


## RESEARCH PAPER

# Information-gathering as a response to manipulated signals in the eastern fence lizard, *Sceloporus undulatus*

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## Abstract

Colorful visual signals are used across taxa to convey information during agonistic male-male encounters, which are important for sexual selection. Although much is known about the information content of color signals, less is known about how receivers interpret this information. Here, using territorial *Sceloporus undulatus* lizards in a natural setting, we examined receiver response to intruders with different color patch sizes to determine (a) if patch size conveys information assessed during male-male interactions and (b) if/how receivers modulate their behavioral responses to different types of behavioral signals. We found that larger lizards had longer and wider patches, indicating that the size of the patches may be one of the many characteristics of these patches that is used by males to convey information. Free-ranging subject males also produced more headbob displays in response to intruders with small patches and took marginally longer to react to intruders with large patches. However, we found no differences in the aggressiveness of the response (i.e., full-shows). This indicates that patch size conveys information that is employed during territorial disputes, but that the response is primarily in terms of timing, allowing lizards to gather more information about intruders, instead of aggressive behavior (i.e., fullshows).

## KEYWORDS

aggression, animal coloration, information content, lizards, *Sceloporus*, visual communication

## 1 | INTRODUCTION

In many taxa, sexual selection acts through male-male competition via the use of weapons or ornaments (reviewed in McCullough, Miller, & Emlen, 2016). During these aggressive male-male interactions, colorful visual signals are often used for conflict resolution (reviewed in Senar, 2006), and signal size often conveys important information about the signaler (e.g., Dey, Dale, & Quinn, 2014; Laubach, Blumstein, Romero, Sampson, & Foufopoulos, 2013; Moreno et al., 2011). For example, experimental manipulations of color signals in pukekos (Dey et al., 2014) and white-crowned sparrows (Laubach et al., 2013) indicate that signaling patch size is positively associated

with dominance status or aggression. Further, forehead patch size in pied flycatchers is positively associated with antioxidant capacity (Moreno et al., 2011) and winning male contests (Järvisvö, Laaksonen, & Calhim, 2013). In addition to conveying information about body size and condition, colored patches may also lead to changes in the behavior of receiving animals that have long-term consequences to territorial competition and mate choice. Recently, paint manipulation studies have offered fresh insight by emphasizing the impact of social interactions on the subsequent behavior of the signaler. For example, in birds, males with artificially decreased patches are less aggressive during social interactions (Järvisvö et al., 2013), and the manipulation itself can lead to decreases in the size of the actual patch (e.g., Dey

et al., 2014). In spiny-footed lizards, adult aggression was reduced toward juveniles with experimentally manipulated red coloration (Fresnillo, Belliure, & Cuervo, 2015). Experimentally painted wasps received more aggression, which changed juvenile hormone levels of both signalers and receivers (Tibbetts, Crocker, & Huang, 2016). Here, using territorial *Sceloporus undulatus* lizards in the wild, we examine receiver response to intruders with different patch sizes to determine (a) if patch size conveys information assessed during male-male interactions and (b) if/how receivers modulate their behavioral responses to different types of signals.

In many territorial species, territoriality is costly to males and appropriately responding to threats is therefore paramount. For example, aggression, fighting, and territory defense are not only energetically costly (e.g., Vehrencamp, Bradbury, & Gibson, 1989; Whiting, 1999) and time-consuming, but may also attract visually oriented predators. Thus, to avoid costs, selection should favor territorial males that respond differently to threatening vs. non-threatening intruder males. In cichlids, for example, males are more aggressive to other ecologically similar males that pose a direct threat to their resources than to non-ecologically similar males (Dijkstra, Seehausen, Fraterman, & Groothuis, 2008; Seehausen & Schluter, 2004). Males are thus capable of distinguishing threatening vs. non-threatening males and responding appropriately.

There are many aspects to color patches that may be rich in information content. Signal size in pied flycatchers is positively associated with winning male contests (Järvisjö et al., 2013), but in other taxa, color may play a more important, or similar role to size during agonistic male-male encounters. For example, in wrasses (Braun, Michiels, Siebeck, & Sprenger, 2014), blue tits (Rémy, Grégoire, Perret, & Doutrelant, 2010) and scrub jays (Tringali & Bowman, 2012) the color of the signaling patches is important for mediating aggression or dominance status. However, in male red-collared widowbirds, both color and size of collar patches independently convey information on dominance status or fighting ability (Pryke, Andersson, Lawes, & Piper, 2002). In lizards, color (e.g., Hamilton, Whiting, & Pryke, 2013; Steffen & Guyer, 2014) and patch size (e.g., Abalos, Pérez i de Lanuza, Carazo, & Font, 2016) are linked to winning contests. However, we still have a poor understanding of how receivers respond to different types of signals in an explicit field context. Here, we focus on a single aspect of the color patch, the size, to determine if this one factor is important for communication during agonistic male-male encounters.

In territorial, polygamous lizard species, female choice for male traits is rare (Sullivan & Kwiatkowski, 2007; Tokarz, 1995; Uller & Olsson, 2008), however, sometimes when territorial cues are absent, females assess multiple aspects of male quality for mate choice (Baird, Fox, & McCoy, 1997; Swierk, Ridgway, & Langkilde, 2012). *Sceloporus* lizards utilize several different channels to communicate with conspecifics. For example, headbob displays (Carpenter, 1978; Martins, 1993) are used by both males and females to broadcast information on individual, sex, and species identity (Martins, 1991; Thompson, Bissell, & Martins, 2008). Most *Sceloporus* lizard species are sexually dimorphic in that males exhibit bright blue belly patches and females

have white bellies (Wiens, 1999). These blue belly patches are posturally displayed during male-male interactions (fullshow, Carpenter, 1978; Martins, 1993) and typically elicit an aggressive response (Carpenter, 1978; Cooper, 1987; Hews & Quinn, 2003; Martins, 1993; Quinn & Hews, 2010; Wiens, 1999) and receive greater attention from males than from females (Martins, Ord, & Davenport, 2005). Aside from individual variation in patch size within a species, perhaps one of the most striking differences in males across species is the size of the blue belly patches—some species have very large, paired blue patches, others have smaller patches, and some species lack patches all together (Wiens, 1999). Species that have lost the patch over evolutionary time may be less conspicuous to predators, but may also transfer the aggressive information content of the color patch to other signals (Martins et al., 2015; Ossip-Drahos, Oyola Morales, Zúñiga-Vega, Hews, & Martins, 2016).

Here, we conduct a field study with male *S. undulatus* lizards to test how receivers respond to males that differ in signal size. Noble (1934) found that male *S. undulatus* respond similarly to experimentally altered belly patches of different hues (e.g., gold, silver, yellow), suggesting that other patch features (e.g., size) may more important. If patch size is indeed an important factor assessed during male-male encounters, we would expect to see differences in behavioral responses to the different intruders. Moreover, we expect the specific types of behavioral responses to shed light on the dynamic social interactions that may impact both sender and receiver. First, we measured natural variation in patch size in a specific population. We then painted intruder males to have small (i.e., non-threatening) or large (i.e., threatening) patches and measured behavioral response of the receiver male when presented with both types of intruders. We thus are able to determine (a) if patch size conveys information assessed during male-male interactions and (b) if/how receivers modulate their behavioral responses to different types of intruder males.

## 2 | MATERIALS AND METHODS

### 2.1 | Subjects and site

The protocols and procedures implemented during this study were ethically reviewed and approved by the Indiana State Department of Natural Resources and Animal Use and Care Protocol from the Indiana University Bloomington Institutional Animal Care and Use Committee. We conducted all behavioral trials during the *S. undulatus* breeding season at Lake Monroe in Bloomington, Indiana between June 13 and July 16, 2013 during hours of high lizard activity, which ranged from 10:00 a.m. to 5:00 p.m. Although the blue color of the belly patch can become greenish at very low body temperatures (e.g., Langkilde & Boronow, 2012), *Sceloporus undulatus* are excellent thermoregulators (Angilletta, 2001) such that the belly patches are a stable and constant blue throughout the active period. This site has been used for other behavioral studies of *S. undulatus* (Hews, Date, Hara, & Castellano, 2011).

## 2.2 | Correlates and allometry of patch size

To understand natural variation in morphology for this population, we captured 34 sexually mature males and measured snout-to-vent length (SVL), mass, patch length, and patch width to search for correlates that might indicate whether patches convey information about male quality. We used Pearson's correlation analyses in R v. 2.12.0 (R Development Core Team, 2010) to estimate pair-wise relationships between mass, SVL, patch length, and patch width. We also used the lmodel2 package (Legendre, 2018) to estimate allometric relationships, log-transforming patch length and width and using major axis regression to estimate the slope of those relationships with SVL and mass.

## 2.3 | Response to paint-manipulated patches

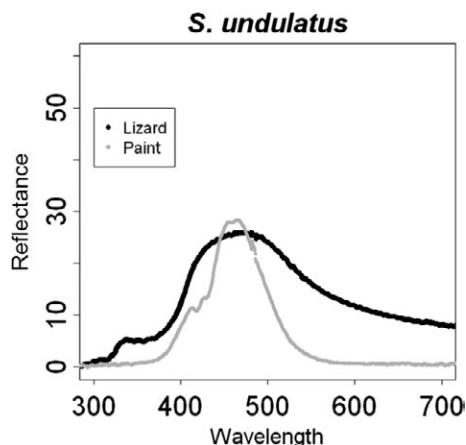
We then measured aggression in a smaller number of lizards by conducting staged territorial intrusions (STIs; e.g., Moore, 1987) whereby a tethered, adult intruder male was presented to a free-ranging, unfamiliar male. We painted male "intruders" with either small or large blue patches using non-toxic Elmer's paint pens chosen to match the peak reflectance (also termed "hue") of male *S. undulatus* bellies (Figure 1). We first painted the bellies white, and then added two blue belly patches with thin black borders, thereby matching the natural ventral coloration of this species (Supporting Information Figure S1; see also Ossip-Drahos et al., 2016 for detailed description and analysis of the natural ventral color of this species). We created patches that were proportional in length and width to the very smallest and largest patches of 34 sexually mature males sampled from this population. Thus, our manipulations closely matched the primary color and patterning of male belly patches.

We then conducted staged-territorial intrusions using our paint-manipulated males as intruders. For each trial, we began by tethering a painted male with fishing line to a long pole. In these lizards, territorial males are often less aggressive toward familiar males (Whiting, 1999). We thus found a second, free-ranging male that was not a near neighbor (at least 20-m away), and presented him with the painted

intruder placed 1 m from the subject male. We video-recorded the behavior of the subject using a Canon Elura 100 camcorder for up to 10 min. We were not able to record the behavior of the stimulus male with a single camera because of the frequent locomotion of the resident lizard and the relatively long distance (1 m) between resident and intruder. In general, however, intruders tended to freeze or to flee, rather than to challenge the resident.

We used a paired design, presenting each focal lizard with both a large- and small-patch intruder on separate days and in randomized order. We excluded trials where we were not confident that the resident male actually saw the intruder (i.e., there was no response to the intruder after 10 min and they did not turn their head or otherwise indicate that they had noticed the presence of another lizard). At the end of the first trial, we captured and paint-marked the subject (with a color stripe near the base of the tail) so that we could identify him on the subsequent day. We stopped the trial early and separated the lizards if they started biting. In order to minimize stress on the paint-manipulated lizards, we used a paint-manipulated male in no more than three trials per day. At the end of each day, we removed all ventral paint using 70% isopropyl alcohol wipes, marked the intruder males at the tail base using Elmer's non-toxic paint, and released all lizards at the site of capture. We presented a total of 16 males successfully with both treatments (i.e., 32 trials total). Although we did not size-match in advance, we found that residents and intruders were within 15% of each other in terms of body size (SVL; median = 2.0 mm or 6%) for all but four residents (the resident was smaller than the intruders in these four cases). Similarly, although we used each of the 13 intruders in multiple trials, sometimes painting the same lizard with two different patch sizes, the average size of intruder painted with a large patch was slightly smaller (67 mm, SE = 0.6) than the average size of intruder painted with a large patch (69 mm, SE = 0.9). This difference in body size was not statistically significant ( $t = 1.7$ ,  $df = 32$ ,  $p = 0.16$ ).

We scored latency to respond (i.e., approach, headbob, charge, or bite) to intruder male, and the number of headbob displays (scoring each species-typical series of up-and-down motions as a single display). Headbob displays are not necessarily aggressive, instead, they are produced most often as broadcasts of individual identity or in courtship (Carpenter, 1978; Martins, 1993). To measure aggression, we also recorded the number of headbob displays, which included the "full-show" posture (arched back and lateral flattening) that exposes the blue belly patches and is an aggressive signal (Carpenter, 1978; Martins, 1993). We used paired  $t$  tests and non-parametric Wilcoxon tests to compare behavioral differences (in terms of raw counts per 10-min trial) between the two treatment groups using the base functions of R v. 2.12.0 (R Development Core Team, 2010).



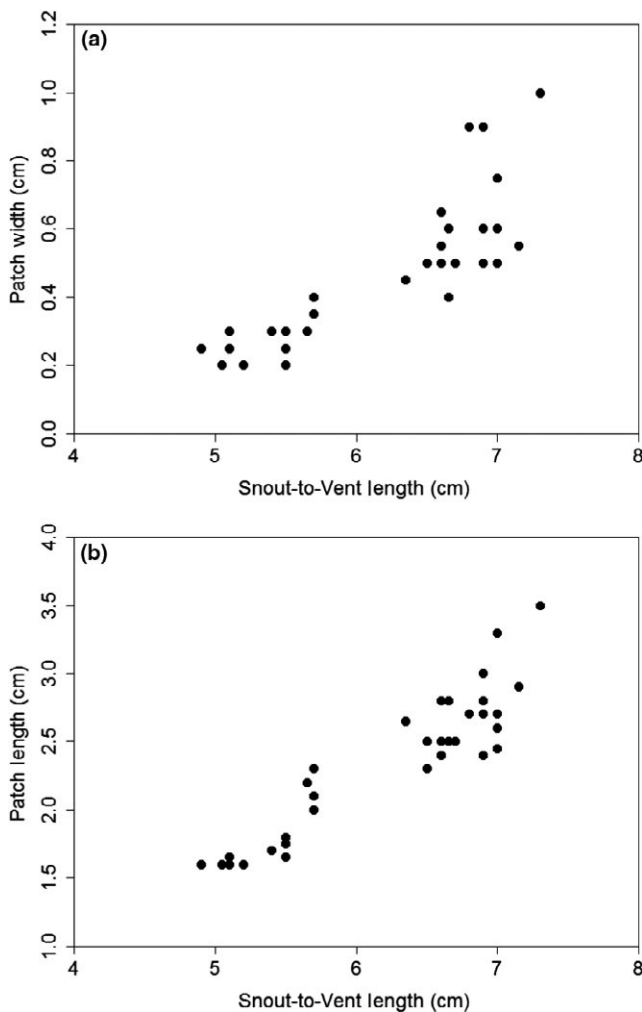
**FIGURE 1** Spectral reflectance curve of a male blue belly (black) and blue paint used for this study (gray)

## 3 | RESULTS

### 3.1 | Morphological correlates

Using our complete data set of 34 adult male lizards (not the reduced set used for the intruder playbacks below), we found that male

lizards ranged in body size between 49 and 73 mm (mean = 63 mm,  $SE = 1.3$ ; Figure 2). Larger lizards (longer SVL) had wider ( $r_{32} = 0.84$ ; Figure 2a) and longer patches ( $r_{32} = 0.92$ , Figure 2b), as did lizards with larger body mass (patch length:  $r_{32} = 0.87$ ; patch width:  $r_{32} = 0.84$ ;  $p < 0.001$  in all cases). However, patch dimensions were not good predictors of relative condition (residuals of regression of body mass on SVL), which was only weakly associated with patch width ( $r_{32} = 0.14$ ,  $p = 0.44$ ) and length ( $r_{32} = -0.03$ ,  $p = 0.88$ ). Tail length was a better predictor of condition ( $r_{32} = 0.34$ ,  $p = 0.04$ ), although it was not closely associated with body size ( $r_{32} = 0.18$ ,  $p = 0.30$ ), mass ( $r_{32} = 0.28$ ,  $p = 0.11$ ), or patch dimensions (length:  $r_{32} = 0.12$ ,  $p = 0.51$ ; width:  $r_{32} = -0.04$ ,  $p = 0.80$ ). Males had a median mass of 10.3 g ( $SE = 0.50$ ), a median SVL of 6.6 cm ( $SE = 0.13$ ), a median tail length of 7.6 cm ( $SE = 0.38$ ), a median patch length of 2.5 cm ( $SE = 0.09$ ), and a median patch width of 0.5 cm ( $SE = 0.04$ ). Both patch width and length exhibited positive allometry, with large lizards having larger patches than predicted by a simple linear relationship with body size. Patch width, in particular, showed a steep



**FIGURE 2** (a) Scatterplot of snout-to-vent length and patch width indicates that longer males have wider patches. (b) Scatterplot of snout-to-vent length and patch length indicates that longer males have longer patches

positive slope (95% CI of slope estimate = 3.4 to 4.8 for SVL, 3.5 to 5.1 for Mass). Patch length also showed positive allometry (95% CI of slope estimate = 1.7 to 2.2 for SVL, 1.8 to 2.4 for Mass).

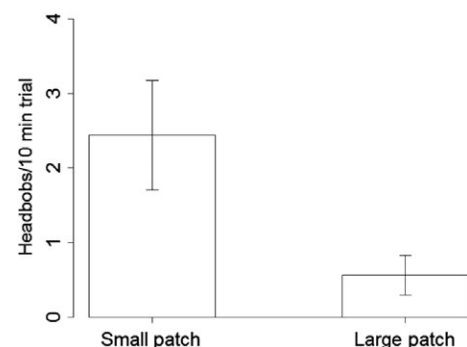
### 3.2 | Behavioral data: lizards differed in information gathering, not aggressive behavior

The median trial duration was 10 min. Five of the 32 behavioral trials were very short (less than 5-min) because the free-ranging male quickly escalated to a high degree of aggression (i.e., biting), and we thus stopped the trial early. Lizards produced between 0 and 11 headbob displays per trial, with an average of 1.5 displays, and a median of zero displays ( $SE = 0.42$ ).

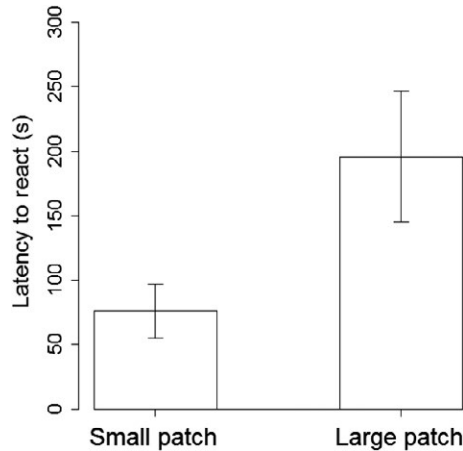
Subject males produced more headbob displays when presented with intruders with small blue belly patches than with intruders with large patches (paired  $t$  test:  $t_{15} = 2.5$ ,  $p = 0.02$ ; Wilcoxon test:  $W = 52$ ,  $p = 0.01$ ; Figure 3). After presentation with a stimulus male, subject males took between 0 s (immediately responded) and 10 min (no response) to react, with an average response time of 136 s (median = 84s,  $SE = 28.27$ ). There was a trend for subject males to have a longer latency to respond to intruders with large blue belly patches than to intruders with small patches (paired  $t$  test:  $t_{15} = -2.0$ ,  $p = 0.07$ ; Wilcoxon test:  $W = 42$ ,  $p = 0.19$ ; Figure 4). Lizards produced between 0 and 8 headbob displays with body postures that exhibited the aggressive blue color (i.e., full shows), with an average of 1.5 full shows per trial and a median of zero full shows ( $SE = 0.39$ ). However, when presented with intruders with small patches and intruders with large patches, there were no treatment differences in rate of headbob displays with the aggressive blue color (i.e., full shows) in the focal males (paired  $t$  test:  $t_{15} = 0.1$ ,  $p = 0.94$ ; Wilcoxon test:  $W = 34$ ,  $p = 0.96$ ; Figure 5).

## 4 | DISCUSSION

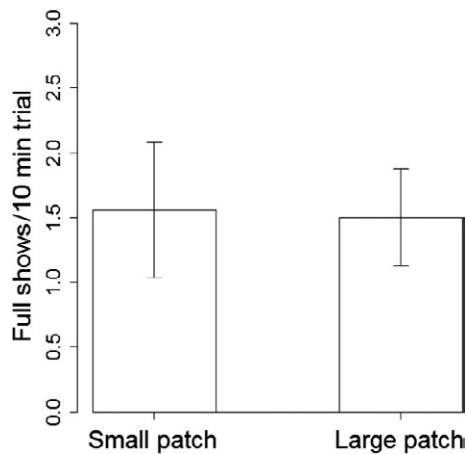
Male-male competition for resources involves complex sender-receiver dynamics, often centering around the use of weapons or



**FIGURE 3** Males performed more headbobs toward intruders with small patches (left) than intruders with large patches (right). Values are estimated means per 10-min trial, and error bars are one standard error



**FIGURE 4** Males had a longer latency to react to intruders with large patches (right) than intruders with small patches (left). Error bars are one standard error



**FIGURE 5** There were no differences in number of headbob displays that exhibited the blue color when males were presented with intruders with small patches (left) and when males were presented with intruders with large patches (right). Values are estimated means per 10-min trial, and error bars are one standard error

ornaments (reviewed in McCullough et al., 2016). Studies manipulating ornament sizes during these aggressive encounters have found positive associations between ornament size and dominance status or aggression (Dey et al., 2014; Laubach et al., 2013). Our study focused on receiver response to color patch manipulation during aggressive male-male interactions. When presented with two signals that varied in size (large and small color patches), we found that differences in receiver response were mostly in terms of ways of gathering information rather than differences in the aggression of the response. Specifically, when presented with an intruder with large patches, we found that the resident male froze (i.e., had a longer latency to respond), whereas when presented with a small-patched intruder, we found that the resident male performed more headbob displays. Residents may be taking longer to respond to a large-patched intruder because they are

reluctant to escalate a risky battle. However, we found no difference in the aggressiveness of the response (i.e., full shows). Thus, differences in the responses of the resident male are primarily in terms of time, and not level of aggression. Bigger patches may give a male a few extra moments of time to approach or aggress, while responding quickly to smaller patches may give a territory holder an edge.

Headbobs in *Sceloporus* convey information about individual, sex and species identity (Martins, 1991; Thompson et al., 2008). Our findings align with previous work in *Sceloporus* that indicates that headbobs are a way for lizards to gain additional information (Thompson et al., 2008). Specifically, when a lizard headbobs toward another lizard, it elicits a reaction in the second lizard (ex. headbob, runaway, etc), which then provides the first lizard with more information. Females of this species have white bellies, and perhaps males headbobbed more toward the small-patched individuals in an attempt to gain additional information to determine the sex of the intruder.

In lizards, color (Hamilton et al., 2013; Steffen & Guyer, 2014) and patch size (Abalos et al., 2016) are linked to winning contests. However, in our study, we found no differences in the aggressiveness of the response to small vs. large patches, indicating that patch size is conveying only some of the information about fighting ability, and there are likely other factors at play. For example, other aspects of the blue patches such as hue, saturation, brightness, shape, and positioning on the body may also convey information that is assessed during these aggressive encounters. Indeed, the color of *S. undulatus* belly patches can change slightly depending on internal body temperature (Langkilde & Boronow, 2012), and may play a role in communication especially during the early morning times when lizards are warming up. Alternatively, chemosensory signals or dynamic visual signals (i.e., headbobs) may be more important in assessing fighting ability of conspecifics males. These chemical and visually dynamic signals are used in *Sceloporus* to broadcast individual, sex, and species identity (Martins, 1991; Thompson et al., 2008), but they could also play an indirect role in intrasexual competition.

In summary, our results highlight the importance of information content in a signaling context. When lizards were presented with an aggressive signal, they responded primarily by gathering more information (i.e., freezing or headbobbing) rather than aggressing. Previous studies have indicated that signals that convey the same type of information co-evolve (Ossip-Klein, Fuentes, Hews, & Martins, 2013), and thus our results add to the growing body of evidence that information content is an important force that shapes signal evolution.

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## CONFLICT OF INTEREST

The authors confirm that there is no conflict of interest.

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## SUPPORTING INFORMATION

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