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SHOWING RED: MALE COLORATION SIGNALS SAME-SEX RIVALS IN AN AUSTRALIAN WATER DRAGON

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ABSTRACT: Sexually dimorphic coloration that plays a role in social signaling during stereotypical displays is well known in lizards. Previous studies on a large Australian agamid lizard (Eastern Water Dragon, *Intellagama lesueurii*) documented male-biased sex differences in ventral coloration, but males were not observed to use postures that displayed their ventral surfaces. Male resource-holding potential (RHP) was determined by body size, with the largest individuals controlling territories in preferred riparian habitat. Both large males that defended territories and those that did not had fully developed ventral coloration. Together these observations suggested that male ventral coloration does not play a role in social communication in male Water Dragons. We tested this hypothesis by recording the behavior of free-ranging males during baseline social conditions and when the level of aggression was much higher because we temporarily removed and then reinstated territory owners. Male Water Dragons performed three behavior patterns that displayed their conspicuous ventral coloration when engaged in agonistic encounters with same-sex rivals, especially when social conditions among neighboring males were unstable. Rival males responded to these displays in all instances. A large, model Water Dragon male in which we manipulated ventral color elicited lower-intensity responses from rival males when the model ventral surface was red than when it was brown. This result is also consistent with the hypothesis that red coloration plays a role in signaling and perhaps in intimidation of rivals. Water Dragon displays that revealed ventral coloration were not given when males interacted with females, suggesting red coloration does not function in advertisement to potential female mates. Our results support the hypothesis that red ventral coloration in Eastern Water Dragons functions in advertisement to rival males similar to the function of red coloration in several other vertebrates.

Key words: Agamidae; Aggression; Communication; Sexual selection, Signaling

VERTEBRATES in many taxa develop conspicuous coloration that is widely hypothesized to function in intraspecific social communication (Andersson, 1994; Whiting et al., 2003), including sex recognition and advertisement to potential mates or signaling same-sex conspecifics (or both; e.g., Vitt and Cooper, 1985; Cooper and Greenberg, 1992; Anderson and Iwasa, 1996). Although females sometimes develop unique coloration that is associated with their reproductive cycles (e.g., Dixon, 1983; Rowland et al., 1991; Hager, 2001; Baird, 2004), conspicuous sex-specific coloration is most widespread in vertebrate males. Conspicuous male coloration, especially red-orange hues, has been associated with social dominance and intimidation of rivals (reviewed by Pryke, 2009) in fishes (Dijkstra et al. 2005; Guderley and Couture, 2005), birds (Crowley and Magrath, 2004; Pryke and Griffith, 2006), primates (Setchell and Wickings, 2005), and lizards

(Sinervo et al., 2000; Healey et al., 2007; Huyghe et al., 2007; Hamilton et al., 2013). Advertisement to mates is another potential function of conspicuous male coloration, and females of several species have been documented to show preferences for brightly colored males (Hill, 1990; Houde and Endler, 1990; Saetre et al., 1994; Sundberg, 1995; Houde, 1997), including some lizards (Baird et al., 1997; Kwiatkowski and Sullivan, 2002).

The signaling function of sexually dimorphic coloration is obvious if conspicuous markings are restricted to parts of the body that are only visible during certain times such as during contests with rival males or when males court females. The function of color patches on body regions that are normally hidden are more difficult to determine, especially in the absence of detailed observations on social behavior. It is possible that some such coloration patterns may function for purposes other than social signaling (Marshall, 2010) whereas in other cases animals may use stereotypical displays to reveal these colorful patches only when social situations demand it

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(Echelle et al., 1971). For example, some lizards have sexually dimorphic coloration on the ventral surface that is visible to conspecifics only when they use display postures that elevate the torso (e.g., Cooper and Burns, 1987; Quinn and Hews, 2000; Hews and Quinn, 2003; Whiting et al., 2003).

In Australian Eastern Water Dragons (Agamidae: *Intellagama lesueurii*; formerly *Physignathus*), the abdomens and chests of large males are completely covered with orange-red to reddish-black coloration that is absent in females (Thompson, 1993; Cuervo and Shine, 2007). Because the colorful ventral patch of males was not visible to conspecifics unless the torso was elevated to reveal it, and no such displays were reported in previous studies (Cuervo and Shine, 2007), the possible signaling function of dimorphic coloration in this species merits further investigation using quantitative observations of individual males, especially under conditions that are socially challenging.

We tested the null hypothesis that male-biased ventral coloration in Eastern Water Dragons does not function in intraspecific social communication by recording focal observations of the behavior of males in the field during stable (unmanipulated) social conditions and during unstable social conditions that we prompted by using temporary removal and reinstatement of territorial males (Baird et al., 2012). Because our results revealed three male displays that revealed red coloration, we describe these displays, determined the frequency with which they were given during periods when the social relationships among males were stable versus unstable, and quantified the responses of recipient males. The resultant data allowed us to clarify whether males display their ventral coloration during displays given to rivals, females, or both. We further explored male responses to ventral coloration by using a model lizard that was larger than resident males and painted with either exaggerated red or brown ventral coloration. Because large body size is an important determinant of resource holding power in many lizards (e.g., Stamps and Krishan 1994; Baird et al., 1997; Lopez and Martin 2001; Radder et al., 2001; Aragón et al., 2004), including Eastern Water

Dragons (Baird et al., 2012), and because red color signals aggression and dominant status in many vertebrates including lizards (reviewed by Pryke, 2009), we expected that enhanced red ventral coloration on our large, high resource-holding potential (RHP) model would intimidate and inhibit the agonistic responses of resident males to the model.

MATERIALS AND METHODS

Study Population

Intellagama lesueurii is a large (up to 1 kg), semi-aquatic, diurnal agamid lizard that occurs in riparian areas throughout Eastern New South Wales and Southern Queensland (Cogger, 1986). We conducted this study on the grounds of the Flynn's Beach Resort in Port Macquarie, NSW, 31°26'S latitude, 152°55'E longitude from 12 September–30 November, 2009, which is the Austral spring when Eastern Water Dragons are reproductively active (Thompson 1993; Harlow, 2001; Cuervo and Shine, 2007). Water Dragons occurred throughout the resort grounds (8980 m²) in naturally vegetated riparian habitat as well as in highly modified areas such as lawns, plant beds, sidewalks, and swimming pool decks. Lizards here were habituated enough to humans that they tolerated approach to within 2 m but retreated when approached more closely (Baird et al., 2012). We captured lizards ($n = 111$) by noose from 15 September–15 October, 2009. At initial capture we measured snout–vent length (SVL) to the nearest millimeter, using a ruler, and total body mass ± 5 g using a spring scale. Males were marked for identification by painting numbers on each side of the upper torso using waterproof white nail polish. Numbers were retouched when necessary, but none of the marked lizards lost their numbers as a consequence of molting.

This population contained 30 large males (SVL = 238–271 mm) that all possessed well-developed coloration that covered the entire ventral surface and extended partially onto the ventrolateral torso and were all sexually mature as indicated by secretion of seminal fluid from everted hemipenes. Smaller males had small (< 1 cm across) patches of light orange scattered on the abdomen (TAB,

personal observation) and the hemipenes either could not be everted or were not secretory. Large size determined RHP in this population (Baird et al., 2012). Fourteen large males defended territories in the limited riparian habitat using high rates of patrol and head display and by aggressively chasing away same-sex intruders. By contrast, 16 mature males remained in this preferred habitat by exhibiting markedly lower rates of patrol and display and usually fleeing territorial males. Territorial males also interacted with females more frequently than did non-territorial males. The plastic nature of these two social tactics was confirmed by non-territorial males adopting territorial tactics in response to experimental removal of territorial males and, in two cases, by spontaneously evicting territorial males and taking over their territories (Baird et al., 2012).

Male Social Behavior

One of us (TAB) recorded the behavior of males during focal observations (*sensu* Altmann, 1974) under stable social conditions and during socially unstable conditions prompted by experimental removal and reinstatement of individual territorial males (described below). Focal observations involved recording all of the displays, aggressive encounters with other males, and courtship interactions with females that were initiated by subject males (Baird, 2013). Focal observations were recorded from 0900 to 1500 h when water dragons show peak activity. Observation sessions lasted 20 min except for a few (< 5%) that were terminated sooner because focal lizards were lost from view. Although lizards at this site were not overtly affected by human presence, we recorded focal observations when human disturbance was minimal. During stable social conditions, we recorded a minimum of five observation sessions per male on different days for an average of 204 (± 17.7 min) observation min/male.

Temporary removal of territory owners can elicit intense aggressive interactions among nearby competitors in lizards, including Water Dragons (Baird and Timanus, 1998; Baird and Curtis, 2010; Baird et al., 2012), and might reveal behavior patterns that involve display of

ventral coloration for social signaling. We performed 11 trials where we removed a different territorial male at 1400 to 1600 h and kept him off-site for 2 d. Removed males were maintained in damp, low-light conditions to mimic cool, rainy conditions when Water Dragons are inactive. From 0900 to 1500 h during the 2-d removal, we recorded at least three, 20-min focal observations per male on the mature nonterritorial males that competed for the territory of the removed male. After nightfall on the second removal day (2000 to 2100 h), we reinstated the removed male to his original territory. On the following day from 0900 to 1500 h, we recorded at least three 20-min focal observations on the same males as during the removal as well as on the reinstated territorial male.

Altogether, we documented behavior in 18 males during stable baseline conditions versus unstable social conditions. The sample during stable conditions included 11 territorial males prior to their removal and seven nonterritorial males during the same period. The sample during unstable social conditions included these same territorial males when they were reinstated following their removal and the seven nonterritorial males that had changed social tactics to establish temporary occupancy of territories when the original owners were removed. Because these data deviated substantially from normality, despite transformation, we used paired Sign-Tests to compare the frequencies of male behavior patterns during stable (prior to removals) with unstable social conditions (during removals and when territory owners were reinstated).

Model-Introduction Experiments

We conducted experiments where we manipulated the coloration of a model Water Dragon that we introduced to territorial ($n = 14$) and nonterritorial ($n = 10$) males to further test the hypothesis that red coloration functions to signal male rivals. The model was a replica of a male Green Iguana (*Iguana iguana*), which is similar in general shape to male *I. lesueurii*. The model was posed with its head elevated and its dewlap extended, its torso flexed slightly to one side, and its tail curled next to that side of the body. In this posture, the ventrolateral torso that is colored

red in male Water Dragons was visible from the side to which the model was flexed. We used water-based artist acrylic colors to paint the model to mimic males at our site using a brown background and black vertical bars on the head, torso, and tail. We fashioned paper dorsal crests to mimic these structures, which are longer in males (comparison of the longest three crests by sex; $t'_{s_{1,96}} = 3.80\text{--}4.47$, $P_s < 0.001$) and glued them to the dorsal surface of the neck and head. The model was 315 SVL, which is 40–74 mm longer than the male subjects to which it was introduced and 81 mm longer than the largest female on the site. Because we only had one model, it was necessary to recolor it to randomize presentation of color treatments. For the red experimental treatment, we used a red felt-tip (Sharpie®) marker to color the ventral side of the torso and chest. We measured the percent reflectance of this red coloration using a JAZ-PX spectrophotometer (Oceanoptics Inc.) for comparison with measurements of abdominal coloration in living male Water Dragons (Cuervo and Shine, 2007). Percent reflectance of the red-painted abdomen of our model was 31–37.7 in the 590–700 nm range, for which living lizards showed lower reflectance (11–18%; Cuervo and Shine, 2007). Therefore, our model was a supernormal social stimulus because it was both larger and more colorful on the abdomen than natural same-sex competitors. Even though the brown model lacked red ventral coloration, it is unlikely that subject males confused it with a female because the model was much larger than females, it had the long dorsal crests characteristic of males, and the model's head was also relatively large, as it is in Water Dragon males (Cuervo and Shine, 2007). It is also unlikely that test males confused the larger model with a predator. Water Dragons fled into the creek whenever they encountered Lace Monitors (*Varanus varius*), suggesting that these large lizards are predators. Lace Monitors lack red color, and Water Dragons never fled the model painted either color.

One of us (TAB) introduced the same model in both color treatments flexed toward test subjects. We conducted a pair of trials (brown versus red model) on each male.

Paired trials on individual males were conducted no fewer than 5 d apart and in a balanced, random color order. The model was placed on the ground 2.0–2.5 m from the subject male with an unobstructed line of sight. The observer then withdrew 6–8 m to the side so as not to be in the test lizard's visual field as he viewed the model. For territorial males, the model was introduced within the boundaries defended by each territory owner. Because nonterritorial males ranged more widely (Baird et al., 2012), we introduced the model wherever we encountered them. We recorded for 10 min any movements on a direct path to within one body length of the model (approaches), displays involving movements of the head, displays that revealed ventral coloration (both described below), and vertical or lateral movements of the tail that function as social signals in some agamid lizards (e.g., Ord and Evans, 2003; Peters and Ord, 2003). Our paired experiments compared responses by subject males to the same model, positioned the same way but just painted differently. This design controls for other variables that might explain different responses to introduction of the model painted brown or red. For statistical analysis of responses by resident males to model introductions, we used repeated-measures analysis of variance (ANOVA) to compare (separate analyses) latency to first response (seconds from placement of the model on the substrate in view of the test male to first response by the test male) and the total number of acts (all displays and approaches to the model pooled) with model color (brown versus red) and resident male social status (territorial versus nonterritorial) as independent factors. We \log_{10} transformed these two dependent variables to meet the assumptions of parametric ANOVA.

RESULTS

Male Social Behavior

Although the most-frequent displays given by Water Dragon males involved only head movements that did not reveal the red ventral coloration, males also exhibited three behavior patterns that revealed their coloration, especially under unstable social conditions when



FIG. 1.—Male Water Dragon performing a full show display which reveals red coloration in the ventrolateral torso region.

aggression was most frequent (Baird et al., 2012). Stationary males performed “full shows” characterized by tilting the snout upward at a 25° angle while holding the mouth open partially, extending the dewlap, slowly elevating on all four legs, and compressing the torso laterally such that coloration on the ventral lateral torso was highly visible (Fig. 1). Ventrolateral coloration was then obscured when males lowered to the substrate. Males sometimes performed only one full show, which they held for a few seconds before lowering, but at other times they elevated and lowered as many as four times in succession. Full shows were occasionally (2 of 38) performed when males were distant (= 5 m) from same-sex rivals, but most (36 of 38, 94.7%) were given when males contested rivals at close (= 1 m) range. Males sometimes confronted rivals by raising the anterior torso and charging their opponent, running on only their hind legs (bipedal charge). As contests continued at close (= 1 m) range, males elevated and compressed the torso laterally, similar to full shows, but while running sideways towards their opponent using a slow, stiff-legged gait (display runs). Even though the mean frequency (acts/min) with which males initiated full shows during unstable conditions was nearly three times higher than that during stable conditions, this difference was not statistically significant (Paired Sign test: $P = 0.289$) as a consequence of high variability (Fig. 2). The frequencies of both display runs ($P = 0.039$) and bipedal charges ($P = 0.016$) were higher during unstable social conditions (Fig. 2).

We recorded 105 total contests between males, defined as the focal male closing to

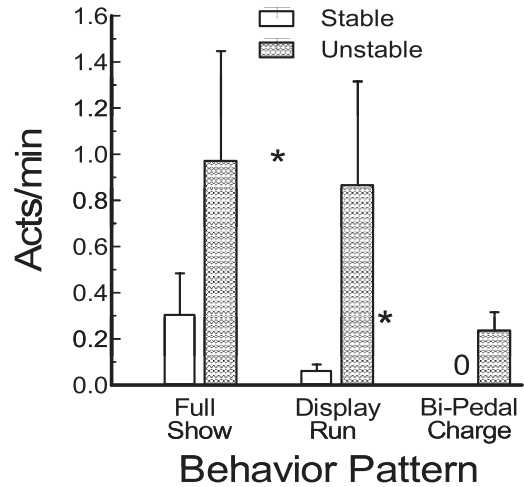


FIG. 2.—Frequency of behavior patterns that revealed ventral coloration in male Water Dragons under stable (open bars) and unstable (hatched bars) social conditions. Data are means ± 1.0 SE. Asterisks indicate significantly higher frequencies ($P < 0.01$) of display runs and bipedal charges during unstable social conditions.

within 1 m of a rival while initiating aggressive behavior, to which the opponent responded by either fleeing or standing his ground and fighting back. Sixty-six contests (62.9%) began without behavior that revealed ventral coloration when focal males approached a rival deliberately, pausing to give head displays ($n = 30$ contests), or charged the rival ($n = 36$), fast running quadrupedally. Opponent males fled in the majority of contests (54, 81.8%) initiated without the display of red whereas they fought back during only 12 (18.2%; Fisher's Exact Test, $\chi^2 = 10.99$, $P = 0.0009$). Focal males began 39 contests (37.1%) by giving one or more displays that revealed red coloration ($n = 6$ bipedal charges, $n = 12$ display runs, $n = 21$ full shows). Opponent males responded in all of these contests. Responses by rivals depended on their social status. Nonterritorial males fled whereas established territorial males or males that were fighting to establish occupancy in response to removal fought back. Recipients fled in 20 (51.3%) contests begun with displays that revealed ventral coloration whereas they fought back in 19 (48.7%) of these contests.

Although we also recorded over 100 encounters where males approached a female

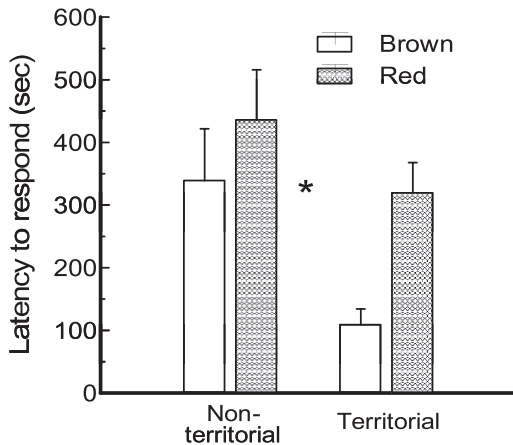


FIG. 3.—Latency (seconds) to first response to an introduced brown- (open bars) or red-painted (hatched bars) male Water Dragon model. Data are means ± 1.0 SE. Asterisk indicates a significant ($P < 0.01$) interaction between male social status and model color.

within one-half a body length (sometimes contacting her), males did not direct full shows, display runs, bipedal chases, or any other behavior that revealed red ventral coloration to females.

Model-Introduction Experiments

Male Water Dragons responded in 21 of 24 (87.5%) introductions of brown models compared with 16 of 24 (66.7%) introductions of red-painted models (Fisher's Exact Test, $\chi^2 = 2.95$, $P = 0.086$). For all trials in which test males did not respond, they maintained their positions instead of moving away from the model. Most (93.7%) of the responses to both brown and red models, pooled, involved head displays whereas 6.3% of response behaviors were approaches and lateral-vertical tail movements (5.2% and 1.3% respectively). Introduction of brown models elicited six display runs (3 trials), one full show, and in one trial the resident male charged and struck the brown model.

For latency to first response, there was a statistically significant interaction (repeated-measures ANOVA: $F_{1,22} = 5.89$, $P = 0.024$) between male social status and model color. Both categories of males took longer ($F_{1,22} = 23.75$, $P < 0.0001$) to respond to the red model, and the influence of male social status approached statistical significance ($F_{1,22} = 3.2$,

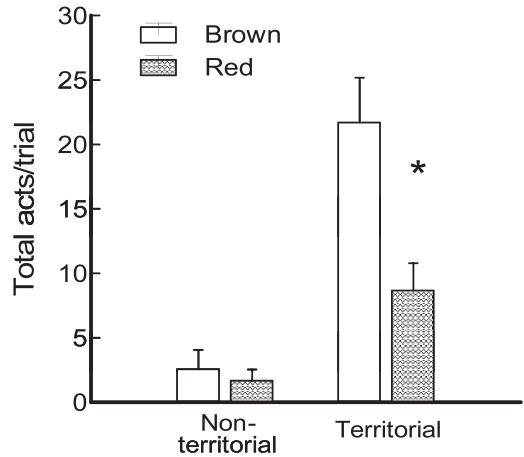


FIG. 4.—Total responses (all displays + approaches per 10 min trial) to an introduced brown- (open bars) and red-painted (hatched bars) male Water Dragon model. Data are means ± 1.0 SE. Asterisk indicates differences between responses to different colored models in territorial males.

$P = 0.087$; Fig. 3). Both male social status ($F_{1,22} = 4.57$, $P = 0.044$) and model color ($F_{1,22} = 44.38$, $P < 0.001$) influenced the total number of acts given per trial, with territorial males responding more to brown-painted models (Fig. 4). The interaction between male social status and model color only approached statistical significance ($F_{1,22} = 3.49$, $P = 0.075$).

DISCUSSION

Although the most-frequent displays given by Water Dragon males are stereotypical movements of the head and the dewlap (head raises, head bobs, dewlap extension), which do not reveal the red venter (Thompson, 1993; Cuervo and Shine, 2007; Baird et al., 2012), our present study clearly shows that communication among males also involves postural displays that reveal this coloration. Focal observations, particularly those recorded when social relationships among neighboring males were unstable, revealed three behavior patterns that males used to display red ventral coloration. Males did not direct these behavior patterns toward females even though intersexual interactions were common (Baird et al., 2012). Decreased responses by males to a large model displaying exaggerated red coloration, relative to the same model when

painted brown, further supports the hypothesis that display of red ventral coloration functions to signal rivals. One likely explanation of reduced responsiveness to the red model is that engagement with a larger intruder giving an aggressive signal (Baird et al., 2012) would carry high costs (Marler and Moore, 1988; Marler et al., 1995).

The judicious use of display patterns that revealed ventral coloration, together with more-frequent head displays that did not, suggests that selection has favored variable signals in male Water Dragons that convey graded aggressive content. Such graded signals have been documented in several other lizards that, similar to Water Dragons (Baird et al., 2012), sometimes engage in intense physical combat (Earley et al., 2002; Jenssen et al., 2005; Stuart-Fox et al., 2006). In Water Dragons, full shows and display runs (Baird et al., 2012) were always preceded by less-intense elevation of the head and extension of the dewlap, and the frequency that the colorful ventral surface was revealed increased only when aggressive contests escalated. Reliance on head displays when social conditions were stable strongly suggests that head posturing is preferred when only lower-intensity advertisement of territory ownership is necessary. When males were challenged, however, their responses more frequently escalated to displays at close range that fully revealed ventral coloration, followed by prolonged physical contests when displays were not sufficient to resolve disputes.

Intraspecific variation in red color patches appears to be involved in establishing social dominance in several vertebrates (e.g., Bakker and Sevensten, 1983; Evans and Norris, 1996; Crowley and Magrath, 2004), but it is sometimes difficult to isolate a specific signaling role for red because many species also have other conspicuous colors (Pryke, 2009). Species characterized by alternative color morphs, some of which are red-orange, are particularly instructive. Red-orange morphs of fishes (Barlow, 1983; Dijkstra et al., 2005) and lizards (Sinervo et al., 2000; Whiting et al., 2006; Healey et al., 2007) use aggression to maintain social dominance over blue, white, or yellow morphs, and there is some evidence that avoidance of red color may be innate

(Pryke, 2009). Orange-red coloration in long-lived Water Dragons first develops when males are much too small to compete for territories and gradually expands and becomes darker red as males grow in total size and head dimensions (TAB, personal observation), both of which are determinants of male RHP (Baird et al., 2012). Whether learned or genetic, the ontogenetic pattern of color development and behavior patterns by males to display it during high-intensity contests adds Eastern Water Dragons to the growing list of species, including other agamid lizards (Hamilton et al., 2013), where red coloration appears to signal aggression and high social status.

Selection may favor graded signals (those that display red and those that do not) in Water Dragons as a consequence of the apparent high, chronic costs of maintaining territories. Mature males were so highly concentrated that several could not acquire territories (Baird et al., 2012), and similar high densities have been reported in another population of this species (Thompson, 1993). High baseline display rates, the immediate transition from nonaggressive to highly aggressive tactics in some males prompted by experimental removal of territory owners, and the spontaneous eviction of territory owners all indicate intense competition among males (Baird et al., 2012). Fights during unstable social conditions involved prolonged (> 1 h) bouts of intense combat, and the high physiological cost of fighting was obvious from the deep breathing of participants, acquisition of fresh, bleeding wounds, and numerous scars borne by males in this population (Baird et al., 2012). Under chronic intense competition, selection may favor frequent use of head displays that are inexpensive to perform and also have the potential to advertise to nearby potential mates (Baird, 2013). When challenged by rivals, it probably becomes cost-effective for males to use more-intense postures (that reveal red coloration) if doing so settles disputes without costly physical attacks. One consequence of this graded set of signals is that short-term observations of display behavior—the kind of data available to Cuervo and Shine (2007)—may fail to detect display postures that utilize this species

spectacularly dichromatic ventral colors. More-intensive observations revealed that the red venter of adult males played no role in routine advertisement displays but is quickly brought into play during escalated interactions when a male's territorial status is under direct challenge. Our data thus provide a cautionary tale about the need for long-term observational data, preferably combined with field-based manipulative studies, to infer the biological function of sexual dichromatism.

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