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Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*

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Abstract. The blue ventral colour patches of the fence lizard, *Sceloporus undulatus*, long believed to be involved in intraspecific communication, allow males to recognize the sex of conspecifics. This was demonstrated experimentally by a field study in which tethered lizards were introduced singly to free-ranging adult males. Males identified those conspecifics having blue belly and throat patches as male, and those that had white belly and throat patches as female. Six experimental groups of tethered lizards consisted of unpainted lizards of each sex, lizards of both sexes painted to match their normal ventral colour patterns, and lizards of each sex painted to match the ventral coloration of the opposite sex. Males responded to unpainted lizards by directing agonistic behaviour to males and courtship to females. Their responses to lizards painted to match the ventral patterns of their own sex were virtually identical to their responses to unpainted lizards, indicating that painting alone did not alter their reactions. Males painted to resemble females in ventral coloration were courted in all but one trial; females painted with the ventral pattern of males were all subjected to aggressive behaviour. Responses to both groups bearing colours of the opposite sex were significantly different from those to unpainted members of their own sex, but were nearly identical to those normally elicited by the opposite sex.

Among animals with colour vision, chromatic signals are widely employed to convey socially important information regarding species membership, sex and reproductive condition and in some cases probable agonistic prowess (see reviews by Hailman 1977; Burtt 1979; Colgan 1983). This is widely assumed to apply to iguanid lizards, which often possess colour patterns that readily allow visual identification of species and sex by biologists. However, pigmentation patterns are known definitely to affect social response in only a few iguanids. Although of great biological interest, distinctive bright female coloration is restricted to a small fraction of iguanid species. Colourful pigments have been shown experimentally to identify reproductively mature females in at least two species, the tropidurine *Tropidurus delanonis* (Werner 1978) and the sceloporine *Holbrookia propinqua* (Cooper 1984). In a third species, *Sceloporus virgatus*, males and females have similar bright blue colour patches, except during the breeding season, when the blue throat patches of females turn orange (Vinegar 1972).

In most sexually dichromatic iguanids, the male is the more brightly coloured. For example, males of many species of *Anolis* possess larger, more brightly coloured dewlaps than do females. However, the social import of this coloration is controversial. Mature males of numerous North American sceloporines have bright colours that are absent or weakly expressed in conspecific females. Preliminary experiments on *Uta stansburiana* (Ferguson 1966) suggest that the male colour pattern may be important in social encounters, but repetitions of experimental treatments necessary for the establishment of statistical significance have not been performed. Dewlap coloration in male *Urosaurus ornatus* is related to agonistic dominance and display frequency (Hover 1985).

Perhaps the best known case of iguanid colour dimorphism in the United States occurs in the fence lizard, which includes the two eastern subspecies of *Sceloporus undulatus*. Adult male fence lizards have bright blue belly patches which extend from the lateral margins of the venter and are bordered medially on each side by a black line. Patches of blue also cover posterior portions of the throat. Females have only small amounts of pale blue in the areas of the throat patches and belly patches, both of which are predominantly white. Similar dimorphisms differing in some cases in details of hue and pattern characterize other populations of *S. undulatus* and several congeners.

Because many biologists are predisposed to interpret obvious sex differences in coloration as cues indicating sex to conspecifics, colour dimorphisms have sometimes been accepted without adequate evidence as conveying social signals. Such is the case for the fence lizard. Noble (1934) is cited as having established that the blue patches identify the male to conspecifics, but close reading of the original article reveals no currently acceptable basis for accepting that conclusion. Noble introduced tethered lizards with altered colour patterns to unrestrained conspecifics in the field and categorized social responses of the latter as indicating recognition of the introduced lizard as male (agonistic display or attack) or female (courtship). The tethered introduction method of studying iguanid behaviour was itself a valuable contribution, but Noble (1934) did not indicate the number of trials in each experimental treatment. In fairness to Noble, it should be noted that statistical hypothesis testing was not in wide use among zoologists in the early 1930s. Nevertheless, it is not possible in retrospect to determine whether any effects of colour were demonstrated.

Thus, acceptable evidence on the role of bright male colours in sex identification by iguanid lizards, especially sceloporines, appears to be lacking. We present here an experimental study of the role of ventral coloration in sex identification in the fence lizard. The study is essentially a replication of much of Noble's (1934) work with slight modifications of the experimental treatments and introduction techniques. The only substantive improvement we have made is the inclusion of frequency data allowing statistical assessment of treatment effects.

METHODS

Lizards used in this study belonged to several populations on the Savannah River Plant in Aiken and Barnwell Counties, South Carolina, near the conjunction of ranges of the geographic races *S. u. undulatus* and *S. u. hyacinthinus*. Because the ventral coloration of several other subspecies may differ from that of the two eastern ones in socially significant ways (especially in *S. u. erythrocheilus* and in some south Texan *S. u. consobrinus*), results of this study should probably not be generalized beyond the two eastern subspecies (see also Carpenter & Ferguson 1977). Stimulus animals were captured prior to field tests and were housed at the Savannah River Ecology Laboratory where they were maintained on crickets and mealworms prior to painting and/or use in trials. All experimental trials were conducted between 25 June and 16 July 1985.

To reveal any effect of ventral coloration on qualitative social responses, reactions of unrestrained adult male fence lizards exposed to conspecifics of six sex and colour categories were recorded. The stimulus conditions were: unpainted male, whitened male (painted to resemble a female by painting the blue patches white), blued male (painted to match normal male coloration), unpainted female, whitened female (painted to match normal female coloration) and blued female (painted to match male coloration by adding blue ventral patches). The blued male and whitened female conditions served as controls for possible responses to the paint rather than to the colour pattern. Testor's model paints were mixed to achieve good visual matches (to human observers) between lizards painted experimentally and unpainted controls. An independent groups design was used in which each unrestrained lizard was tested only once. Re-use of residents was avoided by conducting trials in several populations separated by more than 1 km, and within each population by avoiding subsequent use of any male near the territory of a previously tested resident. Ten trials were conducted for each treatment group.

In each trial a tethered stimulus lizard was presented to an unrestrained male in the field. Stimulus lizards were tethered by a 0·7 m length of waxed dental floss tied around the neck and attached to the end of a 2·5 m rod. To initiate a trial, a tethered lizard was placed approximately 0·7–1·0 m from a free male by slowly lowering it to the substrate, into the field of view of the lizard to be tested. The exact distance between the stimulus and experimental lizards varied somewhat, due to structural constraints on lizard placement. If the unrestrained lizard retreated, the stimulus lizard was left in place for a variable interval to induce interaction, but if the unrestrained lizard fled, the test was cancelled. Thus, the length of an encounter varied, depending upon latency to social response.

The social reactions of unrestrained males to tethered lizards were classified as being typical of either agonistic responses to conspecific males or courtship of females. During the breeding season, male fence lizards and other subspecies of *S. undulatus* reliably perform species-typical agonistic and courtship behaviours (Noble & Bradley 1933; Fitch 1940; Carpenter 1962; Kennedy 1968; Ferguson 1971; Vinegar 1975; Ferner 1976; Rothblum & Jenssen 1978). Upon detecting intruders, males may give species-typical pushup (assertion) displays in which the head and anterior portion of the body are repeatedly moved up and down. Pushups may be directed toward either sex, especially during initial encounter stages. Lateral compression of the body while oriented to display to maximal effect the increased lateral surface to a conspecific is another agonistic response which occurs early in encounters. It may be a response to either sex, but is more often directed toward males (e.g. Cooper 1984). Clear aggressive intent is indicated by challenge displays in which pushups are combined with lateral compression and ventral extension of the dewlap. The dewlap may also be extended and held in its lowered position between pushups. In both cases, dewlap extension is an agonistic display directed much more frequently toward males. Physical attacks in which one male charges another lizard, bites or attempts to bite it, and chases it are easily categorized as aggressive behaviour.

Courtship behaviours by the unrestrained males were considered to denote identification of the stimulus lizard as female. Mounting the female in the species-typical copulatory posture or attempts to do so clearly identified courtship behaviour, as did attempting to grasp the female's nuchal skin between the jaws, a requisite for mounting. No one display pattern is completely sufficient for determining whether a male has identified a conspecific as female. However, in many species shuddering is much more often a response to females than to males. The shudder display (rapid head-bobbing while advancing toward the conspecific) in the absence of dewlapping during the encounter was a major indicator. Shuddering has a courtship function in many iguanids, including *Sceloporus*, but in some cases may indicate general arousal rather than courtship per se (Jenssen 1977; Ruby 1977; Rothblum & Jenssen 1978). Nevertheless, differences in the proportion of encounters with males and females in which the shudder display and other indications of courtship are performed do indicate whether the unrestrained lizards respond to different categories of tethered lizards as male or female.

Following the introduction of a tethered lizard, the experimenter recorded all social behaviours mentioned above for residents and the responses of the tethered lizards, which included courtship rejection behaviours by females. The significance of differences in the frequency of response to stimulus lizards as male or female by test males was calculated by Fisher's exact probability tests (Zar 1974). One-tailed tests of the directional hypotheses were conducted with alpha $=0.05$.

RESULTS

Particular displays by unrestrained males were clearly associated with the sex of unpainted, tethered lizards. In all 10 encounters with unpainted females, males gave shudder displays, whereas only three did so in encounters with unpainted males ($P=0.0015$). Unpainted male lizards elicited dewlap extensions in eight of ten trials as opposed to three of ten for females. This difference was also significant ($P<0.05$). Although the absence of shuddering indicated that an unpainted lizard was not a female in this experiment, in general, observation of other behaviours was required to characterize the response of an unrestrained male as courtship or aggression.

Responses of males to tethered lizards were categorized as courtship or agonistic behaviour (Table I). The reactions of all 10 males to blued females were aggressive. Males initiated displays in

Table I. Numbers of encounters in which unrestrained male fence lizards responded agonistically or with courtship to tethered lizards of the six experimental groups

Experimental group	Courtship	Agonistic behaviour
Unpainted males	0(3)	10(7)
Blued males	0(3)	10(7)
Whitened males	9	1
Unpainted females	10	0
Whitened females	10	0
Blued females	0(2)	10(8)

Where parentheses are present, the primary numbers include encounters with mixed responses because these indicate the probable response to experimental colour modification. The numbers in parentheses represent the most conservative interpretation, in which mixed responses are taken to show no effect of colour treatment.

all encounters. Four of the blued females performed no displays or other courtship or agonistic behaviours, even in response to male aggression. The remaining six blued females sidlehopped (hopped sideways) after male approach or display. Of these, two were bitten after sidlehopping and one sidlehopped only after being attacked. Although two males shuddered during the encounters, they did so only after performing agonistic displays, including dewlap extension. For this group, all of the males were considered to have identified, at least initially, the females as male. Pushups and dewlapping occurred in nine trials, lateral compression in five, and physical attack, including biting, occurred three times.

In contrast, all males courted unpainted females and whitened female controls. In addition to the shuddering performed by males in 10 trials with unpainted females, five males attempted to grasp the skin of such females in their jaws. Nine of the 10 males that responded to whitened females shuddered, and two mounted the females. The frequencies of encounters in which males courted unpainted females and their painted controls were identical ($P > 0{\cdot}10$, Table II). The difference in the response to females painted blue from the response to the unpainted female and whitened female groups was dramatic and highly significant ($P < 0{\cdot}001$ in each case). Even if the two cases of shuddering toward blued females are taken to indicate identification of the introduced lizard as female, the differences remain significant ($P < 0{\cdot}01$ each).

Unpainted tethered males elicited seven initial agonistic responses including lateral compression, dewlap extension and biting (three cases). Three males initially shuddered in response to the tethered males, but switched to agonistic responses upon approaching them. All three of these unrestrained males eventually either dewlapped or attempted to attack the introduced unpainted males. Reactions to painted male controls were similar to those elicited by unpainted males ($P > 0{\cdot}10$). Of the seven males that were initially aggressive toward males, six dewlapped and four attacked. Of the three males that initially shuddered at unpainted males, all subsequently performed dewlap extensions and attacked or chased the tethered lizard. Males painted to resemble females were initially courted in nine of the 10 trials, as indicated by shuddering. In the remaining case the unrestrained male dewlapped immediately upon introduction of the tethered lizard and then attacked. Although resident males initiated displays in all of the trials, whitened males responded aggressively in all but one trial. Nine whitened males performed pushups, six after shuddering by the resident, two after being bitten, and one in response to pushups. One whitened male attempted to bite the resident.

Five unrestrained males never exhibited agonistic behaviour toward whitened males, despite attempts to bite or displays by the stimulus males; two switched to agonistic behaviour which included dewlapping, but not chasing or biting; and two performed agonistic behaviours followed by further shuddering. It is apparent that whitened males elicited responses typically directed toward females in a higher proportion of trials than did either unpainted or blued males. This difference is significant for each comparison ($P < 0{\cdot}01$). More importantly, the same significance levels are attained even if initial shuddering is taken to indicate that unpainted and blued males (three each) were courted.

Males of the unpainted and blued groups were objects of aggressive behaviour in a significantly higher frequency of trials than were unpainted females or whitened females ($P = 0{\cdot}0015$ in all cases). The fraction of trials in which agonistic

Table II. Statistical significance pattern for differences in the numbers of trials in which unrestrained males courted or behaved agonistically toward tethered lizards of the six experimental treatment groups

	Blued males	Whitened males	Unpainted females	Whitened females	Blued females
Unpainted males	NS	0·01	0·01	0·01	NS
Blued males		0·05	0·01	0·01	NS
Whitened males			NS	NS	0·01
Unpainted females				NS	0·01
Whitened females					0·01

behaviour was directed toward blued females, however, was similar to that for unpainted and blued males ($P > 0.10$ each). Whitened males were courted in as high a proportion of trials as were unpainted females and whitened females ($P > 0.10$ each), and in a significantly higher proportion than blued females ($P < 0.001$). Conservative tests in which the occurrence of shuddering at any stage of an encounter is taken to indicate perception of a tethered lizard as female retain significance ($P < 0.01$ in all cases).

DISCUSSION

The results of the present experiment show that the blue colour patches strongly affect the social responses of fence lizards. Male fence lizards react to conspecifics that have dark blue ventral throat and belly patches as if the latter were male, and to those lacking the blue patches as if they were female, regardless of biological sex. The pronounced effects of colour modification on lizard behaviour cannot be attributed to painting because the painted control groups of both sexes elicited responses appropriate for their sexes. Beyond the role of colour patches in the identification of males, much uncertainty remains about the effective stimulus properties of the patches, the functional relationships between chromatic/brightness cues and other reliable indicators of sex, and their selective basis.

The experiments show that the males react to conspecifics bearing blue ventral colour patches as male, but do not establish whether dominant wavelength affects sex recognition. Although lizard retinas possess well-developed cones (Walls 1942), presumably supporting colour vision in the fence lizard, the precise hue of the patches may be relatively unimportant. Noble (1934) reported that female fence lizards that had belly patches painted various bright colours were treated as intruding males. This suggests that brightness and/or contrast may be the effective stimuli to which males respond.

Stimuli unrelated to the colour patches are undoubtedly important in sex recognition. Males may be identified by behavioural cues, particularly courtship and agonistic displays. This presumably explains the mixed responses of unrestrained males to the whitened tethered males. Whitened males responded to an approach by performing typical male agonistic behaviours. Similarly, sidlehopping and failure to respond aggressively to agonistic displays are reliable female behaviours which may have influenced the two males that switched from aggression toward blued females to courtship. Chemical cues may be important once physical contact occurs because body licking allows important chemical discriminations in the closely related *S. occidentalis* (Duvall 1979, 1981, 1982). Alternation between aggression and courtship by some males and continued courtship by others, despite male-like behaviour by the whitened males, suggests continued effectiveness of the coloration upon repeated presentation.

The reproductive importance of sexually dimorphic pigmentation is supported by studies showing that it is under steroidal control in some male scincid lizards (e.g. Edgren 1959; Cooper & Vitt 1984) and some female iguanids (Cooper & Ferguson 1972, 1973; Medica et al. 1973; Cooper & Clarke 1982). A hormonal role has not been demonstrated in the fence lizard, but the black component of male ventral pigment in the closely related *S. occidentalis* is enhanced by androgen administration (Kimball & Erpino 1971).

It is unlikely that the blue coloration is important in species recognition in the genus *Sceloporus* because it is widespread in the genus, even in areas having several sympatric congeners. Furthermore, iguanid lizards, including sceloporines, perform species-typical display action patterns which appear to allow species recognition by the sequence, timing and relative amplitudes of head and body movements (Carpenter 1962; Hunsaker 1962; Jenssen 1970; Carpenter & Ferguson 1977). The possibility that redundant cues support species recognition cannot be dismissed, but it is unlikely that species recognition is the primary selective force that currently favours blue ventral patches.

Territorial male fence lizards often initially display to intruding males without extending the dewlap, but indicate stronger aggressive intent by performing pushups with the dewlap extended. The blue belly patches, completely or partly concealed while the male is at rest, are emphasized during these displays by lateral compression of the body. The male frequently orients at right angles to the intruder, which maximizes the visibility of the blue patches. Blue throat patches are obvious only when the dewlap is extended. Although males perform less intense pushups when interacting with females, male coloration is visible to both sexes during social encounters. Similarly, lizards of both sexes may respond by displaying their own ventral coloration. A female that is being courted may show a rejection display in which she presents a lateral view to the male, arches her back upward, performs shuddering pushups, and often hops sideways (sidlehopping). She may even attack the male. Lateral compression during the rejection display clearly reveals the lack of bright blue belly patches.

Thus, the ventral coloration of both sexes is displayed during social encounters. In intraspecific encounters, males may gain a selective advantage by using the presence of blue ventral coloration to identify appropriate objects of agonistic behaviour and its absence to indicate individuals suitable for courtship. Revealing the lack of blue ventral coloration in the rejection display may benefit females through a reduction of male aggression. Nevertheless, these current roles of coloration may not account for its evolution. If sex recognition were the sole effect of bright pigmentation in iguanids, each sex might be equally likely to be the brighter. On the contrary, males are more brightly coloured in most chromatically dimorphic iguanid species. Countervailing selection for crypticity may be stronger in females due to the reduced ability to avoid predators while gravid (Shine 1980), which could produce the observed colour distribution.

A potential selective force favouring the blue coloration of males is epigamic selection. In the anoline iguanids, dewlap coloration is brighter in males and varies interspecifically in a manner allowing its use in specific recognition (Rand & Williams 1970; Williams & Rand 1977; Losos 1985). However, investigations of the effects of male dewlap coloration on female choice have produced contradictory results (Greenberg & Noble 1944; Crews 1975; Sigmund 1983). The importance of epigamic selection in the evolution of the blue coloration of the males cannot be properly evaluated because female response to it is unknown in *S. undulatus* (or its ancestors in which the colour evolved).

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