grouped as the yellow morph. Percentages are given in parentheses.

Table 2); however, there was no significant difference in the likelihood of the orange and the yellow morph attacking (orange versus yellow: t test: $t_{155} = 0.47$, $P = 0.638$; Table 2). There was no significant difference in attack response to different model colours (chi-square test: $\chi^2_3 = 5.78$, $P = 0.127$) and no significant interaction between focal male morph and model colour (chi-square test: $\chi^2_6 = 2.26$, $P = 0.893$).

Flight Distance

There was no difference in FID between years (ANCOVA: $F_{1, 57} = 0.08$, $P = 0.772$) so we combined FID scores from the 2 years. With perch temperature as a covariate, the ΔAICi for the four-morph model was <2 compared to the models for three morphs with orange-yellow grouped with either the orange or yellow morph (Table 1). Therefore, there was no distinguishable difference in the explanatory power of the three models. For all three models, FID differed between colour morphs (three morphs with OY as orange ANCOVA: $F_{2, 55} = 3.52$, $P = 0.037$; Fig. 4a; three morphs with OY as yellow: ANCOVA: $F_{2, 55} = 3.66$, $P = 0.032$; Fig. 4b; four morphs: ANCOVA: $F_{3, 54} = 2.83$, $P = 0.047$, ANCOVA: $F_{3, 54} = 2.83$, $P = 0.047$; Fig. 4c). FID was greatest for the grey morph, followed by orange, yellow and orange-yellow (Table A4) and post hoc comparisons for the four-morph model showed that grey morphs had significantly larger FIDs than orange-yellow and yellow morphs (t tests: orange-yellow: $t_{54} = 2.86$, $P = 0.006$; yellow: $t_{54} = 2.01$, $P = 0.049$). All other comparisons between morphs were not significantly different: grey and orange (t test: $t_{54} = 1.65$, $P = 0.105$), orange and orange-yellow (t test: $t_{54} = 1.19$, $P = 0.238$), orange and yellow (t test: $t_{54} = 0.209$, $P = 0.835$) and orange-

yellow and yellow (t test: $t_{54} = 1.090$, $P = 0.280$; Fig. 4c). When the orange-yellow morph was classified as an orange morph, the grey morph had a significantly larger FID than the orange morph (t test: $t_{54} = 2.60$, $P = 0.012$; Fig. 4a) and the yellow morph (t test: $t_{54} = 2.02$, $P = 0.048$; Fig. 4a); whereas there was no significant difference in FID between the orange and yellow morph (t test: $t_{54} = 0.496$, $P = 0.622$). Finally, when the orange-yellow morph was classified as a yellow morph, the grey morph had significantly higher FID than the yellow morph (t test: $t_{54} = 2.71$, $P = 0.009$; Fig. 4b); whereas there were no significant FID differences between the grey and orange morph (t test: $t_{54} = 1.65$, $P = 0.105$) or the orange and yellow morphs (t test: $t_{54} = 0.71$, $P = 0.480$). In 80% of FID trials the lizard was less than 1 m from its refuge and for over 91.4% of trials lizards were less than 2 m from their refuge. There was no relationship between FID and the distance to the refuge ($F_{1, 34} = 1.89$, $P = 0.178$, adjusted $r^2 = 0.026$) and morphs did not differ in their distance to the refuge (ANOVA: $F_{3, 34} = 0.87$, $P = 0.465$).

DISCUSSION

Our results show that tawny dragon colour morphs have different behavioural responses to both simulated conspecifics and predators. For aggression, the data best fitted a three-morph model (orange, yellow, grey) with orange-yellow individuals classified as yellow. The orange morph showed consistently high aggression and the grey morph consistently low aggression to all other morphs; in contrast, the aggression level of the yellow morph was conditional on the throat colour of the intruder with yellow males displaying more aggression to the yellow and orange morphs than the grey morph. Furthermore, based on the three-morph model with orange-yellow classified as yellow, the orange morph and the yellow morph were more likely to attack the model intruder than the grey morph. For boldness towards a simulated predator, three- and four-morph models were equally likely. Under both three- and four-morph models for boldness, the grey morph was the least bold compared with the boldest morph. For the four-morph model, the orange-yellow morph was the boldest and grouping orange-yellow individuals with either the yellow or orange morph category in the three-morph model resulted in the yellow and orange morph having the highest boldness, respectively. Thus, there are some consistencies between aggressive and bold behaviours as the grey morph was the least bold and the least aggressive; however, levels of boldness and aggression were not entirely congruent for the other morphs. Nevertheless, the clear differences in aggressive
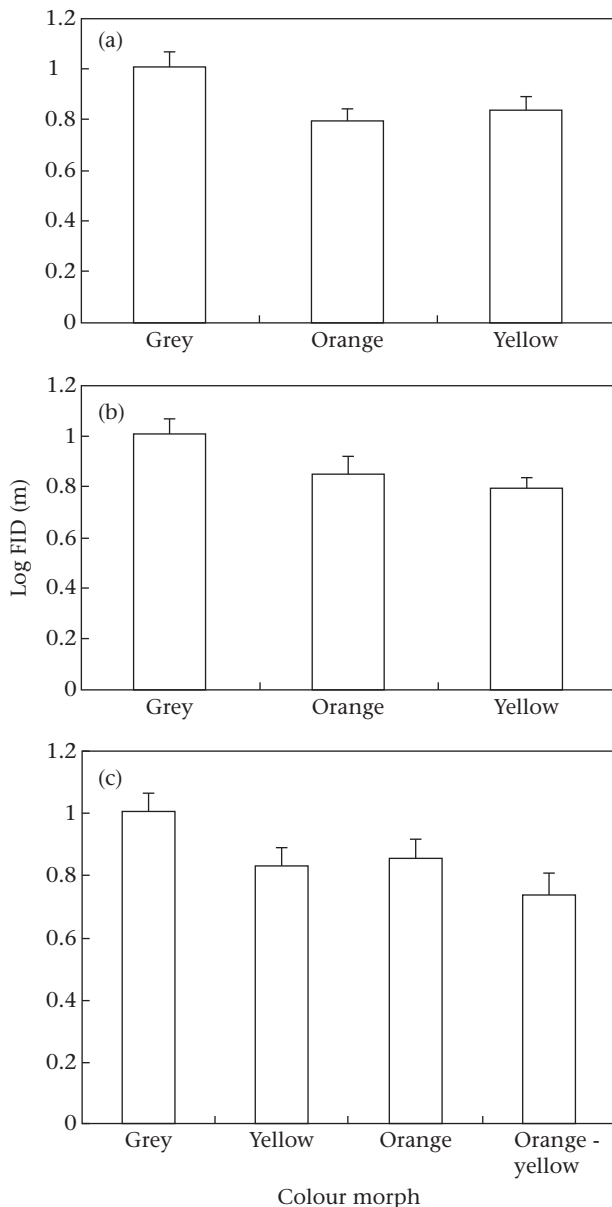
Figure 4. Flight initiation distance (FID) ANCOVA models comparing four morphs and three morphs with orange-yellow classified as either an orange or a yellow morph. (a) Three-morph model with orange-yellow individuals classified as orange morphs: log FID (m) for grey ($N = 14$), orange ($N = 26$) and yellow ($N = 19$) morphs. (b) Three-morph model with orange-yellow individuals classified as yellow morphs: log FID (m) for grey ($N = 14$), orange ($N = 13$) and yellow ($N = 32$) morphs. (c) Four-morph model: log FID (m) for grey ($N = 14$), orange ($N = 13$), orange-yellow ($N = 13$) and yellow ($N = 19$) morphs. Values shown are mean $\pm$ SE of FIDs.

behaviour between morphs and consistency within the grey morph of low aggression and boldness suggest that colour morphs of the tawny dragon lizard may exhibit different behavioural strategies. More broadly, our study highlights that in species with complex colour polymorphism, the manner by which visually discrete colour morphs correspond to behavioural, life history or physiological traits should be explicitly tested rather than assumed in statistical models (in this case, three morphs versus four morphs).

Levels of aggression can reflect dominance (Francis, 1988) which is an important indicator of alternative strategies in colour-

polymorphic species (Ficken, Ficken, & Hailman, 1978; Sinervo & Lively, 1996; Thompson & Moore, 1991). The high aggression of the tawny dragon lizard orange morph is concordant with behavioural studies in fish (de Fraipont, FitzGerald, & Guderley, 1993; McKinnon, 1996), birds (Attrill, Gresty, Hill, & Barton, 2008; Pryke, 2006; Pryke, Lawes, & Andersson, 2001), primates (Setchell & Jean Wickings, 2005), including humans (Attrill et al., 2008; Little & Hill, 2007), and lizards (Hamilton, Whiting, & Pryke, 2013; Stapley & Keogh, 2006) in which red and orange coloration are associated with dominance or win/loss status. In colour polymorphic lizard species in which aggression and associated dominance or win/loss status have been examined, several but not all orange or red morphs are dominant or most aggressive (*Ctenophorus pictus*; Healey et al., 2007; *Podarcis melisellensis*; Huyghe, Vanhooydonck, Herrev, Tadic, & Van Dammet, 2007; *Sceloporus consobrinus*; Rand, 1988; *U. stansburiana*; Sinervo & Lively, 1996) although there are exceptions (*Sceloporus grammicus*; Bastiaans, Morinaga, Castañeda Gaytán, Marshall, & Sinervo, 2013; *Urosaurus ornatus*; Carpenter, 1995). Generally, and specifically in colour-polymorphic species, dominance is usually related to size with larger individuals being more dominant (Haley, Deutsch, & Le Boeuf, 1994; Sinervo & Lively, 1996; Tokarz, 1985); however, tawny dragon lizard colour morphs do not differ in their body size, weight, condition or head dimensions (Teasdale et al., 2013; Yewers & Stuart-Fox, 2013a) and body size did not significantly affect levels of aggression in this study. Despite similar morphology, aggression and associated dominance or win/loss status are likely to be important to male tawny dragon lizard colour morphs due to high competition for space and mates (Gibbons, 1979; Osborne, 2004; Stuart-Fox & Johnston, 2005; Umbers et al., 2012; M. S. Yewers, S. Pryke, & D. Stuart-Fox, personal observations). Indeed aggressive displays are energetically costly in the tawny dragon lizard (Osborne, 2005a) and staged captive contests are readily observed (Osborne et al., 2013; Umbers et al., 2012); however, males reduce their aggression in repeat interactions with familiar competitors (Osborne, 2005b; Stuart-Fox & Johnston, 2005) and territory sizes are often maintained over consecutive years (Yewers & Stuart-Fox, 2012) suggesting dominance structure. Thus, as for other colour polymorphic lizard species, differences in behaviour are likely to reflect alternative behavioural strategies (Healey & Olsson, 2008; Sinervo & Lively, 1996). We can only speculate about how behavioural strategies relate to reproductive strategies. For example, males employing a dominant strategy that entails patrolling territories to the exclusion of all other males are expected to be aggressive to all intruders, males employing a mate-guarding strategy may exhibit aggression conditional on the colour of the intruder, while males that have a sneaking strategy may have overall low levels of aggression (Sinervo & Lively, 1996). The grey morph with its low aggression and low boldness may gain paternity with a cautious strategy (e.g. by sneaking extraterritorial copulations). To further quantify the possible dominant or more aggressive strategy of the orange morph and the cautious strategy of the grey morph, investigations into other potential behavioural, morphological and physiological correlates such as territorial behaviour, testes size and testosterone levels would be informative.

In contrast to the orange and grey morphs, the yellow morph appears to exhibit aggression that is conditional on the colour morph of the intruder. Specifically, the yellow morph was more aggressive to both the yellow model and the orange model than the grey model. Furthermore, the yellow morph directed the least aggression to grey-throated territorial intruders and therefore may not perceive them as a threat. The ability of the yellow morph to

moderate aggression in relation to intruder colour morph could be due to differences in the threat represented by each morph; but it could also reflect the behavioural plasticity of colour morphs. Levels of behavioural plasticity can indicate behavioural differences (Dingemanse, Kazem, Réale, & Wright, 2010; Wolf, Van Doorn, & Weissing, 2008). For example, in laboratory rodents bred to be aggressive, males can either adjust their aggressive behaviour depending on social context or show repetitive aggressive responses insensitive to the social context (Natarajan, de Vries, Saaltink, De Boer, & Koolhaas, 2009). Moreover, male stream water striders, *Aquarius remigis,* that are more active and aggressive show greater behavioural plasticity in changing social conditions (Sih, Chang, & Wey, 2014). Therefore, behavioural plasticity could be a promising area for further research on the behavioural strategies of the colour morphs. Lastly, our results do not support like-colour morph aggression bias, which therefore cannot account for the maintenance of colour polymorphism, nor promote divergence between colour morphs.

We found consistency between aggression and boldness for the grey morph, which is both the least aggressive and least bold morph, implying a cautious strategy. Bold antipredator behaviour is often correlated with high levels of aggressive behaviour to conspecifics (Kortet & Hedrick, 2007; Reaney & Backwell, 2007). However, the high aggression and suggested dominant strategy of the orange morph was not necessarily associated with the highest levels of boldness in the face of predators. The orange morph was only the most bold for the three-morph model with orange-yellow individuals classified as orange morphs, whereas it had intermediate levels of boldness for the three-morph model with orange-yellow individuals classified as the yellow morph and the four-morph model. However, we do not necessarily expect exactly the same rank order of mean aggression and boldness in a three- or four-morph system compared with a binary system (e.g. two morphs or bold versus shy), when some morphs show a conditional strategy (high or low aggression depending on the intruder). It would be informative to test boldness and aggression in the same individuals to see whether these traits correlate perhaps forming a behavioural syndrome or personality type.

Bolder individuals that take risks in response to predators are expected to show more risky behaviour in other contexts, including conspecific aggression (Coleman & Wilson, 1998). Thus the boldest morph may show similar risk-taking behaviours to secure matings (e.g. more conspicuous courtship displays). Signalling to potential mates is a risky behaviour and there is likely to be a trade-off between the benefits of attracting a mate and the cost of being more conspicuous to predators (Endler, 1980; Huhta, Rytkönen, & Solonen, 2003; Magnhagen, 1991; Zuk & Kolluru, 1998). To further explore the possibility of alternative behavioural strategies in the tawny dragon lizard, future studies would need to quantify reproductive tactics in relation to mating success (although this is challenging in *C. decresii*). Furthermore, as boldness is associated with differences in investment in current versus future reproductive success (Wolf et al., 2007), ideally one would need to quantify reproductive success and survival of morphs over time; we would predict bolder morphs to have a greater current reproductive success but lower survival than the grey morph.

Here, we have shown that male colour morphs of the tawny dragon lizard differ behaviourally in two contexts, conspecific aggression and risk in antipredator response. Aggression levels best fit a statistical model representing three colour morphs with orange-yellow individuals classified as yellow morphs. There is ambiguity for the boldness data with models representing four or three colour morphs being equally likely. In any case, the grey morph is both the least bold and least aggressive, implying a cautious behavioural strategy. Furthermore, the orange morph shows high aggression to all morphs regardless of colour, potentially indicating a dominant or more aggressive behavioural strategy, while the yellow morph appears to exhibit a conditional strategy, with aggression varying depending on the morph of the intruder. Our results therefore support the view that tawny dragon lizard colour morphs may exhibit alternative behavioural strategies. More research on other potentially correlated behavioural traits, as well as life history and physiological traits, is required to further qualify these potential strategies, which can provide insight into the mechanisms maintaining colour polymorphism in this system.

References

Alonzo, S. H., & Sinervo, B. (2001). Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard, *Uta stansburiana. Behavioral Ecology and Sociobiology, 49*(2–3), 176–186. http://dx.doi.org/10.1007/s002650000265.

Ariyomo, T. O., & Watt, P. J. (2012). The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Animal Behaviour, 83*(1), 41–46. http://dx.doi.org/10.1016/j.anbehav.2011.10.004.

Attrill, M. J., Gresty, K. A., Hill, R. A., & Barton, R. A. (2008). Red shirt colour is associated with long-term team success in English football. *Journal of Sports Sciences, 26*(6), 577–582. http://dx.doi.org/10.1080/02640410701736244.

Barlow, G. W. (1976). Competition between color morphs of the polychromatic Midas cichlid *Cichlasoma citrinellum. Science, 179*(4075), 806–807. http://dx.doi.org/10.1126/science.179.4075.806.

Bastiaans, E., Morinaga, G., Gaytán, J. G. C., Marshall, J. C., & Sinervo, B. (2013). Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. *Behavioral Ecology, 24*(4), 968–981. http://dx.doi.org/10.1093/beheco/art010.

Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters, 10*(9), 828–834. http://dx.doi.org/10.1111/j.1461-0248.2007.01081.x.

Bleay, C., Comendant, T., & Sinervo, B. (2007). An experimental test of frequency-dependent selection on male mating strategy in the field. *Proceedings of the Royal Society B: Biological Sciences, 274*(1621), 2019–2025. http://dx.doi.org/10.1098/rspb.2007.0361.

Brace, R. C., Pavey, J., & Quicke, D. L. J. (1979). Intraspecific aggression in the colour morphs of the anemone Actinia equina: the 'convention' governing dominance ranking. *Animal Behaviour, 27,*(2), 553–561. http://dx.doi.org/10.1016/0003-3472(79)90190-8.

Bremner-Harrison, S., Prodohl, P. A., & Elwood, R. W. (2004). Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation, 7*(3), 313–320. http://dx.doi.org/10.1017/s1367943004001490.

Calsbeek, R., & Cox, R. (2012). An experimental test of the role of predators in the maintenance of a genetically based polymorphism. *Journal of Evolutionary Biology, 25*(10), 2091–2101. http://dx.doi.org/10.1111/j.1420-9101.2012.02589.x.

Carpenter, G. C. (1995). Modeling dominance: the influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetological Monographs, 9*, 88–101. http://dx.doi.org/10.2307/1466998.

Coleman, K., & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour, 56*(4), 927–936. http://dx.doi.org/10.1006/anbe.1998.0852.

Colléter, M., & Brown, C. (2011). Personality traits predict hierarchy rank in male rainbowfish social groups. *Animal Behaviour, 81*(6), 1231–1237. http://dx.doi.org/10.1016/j.anbehav.2011.03.011.

Cooper, W. E., Jr. (2000). Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour, 137*, 1299–1315. http://dx.doi.org/10.1163/156853900501935.

Cooper, W. E., Jr. (2011). Influence of some potential predation risk factors and interaction between predation risk and cost of fleeing on escape by the lizard *Sceloporus virgatus*. *Ethology, 117*(7), 620–629. http://dx.doi.org/10.1111/j.1439-0310.2011.01911.x.

Cooper, W. E., Jr., Martin, J., & Lopez, P. (2003). Simultaneous risks and differences among individual predators affect refuge use by a lizard, *Lacerta monticola*. *Behaviour, 140*, 27–41. http://dx.doi.org/10.1163/156853903763999872.

Cox, R. M., & Calsbeek, R. (2011). An experimental test for alternative reproductive strategies underlying a female-limited polymorphism. *Journal of Evolutionary Biology, 24*(2), 343–353. http://dx.doi.org/10.1111/j.1420-9101.2010.02171.x.

Da Silva, A., Van Den Brink, V., Emaresi, G., Luzio, E., Bize, P., Dreiss, A. N., et al. (2013). Melanin-based colour polymorphism signals aggressive personality in nest and territory defence in the tawny owl (*Strix aluco*). *Behavioral Ecology and Sociobiology, 67*(7), 1041–1052. http://dx.doi.org/10.1007/s00265-013-1529-2.

Dahlbom, S. J., Lagman, D., Lundstedt-Enkel, K., Sundström, L. F., & Winberg, S. (2011). Boldness predicts social status in zebrafish (*Danio rerio*). *PloS One, 6*(8), e23565. http://dx.doi.org/10.1371/journal.pone.0023565.

Dijkstra, P. D., & Groothuis, T. G. (2011). Male–male competition as a force in evolutionary diversification: evidence in haplochromine cichlid fish. *International Journal of Evolutionary Biology, 2011*, 689254. http://dx.doi.org/10.4061/2011/689254.

Dijkstra, P. D., Lindström, J., Metcalfe, N. B., Hemelrijk, C. K., Brendel, M., Seehausen, O., et al. (2010). Frequency-dependent social dominance in a color polymorphic cichlid fish. *Evolution, 64*(10), 2797–2807. http://dx.doi.org/10.1111/j.1558-5646.2010.01046.x.

Dijkstra, P. D., Seehausen, O., Pierotti, M. E., & Groothuis, T. (2007). Male–male competition and speciation: aggression bias towards differently coloured rivals varies between stages of speciation in a Lake Victoria cichlid species complex. *Journal of Evolutionary Biology, 20*(2), 496–502. http://dx.doi.org/10.1111/j.1420-9101.2006.01266.x.

Dill, L. M., & Houtman, R. (1989). The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Canadian Journal of Zoology, 67*(1), 233–235. http://dx.doi.org/10.1139/z89-033.

Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution, 25*(2), 81–89. http://dx.doi.org/10.1016/j.tree.2009.07.013.

Dingemanse, N. J., Wright, J., Kazem, A. J., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology, 76*(6), 1128–1138. http://dx.doi.org/10.1111/j.1365-2656.2007.01284.x.

Dominey, W. J. (1980). Female mimicry in male bluegill sunfish—a genetic polymorphism? *Nature, 284*, 546–548. http://dx.doi.org/10.1038/284546a0.

van Doorn, G. S., Dieckmann, U., & Weissing, F. J. (2004). Sympatric speciation by sexual selection: a critical reevaluation. *The American Naturalist, 163*(5), 709–725. http://dx.doi.org/10.1086/383619.

Dugatkin, L. A. (1992). Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). *Behavioral Ecology, 3*(2), 124–127. http://dx.doi.org/10.1093/beheco/3.2.124.

Endler, J. A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution, 34*(1), 76–91. http://dx.doi.org/10.2307/2408316.

Ficken, R. W., Ficken, M. S., & Hailman, J. P. (1978). Differential aggression in genetically different morphs of the white-throated sparrow (*Zonotrichia albicollis*). *Zeitschrift für Tierpsychologie, 46*(1), 43–57.

Ficken, M. S., Weise, C. M., & Popp, J. W. (1990). Dominance rank and resource access in winter flocks of black-capped chickadees. *The Wilson Bulletin*, 623–633.

Ford, E. B. (1945). Polymorphism. *Biological Reviews of the Cambridge Philosophical Society, 20*, 73–88.

de Fraipont, M., FitzGerald, G. J., & Guderley, H. (1993). Age-related differences in reproductive tactics in the three-spined stickleback, Gasterosteus aculeatus. *Animal Behaviour, 46*(5), 961–968. http://dx.doi.org/10.1006/anbe.1993.1277.

Francis, R. C. (1988). On the relationship between aggression and social dominance. *Ethology, 78*(3), 223–237. http://dx.doi.org/10.1111/j.1439-0310.1988.tb00233.x.

Gibbons, J. R. H. (1977). *Comparative ecology and behaviour of lizards of the* Amphibolurus decresii *species complex* (Unpublished Ph.D. thesis). Adelaide, Australia: University of Adelaide.

Gibbons, J. R. H. (1979). The hind leg pushup display of the *Amphibolurus decresii* species complex (Lacertilia: Agamidae). *Copeia*, (1), 29–40. http://dx.doi.org/10.2307/1443725.

Gibbons, J. R. H., & Lillywhite, H. B. (1981). Ecological segregation, color matching, and speciation in lizards of the *Amphibolurus decresii* species complex (Lacertilia: Agamidae). *Ecology, 62*(6), 1573–1584. http://dx.doi.org/10.2307/1941513.

Gross, M. R. (1991). Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 332*(1262), 59–66. http://dx.doi.org/10.1098/rstb.1991.0033.

Gullberg, A., Olsson, M., & Tegelström, H. (1997). Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: behavioural and molecular genetics data. *Molecular Ecology, 6*(2), 105–112. http://dx.doi.org/10.1046/j.1365-294X.1997.t01-1-00156.x.

Haley, M. P., Deutsch, C. J., & Le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, Mirounga angustirostris. *Animal Behaviour, 48*(6), 1249–1260. http://dx.doi.org/10.1006/anbe.1994.1361.

Hamilton, D. G., Whiting, M. J., & Pryke, S. R. (2013). Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards. *Behavioral Ecology*. http://dx.doi.org/10.1093/beheco/art041.

Healey, M., & Olsson, M. (2008). Territory acquisition in a polymorphic lizard: an experimental approach. *Austral Ecology, 33*(8), 1015–1021. http://dx.doi.org/10.1111/j.1442-9993.2008.01871.x.

Healey, M., Uller, T., & Olsson, M. (2007). Seeing red: morph-specific contest success and survival rates in a colour-polymorphic agamid lizard. *Animal Behaviour, 74*(2), 337–341. http://dx.doi.org/10.1016/j.anbehav.2006.09.017.

Hertz, P. E., Huey, R. B., & Nevo, E. (1982). Fight versus flight: body temperature influences defensive responses of lizards. *Animal Behaviour, 30*(3), 676–679. http://dx.doi.org/10.1016/S0003-3472(82)80137-1.

Horton, B. M., Hauber, M. E., & Maney, D. L. (2012). Morph matters: aggression bias in a polymorphic sparrow. *PLoS One, 7*(10), e48705. http://dx.doi.org/10.1371/journal.pone.0048705.

Houston, T. F. (1974). Revision of the *Amphibolurus decresii* (Lacertilia: Agamidae) of South Australia. *Transactions of the Royal Society of South Australia, 98*, 49–60. http://dx.doi.org/10.2307/1443725.

Houston, T. F. (1998). *Dragon lizards and goannas of South Australia*. Adelaide: South Australia, Australia: South Australian Museum.

Hugall, A. F., & Stuart-Fox, D. (2012). Accelerated speciation in colour-polymorphic birds. *Nature, 485*(7400). http://dx.doi.org/10.1038/nature11050, 631-+.

Huhta, E., Rytkönen, S., & Solonen, T. (2003). Plumage brightness of prey increases predation risk: an among-species comparison. *Ecology, 84*(7), 1793–1799. http://dx.doi.org/10.1890/0012-9658(2003)084[1793:PBOPIP]2.0.CO;2.

Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour, 24*(2), 245–260. http://dx.doi.org/10.1016/S0003-3472(76)80034-6.

Huxley, J. (1955). Morphism in birds. *International Congress of Ornithology XI*, 309–389.

Huyghe, K., Vanhooydonck, B., Herrev, A., Tadic, Z., & Van Dammet, R. (2007). Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Integrative and Comparative Biology, 47*(2), 211–220. http://dx.doi.org/10.1093/icb/icm043.

Iii, E. D. B. (1992). Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution, 46*(5), 1284–1298. http://dx.doi.org/10.2307/2409937.

Kortet, R., & Hedrick, A. (2007). A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biological Journal of the Linnean Society, 91*(3), 475–482. http://dx.doi.org/10.1111/j.1095-8312.2007.00812.x.

Lank, D. B., Smith, C. M., Hanotte, O., Burke, T., & Cooke, F. (1995). Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature, 378*(6552), 59–62. http://dx.doi.org/10.1038/378059a0.

Little, A., & Hill, R. (2007). Attribution to red suggests special role in dominance signalling. *Journal of Evolutionary Psychology, 5*(1), 161–168. http://dx.doi.org/10.1556/jep.2007.1008.

Mafli, A., Wakamatsu, K., & Roulin, A. (2011). Melanin-based coloration predicts aggressiveness and boldness in captive eastern Hermann's tortoises. *Animal Behaviour, 81*(4), 859–863. http://dx.doi.org/10.1016/j.anbehav.2011.01.025.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution, 6*(6), 183–186. http://dx.doi.org/10.1016/0169-5347(91)90210-O.

McKinnon, J. S. (1996). Red coloration and male parental behaviour in the threespine stickleback. *Journal of Fish Biology, 49*(5), 1030–1033. http://dx.doi.org/10.1111/j.1095-8649.1996.tb00099.x.

McKinnon, J. S., & Pierotti, M. E. R. (2010). Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Molecular Ecology, 19*(23), 5101–5125. http://dx.doi.org/10.1111/j.1365-294X.2010.04846.x.

McLean, C. A., Moussalli, A., Sass, S., & Stuart-Fox, D. (2013). Taxonomic assessment of the *Ctenophorus decresii* complex (Reptilia: Agamidae) reveals a new species of dragon lizard from Western New South Wales. *Records of the Australian Museum, 65*(3), 51–63. http://dx.doi.org/10.3853/j.2201-4349.65.2013.1600.

McLean, C. A., Moussalli, A., & Stuart-Fox, D. (2014). Local adaptation and divergence in colour signal conspicuousness between monomorphic and polymorphic lineages in a lizard. *Journal of Evolutionary Biology, 27*(12), 2654–2664. http://dx.doi.org/10.1111/jeb.12521.

McLean, C. A., Stuart-Fox, D., & Moussalli, A. (2015). Environment, but not genetic divergence, influences geographic variation in colour morph frequences in a lizard. *BMC Evolutionary Biology, 15*(1), 1–10. http://dx.doi.org/10.1186/s12862-015-0442-x.

Mettke-Hofmann, C. (2012). Head colour and age relate to personality traits in Gouldian finches. *Ethology, 118*(9), 906–916. http://dx.doi.org/10.1111/j.1439-0310.2012.02079.x.

Miles, D. B., Sinervo, B., Hazard, L. C., Svensson, E. I., & Costa, D. (2007). Relating endocrinology, physiology and behaviour using species with alternative mating strategies. *Functional Ecology, 21*(4), 653–665. http://dx.doi.org/10.1111/j.1365-2435.2007.01304.x.

Natarajan, D., de Vries, H., Saaltink, D.-J., De Boer, S. F., & Koolhaas, J. M. (2009). Delineation of violence from functional aggression in mice: an ethological approach. *Behavior Genetics, 39*(1), 73–90. http://dx.doi.org/10.1007/s10519-008-9230-3.

Olsson, M., Healey, M., Wapstra, E., Schwartz, T., Lebas, N., & Uller, T. (2007). Mating system variation and morph fluctuations in a polymorphic lizard. *Molecular Ecology, 16*(24), 5307–5315. http://dx.doi.org/10.1111/j.1365-294X.2007.03578.x.

Olsson, M., Stuart-Fox, D., & Ballen, C. (2013). Genetics and evolution of colour patterns in reptiles. *Seminars in Cell and Developmental Biology, 24*(6–7), 529–541. http://dx.doi.org/10.1016/j.semcdb.2013.04.001.

Osborne, L. (2004). *Male contest behaviour and information content of signals used by the Australian Tawny Dragon* (Unpublished Ph.D. dissertation). Canberra, Australia: Australian National University.

Osborne, L. (2005a). Information content of male agonistic displays in the territorial tawny dragon *(Ctenophorus decresii). Journal of Ethology, 23*, 189–197. http://dx.doi.org/10.1007/s10164-005-0151-9.

Osborne, L. (2005b). Rival recognition in the territorial tawny dragon (*Ctenophorus decresii*). *Acta Ethologica, 8*(1), 45–50. http://dx.doi.org/10.1007/s10211-005-0108-6.

Osborne, L., Umbers, K. D., Backwell, P. R., & Keogh, J. S. (2012). Male tawny dragons use throat patterns to recognize rivals. *Naturwissenschaften, 99*(10), 869–872. http://dx.doi.org/10.1007/s00114-012-0968-3.

Osborne, L., Umbers, K. D., & Keogh, J. S. (2013). The effects of perch height, time in residence and distance from opponent on aggressive display in male lizards. *Acta Ethologica, 16*(1), 41–46. http://dx.doi.org/10.1007/s10211-012-0135-z.

Pauers, M. J., Kapfer, J. M., Fendos, C. E., & Berg, C. S. (2008). Aggressive biases towards similarly coloured males in Lake Malawi cichlid fishes. *Biology Letters, 4*(2), 156–159. http://dx.doi.org/10.1098/rsbl.2007.0581.

Paulson, D. R. (1973). Predator polymorphism and apostatic selection. *Evolution*, 269–277. http://dx.doi.org/10.2307/2406967.

Pryke, S. R. (2006). Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proceedings of the Royal Society B: Biological Sciences, 273*(1589), 949–957. http://dx.doi.org/10.1098/rspb.2005.3362.

Pryke, S. R. (2007). Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behavioral Ecology, 18*(3), 621–627. http://dx.doi.org/10.1093/beheco/arm020.

Pryke, S. R., Astheimer, L. B., Buttemer, W. A., & Griffith, S. C. (2007). Frequency-dependent physiological trade-offs between competing colour morphs. *Biology Letters, 3*(5), 494–497. http://dx.doi.org/10.1098/rsbl.2007.0213.

Pryke, S. R., Lawes, M. J., & Andersson, S. (2001). Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. *Animal Behaviour, 62*(4), 695–704. http://dx.doi.org/10.1006/anbe.2001.1804.

Qvarnström, A., Vallin, N., & Rudh, A. (2012). The role of male contest competition over mates in speciation. *Current Zoology, 58*(3), 493–509.

Rand, M. S. (1988). Courtship and aggressive behavior in male lizards exhibiting two different sexual colorations. *American Naturalist, 28*(4), 153.

Rankin, K. (2014). *Genetic and environmental influences on male throat colouration in the colour polymorphic tawny dragon lizard* Ctenophorus decresii (Unpublished MSc thesis). Melbourne, Australia: The University of Melbourne.

Reaney, L. T., & Backwell, P. R. (2007). Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behavioral Ecology, 18*(3), 521–525. http://dx.doi.org/10.1093/beheco/arm014.

Rice, G. E., & Bradshaw, S. D. (1980). Changes in dermal reflectance and vascularity and their effects on thermoregulation in *Amphibolurus nuchalis* (reptilia: Agamidae). *Journal of Comparative Physiology, 135*(2), 139–146.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology, 86*(10), 2805–2814. http://dx.doi.org/10.1890/05-0074.

Roulin, A. (2004). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews, 79*(4), 815–848. http://dx.doi.org/10.1017/s1464793104006487.

Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews, 85*(2), 217–246. http://dx.doi.org/10.1111/j.1469-185X.2009.00101.x.

Seehausen, O., & Schluter, D. (2004). Male–male competition and nuptial–colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proceedings of the Royal Society B: Biological Sciences, 271*(1546), 1345–1353. http://dx.doi.org/10.1098/rspb.2004.2737.

Setchell, J. M., & Jean Wickings, E. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology, 111*(1), 25–50. http://dx.doi.org/10.1111/j.1439-0310.2004.01054.x.

Sih, A., Chang, A. T., & Wey, T. W. (2014). Effects of behavioural type, social skill and the social environment on male mating success in water striders. *Animal Behaviour, 94*(0), 9–17. http://dx.doi.org/10.1016/j.anbehav.2014.05.010.

Simon, V. B. (2011). Communication signal rates predict interaction outcome in the brown anole lizard, *Anolis sagrei. Copeia, 2011*(1), 38–45. http://dx.doi.org/10.1643/ce-08-022.

Sinervo, B., & DeNardo, D. F. (1996). Costs of reproduction in the wild: path analysis of natural selection and experimental tests of causation. *Evolution, 50*(3), 1299–1313. http://dx.doi.org/10.2307/2410670.

Sinervo, B., & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature, 380*(6571), 240–243. http://dx.doi.org/10.1038/380240a0.

Sinervo, B., & Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity, 89*, 329–338. http://dx.doi.org/10.1038/sj.hdy.6800148.

Sinervo, B., Svensson, E., & Comendant, T. (2000). Density cycles and an offspring quantity and quality game driven by natural selection. *Nature, 406*(6799), 985–988. http://dx.doi.org/10.1038/35023149.

Sinervo, B., & Zamudio, K. R. (2001). The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. *Journal of Heredity, 92*(2), 198–205. http://dx.doi.org/10.1093/jhered/92.2.198.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology, 19*(2), 448–455. http://dx.doi.org/10.1093/beheco/arm144.

Stamps, J. A., & Krishnan, V. V. (1997). Functions of fights in territory establishment. *The American Naturalist, 150*(3), 393–405. http://dx.doi.org/10.1086/286071.

Stapley, J., & Keogh, J. S. (2006). Experimental and molecular evidence that body size and ventral colour interact to influence male reproductive success in a lizard. *Ethology Ecology & Evolution, 18*(4), 275–288. http://dx.doi.org/10.1080/08927014.2006.9522696.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford, U.K.: Oxford University Press.

Stuart-Fox, D., & Johnston, G. R. (2005). Experience overrides colour in lizard contests. *Behaviour, 142*, 329–350. http://dx.doi.org/10.1163/1568539053778265.

Stuart-Fox, D., Moussalli, A., Marshall, N. J., & Owens, I. P. (2003). Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour, 66*(3), 541–550. http://dx.doi.org/10.1006/anbe.2003.2235.

Sundström, L. F., Petersson, E., Höjesjö, J., Johnsson, J. I., & Järvi, T. (2004). Hatchery selection promotes boldness in newly hatched brown trout (Salmo trutta): implications for dominance. *Behavioral Ecology, 15*(2), 192–198. http://dx.doi.org/10.1093/beheco/arg089.

Teasdale, L., Stevens, M., & Stuart-Fox, D. (2013). Discrete colour polymorphism in the tawny dragon lizard (*Ctenophorus decresii*) and differences in signal conspicuousness among morphs. *Journal of Evolutionary Biology, 26*(5), 1035–1046. http://dx.doi.org/10.1111/jeb.12115.

Thompson, C. W., & Moore, M. C. (1991). Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus. Animal Behaviour, 42*(5), 745–753. http://dx.doi.org/10.1016/S0003-3472(05)80120-4.

Tokarz, R. R. (1985). Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Animal Behaviour, 33*(3), 746–753. http://dx.doi.org/10.1016/S0003-3472(85)80006-3.

Tokarz, R. R. (1998). Mating pattern in the lizard Anolis sagrei: implications for mate choice and sperm competition. *Herpetologica, 54*(3), 388–394.

Umbers, K. D. L., Osborne, L., & Keogh, J. S. (2012). The effects of residency and body size on contest initiation and outcome in the territorial dragon, *Ctenophorus decresii. PLoS One, 7*(10), 1–5. http://dx.doi.org/10.1371/journal.pone.0047143.

Vercken, E., Massot, M., Sinervo, B., & Clobert, J. (2007). Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara. Journal of Evolutionary Biology, 20*(1), 221–232. http://dx.doi.org/10.1111/j.1420-9101.2006.01208.x.

Williams, L. J., King, A. J., & Mettke-Hofmann, C. (2012). Colourful characters: head colour reflects personality in a social bird, the Gouldian finch, *Erythrura gouldiae. Animal Behaviour, 84*(1), 159–165. http://dx.doi.org/10.1016/j.anbehav.2012.04.025.

Wolf, M., Van Doorn, G. S., & Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America, 105*(41), 15825–15830. http://dx.doi.org/10.1073/pnas.0805473105.

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature, 447*(7144), 581–584. http://dx.doi.org/10.1038/nature05835.

Yewers, M. S., McLean, C. A., Moussalli, A., Stuart-Fox, D., Bennett, A. T., & Knott, B. (2015). Spectral sensitivity of cone photoreceptors and opsin expression in two colour-divergent lineages of the lizard *Ctenophorus decresii. The Journal of Experimental Biology, 218*(10), 1556–1563. http://dx.doi.org/10.1242/jeb.119404.

Yewers, M. S., & Stuart-Fox, D. (2012). *[Territory size and spatial arrangement of male colour morphs of the tawny dragon lizard]*. Unpublished raw data.

Yewers, M. S., & Stuart-Fox, D. (2013a). *[Hormone profiles, performance and morphology do not predict to behavioural strategies of* Ctenophorus decresii *colour morphs]*. Unpublished manuscript.

Yewers, M. S., & Stuart-Fox, D. (2013b). *[Recapture rate of a colour polymorphic population of male tawny dragon lizards]*. Unpublished raw data.

Zuk, M., & Kolluru, G. R. (1998). Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology*, 415–438.
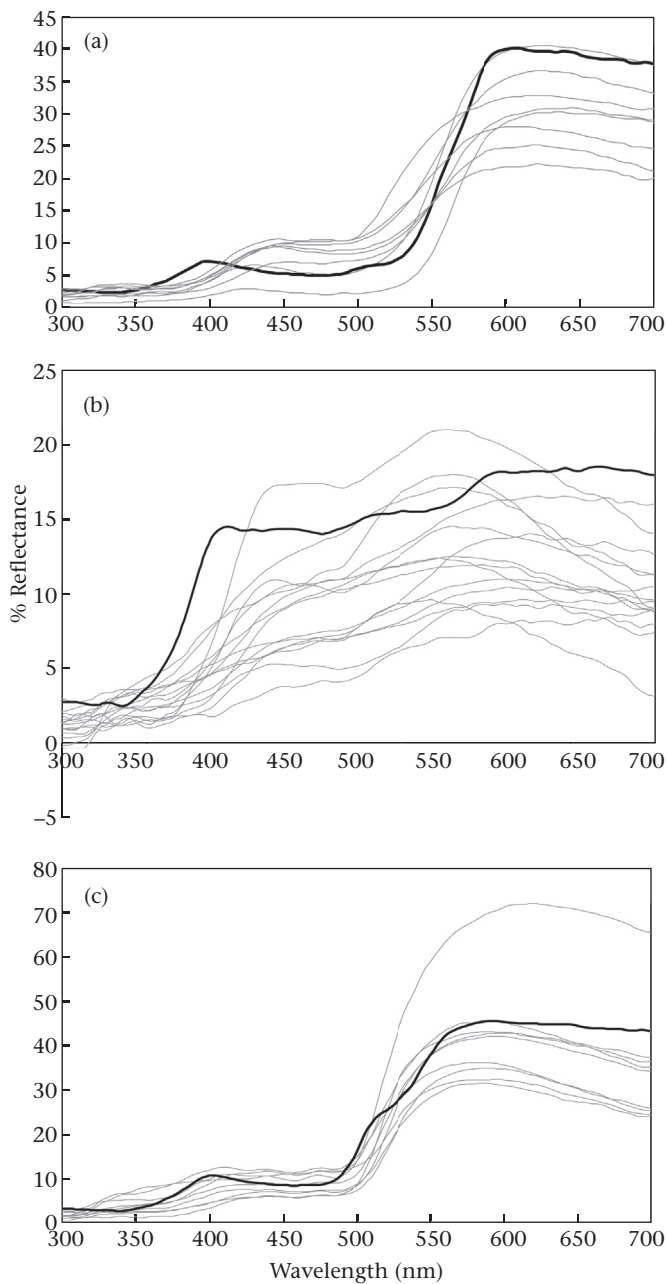
Appendix 1. Supplementary methods

Fig. A1. Reflectance spectra of natural variation of (a) orange colour, (b) grey colour and (c) yellow colour on male lizards (grey lines) compared with the colour-matched acrylic paint on the model lizards (black line).

We measured the spectral reflectance of the throat of wild-caught lizards using an Ocean Optics USB2000+ spectrometer and PX-2 Pulsed Xenon light source both connected to a probe via a bifurcated fibre-optic cable. Measurements were an oval point sample 2×4 mm, expressed relative to a 99% diffused white reflectance standard and taken at a $45°$ angle to the surface of the throat. Body temperature can affect reflectance in reptiles (Rice & Bradshaw, 1980) so we heated lizards to an average of 32.5 ± 0.2 °C when measuring reflectance. For each lizard we took two to four measurements of both the primary (central) and secondary (surrounding) throat colours.

Appendix 2. Results of four-morph models

Table A1

Aggression level candidate models, second-order Akaike's information criterion and Akaike weights for conspecific aggression by the four male tawny dragon colour morphs to model intruder lizards

Categorization of morphs	Model	AICc	ΔAICi	Akaike weight (wi)
4-Morph model	Null	495.6	10.00	0.003
	Weight	501.7	18.00	0.000
	SVL	485.6	2.40	0.122
	Residuals head length	485.6	1.90	0.156
	Residuals head depth	483.7	0.50	0.315
	Residuals head width	483.6	0.00	0.404
3-Morph model OY as orange	Null	229.74	6.19	0.02
	Weight	237.50	13.95	0.00
	SVL	236.14	12.59	0.00
	Residuals head length	225.66	2.11	0.154
	Residuals head depth	223.85	0.30	0.381
	Residuals head width	223.55	0.00	0.443
3-Morph model OY as yellow	Null	221.52	7.75	0.01
	Weight	227.74	13.97	0.00
	SVL	226.72	12.95	0.00
	Residuals head length	215.51	1.74	0.189
	Residuals head depth	214.29	0.52	0.348
	Residuals head width	221.52	0.00	0.452

The best model is indicated by the smallest AICc and the smallest ΔAICi with ΔAICi < 2 considered equally as good a fit (Richards, 2005). Akaike weight is the probability that the associated model is the best in the set.

Table A2

Test of fixed effects for the linear mixed model for levels of aggression of the four visually discrete colour morphs

Fixed term	Numerator df	F	Denominator df	Pr>F
Model	4	11.84	118.8	<0.001
Morph	3	2.94	28.5	0.050
Model∗Morph	12	2.11	118.9	0.021
Head width	1	3.64	28.2	0.067

Table A3

Parameter estimates (and SEs) of the interaction between the four colour morphs and five coloured models for the final linear mixed model for levels of aggression

Model colour	Morph			
	Grey	Orange	Orange-yellow	Yellow
Control	0	0	0	0
Grey	0	0.556 (0.746)	−0.944 (0.746)	−1.556 (0.724)
Orange	0	1.333 (0.746)	0.224 (0.760)	0.556 (0.724)
Orange-yellow	0	−0.153 (0.746)	0.347 (0.746)	−0.667 (0.724)
Yellow	0	0.500 (0.746)	0.500 (0.746)	0.778 (0.724)

Levels of aggression LMM includes morph colour, model colour, head width residuals and the intercept of model colour and morph colour. The first level of each categorical variable was set to zero by default forming the reference level factor.

Table A4

Parameter estimates (and SEs) of the four colour morphs for flight initiation distance (FID) ANCOVA

Morph	Parameter estimate
Grey	0
Orange	−0.152 (0.092)
Orange-yellow	−0.264 (0.093)
Yellow	−0.170 (0.084)

We performed an ANCOVA with FID as the response variable and rock temperature as the covariate. The first level of each categorical variable was set to zero by default forming the reference level factor.