

Signals and behavioural responses are not coupled in males: aggression affected by replacement of an evolutionarily lost colour signal

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Male *Sceloporus virgatus* lack the blue abdominal patches which are used during aggressive encounters in other *Sceloporus* lizards. Herein we report that, despite having lost this signal, males have retained a behavioural response to experimentally restored blue abdominal patches. We tested two adaptive hypotheses: selection acted primarily upon signallers or selection acted upon both signallers and receivers. The first predicts that only the signal is lost and that male interactions should be affected by the restoration of blue patches. The latter predicts that both the signal and behavioural response are lost and the display of the restored blue patches should have no effect on male–male interactions. We compared the behaviour of receivers in paired encounters where one male (signaller) had blue-painted abdominal patches to a set of trials where both males had white-painted abdomens, unmanipulated abdomens or a novel-painted pattern. The receivers of the blue-painted signal were more likely to display submissive behaviour. The receivers in either the unmanipulated, white-painted or novel-painted signal trials were more likely to display neutral behaviour. These results support the hypothesis that receivers have retained a behavioural response and selection has acted primarily on the signaller. We believe this is the first documentation of males responding to an evolutionarily lost signal in conspecific males.

Keywords: animal communication; colour; evolutionary loss; receiver; *Sceloporus virgatus*; signal

1. INTRODUCTION

Communication is an important component of animal social interactions and diverse types of information can be transmitted, including reproductive condition, aggressive status and species identity (Bradbury & Vehrencamp 1998). Many signals are sexually selected and studies regarding the origin and maintenance of conspicuous secondary sex characteristics have focused primarily on female responses to male signals (Andersson 1994). These studies suggest that signallers and receivers have coevolved and that changes in the signal parallel changes in the receiver (Butlin & Ritchie 1989). However, studies of pre-existing bias have revealed that females of a given species may respond to signals which have not yet evolved in that species (Ryan 1990; Basolo 1996). The degree of coevolution can be influenced by many factors, including the sex of the signaller and receiver and selective forces which may act differently on signallers and receivers (Morris & Ryan 1996).

While there has been much study of signals which are present or signals which have not yet evolved, relatively little empirical work has examined taxa with evolutionary loss of male signals. The evolutionary loss of male signals may be more common than gains (Wiens 1999) and occurs in many lineages, e.g. mammals (Wright 1993), birds (Peterson 1996), fishes (Basolo 1996; McLennan 1996) and reptiles (Wiens 1999). Non-adaptive hypotheses such as genetic drift have been generated in order to explain the loss of male traits (Hill 1994; Peterson 1996), as have adaptive hypotheses (Endler 1980).

To examine the coevolution of signallers and receivers in a communication system with male loss of a sexually dimorphic trait, we recorded behaviour during male–male encounters in the phrynosomatid lizard *Sceloporus virgatus*. Most male *Sceloporus* have a pair of sexually dimorphic blue abdominal patches which are displayed during male–male and male–female interactions. Using well-corroborated phylogenies based on molecular and morphological traits (Reeder & Wiens 1996; Wiens & Reeder 1997), phylogenetic analyses have indicated that at least nine independent male losses of this trait have occurred in *Sceloporus* (Wiens 1999). Some species have a derived state in which neither sex has blue abdominal patches such as the study species *S. virgatus*, while others have an alternative derived state in which both sexes have patches.

We asked whether selection has acted upon signallers and receivers in a similar manner. The loss of abdominal patches in *Sceloporus* lizards is associated with a ground-dwelling habit (Wiens 1999), suggesting that natural selection may be involved in the signal loss (e.g. Endler 1980). However, some major qualitative features of the agonistic behavioural patterns of *Sceloporus* lizards are conserved throughout the genus whereas other qualitative and quantitative aspects are highly variable (Martins 1993; Wiens 2000). We propose two hypotheses for examining how selection has altered this communication system. The one-loss hypothesis states that selection has acted more strongly on signallers than on receivers and predicts that receivers should retain an ability to respond to abdominal patches. The two-loss hypothesis states that selection has been relatively strong on both signallers and receivers and predicts that the signal and the male response to abdominal patches will be absent. To test these predictions we manipulated the abdominal

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colour of male *S. virgatus* by restoring lost abdominal patches to the levels seen in the sister species *Sceloporus undulatus*. We then determined whether this replacement altered aggressive interactions between pairs of males in staged encounters.

2. MATERIAL AND METHODS

We studied a population of *S. virgatus* in the Chiricahua Mountains of south-eastern Arizona near the Southwestern Research Station of the American Museum of Natural History, which is located at the northern edge of the species' range (elevation *ca.* 1650 m). We captured adult (greater than 50 mm snout–vent length (SVL)) (Vinegar 1975) males and females and measured their SVL and body mass. The lizards were captured in the afternoon, maintained in an environment which simulated overnight temperatures and used in trials the following morning.

We conducted two trials per day in large outdoor arenas (6 m × 10 m) from 18 May to 11 June 1998 and from 16 May to 6 June 1999 between 08.00 and 12.00 h. During a trial, we recorded lizard behaviour viewed through a one-way glass window. Before the start of each trial, we placed three still-cool lizards on a board (20 cm × 60 cm) in the arena in the following positions: male, female, male. To avoid a side bias, the positions of the males were alternated. We placed three opaque containers over the lizards, raised the containers remotely and began the trial at the first lizard movement. To decrease the variation in competitive ability between paired males, we matched males with similar SVL (within 2 mm measured using a transparent ruler), tail status (broken or intact), mass (within 1 g measured using a Pesola spring scale) and date of capture. Females were included in all sets of trials in order to enhance the likelihood of male–male interactions (Thompson & Moore 1991).

We manipulated their abdominal signals using a non-toxic latex paint (Tulip Pearl Fabric Paint, Tulip, Clovis, CA, USA) which is flexible when dried, allowing painted males to extend their ventral surface fully when engaged in aggressive postural signals (see the behaviours described below). We assigned one of four treatments to a randomly selected member (hereafter the signaller) of each pair of males: unmanipulated, white painted, blue painted or novel painted. Signallers in the unmanipulated group were not painted on the abdomen, signallers in the white-painted group were painted with 'snow white' and signallers in the blue-painted group were painted with 'blue'. Signallers in the novel group were painted with a series of black dots on the abdomen. As an internal paint control, the other male (hereafter the receiver) was painted with snow white in a pattern which matched the abdominal paint of the signaller of that pair (i.e. a patch or dots). In unmanipulated trials both the signaller and receiver were unpainted. Males given patches had two stripes (*ca.* 5 mm × 20 mm) of the appropriate paint colour applied to the abdomen. Since paint could alter a possible UV signal or alter their ability to perform a full show, a white-painted treatment group was used. Males given black dots had a series of ten to 16 dots (the number varied with the size of the animal), each 1 mm in diameter, painted on the abdomen. For purposes of identification during the trial, we also applied a dot of white paint on the head of one male and on the tail base of the other male (randomly assigned). In 1998 we conducted 19 unmanipulated and 18 blue-painted trials and in 1999 we ran nine white-painted, eight additional blue-painted and eight novel-painted trials.

We were interested in the receivers' behavioural responses to restored abdominal patches (the signal). For abdominal patches to be viewed by receivers, senders must perform one of two postural displays: the challenge display and the face-off display (Carpenter 1978). In the challenge display, signallers are perpendicularly orientated to receivers at close range (one to three body lengths). In the face-off display, signallers and receivers are in parallel body positions but orientated head to tail at close range. The body postures in both challenge and face-off displays are similar: signallers expand their dewlap (throat fan) ventrally, arch their back dorsally and compress their trunk ventrally and laterally. This alteration in body posture exposes abdominal patches (Carpenter 1978; V. S. Quinn, personal observation). We combined these displays into one category (full show), since they differ only in the relative positions of opponents and not the body posture of signallers. If abdominal patches in *S. virgatus* are perceived as an aggressive signal, the receiver's response immediately following the signaller's first full show is the best measure of the response to abdominal patches. Therefore, we analysed the first behaviour of receivers immediately following the signaller's first full show (hereafter post-full show behaviour). Behavioural responses were categorized as follows: (i) aggressive, which included moves towards, approaches and bites, (ii) submissive, which included moves away and retreats, or (iii) neutral, which included nose tapping or licking the substrate and head bobs. Moves towards and approaches involve movement towards the signaller. Moves away and retreats involve movement away from the signaller. Nose tapping and licking the substrate are chemoreception behaviours which occur in both social and non-social contexts, as is the head bob display (Carpenter 1978).

If blue abdominal patches are an aggressive visual signal and *S. virgatus* has retained the ability to respond to this signal, we would expect the post-full show behaviour to differ between the blue-painted trials and both the unmanipulated and white-painted trials. An alternative hypothesis to explain why males may respond to abdominal patches differentially is that males display a general fear reaction to a novel signal. This hypothesis predicts that males perceiving a novel signal would also respond differently than males perceiving a white-painted abdomen. Thus, if blue abdominal patches are simply being responded to as a novel signal and *S. virgatus* responds to all novel signals in the same way, this novel signal hypothesis predicts that post-full show behavioural responses will not differ between novel-painted (black dot) and blue-painted trials, but that these responses would differ from unmanipulated and white-painted trials. Differences in the frequencies of trials having neutral, submissive or aggressive behavioural responses to the first full show were compared using log-linear *G*-tests (Norusis 1990).

3. RESULTS

The number of trials in which a full show occurred in 1998 (32 out of 37) did not differ from the number in 1999 (23 out of 25) ($\chi^2 = 0.0716$, d.f. = 1 and $p > 0.5$); thus, we combined these data. The one-loss hypothesis states that abdominal patches have been lost in *S. virgatus* and that a behavioural response to this signal remains. This hypothesis predicts that the first post-full show behaviour should differ among receivers exposed to the blue signal and those not exposed. Our data support this hypothesis (figure 1). There was a significant association between treatment and post-full show behavioural

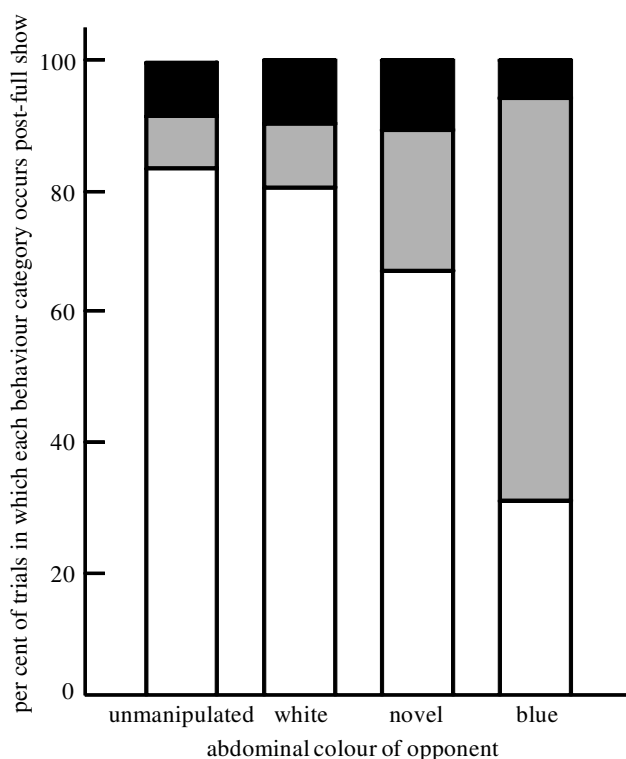


Figure 1. The percentage of trials in which each behavioural response (neutral, open bars; submissive, grey bars; or aggressive, black bars) was performed by the receiver immediately following the first full show by the signaller. Full show is a postural display revealing the abdomen. In the unmanipulated trials ($n = 10$) abdominal coloration was not altered. In the white-painted trials ($n = 12$) we painted white abdominal patches on both the signallers and receivers. In the novel trials ($n = 9$) we painted black dots on the signallers and white dots on the abdomen of the receivers. In the blue-painted trials ($n = 16$) we painted blue abdominal patches on the signallers and white-painted patches on the receivers. The treatments and behavioural responses were significantly associated ($\chi^2 = 13.407$, d.f. = 6 and $p = 0.0403$).

categories ($\chi^2 = 13.407$, d.f. = 6 and $p = 0.0403$). Neutral behaviours were the most frequent response category to the first full show in the unmanipulated, white-painted and novel-painted trials and submissive behaviours were the most frequent response in blue-painted trials. Aggressive responses occurred at the lowest frequency in all four trial types.

4. DISCUSSION

The results of our manipulative paint study clearly demonstrate that a response to male abdominal patches is present in *S. virgatus*, even though this signal has been lost. We did not measure the spectral reflectance of either the blue paint or the natural abdominal patches. The colour vision abilities of *Sceloporus* lizards is also not known, but the fact that the lizards responded to the blue paint in a comparable manner to natural abdominal patches suggests that this is not a problem. The frequency of trials in which the receiver displayed submissive behaviours after the first full show was greater in the blue-painted trials and more trials with neutral responses post-full show occurred in the control or novel-painted trials. Our data do not support the hypothesis that male

S. virgatus perceive the blue abdominal patches as an unknown signal and avoid this stimulus, because the post-full show behaviour by signallers with the novel-painted pattern did not differ from the response to control males. These results support the conclusion that blue-painted patches were retreated from because of a specific response to the patches. These patches are aggressive visual signals in other *Sceloporus* lizards (Cooper & Burns 1987) and the response to this restored signal in *S. virgatus* was submissive, suggesting that receivers perceived signallers as aggressive and retreated (e.g. Rowher 1985).

Another interpretation of these results is that the receivers of abdominal patches perceived the signaller as a heterospecific and avoided this animal due to the effects of interspecific competition or predation. However, available evidence suggests that heterospecific avoidance is not the most parsimonious explanation. Heterospecific lizards with blue abdominal coloration overlap with *S. virgatus* at this study site, but differ in body size, shape and dorsal coloration. Therefore, features other than the presence or absence of abdominal patches are present and more readily available for species identification. The mountain spiny lizard *Sceloporus jarrovi* (both males and females have blue abdomens) overlaps with *S. virgatus* and these two species inhabit different microclimates, suggesting that these species may not often interact (G. Middendorf, personal communication). Another species co-occurring at this study site is the common tree lizard *Urosaurus ornatus* (males have blue abdomens and females have white abdomens). This lizard does not compete with *S. virgatus* (Smith 1981) suggesting that these similar-sized species also may not interact aggressively.

Interestingly, display morphology tends to be more labile than display behaviour in *Sceloporus* lizards. Multiple, independent losses of abdominal patches and the maintenance of a variety of aspects of display behaviour have occurred in *Sceloporus* (Martins 1993; Wiens 2000). Morphological traits and behaviour may not be tightly linked because other traits can convey the same information as the lost morphological trait (e.g. Prum 1990). Redundant signals decrease the likelihood of coupled evolution between signallers and receivers.

The conservation of some components of display behaviour in *Sceloporus* is consistent with our results that selection has acted primarily on the signaller, favouring the loss of the male signal (Martins 1993; Wiens 2000). Selection against male signals may have been greater in terrestrial than arboreal habitats, possibly due to predation (Wiens 1999). Increased natural selection against male signals due to predation in some habitats has been shown to favour the loss of sexually selected signals (Endler 1980). Omland (1997) suggested a decrease in female preference as a possible explanation for male signal loss.

Traditionally, studies examining the roles of sexually selected signals have focused on female responses to signals which are present in males. However, sexually selected signals can have dual functions, including the deterrence of rival males and attraction of females. Because the sexes often face different selective pressures (Andersson 1994), selection could act differently on male versus female receivers. A growing number of studies

have revealed that one or both sexes may respond to male signals and that species may vary as to which sex does or does not respond (Ryan & Wagner 1987; Searcy & Brenowitz 1988; McKinnon & McPhail 1996; Morris & Ryan 1996; Ryan & Rand 1998). For example, female preference for the lost blue abdominal patches would suggest that selection may have acted upon male signalers, but not upon female receivers. Future work will test for female responses to this male trait in *S. virgatus* and in the sister species *S. undulatus*, which has male abdominal patches.

A powerful method for studying the evolution of communication systems and the signallers and receivers of these systems is the use of phylogenetic comparisons. Understanding the evolutionary relationships between closely related species as well as the pattern of losses and gains of morphological and behavioural traits within these phylogenies may lead to more specific hypotheses of the function of male signalling traits and the selective forces leading to the gains and losses of these traits.

We thank M. Galloway, C. Johnson, M. Westphal and R. Worthington for their assistance in the field. In addition, A. Abell, S. Lima, G. Middendorf, N. Rattenborg, P. Scott, P. Zollner and two anonymous referees gave helpful reviews of this manuscript and thoughtful discussion. This study was supported by the School of Graduate Studies of Indiana State University, Indiana Academy of Science, Southwestern Research Station's Graduate Student Fund and Theodore Roosevelt Graduate Student Fund of the American Museum of Natural History (all to V.S.Q.) and United States National Science Foundation IBN-9629783 (to D.K.H.).

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