

Original Article

Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards

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Conspicuous color signals are commonly used by a wide diversity of animals to advertise some specific aspect of their competitive ability. In particular, orange and red colors are often used as an aggressive signal to potential rivals. The iconic Australian frillneck lizard (*Chlamydosaurus kingii*) has a large and extensible frill that varies geographically in the extent of yellow, orange, and red present. Focusing on the red-orange lizards found in Western Australia, we first established that, in contrast to most lizards studied to date, the red-orange-colored frill is carotenoid rather than pterin based. Second, we measured chromatic and achromatic aspects of male frills before staging dyadic contests between males to determine whether color is used to signal fighting ability. Both chromatic and achromatic measures of the red-orange patches on the lizard's frills, as well as similarly colored patches on their throats, were reliable predictors of competitive ability; males possessing more colorful displays dominated size-matched competitors in dyadic contests. Apart from large differences in body size and mass (>10%), no other colorimetrics (e.g., white patches), frill traits (e.g., size, relative and absolute patch sizes), or morphological measures (e.g., head size, bite force) were found to predict the outcome of contests. To the best of our knowledge, this is the first example of carotenoid-based patches signaling male fighting ability in a lizard.

Key words: *Chlamydosaurus kingii*, color signal, communication, fighting ability, reflectance, visual modeling.

INTRODUCTION

Carotenoid pigmentation is responsible for many of the conspicuous yellow, orange, and red colors displayed by vertebrates (Evans and Norris 1996; Badyaev and Hill 2000; Hill 2000; Pryke et al. 2002; McGraw et al. 2006; Svensson and Wong 2011). Carotenoids are also vital nutrients for all animals (Lozano 1994; Olson and Owens 1998), and because of the costs of foraging, parasite-inhibited uptake, and competing physiological functions (e.g., Lozano 1994; Olson and Owens 1998; Moller et al. 2000; Fitz et al. 2009; Svensson and Wong 2011), carotenoid displays are often invoked as honest signals of individual quality to potential mates and/or rivals (Hill 2002; Blount 2004; Hill and McGraw 2006; Mougeot et al. 2007). In birds, carotenoid-based signals are frequently used in female mate choice and/or male conflict resolution (Dufva and Allander 1995; Matéos and Carranza 1997; Pryke and Andersson 2003; McGraw et al. 2006; Pryke and Griffith 2006; Griggio et al. 2007; Webster et al. 2008; Pryke 2009; Alonso-Alvarez et al. 2012). In contrast, the role of carotenoid coloration in reptiles has been largely neglected and remains controversial. For example, recent studies suggest that carotenoids may play a minor

role in producing their conspicuous coloration (Olsson et al. 2008), which may instead be primarily determined by pterins (Steffen and McGraw 2007; Weiss et al. 2012). Studies of lizards that do display carotenoid-based signals (e.g., anoles; Macedonia et al. 2000; Steffen and McGraw 2007) suggest that carotenoid-based signals may also be condition dependent (common lizard, *Zootoca vivipara*: Fitz et al. 2009) but have either not identified or investigated a signaling function of carotenoid coloration. Furthermore, *Anolis sagrei* whose diets were supplemented with carotenoids did not experience any significant change to the color of their dewlap (Steffen et al. 2010). Together, this has left the relative signal function of carotenoid pigmentation in lizards unclear.

In many vertebrate systems, males compete directly for females or for resources that are necessary for attracting females (Andersson 1994). Sexual selection through male contest competition can therefore be severe and may, like female choice, drive the evolution of conspicuous male traits (Charles and Ord 2012) and dramatic sexual dichromatism (Macedonia et al. 2002; Stuart-Fox and Ord 2004; Hofmann et al. 2008). Many studies indicate that selection for male competitive ability may favor the evolution of conspicuous signals in both birds (e.g., Matéos and Carranza 1997; Crowley and Magrath 2004; Pryke and Griffith 2006) and lizards (e.g., Whiting et al. 2003; Olsson et al. 2005; Stapley and Whiting 2006; Whiting

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et al. 2006; Healey et al. 2007; Qi et al. 2011). Such signals may help individuals to immediately assess the relative competitive ability of rivals, without having to revert to costly escalated interactions (and physically fighting) when establishing dominance relationships. Indeed, some of the most conspicuous and elaborate color signals seen in birds and lizards are used for signaling status and resolving male contests (reviewed in Whiting et al. 2003).

In lizards, color signaling is highly developed, often permitting effective communication when prominently displayed over long distances, even in complex environments (Fleishman et al. 2009). However, the evolution of conspicuous color patterning is typically restricted by predation pressure, which favors more cryptic coloration through natural selection (Stuart-Fox et al. 2003; Stuart-Fox and Ord 2004). Many lizards overcome this trade-off by displaying conspicuous color signals on the underparts of their body, which are often not visible to predators, or by displaying color on body areas or morphological structures that can be distended and retracted (i.e., with the color hidden when not displayed; Whiting et al. 2003). These ornaments are evident in many different forms; for example, modification of the dewlap (on the throat), such as in the *Anolis* species complex (Nicholson et al. 2007), or the spectacularly colored tongues of blue-tongue skinks, *Tiliqua* species (Cogger 2000). However, perhaps one of the most dramatic and unusual color displays is found in the frillneck lizard, *Chlamydosaurus kingii* (Shine 1990; Christian et al. 1995).

Frillneck lizards are characterized by an elaborately colored frill around their necks (Figure 1), which can be erected through use of the hyoid musculature (Shine 1990). Frill color shows marked geographic variation across their range in tropical northern Australia; in their western range (Western Australian and Northern Territory populations), lizards typically display a red-orange coloration in the frill (Figure 1), whereas lizards in more eastern populations (Arnhemland and Queensland) predominantly display yellow or white frills (Cogger 2000; Wilson and Swan 2010). Frill size is also sexually dimorphic, with males displaying larger and more brightly colored frills than females. Observations of males in the wild suggest that the frill may function in both territory defense and courtship (Shine 1990; Christian et al. 1995); however, no correlative or experimental studies have investigated the relative function of the colored frill in resolving male conflicts and thus its signal function remains unclear.

To determine the signal function of the red-orange frill color of lizards in western populations, we first established whether the color patch was pterin or carotenoid based. Second, to quantify color signal expression as perceived by rival lizards, rather than the human visual system, we measured spectral reflectance of color patches (using a reflectance spectrometer) and applied a model of color perception based on the visual pigment sensitivities for a closely related agamid (*Ctenophorus ornatus*; Barbour et al. 2002). In addition, because correlates of the frill and/or different male traits may be related to fighting ability, we also examined a range of frill traits (relative size, relative and absolute patch size) and other morphological traits known to be important in resolving contests in lizards (e.g., bite force, body size, and mass). Lastly, to experimentally test the role of the red-orange frill in resolving male contests, we staged dyadic contests between unfamiliar males of similar sizes. Males are highly territorial during their reproductive season (Shine 1990; Griffiths 1999) and typically compete for access to prominent trees from which to display to females (and defend their territories). Therefore, contests were staged to coincide with territorial establishment (i.e., when competition is most intense) and over access to a single tree trunk (i.e., a valued resource).

Because territory establishment and maintenance is likely to be critical for male mating success (Andersson 1994), any signal trait that increases the efficiency (or decreases the cost) of frequent contests between males should be favored.

MATERIALS AND METHODS

Study system

The frillneck lizard is a large agamid (mean adult snout–vent length [SVL] in the study population is 231.15 mm [95% CI = 225.10–237.20 mm; range = 210–255 mm], but individuals from the eastern populations are often larger; see Christian et al. 1995), which is restricted to the northern tropical savannas of Australia. Although they have a restricted distribution, frillneck lizards are locally abundant. We studied 2 wild populations of frillneck lizards in the eastern Kimberley region of northwestern Australia, which are situated more than 100 km apart (Wyndham: 15.49°S, 128.12°E; Kununurra: 15.77°S, 128.74°E). The eastern Kimberley experiences a strongly seasonal monsoonal climate consisting of a dry season (May to September), a wet season (November to March), and 2 short transitional seasons. All fieldwork was conducted during the wet season, as this is when the lizards are reproductively active, with males actively defending their territories (Christian and Bedford 1995). Studies of Northern Territory populations indicate that adult males can occupy territories more than 2.5 ha in area (Shine and Lambeck 1989; Griffiths 1999) but also often reach high population densities in good quality foraging environments (i.e., open understory) where competition for trees can be common.

Male lizards were captured either by hand or by noosing (Shine 1990; Christian et al. 1995). Lizards were sexed by head and SVL measurements (Christian et al. 1995), and hemipene eversion (Harlow and Shine 1999) was used in 2 cases where body measurements were ambiguous. Capture location was recorded on a handheld GPS, and all lizards were released at their capture location within 72 h. To ensure that male lizards could be reliably and rapidly located for the dyadic contests, individuals were fitted with radio transmitters (Sirtrack V1G 118) when first captured (November 2011–January 2012). Transmitters were glued to a small square of nylon mesh and then attached to the base of the tail using nontoxic silicon adhesive. Attachments weighed 0.8–2.4% of the lizards' body mass and did not noticeably interfere with any behavior. Transmitter-bearing lizards were released within 12 h of capture and then later relocated for use in staged contests.

Male morphology and bite force

All lizards were permanently marked for future identification using passive integrated transponder tags (Hongteng Barcode Company) implanted subcutaneously under a loose fold of skin on the neck (Griffiths and Christian 1996) and temporarily marked with nontoxic paint pens for identification during trials. Maximal bite force for each lizard was measured using a piezoelectric transducer (Kistler type 9203 force transducer ± 500 N). Individuals were induced to bite forcefully on specially constructed plates (measuring bite intensity) by placing the plates between a lizard's open jaws. As this measure is designed to capture an individual's maximum performance (Anderson et al. 2008), the highest value of 3 measures was recorded as the lizard's maximum bite force (e.g., Vanhooydonck et al. 2010). Only vigorous bites where the lizard exerted a high degree of force were recorded; nonvigorous bites (i.e., those producing anomalously low readings) were discarded (Anderson et al. 2008; Vanhooydonck et al. 2010). Body size (SVL),

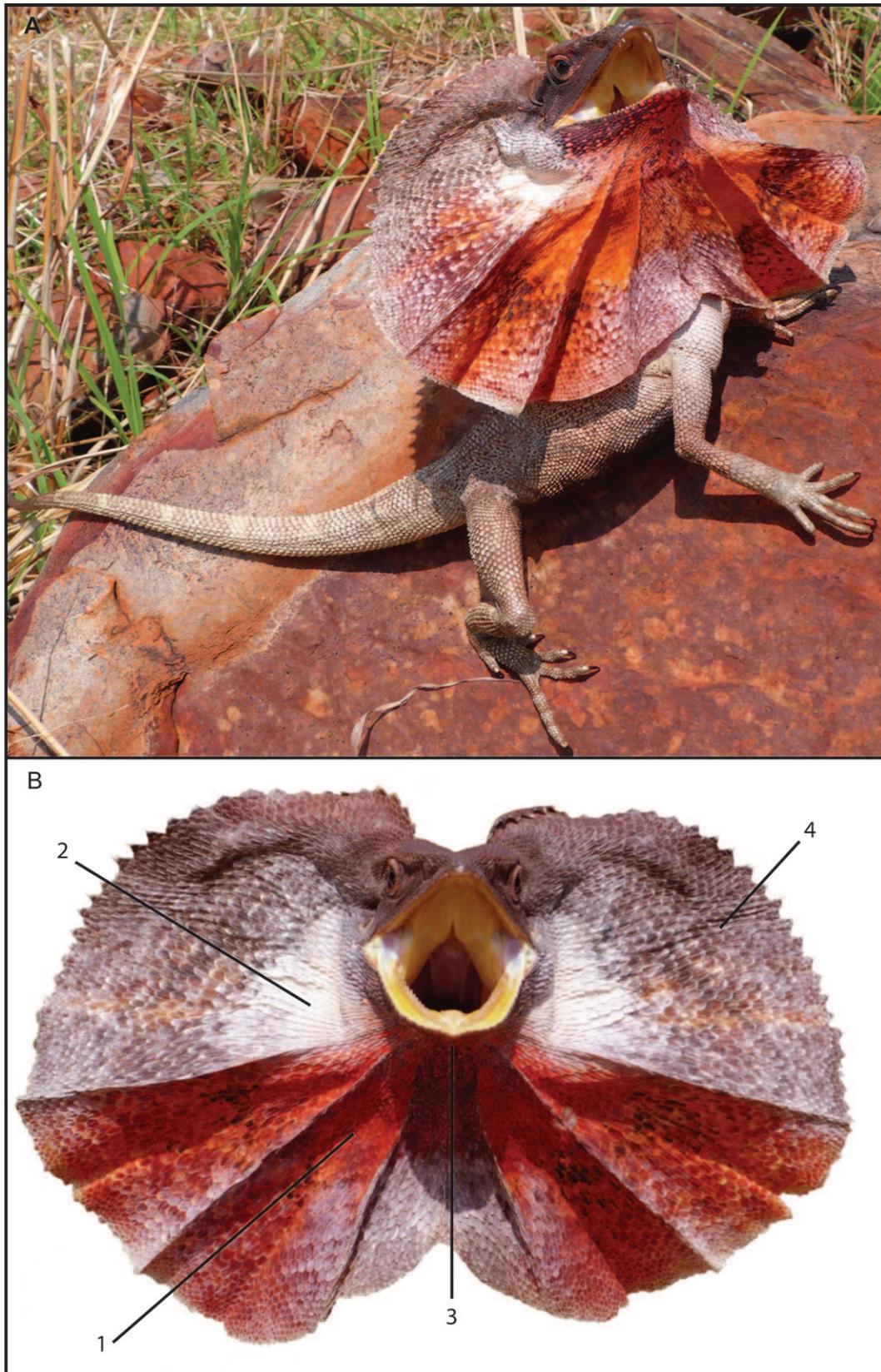


Figure 1

(A) Adult male frillneck lizard from Western Australia displaying his colored throat and frill. (B) The color patches measured on frillneck lizards using a reflectance spectrometer: (1) red-orange frill; (2) white frill; (3) red-orange throat (clearly shown in A); and (4) background (brown) frill. Three measurements were taken of each patch (left and right in the case of 1, 2, and 4) on all individuals and averaged for each color patch (and left and right red-orange and white patches were averaged).

head length, head width, head height, tail length, hindlimb length, and frill length (from the bony ridges on the top of the head to the furthest extremity of the frill in a line parallel to the main axis of the body; Christian et al. 1995) were measured to the nearest millimeter, and mass to the nearest 0.1 g, immediately after capture. Because the 3 head measurements were intercorrelated, we used the first axis of a principal component analysis (PCA), which explained 99.91% of the variation, as an independent measure of head size. Because frill size was positively correlated with body size (see Results), we calculated relative frill size as the residuals from frill size linearly regressed on body size (SVL). Similarly, we calculated body condition using the residuals of mass/SVL. Finally, standardized digital photos of the erect frill were taken against a standardized white background. Color patch area (Figure 1) was calculated as a percentage of total frill size using the graphics software Scion Imaging Software Beta 4.02 (Scion Corporation, Frederick, MA).

Male coloration and visual modeling

Immediately prior to commencement of the tournament, we quantified male coloration using a USB2000 spectrometer (Ocean Optics, Dunedin, FL) with illumination from a PX-2 light source. For each individual, we took measurements of each side (i.e., left and right) of the red-orange and white patches on the frill and throat and the brown background of the frill (Figure 1). Three consecutive scans (removing the probe between each) of different locations in the center of each patch were taken with a fiber-optic reflectance probe and in relation to a WS-2 white standard scanned prior to each individual. For analysis, we averaged spectral reflectance of all 3 scans over each 5-nm interval in the range of 320–700 nm, the visual spectrum for most diurnal lizards (Loew et al. 2002). As there was no variation observed between left and right sides of the frill, for the red-orange and white frill patches, we collated the measurements of both sides to obtain the average spectral reflectance (see Figure 2 for average wavelength curves of the measured patches).

As visual systems encode signals as contrasts between adjacent colors, we analyzed the color variation as changes in the contrast (relative to the lizard visual system) between the 3 frill colors: red-orange (frill and throat), white (frill) coloration, and the surrounding brown frill background (see Figure 1). To estimate contrasts, we applied the Vorobyev–Osorio model (Vorobyev and Osorio 1998; Osorio and Vorobyev 2008), which estimates the discriminability of 2 colors (e.g., the red-orange frill and the surrounding brown frill background) in units of discrimination thresholds (or “just noticeable differences”) and assumes that visual discrimination is limited by photoreceptor noise. The model produces a measure of the chromatic (color) contrast based on the 4 single cones used for color perception and a measure of achromatic (luminance) contrast based on the double cone used for luminance perception (Vorobyev and Osorio 1998). Contrast measures provide an indication of conspicuousness against adjoining color patches (e.g., frill background). We used the model calculations detailed in Siddiqi et al. (2004).

Following other studies of coloration in agamids (Chan et al. 2009; Jessop et al. 2009), to quantify male frill color variation, as perceived by conspecifics, we used data on the spectral sensitivities of a closely related dragon, *C. ornatus* (Barbour et al. 2002). As in other related diurnal lizards, this species has both single and double cones. However, Barbour et al. (2002) identified only 3 visual pigments, a short wavelength-sensitive ($k_{\max} = 440$ nm), medium wavelength-sensitive ($k_{\max} = 493$ nm), and long wavelength-sensitive

($k_{\max} = 571$ nm) type, and failed to identify the rare ultraviolet-sensitive (UVS) photoreceptor (which has been found in all other related lizards) in their small sample of microspectrophotometric data. Therefore, following Chan et al. (2009), we repeated all model calculations with and without a fourth UVS photoreceptor ($k_{\max} = 360$ nm). Nevertheless, color variation for both the red-orange and white patches was qualitatively unchanged; therefore, we only present results based on the 3 published photoreceptor sensitivities.

For model calculations, the absorbance curves for each visual pigment were first multiplied by the oil droplet spectrums and ocular media (lens and cornea; assumed to have a $k_{\max} = 350$ nm as in other lizards) and then normalized to equal area (Endler and Mielke 2005). Receptor quantum catches for each cone were then derived over the visible spectrum (Vorobyev and Osorio 1998; Endler and Mielke 2005) before applying the von Kries transformation to account for receptor adaptation to the light environment (Vorobyev and Osorio 1998; Siddiqi et al. 2004; Endler and Mielke 2005). Because frillneck lizards are diurnal and their habitat is open, we assumed that photoreceptor noise (ω_i) for the long wavelength-sensitive photoreceptor was 0.05 (see Stuart-Fox et al. 2003; Chan et al. 2009) and then derived ω_i for the other photoreceptor classes (Stuart-Fox et al. 2003; Siddiqi et al. 2004). For the 3 photoreceptor classes, we used a ratio of 1:3.5:6 (Barbour et al. 2002). As found in other vertebrates (Osorio and Vorobyev 2005), it was assumed that the 3 single cones are used for chromatic (“color”) discrimination, whereas the long wavelength-sensitive photoreceptors are thought to function in achromatic (“brightness”) discrimination.

Carotenoid and pterin assays

Small tissue samples of the colored frill were collected from male frillnecks (during measurements described above) and stored at -20 °C until the carotenoid and pterin assays were conducted. For both assays, we tested 17 males. To determine whether carotenoids were present in the red-orange-colored frill, we performed a simple chemical assay following McGraw et al. (2005). Briefly, the assays involved placing 3–5 mg of the frill tissue in 1 mL of acidified pyridine (acidified with 38% hydrochloric acid; 4 drops of HCl for every 100 mL of pyridine). Samples were placed along with negative controls in a 95 °C water bath for 4 h to unbind carotenoids from the tissues. If the solution was colored (compared with the negative control; McGraw et al. 2005), 2 mL of distilled water and 1 mL of 1:1 hexane:tert-butyl methyl ether (TBME) were added to the vial. This separated carotenoids into a top lipid layer when the mixture was allowed to settle overnight. Any color remaining in the upper phase is attributed to the presence of carotenoids (McGraw et al. 2005).

We assayed for pterins in the red-orange-colored frill following Kikuchi and Pfennig (2012). Briefly, finely diced tissue samples were placed in 0.5 mL of 1 N NH_4OH (which dissolves pteridines). Before centrifuging, a further 0.5 mL of 1 N NH_4OH was added (to make up 1 mL) and then 1 mL of 1:1 hexane:TBME solution was added. Tubes were vortexed for 30 s to extract any carotenoids into the hexane:TBME phase. The hexane:TBME phase was then separated from the NH_4OH phase by centrifuging for 5 min at 8000 rpm. Any visible color (in the lower (NH_4OH) phase) is then attributed to the presence of pterins (Kikuchi and Pfennig 2012).

Male contest experiments

Staged contests were carried out during January 2012 using a total of 20 males (13 from the Wyndham sites and 7 from the Kununurra

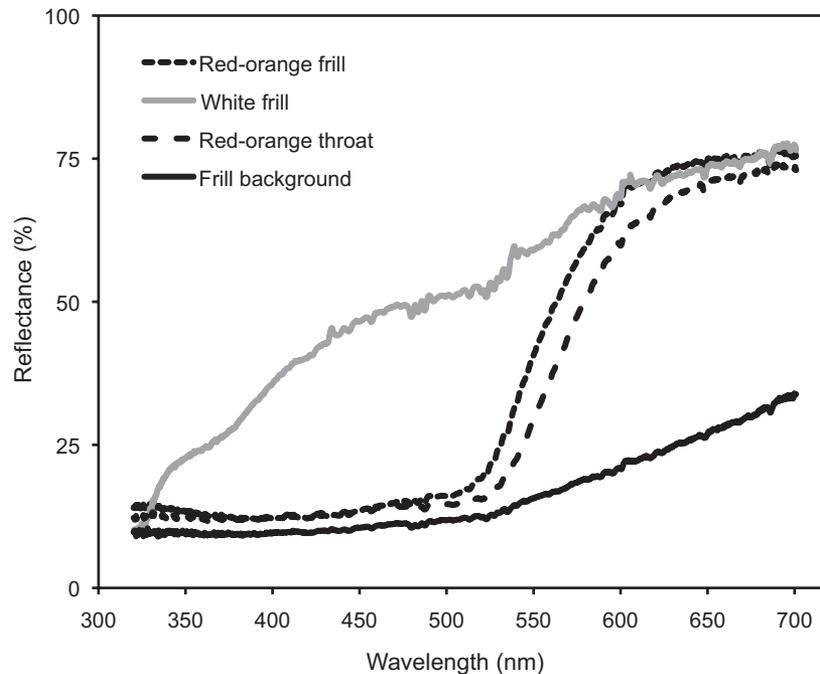


Figure 2

Average reflectance (across all individuals) of the red-orange and white color patches on the frill and throat and the brown background of the frill.

sites). Trials were conducted in an indoor arena (100 × 80 × 200 cm high) with a single vertical tree trunk in the center, which provided the best access to an overhead basking lamp. Because frillneck lizards typically acquire and defend prominent trees in their territories (Shine 1990), and because the tree trunk provided the only elevated display point in the arena, as well as an optimum basking spot, this provided a valued resource for lizards to compete for. Our observations of interactions between frillneck males in the wild reveal that, following contests, the dominant male will typically reassume an elevated position from which to continue displaying, whereas the loser assumes a submissive posture low to the ground. In our experimental contests, the tree perch was never used as an escape route for the subordinate (losing) male. Lizards were kept in standardized conditions (temperature-controlled room at 26 °C) for at least 12 h prior to the trials, but given 10 min under a heat lamp immediately before trials commenced. This ensured that all competitors were kept at a constant temperature, below that of optimum basking, to standardize and maximize their motivation to compete for access to the heat source.

Standardized dyadic contests were performed (see Stuart-Fox et al. 2006) in which 2 males were placed opposite one another (but equidistant from the basking/display platform) in the arena before the observer quickly withdrew. Contests were videotaped and also monitored by an observer once every 10 min from behind a thick shade-cloth screen. We terminated interactions once a clear winner was identified or if no interaction had occurred after 30 min. Winners were identified as the individual to reach the optimum basking position after passive or active interactions with its opponent. Typically, this involved the winner turning and facing its rival, elevating its head and/or body, and erecting its frill, which would result in its rival adopting a submissive posture (head and body low to the ground, no frill erection). Interactions varied from active (threat displays) to passive supplants where a lizard simply fled if approached by its opponent, but no physical interaction (fighting) was observed. If an individual reached the basking refuge first,

without any interaction with its opponent, the trial was rerun ($n = 3$ trials). Contestants were given a minimum of 12 h between trials.

Contests between males were performed as part of a “tournament,” where the relative fighting ability of males was estimated based on their interactions between different “players” (Whiting et al. 2006). Males were initially size matched within 10% of SVL (of the smaller individual), as is common practice in staged lizard contests (Stuart-Fox and Johnston 2005; Stuart-Fox et al. 2006; Healey et al. 2007). Following these initial trials, individuals with the same records (e.g. win–win, loss–win) were then paired against each other (to avoid potential winner–loser effects). All paired contests were between unfamiliar individuals captured from different localities. Lizards generally underwent 3 trials each, unless there was no size-matched (within 10% SVL) opponent available with an identical contest record ($n = 4$). In addition, 2 lizards were used in 5 trials, and a further 2 underwent 4 trials. In total, 31 trials were conducted (with 20 males); only 1 trial was terminated with no discernible winner.

Statistical analysis

The interrelations between morphological variables (SVL, mass, condition, head size, relative frill length, red-orange and white patch sizes, and hindlimb length), bite force, and spectral measures (chromatic and achromatic contrasts) were analyzed using Pearson’s correlations. Generalized linear models (GLM) with a logarithmic link function and Poisson distribution were used to evaluate the relative contribution of these potentially interacting variables on color expression. The significance of these predictor variables was tested by the change in deviance of the different models using a chi-square approximation.

Contest outcomes were analyzed using the Bradley–Terry (B-T) model for paired comparisons (full details of the B-T model are provided in Firth 2005; Stuart-Fox et al. 2006; Whiting et al. 2006). Briefly, B-T models assume that in a contest between 2 competitors,

the odds of winning are positive-valued parameters representing their “fighting ability,” such that the result of any contest is the ratio of the abilities of the 2 contestants (Firth 2005). This form of GLM takes proper account of dependency within and between contests and can also accommodate an incomplete matrix of possible interactions (Bradley and Terry 1952; Firth 2005). The B-T models were run using the statistical program R (Firth 2005; R Development Core Team 2005), with site (Wyndham or Kununurra), morphological variables (SVL, mass, body condition, head size, relative frill length, red-orange and white frill patch size, and hindlimb length), bite force, and spectral measures (chromatic and achromatic contrast) for all color patches (Figure 1) as the independent predictor variables. To effectively examine the relative magnitudes of different effects, we used standardized regression coefficients with all predictor variables scaled to have unit standard deviations.

For all models (both colorimetric and B-T), all possible effects, combinations, and interactions were initially modeled. Second-order Akaike information criterion (AIC_C) weights were calculated for each model. The AIC_C (used for smaller sample sizes) balances the fit of the model against the number of parameters and was used to objectively compare different models and select the best-fitting and most parsimonious model; the model with the lowest AIC_C value (and a ΔAIC_C of ≤ 2) is accepted as the model best fitting the data (Burnham et al. 2011). Because all of the best-fitting models were the only models with $\Delta AIC_C < 2$ (and an AIC_C weight of at least 74% compared with other potential models), for simplicity, the top models are presented (i.e., summaries of the competing models).

RESULTS

Carotenoid and pterin assays

For all 17 males, the red-orange frill samples were bright yellow to orange (compared with the transparent negative control), indicating the presence of carotenoids (McGraw et al. 2005). In contrast, all samples tested for pterins were transparent (no color), indicating that pterins are absent and not responsible for the bright red-orange coloration displayed in male frills.

Frill colorimetrics

As expected, the majority of body size variables (e.g., mass, SVL, and head size) were positively correlated (see Table S1); thus, heavier males had larger heads and longer SVL and hindlimbs. Additionally, the achromatic and chromatic measures for the different colored patches were intercorrelated (see Table S2). In particular, both the red-orange frill and throat patches were similarly colored, but the red-orange color on the throat was less intense than on the frill (Figure 2).

Using a GLM to test for the morphological traits that were related to color expression, the best-fitting model for achromatic red-orange brightness identified both body mass ($F_{1,24} = 5.39$, $P = 0.03$; Figure 3) and SVL ($F_{1,24} = 4.07$, $P = 0.05$; Table 1). Substituting chromatic red-orange coloration produced a similar model with body mass as the single best predictor ($F_{1,24} = 6.09$, $P = 0.005$; Figure 3 and Table 2). Similarly, the best-fitting models for both achromatic and chromatic red-orange throat also identified both SVL (achromatic: $F_{1,24} = 4.18$, $P = 0.04$; Table 1; chromatic: $F_{1,24} = 2.96$; $P = 0.06$; Table 2) and body mass (achromatic: $F_{1,24} = 5.29$, $P = 0.003$; Table 1; chromatic: $F_{1,24} = 5.30$, $P = 0.003$; Table 2) as the sole predictors. Thus, larger and heavier males produced brighter and more intensely colored red-orange frill and throat patches than their smaller counterparts.

In contrast, the white frill patches were unrelated to spectral measures of the red-orange patches (Table S2), as well as size traits (e.g., body, head, or frill size). Instead, the size of the white patch was the sole predictor of the achromatic ($F_{1,24} = 7.94$, $P = 0.01$) and chromatic measures of the white patch ($F_{1,24} = 16.42$, $P < 0.001$).

Predictors of contest success

Two male traits were identified as significant predictors of contest success in the final best-fitting model: body mass and the chromatic contrast (color) of the red-orange frill patches (Table 3). Indeed, of the 30 staged contests, 25 (83%) were won by the heavier male, and 27 (90%) were won by the male with the more colorful (greater chromatic contrast) patch (Figure 4). Although the chromatic contrast of the red-orange frill appears to be the stronger predictor of fighting ability (predicts 90% of wins; $P = 0.003$), the estimated effect sizes of the body mass and red-orange patch chromatic contrast, as measured by standardized regression coefficients (Table 3), suggest that body mass may explain more of the variability. However, the coefficient estimate of this variable may be confounded by the much greater variability in body mass (225–706 g) of males. Indeed, of the 10 contests that had weight-matched males (within 10%), males with “redder” frills won 9 (90%) of the contests (only 5 [50%] of the heavier males won), whereas in the 20 contests between males that differed by more than 10%, 20 (100%) were won by the larger males and only 18 (90%) by the “redder” male. This suggests that chromatic variability is being used to assess the relative fighting ability of an opponent in situations where there is no clear discrepancy in body mass between opponents.

DISCUSSION

Our results indicate that the red-orange frill patches are carotenoid based and are a reliable predictor of competitive ability and contest success in male frillneck lizards. Body size (SVL and/or mass) is a common determinant of contest outcome in many lizard species (e.g., López and Martín 2001; Hibbitts et al. 2007; Qi et al. 2011) and also represented a significant predictor of fighting ability in this species. Although body mass appears to be a better predictor of contest outcome than variation in frill coloration, more intense red-orange frill coloration also plays an important role in resolving contests, especially among size-matched rivals. Furthermore, the relationship between body mass and red-orange frill colorimetrics suggests that larger (older) males may have “redder” frills and adds to growing evidence in reptiles that carotenoid-based signals (although relatively rare in reptiles; Olsson et al. 2008; Weiss et al. 2012) are also condition-dependent signals (Fitze et al. 2009; Cote et al. 2010). To the best of our knowledge, this is the first example of a carotenoid-based color patch signaling fighting ability in a lizard.

Much attention has been given to the reliability of carotenoid-based signals (Blount 2004; Hill and McGraw 2006; Svensson and Wong 2011), especially in birds and fish, as such signals are typically thought to have direct honesty-enforcing production costs. In particular, because carotenoid pigments cannot be synthesized and have to be acquired from the diet, carotenoid-based trait expression is typically thought to be related to the male’s ability to obtain, physiologically transport, process, and deposit carotenoid pigments into colored patches (Goodwin 1984; Brush 1990). A male’s foraging ability, nutritional condition, parasite susceptibility, and immunocompetence may all influence carotenoid expression, as well as the amount of carotenoids an individual is able to invest in a sexual

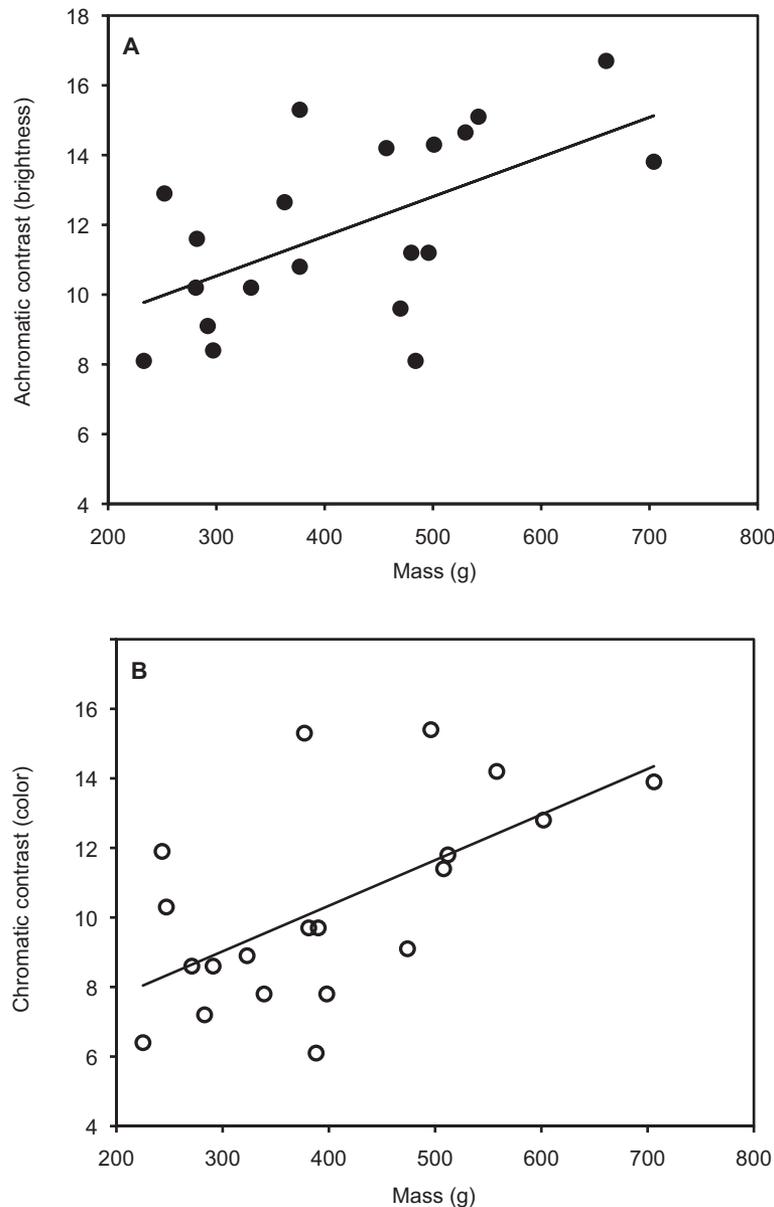


Figure 3

(A) Achromatic contrast (brightness) and (B) chromatic contrast (color) of the red-orange frill patches in relation to total mass (g) of male frillneck lizards.

signal (Lozano 1994; McGraw and Ardia 2003; Svensson and Wong 2011). For example, if there is interference competition over the food source from which the pigments are derived (e.g., carotenoid-rich invertebrates), possibly because territories overlap high-quality food patches, carotenoid coloration can be directly related to competitive ability. We do not know whether such feeding competition exists to the extent that it imposes a limitation on access to carotenoid pigments, but frillneck lizards feed almost exclusively on termites, dragonflies, moths, butterflies, grasshoppers, and other small arthropods (Shine and Lambeck 1989; Griffiths and Christian 1996), and carotenoid-rich invertebrate sources may be rare or patchy in space. In addition, variation in carotenoid-based pigmentation is influenced by environmental stresses such as parasites and pathogens (Olson and Owens 1998) and aspects of immunocompetence and may thus indicate a male's vigor, such as superior health, and/or their ability to forage for scarce carotenoid-rich prey. However, further studies are required to understand the constraints

on color expression in this species, as well as in reptiles in general (Olsson et al. 2008).

The lack of aggression observed here in settling disputes and contests is not unusual and is common in the resolution of many animal contests (e.g., Clutton-Brock and Albon 1979; Whiting et al. 2003, 2006; Morrell et al. 2005). Indeed, passive conflict resolution provides further support that red-orange coloration reliably functions as a traditional status signal used to settle costly interactions (Whiting et al. 2003). All males staged in dyads were unfamiliar, so previous win/loss experience (familiarity) cannot be attributed to the lack of aggressive interactions (Whiting 1999; Osborne 2005). Although males were randomly size matched, it may be that color differences between staged opponents were sufficiently different for the competitively superior male to effectively signal their status without fighting. For example, the chromatic contrast (color) differences between winners and losers were relatively large (e.g., winners often displayed a frill twice as chromatic as their opponent;

Table 1
Summary of GLM models showing main predictors of achromatic red-orange frill and throat coloration

Model	Variable	Coefficient	SE	Standardized coefficient	AIC _C	ΔAIC _C	AIC _C weight
Frill coloration							
1	Mass	0.02	0.005	2.59	28.32	0	0.92
	SVL	0.08	0.04	1.58			
3	Mass	0.02	0.02	2.19	33.21	4.89	0.08
	SVL	0.05	0.07	1.01			
	Head size	0.005	0.32	1.07			
2	Body condition	0.008	0.003	1.25	35.43	7.11	0.02
Throat coloration							
1	Mass	0.02	0.005	2.67	40.87	0	0.93
	SVL	0.09	0.04	1.76			
2	Body condition	0.007	0.003	1.17	47.36	6.49	0.03
3	Mass	0.006	0.02	1.11	48.81	7.94	0.017
	SVL	0.04	0.08	0.99			
4	Head size	0.23	0.34	0.81	48.89	8.02	0.016
	Body condition	0.001	0.01	0.17			
	Head size	0.29	0.31	1.42			

The first models are the best-fitting models (i.e., only model with ΔAIC_C < 2). Only the top 3 models are reported here; all the other models had very low (≤0.01) model weights. SE, standard error.

Table 2
Summary of GLM models showing main predictors of chromatic red-orange frill and throat coloration

Model	Variable	Coefficient	SE	Standardized coefficient	AIC _C	ΔAIC _C	AIC _C weight
Frill coloration							
1	Mass	0.02	0.006	2.73	42.32	0	0.84
	SVL	0.08	0.042	1.73			
2	Mass	0.02	0.006	2.7	46.01	3.69	0.13
	SVL	0.07	0.06	1.42			
	Hindlimb length	0.02	0.05	0.33			
3	Body condition	0.008	0.003	1.72	51.03	8.71	0.011
4	Mass	0.02	0.02	2.01	51.09	8.77	0.011
	SVL	0.07	0.08	1.41			
	Head size	0.04	0.37	0.19			
Throat coloration							
1	Mass	0.016	0.005	2.48	37.39	0	0.75
	SVL	0.07	0.04	1.47			
2	Body condition	0.01	0.01	1.71	39.76	2.37	0.23
	Head size	0.02	0.29	0.08			
3	Mass	0.02	0.005	2.09	44.43	7.04	0.02
	SVL	0.03	0.05	0.73			
	Hindlimb length	0.05	0.04	0.79			

The first models are the best-fitting models (i.e., only model with ΔAIC_C < 2). Only the top 4 models are reported here; all the other models had very low (≤0.01) model weights. SE, standard error.

Table 3
Bradley–Terry models showing the best-fitting predictors of contest outcomes for frillneck lizard contests

Model	Variable	Coefficient	SE	Standardized coefficient	AIC _C	ΔAIC _C	AIC _C weight
1	Mass	1.01	0.33	5.23	9.84	0	0.74
	Chromatic red-orange	0.04	0.02	2.54			
2	Mass	0.05	0.03	4.21	13.59	3.75	0.07
	Achromatic red-orange	1.18	0.80	2.03			
3	Mass	0.05	0.04	4.23	14.52	4.68	0.11
	Chromatic red-orange	0.98	2.83	2.83			
	Achromatic red-orange	0.20	2.23	2.23			
4	Mass	0.04	0.02	4.23	15.65	5.81	0.04
	Achromatic red-orange	0.745	0.78	2.08			
5	Mass	0.04	0.02	4.23	17.75	7.91	0.01
	Head PCA	0.16	0.19	2.67			

The first model is the best-fitting model (i.e., only model with ΔAIC_C < 2). Only the top 5 models are reported here; all the other models had very low (≤0.01) model weights. SE, standard error.

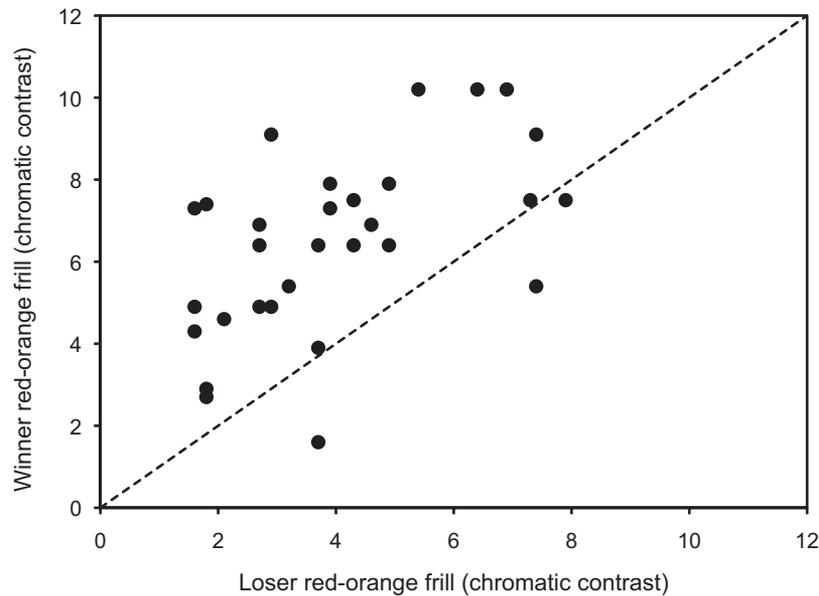


Figure 4

Chromatic contrast (color) of red-orange patches of winners and losers in the staged contests. The dashed line provides equal colorimetric values for both winners and losers; values above the dashed line show contests in which the more chromatic male won, whereas values below the line show contests where the less chromatic male won.

Figure 4); thus, this discrepancy and mismatch in signaling status between opponents may have been sufficient for conflict resolution without the need to escalate aggression and fight.

Because no contest progressed to physical combat, it seems likely that rivals were assessing one another's competitive ability using visual cues (red-orange coloration and body size). Visual indicators of some specific aspect of competitive fitness are common in birds (e.g., Pryke and Griffith 2007; Senar et al. 2008), lizards (e.g., Olsson et al. 2005; Whiting et al. 2006; Healey et al. 2007), and fish (e.g., Evans and Norris 1996; Dijkstra et al. 2008). However, many studies have shown that differences in color patch size, as opposed to color per se, are the most important aspect of the signal. For example, in dwarf chameleons (*Bradypodion pumilum*), the relative area of the colored patch predicted contest outcome (Stuart-Fox et al. 2006), with similar results being found in other studies of lizards (Thompson and Moore 1991; Whiting et al. 2003; López et al. 2004). In this study, however, the size of the red-orange and white frill patches did not predict contest outcome and was also unrelated to any aspects of male competitive ability (e.g., red-orange coloration, body mass, and size). Instead, our results suggest that it is the concentration (intensity) rather than the patch size of the carotenoid pigmentation that is most informative to male frillneck lizards. This may be because signal intensity, rather than size, has the greatest impact when displayed in close contact with a rival and/or predator. This is typically the case for the frillneck lizard where the frill is suddenly displayed and then flapped open and closed at regular intervals in close proximity to rivals and predators (Shine 1990). Color intensity is also an important component of signals that are assessed in a noisy visual environment (Stuart-Fox et al. 2007; Fleishman et al. 2009), which may also be relevant to frillneck lizards that display to conspecifics through habitat, which is dominated by large trees.

The throat patch was similar to the red-orange frill patch and may also function as a signal in male contests. The throat patch was less intense than the red-orange color displayed on the frill (Figure 2) and may function either as a static display or as a

precursor to the frill display. A static display such as a throat-based color signal could circumvent the need to erect the frill, particularly when rivals are clearly conditionally (and thus chromatically) mismatched. This supports the chin-up posture that males frequently adopt when facing rivals on the ground and is also a common feature of many dragon species, which use colored throat displays for signaling status and intent (e.g., bearded dragons, *Pogonia*: Carpenter et al. 1970; *Ctenophorus* spp.: Stuart-Fox et al. 2004). In addition, the throat patch may act as a “backup” signal (Johnstone 1996) to the frill, conveying the same information and thereby increasing the likelihood of successfully conveying information to a rival about fighting ability or dominance.

The potential signal function of the large white areas on the frill is less clear. The size and colorimetrics of the white patches did not correlate with any aspect of male morphology or fighting ability. However, the adjacent location of the red-orange and white frill patches (see Figure 1) may serve to maximize the conspicuousness of the color signal (Charles and Ord 2012) and thereby act as an “amplifier” (Castellano and Cermelli 2010). This certainly appears to be the case in frillneck lizards, where the frill's red-orange coloration becomes markedly more conspicuous when viewed against a background of white, which has uniformly high reflectance (Figure 2). Furthermore, the red-orange is also conspicuous against adjacent brown patches on the frill because brown has low overall reflectance, whereas the red-orange has a steeper slope and a clear peak. When adjacent colors have high and low chromaticity or they do not share wavelengths in common (complimentary colors), they are more conspicuous (Endler 1993).

This study adds to growing evidence that variation in carotenoid-based coloration may play a key role in resolving conflicts in animals (e.g., Evans and Norris 1996; Crowley and Magrath 2004; Hill and Barton 2005; Pryke 2009; Griggio et al. 2010). Furthermore, red coloration (irrespective of its production) has often been associated with aggression and dominance in a wide range of taxa, including fish (Dijkstra et al. 2005; Guderley and Couture 2005), reptiles (Sinervo et al. 2000; Healey et al. 2007; Huyghe et al. 2007; Baird

et al. 2013), birds (Pryke et al. 2002; Crowley and Magrath 2004; Pryke and Griffith 2006, 2009), humans (Hill and Barton 2005; Little and Hill 2007), and other primates (Setchell and Wickings 2005). Indeed, recent studies suggest that the color red is inherently (genetically determined) intimidating to rivals (Healey et al. 2007; Pryke 2009) and thus may be a general signal of intimidation. In frillneck lizards, the avoidance of opponents with redder frills suggests that the variable carotenoid-based coloration displayed by males functions as a status signal. Although color variation has frequently been shown to correlate with ecological variables in agamids (LeBas and Marshall 2000; Stuart-Fox et al. 2004; Chen et al. 2012), few studies have conclusively demonstrated a status signaling function (e.g., Cuervo and Shine 2007). Frillneck lizards are also well known for extending their frills to startle or intimidate predators and both males and females have frills. This suggests that in males, frills may have a dual function as an antipredator signal and a sexual signal used during male contest competition. In addition, they may also function as an ornament for female choice, although to the best of our knowledge this has never been tested. Given the considerable geographic variation in frill color and the multiple roles frills may play in signaling to conspecifics and predators, further studies investigating both behavioral (e.g., female mate choice) and ecological (e.g., predation) pressures on different populations will help illuminate the relative roles of sexual and natural selection on frill color expression in one of Australia's most enigmatic lizards.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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REFERENCES

- Alonso-Alvarez C, Pérez-Rodríguez L, Ferrero ME, García de-Blas E, Casas F, Mougeot F. 2012. Adjustment of female reproductive investment according to male carotenoid-based ornamentation in a gallinaceous bird. *Behav Ecol Sociobiol.* 66:731–742.
- Anderson RA, McBrayer LD, Herrel A. 2008. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biol J Linn Soc.* 93:709–720.
- Andersson M. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Badyaev AV, Hill GE. 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based plumage coloration. *Biol J Linn Soc.* 69:153–172.
- Baird TA, Baird TD, Shine R. Forthcoming 2013. Showing red: male dimorphic coloration signals aggressive intent in water dragons. *Herpetologica*.
- Barbour HR, Archer MA, Hart NS, Thomas N, Dunlop SA, Beazley LD, Shand J. 2002. Retinal characteristics of the ornate dragon lizard (*Ctenophorus ornatus*). *J Comp Neurol.* 450:334–344.
- Blount JD. 2004. Carotenoids and life-history evolution in animals. *Arch Biochem Biophys.* 430:10–15.
- Bradley RA, Terry ME. 1952. Rank analysis of incomplete block designs I: the method of paired comparisons. *Biometrika.* 39:324–345.
- Brush AH. 1990. Metabolism of carotenoid pigments in birds. *FASEB J.* 4:2969–2977.
- Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations and comparisons. *Behav Ecol Sociobiol.* 65:23–25.
- Carpenter CC, Badham JA, Kimble B. 1970. Behavior patterns of three species of *Amphibolurus* (Agamidae). *Copeia.* 3:497–505.
- Castellano S, Cermelli P. 2010. Attractive amplifiers in sexual selection: where efficacy meets honesty. *Evol Ecol.* 24:1187–1197.
- Chan R, Stuart-Fox D, Jessop TS. 2009. Why are females ornamented? A test of the courtship stimulation and courtship rejection hypotheses. *Behav Ecol.* 20:1334–1342.
- Charles GK, Ord TJ. 2012. Factors leading to the evolution and maintenance of a male ornament in territorial species. *Behav Ecol Sociobiol.* 66:231–239.
- Chen IP, Stuart-Fox D, Hugall AF, Symonds MRE. 2012. Sexual selection and the evolution of complex color patterns in dragon lizards. *Evolution.* 66:3605–3614.
- Christian KA, Bedford GS. 1995. Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. *Ecology.* 76:124–132.
- Christian KA, Bedford GS, Griffiths AD. 1995. Frillneck lizard morphology: comparison between sexes and sites. *J Herpetol.* 29:576–583.
- Clutton-Brock TH, Albon SD. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour.* 69:145–170.
- Cogger HG. 2000. *Reptiles and amphibians of Australia*. Sydney (Australia): Reed New Holland.
- Cote J, Meylan S, Clobert J, Voituren Y. 2010. Carotenoid-based coloration, oxidative stress and corticosterone in common lizards. *J Exp Biol.* 213:2116–2124.
- Crowley CE, Magrath RD. 2004. Shields of offence: signalling competitive ability in the dusky moorhen, *Gallinula tenebrosa*. *Aust J Zool.* 52:463–474.
- Cuervo JJ, Shine R. 2007. Hues of a dragon's belly: morphological correlates of ventral coloration in water dragons. *J Zool.* 273:298–304.
- Dijkstra PD, Seehausen O, Fraterman RE, Groothuis TGG. 2008. Learned aggression biases in males of Lake Victoria cichlid fish. *Anim Behav.* 76:649–655.
- Dijkstra PD, Seehausen O, Groothuis TGG. 2005. Direct male-male competition can facilitate invasion of new colour types in Lake Victoria cichlids. *Behav Ecol Sociobiol.* 58:136–143.
- Dufva R, Allander K. 1995. Intraspecific variation in plumage colouration reflects immune response in great tit (*Parus major*) males. *Funct Ecol.* 9:785–789.
- Endler JA. 1993. Some general comments on the evolution and design of animal communication systems. *Philos Trans R Soc Lond B Biol Sci.* 340:215–225.
- Endler JA, Mielke PW. 2005. Comparing entire colour patterns as birds see them. *Biol J Linn Soc.* 86:405–431.
- Evans MR, Norris K. 1996. The importance of carotenoids in signaling during aggressive interactions between male firemouth cichlids (*Cichlasoma meeki*). *Behav Ecol.* 7:1–6.
- Firth D. 2005. Bradley-Terry models in R. *J Stat Soft.* 12:1–12.
- Fitze PS, Cote J, San-Jose LM, Metlan S, Isaksson C, Andersson S, Rossi JM, Clobert J. 2009. Carotenoid-based colours reflect the stress response in the common lizard. *PLoS ONE.* 4:e5111.
- Fleishman IJ, Leal M, Persons MH. 2009. Habitat light and dewlap color diversity in four species of Puerto Rican anoline lizards. *J Comp Physiol A.* 195:1043–1060.
- Goodwin TW. 1984. *The biochemistry of the carotenoids*. New York (NY): Chapman and Hall.
- Griffiths AD. 1999. Demography and home range of the frillneck lizard, *Chlamydosaurus kingii* (Agamidae), in Northern Australia. *Copeia.* 4:1089–1096.
- Griffiths AD, Christian KA. 1996. Diet and habitat use of frillneck lizards in a seasonal tropical environment. *Oecologia.* 106:39–48.
- Griggio M, Serra L, Licheri D, Monti A, Pilastro A. 2007. Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behav Ecol Sociobiol.* 61:423–433.
- Griggio M, Zanollo V, Hoi H. 2010. Female ornamentation, parental quality and competitive ability in the rock sparrow. *J Ethol.* 28:455–462.

- Guderley H, Couture P. 2005. Stickleback fights: why do winners win? Influence of metabolic and morphometric parameters. *Physiol Biochem Zool.* 78:173–181.
- Harlow PS, Shine R. 1999. Temperature-dependent sex determination in the frillneck lizard, *Chlamydosaurus kingii* (Agamidae). *Herpetologica.* 55:205–212.
- 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.
- Hibbitts TJ, Whiting MJ, Stuart-Fox DM. 2007. Shouting the odds: vocalization signals status in a lizard. *Behav Ecol Sociobiol.* 61:1169–1176.
- Hill GE. 2002. A red bird in a brown bag: the function and evolution of colourful plumage in the house finch. New York (NY): Oxford University Press.
- Hill GE, McGraw KJ. 2006. Bird coloration: mechanisms and measurements. Vol. I. London: Harvard University Press.
- Hill J. 2000. Energetic constraints on expression of carotenoid-based plumage coloration. *J Avian Biol.* 31:559–566.
- Hill RA, Barton RA. 2005. Red enhances human performance in contests. *Nature.* 435:293.
- Hofmann CM, Cronin TW, Omland KE. 2008. Evolution of sexual dichromatism. 2. Carotenoids and melanins contribute to sexual dichromatism in New World orioles. *Auk.* 125:790–795.
- 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 Biol.* 47:211–220.
- Jessop TS, Chan R, Stuart-Fox D. 2009. Sex steroid correlates of female-specific coloration, behaviour and reproductive state in Lake Eyre dragon lizards, *Ctenophorus maculosus*. *J Comp Physiol A.* 195:619–630.
- Johnstone RA. 1996. Multiple displays in animal communication: 'Backup Signals' and 'Multiple Messages'. *Philos Trans R Soc Lond B Biol Sci.* 351:329–338.
- Kikuchi DW, Pfennig DW. 2012. A Batesian mimic and its model share color production mechanisms. *Curr Zool.* 58:658–667.
- LeBas NR, Marshall NJ. 2000. The role of colour in signalling and mate choice in the agamid lizard *Ctenophorus ornatus*. *Proc R Soc Lond B Biol Sci.* 267:445–452.
- Little AC, Hill RA. 2007. Attribution to red suggests special role in dominance signalling. *J Cult Evol Psychol.* 5:87–94.
- Loew ER, Fleishman LJ, Foster RG, Provencio I. 2002. Visual pigments and oil droplets in diurnal lizards: a comparative study of Caribbean anoles. *J Exp Biol.* 205:927–938.
- López P, Martín J. 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards. *Behav Ecol Sociobiol.* 49:111–116.
- López P, Martín J, Cuadrado M. 2004. The role of lateral blue spots in intrasexual relationships between male Iberian rock-lizards, *Lacerta monticola*. *Ethology.* 110:543–561.
- Lozano GA. 1994. Carotenoids, parasites and sexual selection. *Oikos.* 70:309–311.
- Macedonia JM, Brandt Y, Clark DL. 2002. Sexual dichromatism and differential conspicuousness in two populations of the common collared lizard (*Crotaphytus collaris*) from Utah and New Mexico, USA. *Biol J Linnean Soc.* 77:67–85.
- Macedonia JM, James S, Wittle LW, Clark DL. 2000. Skin pigments and coloration in the Jamaican radiation of *Anolis* lizards. *J Herpetol.* 34:99–109.
- Matéos C, Carranza J. 1997. The role of bright plumage in male-male interactions in the ring-necked pheasant. *Anim Behav.* 54:1205–1214.
- McGraw KJ, Ardia DR. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *Am Nat.* 162:704–712.
- McGraw KJ, Hudon J, Hill GE, Parker RS. 2005. A simple and inexpensive chemical test for behavioral ecologists to determine the presence of carotenoid pigments in animal tissues. *Behav Ecol Sociobiol.* 57:391–397.
- McGraw KJ, Medina-Jerez W, Adams H. 2006. Carotenoid-based plumage coloration and aggression during molt in male house finches. *Behaviour.* 144:165–178.
- Moller AP, Biard C, Blount JD, Houston DC, Nimni P, Saino N, Surai PF. 2000. Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? *Poult Avian Biol Rev.* 11:137–159.
- Morrell LJ, Backwell PRY, Metcalfe NB. 2005. Fighting in fiddler crabs *Uca mjobergi*: what determines duration? *Anim Behav.* 70:653–662.
- Mougeot F, Pérez-Rodríguez L, Martínez-Padilla J, Leckie F, Redpath SM. 2007. Parasites, testosterone and honest carotenoid-based signalling of health. *Funct Ecol.* 21:886–898.
- Nicholson KE, Harmon LJ, Losos JB. 2007. Evolution of *Anolis* lizard dewlap diversity. *PLoS ONE.* 3:1–12.
- Olson VA, Owens IPF. 1998. Costly sexual signals: are carotenoids rare, risky or required? *Trends Evol Ecol.* 13:510–514.
- Olsson M, Madsen T, Wapstra E, Silverin B, Ujvari B, Wittzell H. 2005. MHC, health, color, and reproductive success in sand lizards. *Behav Ecol Sociobiol.* 58:289–294.
- Olsson M, Wilson M, Isaksson C, Uller T, Mott B. 2008. Carotenoid intake does not mediate a relationship between reactive oxygen species and bright coloration: experimental test in a lizard. *J Exp Biol.* 211:1257–1261.
- Osborne L. 2005. Rival recognition in the territorial tawny dragon (*Ctenophorus decresii*). *Acta Ethol.* 8:45–50.
- Osorio D, Vorobyev M. 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc R Soc Lond B Biol Sci.* 272:1745–1752.
- Osorio D, Vorobyev M. 2008. A review of the evolution of animal colour vision and visual communication signals. *Vis Res.* 48:2042–2051.
- Pryke SR. 2009. Is red an innate or learned signal of aggression and intimidation? *Anim Behav.* 78:393–398.
- Pryke SR, Andersson S. 2003. Carotenoid-based epaulettes reveal male competitive ability: experiments with resident and floater red-shouldered widowbirds. *Anim Behav.* 66:217–224.
- Pryke SR, Andersson S, Lawes MJ, Piper SE. 2002. Carotenoid status signalling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behav Ecol.* 13:622–631.
- Pryke SR, Griffith SC. 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc R Soc Lond B Biol Sci.* 273:949–957.
- Pryke SR, Griffith SC. 2007. The relative role of male vs. female mate choice in maintaining assortative pairing among discrete colour morphs. *J Evol Biol.* 20:1512–1521.
- Pryke SR, Griffith SC. 2009. Socially mediated trade-offs between aggression and parental effort in competing color morphs. *Am Nat.* 174:455–464.
- Qi Y, Wan H, Gu H, Wang Y. 2011. Do displays and badges function in establishing the social structure of male toad-headed lizards, *Phrynocephalus vlangalii*. *J Ethol.* 29:381–387.
- R Development Core Team. 2005. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Senar JC, Negro JJ, Quesada J, Ruiz I, Garrido J. 2008. Two pieces of information in a single trait? The yellow breast of the great tit (*Parus major*) reflects both pigment acquisition and body condition. *Behaviour.* 145:1195–1210.
- Setchell JM, Wickings EJ. 2005. Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology.* 111:25–50.
- Shine R. 1990. Function and evolution of the frill of the frillneck lizard, *Chlamydosaurus kingii* (Sauria: Agamidae). *Biol J Linnean Soc.* 40:11–20.
- Shine R, Lambeck R. 1989. Ecology of frillneck lizards, *Chlamydosaurus kingii* (Agamidae), in tropical Australia. *Aust Wildl Res.* 16:491–500.
- Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol.* 207:2471–2485.
- Sinervo B, Miles DB, Frankino WA, Klukowski M, DeNardo DF. 2000. 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.
- Stapley J, Whiting MJ. 2006. Ultraviolet signals fighting ability in a lizard. *Biol Lett.* 2:169–172.
- Steffen JE, Hill GE, Guyer C. 2010. Carotenoid access, nutritional stress, and the dewlap color of male brown anoles. *Copeia.* 2010:239–246.
- Steffen JE, McGraw KJ. 2007. Contributions of pterin and carotenoid pigments to dewlap coloration in two anole species. *Comp Biochem Physiol B.* 146:42–46.
- Stuart-Fox D, Moussalli A, Whiting MJ. 2007. Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *Am Nat.* 170:916–930.
- Stuart-Fox DM, Firth D, Moussalli A, Whiting MJ. 2006. Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. *Anim Behav.* 71:1263–1271.

- Stuart-Fox DM, Johnston GR. 2005. Experience overrides colour in lizard contests. *Behaviour*. 142:329–350.
- Stuart-Fox DM, Moussalli A, Johnston GR, Owens IPF. 2004. Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. *Evolution*. 58:1549–1559.
- Stuart-Fox DM, Moussalli A, Marshall NJ, Owens IPF. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Anim Behav*. 66:541–550.
- Stuart-Fox DM, Ord TJ. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proc R Soc Lond B Biol Sci*. 271:2249–2255.
- Svensson PA, Wong BBM. 2011. Carotenoid-based signals in behavioural ecology: a review. *Behaviour*. 148:131–189.
- Thompson CW, Moore MC. 1991. Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. *Anim Behav*. 42:745–753.
- Vanhooydonck B, Cruz FB, Abdala CS, Moreno Azócar DL, Bonino MF, Herrel A. 2010. Sex-specific evolution of bite performance in *Liolaemus* lizards (Iguania: Liolaemidae): the battle of the sexes. *Biol J Linn Soc*. 101:461–475.
- Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. *Proc R Soc Lond B Biol Sci*. 265:351–358.
- Webster MS, Varian CW, Karubian J. 2008. Plumage color and reproduction in the red-backed fairy-wren: why be a dull breeder? *Behav Ecol*. 19:517–524.
- Weiss SL, Foerster K, Hudon J. 2012. Pteridine, not carotenoid, pigments underlie the female-specific orange ornament of striped plateau lizards (*Sceloporus virgatus*). *Biochem Mol Biol Int*. 161:117–123.
- Whiting MJ. 1999. When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. *Behav Ecol Sociobiol*. 46:210–214.
- Whiting MJ, Nagy KA, Bateman PW. 2003. Evolution and maintenance of social status signalling badges: experimental manipulations in lizards. In: Fox SF, McCoy JA, Baird TA, editors. *Lizard social behavior*. Baltimore (MD): Johns Hopkins University Press. p. 47–82.
- Whiting MJ, Stuart-Fox D, O'Connor D, Firth D, Bennett NC, Blomberg SP. 2006. Ultraviolet signals ultra-aggression in a lizard. *Anim Behav*. 72:353–363.
- Wilson S, Swan G. 2010. *A complete guide to reptiles of Australia*. Sydney: New Holland Publishing.