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Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards: an experiment

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In the lizard *Psammodromus algirus,* larger and older males show orange nuptial coloration on most of the head and are dominant over smaller and younger, albeit sexually mature, males which do not show such extensive nuptial coloration. This raises the question of why young, small males delay the development of nuptial coloration until a later breeding season. We tested the hypothesis of social costs by manipulating the color of the head of small males. The results of agonistic interactions suggested that small males may pay a cost in terms of being punished by large males. Small males with heads painted orange were still recognized as small by other small males, suggesting that they would not gain in social status relative to normal, dull, small males. We also manipulated the coloration of large males. Small males showed a similar response toward all large males, independent of coloration. This suggests that in short-distance communication, males used other cues, such as body size and behavior, when judging fighting ability. In staged experiments without male competition, female acceptance of matings was influenced by male body size but not by coloration because large males were more successful in obtaining matings than were small males, and within each age/size category there was no difference in mating success between experimental and control males. *Key words:* lizards, mating success, nuptial coloration, *Psammodromus algirus,* signals, social status. *[Behav Ecol 10:396–400 (1999)]*

In many vertebrates, such as birds and lizards, conspicuous patches of color that may reliably signal fighting ability have evolved (Rohwer, 1982; Whitfield, 1987). For instance, males of many species of lizards show breeding colors during the mating season that may function as social releasers (review in Cooper and Greenberg, 1992). These conspicuous badges are important for sex recognition (e.g., Cooper and Burns, 1987) and may function as reliable signals of status in competition between males (Olsson, 1994a; Thompson and Moore, 1991; Zucker, 1994). In the lizard *Psammodromus algirus,* two age categories of sexually mature males occur: larger and older ones with orange coloration on most of the head during the breeding season, and smaller and younger (albeit sexually mature) males lacking orange coloration except on a few infralabial scales at each side of the mouth (for more detailed descriptions of coloration and behavior, see Díaz, 1993; Díaz et al., 1994; Salvador et al., 1995, 1996, 1997). The larger, older males are dominant over the smaller, younger males, although our field recapture data indicate that young, small males attain the size and coloration of large males in the next breeding season, and then become dominant over smaller males (Martín and Forsman, unpublished data; see also Díaz, 1993). Nevertheless, small males (snout-to-vent length >70 mm) with some orange mouth scales are already sexually mature, based on observations of spermatogenic activity (Díaz et al., 1994), active testosterone-dependent secretion from the femoral pores, courting behavior, protrusion of hemipenes, and attempted copulation (Martín and Forsman, unpublished data; see also Salvador et al., 1995, 1997).

When males of different age classes exhibit different badges, individuals may use these badges to judge relative fighting ability and to modify their own behavior accordingly (Enquist and Leimar, 1983; Maynard Smith and Price, 1973; Parker, 1974). Thereby males may avoid the costs associated with escalated aggressive interactions (Marler and Moore, 1988, 1989; Marler et al., 1995; Rohwer and Ewald, 1981). However, if status signaling is based on features (e.g., coloration) that are not directly related to fighting ability, individuals might benefit from "cheating"—that is, signaling at too high a level (Krebs and Dawkins, 1983). Nuptial coloration might not only give a preliminary advantage in intrasexual contests, but small males with nuptial coloration might also attain a higher mating success, if females prefer brighter males. This raises the question of why young but sexually mature small males delay the development of nuptial coloration until a later breeding season.

Although several explanations have been proposed, little is known about what mechanisms delay the appearance of nuptial coloration in lizards. One explanation is that it may be physiologically or morphologically impossible for a young individual to signal too high a dominance status (Rohwer and Rohwer, 1978; Salvador et al., 1997). An alternative hypothesis is that it may be physiologically possible, but too costly, to produce an exaggerated signal. For instance, the signal may be selected against because it decreases crypsis and cause a higher susceptibility to predators (e.g., Forsman and Shine, 1995; Møller, 1989; but see Olsson, 1993b) or parasites (Folstad and Karter, 1992; Salvador et al., 1996). Costs may also be imposed by the targeted receivers. Thus, if the status signal is incongruent with behavior, deception may be detected and punished by genuinely dominant and aggressive individuals (Møller, 1987; Olsson, 1994b; Rohwer and Rohwer, 1978). However, at least to our knowledge, no study has examined experimentally whether social costs may contribute to preventing the appearance of nuptial coloration in lizards.

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To test the hypothesis that social costs account for deferring development of nuptial coloration in small, subordinate lizards, we experimentally manipulated the head coloration of small, young *P. algirus* males, thereby creating a group of experimental small males with the orange nuptial coloration of large males. Using data from staged agonistic encounters, we compared the response of large males to experimental small males with their response to control small males painted brown to resemble their natural lack of nuptial coloration. We also tested whether experimental orange small males might gain any social advantage against normal, dull, small males.

One characteristic of lizards' social relationships is that dominance may be based on differences in body size per se (Cooper and Vitt, 1987; Olsson, 1992; Tokarz, 1985). Therefore, when there is a conflict between the color badge signal and body size, lizards may rely primarily on body size and ignore the presence or absence of a badge. To evaluate this hypothesis, we manipulated the coloration of large males and analyzed the responses of both large and small males to these large males without nuptial coloration. Finally, to examine how the nuptial coloration and body size influence female acceptance of matings, we compared the copulatory success between control and experimentally manipulated males of both age/size classes in staged situations without male competition.

METHODS

Study animals

We captured adult *P. algirus* lizards [large males: snout-to-vent length (SVL), $\bar{x}$ = 83.2 mm, SE = 9.8; small males: SVL, $\bar{x}$ = 75.3 mm, SE = 9.9; females: SVL, $\bar{x}$ = 80.2 mm, SE = 11.2) in an oak forest near Cercedilla (40°44′ N, 4°02′ W), Madrid Province, Spain. To ensure that individuals had not been in previous contact, which may affect the outcome of the interactions (Olsson, 1992), we captured lizards in different places and years over a large area. Lizards were housed individually in seminatural outdoor enclosures (1.5 × 1.5 m) located at ''El Ventorrillo'' Field Station (5 km from the capture site). The enclosures were made of plastic walls supported on the outside by a wooden framework. The habitat inside the enclosures consisted of short grass, some rocks, and oak leaf litter that provided invertebrate prey. We provided mealworms as supplementary food and water ad libitum. The experiments were carried out during April and May 1995 and 1996, which coincides with the mating season of lizards in their original natural population. Additional control tests with new males were made during April and May 1998. Tests were made when lizards were fully active. All lizards were alive at the end of the experiment and were released at their capture sites.

By experimentally manipulating phenotypes of individuals, we created 4 groups of 12 males each: large orange males (painted orange to resemble their natural orange coloration); large brown males (painted brown to eliminate their orange coloration and resemble normal brown-colored small males); small brown males (painted brown to resemble their natural coloration); and small orange males (painted orange to resemble colored large males). Males within each class were matched by SVL and randomly assigned to the different treatments. We used flexible nontoxic Testor's paints for model airplanes, mixing them to achieve good visual matches with the natural color of the lizards. Individuals were cold anesthetized, their heads painted, and then were placed in the refrigerator until the paint had dried. Lizards were painted the day before the trials, and the paint was removed with water immediately after a male had completed all the trials. We did not observe any necrosis of tissue due to the paint that might influence male behavior. Responding males were similarly manipulated but not painted.

Lizards might respond to cues that are not in the spectrum visible for the human eye as, for example, ultraviolet radiation (Fleishman et al., 1993), which might not be accurately imitated or concealed by the paint used. We tried to assess whether the experimental manipulation accurately mimicked natural variation in head coloration by conducting pilot observations of the responses of a group of small males toward unmanipulated, large orange males and large orange males that were painted orange. The results suggested that neither small nor large males changed their normal expected behavior as a result of this manipulation. Also, other lizard species seem to respond normally to individuals painted to resemble natural colorations (e.g., Cooper and Vitt, 1988; Olsson, 1994a; Thompson and Moore, 1991).

Staged agonistic interactions

We staged encounters between pairs of males to test (1) responses of large males to control small males painted brown and to experimental small males painted orange, (2) responses of small males to control small males painted brown and to experimental small males painted orange, (3) responses of small males to control large males painted orange and to experimental large males painted brown, and (4) responses of large males to control small males painted brown and experimental large males painted brown. We used an independent-subjects design. Thus, in each test, the group of males (24 large and 24 small) responding to experimental individuals was different from the group of males (24 large and 24 small) responding to control individuals.

To avoid the effect of prior residence advantage (Cooper and Vitt, 1987; Olsson, 1992), we performed all the experiments in a neutral, previously unoccupied arena, consisting of a 1.5×1.5 m enclosure that could be divided into two equal compartments by the use of a plywood partition. Males were placed in separate compartments and given 15 min to habituate to the new environment before the partition was removed. To avoid disturbing the lizards, we made all observations from an elevated viewpoint behind a blind (a sheet of black plastic). Each responding male was used twice, facing males of different categories in randomized sequence, but each participated in only one interaction per day. In each test the two contestants had never been together before the trials, and this pair of males was not used again in other trials.

We scored the intensity of the aggressive behavioral response of males on a ranked scale as: ''retreat'' (running away from the other male), ''neutral'' (males are closer but no aggressive, approach, or retreat response occur), ''approach'' (approaching another male without aggressive display, yet frequently making the other male retreat), and ''challenge display'' (approaching with head lowered, neck and throat inflated, back arched and the body raised, frequently followed by a pursuit). A contest was interrupted as soon as any aggressive interaction occurred (retreat, approach, or challenge display) or after 20 min if no aggressive interaction occurred (neutral response). Because their lack of a response could be induced by the test situation, males that exhibited neutral responses were tested again subsequently with a different male. They then exhibited other aggressive or submissive responses. However, only data for the first neutral response were analyzed. Two males that consistently exhibited a neutral response were excluded and replaced by new individuals. In the analysis we used the outcome of the first encounter of each responding male with another male belonging to a given category.

Table 1

Number of large males and number of small males showing "retreat," "neutral," "approach," or "challenge" behaviors to small males painted brown (control), small males painted orange (experimental), large males painted orange (control), and large males painted brown (experimental)

	Retreat	Neutral	Approach	Challenge
Large males response to				
Small brown	0	14	10	0
Small orange	0	9	8	7
Large brown	5	6	8	5
Small males response to				
Large orange	15	9	0	0
Large brown	14	10	0	0
Small brown	5	14	5	0
Small orange	7	12	5	0

Mating success

To examine the relative importance of body size and nuptial coloration in female acceptance of matings, we compared the copulatory success of control and experimentally manipulated males of both size categories in staged situations without male competition. We presented a female (randomly chosen) to a male in his enclosure and recorded whether the male attempted to copulate (attempting to grasp the female's tail or nuchal skin between the jaws as a requisite for mounting), and if it was successful (mounting the female in the species-typical copulatory posture). We also noted whether the female accepted the mating attempt, tried to reject the male by biting him, or fled when the male approached before a mating attempt occurred. If the male did not approach or court the female within 30 min, we considered it a neutral response, and then repeated the test after 2 days with a different female to ensure that lack of motivation of the male was not due to female characteristics (e.g., unreceptiveness).

Data analysis

We analyzed the results using the outcome of the first encounter of each responding male with another male belonging to a given category. We used *G* tests to determine if the frequency distribution of response behaviors was independent of whether the encountered male was an experimental or a control individual (Sokal and Rohlf, 1995). We also used *G* tests to evaluate differences in mating success between small and large males (Sokal and Rohlf, 1995). Significance levels for the set of tests for male interactions and for the set of tests for mating success were calculated separately by using the sequential Bonferroni adjustment of Rice (1989) for multiple comparisons (Chandler, 1995).

RESULTS

Agonistic interactions

Response of large males toward small males painted brown and small males painted orange

The response of large males was different depending on whether they encountered a control small male painted brown or an experimental small male painted orange. In their first encounter with a small male painted brown, large males were either neutral or approached, but never challenged, whereas some large males aggressively challenged small males painted orange ($G = 11.02$, df = 2, $p = .004$; Table 1). This result suggests that small males with nuptial coloration have to pay a cost in terms of being punished by large males.

Response of small males toward small males painted orange

Small males appeared to regard the experimental (painted orange) small males as naturally colored small males. Small males mainly retreated from control large orange males, and never approached them. When encountering a small male painted orange, however, most of small males were neutral, and a similar number retreated or approached ($G = 10.34$, df = 2, $p = .0057$; Table 1).

This comparison of responses might be due to differences in body size. Thus, we also compared the responses of small males to control small males painted brown versus their response to experimental small males painted orange. The responses in their first encounter with another small male painted orange were similar to the responses in their first encounter with another small male painted brown ($G = 1.0$, df = 1, $p = .32$; Table 1). These results suggest that small males with nuptial coloration would not gain in social status relative to normal, dull, small males.

Response of small males toward large males painted orange and large males painted brown

Small males showed a similar response toward all large males, independently of the color of their heads. The most common response of a small male encountering a large male, whether brown or orange, was to retreat (Table 1). Responses by small males to the two categories of large males did not differ significantly ($G = 0.09$, df = 1, $p = .77$; Table 1). This suggests that small males use cues other than, or in addition to, color (such as body size and behavior) when judging fighting ability of other males.

Response of large males toward small and large males painted brown

Large males showed different behaviors toward control small males painted brown than toward experimental large males painted brown. When considering data from the first encounter with a large male painted brown, large males exhibited the full range of behaviors. In the first encounter with small males painted brown, large males approached or showed a neutral response, but large males never retreated or challenged small males painted brown ($G = 17.38$, df = 3, $p = .0006$; Table 1).

Mating success

Our experimental results from interactions between male and female lizards suggest that female acceptance of matings is influenced by male body size but not by male coloration. Copulation attempts were nearly twice as common by large (87.5% of 24) as by small males (45.8% of 24) ($G = 9.92$, df = 1, $p = .0016$; Figure 1). Females tended to retreat when approached by small males (20 of 24), but not by large males (5 of 24). Within each size class, however, the number of males attempting copulations was independent of experimental manipulation. Thus, copulation attempts were equally common among large males painted orange and large males painted brown ($G = 0.39$, df = 1, $p = .53$), and among small males painted orange and small males painted brown ($G = 0.17$, df = 1, $p = .68$; Figure 1).

Not only were copulation attempts more common among large males, large males were also more successful in obtaining matings than were small males ($G = 8.68$, df = 1, $p = .003$; Figure 1). However, experimental large males painted brown were not significantly less successful than were control large males painted orange ($G = 0.02$, df = 1, $p = .89$), and

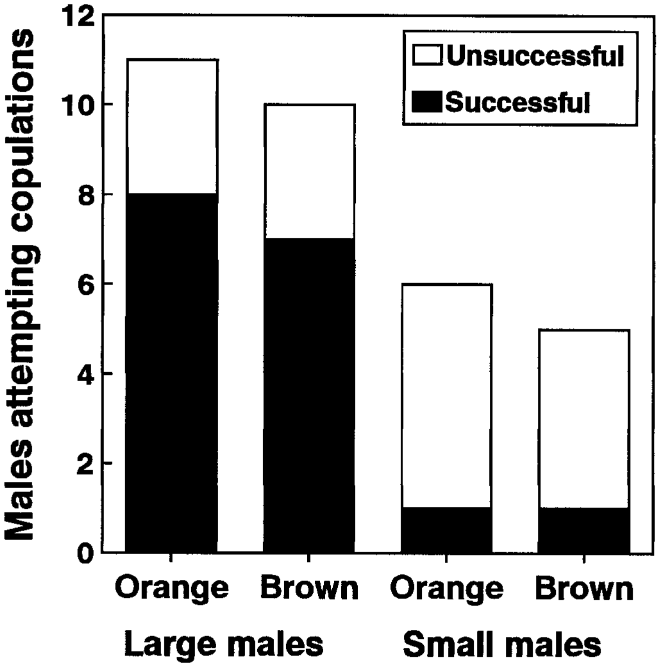

Figure 1
Number of males (n = 12 males tested in each category) that attempted copulations with females and that were successful in getting copulations.

experimental small males painted orange were not more successful than control small males painted brown ($G = 0.02$, df = 1, $p = .89$).

DISCUSSION

The results from our experiment show that large male *P. algirus* responded more aggressively toward experimental small males with heads painted orange than toward control small males painted brown. Bright orange head coloration has been found to be an important releaser of aggressive behavior in males of the lizard *Agama agama* (Harris, 1964; Madsen and Loman, 1987) and the skink *Eumeces laticeps* (Cooper and Vitt, 1988). Behavioral observations of *P. algirus* lizards in the field and in seminatural enclosures have revealed that fights between males are frequent, with social status being correlated with mating success (Salvador et al., 1995). Body size has been found to be an important determinant of dominance in numerous lizards, with larger males usually being dominant in contests with smaller males (Cooper and Vitt, 1987; Olsson, 1992; Tokarz, 1985). In free-ranging *P. algirus,* interactions between large and small males are always initiated by the large male, which chases the smaller male whenever it approaches a female or the large male too closely (Salvador et al., 1995). This suggests that in a natural situation, dominant large males frequently would challenge newcomers that signal high dominance rank. Small males with nuptial coloration probably would pay a cost in that they would elicit aggressive behavior and be punished by larger, dominant males. Display of nuptial coloration may have additional costs. Recent evidence suggest that the immunosuppressive consequences of high testosterone levels associated with the development of nuptial coloration renders orange large males more susceptible to parasites (Salvador et al., 1996). Color pattern also influences predation risk (e.g., Forsman and Shine, 1995), and it is quite likely that more brightly colored males would be more conspicuous to visually guided predators (Martín and López, 1999).

The permanent association of small *P. algirus* males as subordinates within the home ranges of large males suggests that small males may adopt a satellite-sneaking mating strategy (Salvador et al., 1995). In this context, dull coloration may be a reliable signal of subordinance (Lyon and Montgomerie, 1986). By signaling subordinance, a small male with a low resource-holding potential might evade aggression and be able to remain within the home range of a larger, old dominant male. By taking advantage of the large males' difficulty in guarding several females, smaller males may not only obtain some forced matings (if they are able to subdue the female), but also gain experience that may increase their reproductive success in subsequent seasons. Further studies are clearly necessary to determine whether small male *P. algirus* lizards have a similar reproductive success to larger males or whether small dull males are simply making the best of a bad job until they are older and larger and become dominant.

Our experiment failed to reveal any benefits of nuptial coloration accruing to small males. Small males were apparently able to distinguish between other small males and large males, independent of head coloration, suggesting that the development of orange head coloration would not translate into increased social dominance. Furthermore, agonistic interactions between small males are rare in the field (Salvador et al., 1995, 1997). Thus, direct competition between small males for territories or females is probably quite weak. Nor did our results reveal any effect of male coloration on copulatory success, suggesting that small males developing nuptial coloration would not enjoy higher mating success. In fact, female mate choice appears to be rare in lizards (Olsson and Madsen, 1995; Tokarz, 1995), although female choice based on male body size has indeed been demonstrated in two lizard species (Censky, 1997; Cooper and Vitt, 1993). Our results suggest that male body size influences female acceptance of matings also in *P. algirus.* Females tended to flee more often from small males than from large males, and large males were more successful in obtaining matings. However, our experiment does not demonstrate female preference for large body size per se because the responses of females may have been dependent on male behavior. In the field, large males court females during long time periods before they attempt to copulate and also guard them after the copulations (Salvador et al., 1995, see also Olsson, 1993a; Vitt and Cooper, 1985). Small males, in contrast, do not court but instead seek forced copulations when the large male is absent (Salvador et al., 1995). Perhaps female receptivity requires a previous courtship, something that younger, and presumably less experienced, males may not perform satisfactorily. Nevertheless, females might not accept small males even if they do court for longer, and forced copulations therefore may be their only option.

Although our findings suggest that coloration is of little importance in determining the outcome of agonistic interactions in this species, it is possible that the relative importance of size and color depends on interindividual distances. Body size (or another trait correlated with fighting ability) may be the most important character when two individuals are close together, whereas coloration may be more important in long-distance communication, when body size is difficult to assess accurately. Our experimental setup did not enable us to examine such long-distance communication. Nevertheless, the ability to recognize large, dominant males may enable small males to retreat before being located, thereby deferring agonistic interactions and avoiding the costs of fighting (Cooper and Vitt, 1987; Pough and Andrews, 1985). By the same token, large, brightly colored dominant males may be able to chase away competitors without having to approach them and engage in escalated and potentially costly fights.

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