Context-dependent response to red coloration in stickleback

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Abstract. Although Tinbergen found that red nuptial coloration of male three-spined stickleback, Gasterosteus aculeatus, elicited attack by other males, subsequent researchers have had difficulty replicating his results (Tinbergen 1948, Wilson Bull., 60, 6–51; 1951, The Study of Instinct. Oxford: Oxford University Press). Rowland et al. (1995, Anim. Behav., 50, 267–272) found that males tested in neutral tanks attacked a moderately coloured video image of a conspecific male more than either a bright or dull image in simultaneous presentations. These results suggest that a dual-effect process representing an interaction between aggression and fear might determine attack response. Based on this hypothesis, males tested in home tanks should attack the video images more than males tested in neutral tanks and should attack the brighter images most because their attack:fear ratio is higher. Males in their own territories spent more time attacking video images than males in neutral tanks. Males in their own territories also spent more time attacking the brighter image than they spent attacking either the moderate or the dull image. These results demonstrate the influence of spatial location on the response of male stickleback to rivals. Furthermore, a dual-effect model provides a heuristic tool for understanding the agonistic behaviour of male stickleback.

The effect of red nuptial coloration on territorial aggression of male three-spined stickleback has been the focus of much attention (Muckensturm 1968; Rowland 1982, 1994; Baerends 1985; Rowland & Sevenster 1985; Collias 1990) ever since Tinbergen (1948, 1951) concluded that red is a sign stimulus for aggression. This concept was based in part on the observation that a model of a male stickleback with a red ventral area elicited more attack from conspecific males than did models without red (ter Pelkijkwijk & Tinbergen 1937). Subsequent experiments revealed, however, that red did not act merely as a releaser of aggression in this species (Peeke et al. 1969; Wootten 1971; Rowland 1982; Rowland & Sevenster 1985), and it is difficult to conceive how a trait that releases attack from rivals would evolve through intra-sexual selection processes (Rowland 1982).

We recently re-tested the response of male stickleback to variations in red coloration using video playback and offered an explanation for why males do not always attack the brighter red male (Rowland et al. 1995). We found that males in a neutral tank spent more time attacking a moderately coloured image of a conspecific male when it was paired and presented with either a grey-tone or a brightly coloured video image of the same male. There was no difference, however, between the amount of time males spent attacking grey-tone or bright images when these were paired and presented together. We suggested that an interaction between aggression and fear, a dual-effect process, could explain the variability in response to red coloration. Under this model, brightly coloured males would stimulate high levels of both aggression and fear such that fear could decrease attacks. Dull-coloured males, however, would stimulate low levels of both aggression and fear, resulting in similarly lower levels of overt aggression. Moderately coloured males would elicit the most attacks, because they stimulate high levels of aggression but relatively low levels of fear.

In these initial video playback experiments (Rowland et al. 1995), space limitation in our
laboratory required us to test territorial males in neutral, unfamiliar tanks; a male might respond differently to variations in red coloration when an intruder is in its own territory, however. Differences in behavioural responses to a given intruder based on the location of the encounter have been shown in several species, including mammals (Miczek 1977), birds (Hinde 1956; Simpson 1985), fish (Myrberg & Thresher 1974; Giraldeau & Ydenberg 1987), and stickleback (Tinbergen 1953; van Iersel 1958; van den Assem 1967; Huntingford 1977; Rowland 1983; Collias 1990). Most studies revealed that males attack an intruder more when the encounter occurs on rather than off the defender’s territory especially when the intruder is close to the defender’s nest. The effect of red nuptial coloration might therefore differ in various spatial contexts and result in different attack rates.

We previously predicted that a male stickleback should respond more to conspecifics intruding into its own territory because it would be highly motivated to defend its nest (Rowland et al. 1995). Furthermore, bright red coloration should elicit more aggression from a male tested in his own territory than from a male tested in a neutral area. This increase in aggression should occur because (1) the male has more to lose in his home tank (his territory and nest) and (2) male red colour intensity is positively correlated with his tendency to attack (Rowland 1984; McLennan & McPhail 1989) and thus reflects a greater threat to the defending male and his nest. In the present study, we tested our hypothesis by comparing the response of nesting male stickleback to bright, moderate and dull video images of a conspecific male ‘intruder’ presented at the edge of the defender’s territory.

MATERIALS AND METHODS

Subjects

We collected male three-spined stickleback from Long Island, New York (April–May 1994) and held them in groups in laboratory stock tanks maintained at spring conditions (16:8 h light:dark, 18°C; brackish water, 12–14 ppt salinity). All males were fed frozen brine shrimp, Artemia spp., throughout the study period. We then chose males with slight nuptial coloration, indicating they had entered reproductive condition, and placed them individually into a territory tank (50 × 25 × 30 cm) that contained a sand-filled nesting dish with an artificial plant placed in the centre, a water filter and filamentous algae (Rhizoclonium spp.). Within 1–3 days, the coloration of the males intensified, and they built and continued to maintain a nest, indicating that each male had established the tank as its territory.

Testing Procedures

Testing procedures were similar to those used by Rowland et al. (1995). Each subject was simultaneously presented with two versions of the same video sequence (S-VHS Olympus VX-S405-KU) of a male three-spined stickleback directing zigzags, charges and bites towards the viewer. The video sequence was 2 min long and appeared on separate high-resolution colour monitors (27 × 20 cm; Panasonic CT-1382Y). The monitors were located 10 cm from each end of the territory tank, and their hue intensity was controlled by setting their digital controls to one of three predetermined settings: dull, moderate or bright. To our eyes, the dull image appeared grey-tone, the moderate image matched the coloration of most males, and the bright image looked redder than the average males found in this population. These settings do not vary the overall luminance of the image (Rowland et al. 1995).

We randomly presented males with paired combinations of dull, moderate and bright images twice so that we could reverse the colour settings in each pairing to control for possible position effects. At the end of each 2-min playback, males received 2 min of rest. Each male received 12 min of video playback.

We recorded each subject’s response with a Hi-8 video camera-recorder (Nikon VN-750) and analysed the videotapes using the Observer event recording program (Noldus Information Technology, Wageningen, The Netherlands). We measured visit time as the amount of time males spent within one body length of each tank wall and facing the adjacent video image. We were unable to reliably distinguish between closed-mouth and open-mouth contact and so measured these together as butt/bite time on each corresponding tank wall exclusive of our visit time measurements.
RESULTS

All subjects responded to the video images. Because fish in this population tend to show consistent behaviour patterns from year to year (W. J. Rowland, personal observation), we compared the overall pattern of the subjects’ responses to those in our previous study (Rowland et al. 1995). Males tested in their home tanks spent more time butting/biting the video images in the dull versus bright ($P=0.043$) and dull versus moderate test series ($P=0.004$; two-tailed Mann–Whitney $U$-test) than males that had been tested in neutral tanks. Moreover, a $3 \times 2$ factor repeated measures ANOVA on the square root transformed data revealed that males in the present study spent more time butting/biting the bright image than the moderate or dull images and marginally more time butting/biting the moderate than the dull image (Fig. 1a). Males also spent more time visiting the bright image than either the dull or moderate images and more time visiting the moderate than the dull image (Fig. 1b).

DISCUSSION

Our results demonstrate that male three-spined stickleback attack more frequently when they are in their own territories than when they are outside them. This finding supports the proposal that male stickleback attain a maximal level of aggression when in the presence of their nest (Tinbergen 1953; van Iersel 1958; Wootton 1970). Our results are consistent with the hypothesis that proximity to the nest increases the intensity of a male’s aggressive response. More importantly, the relative response to the degree of red coloration of intruders differs for males tested in home tanks in which they had a nest versus neutral tanks in which they did not have a nest. Home-tested males attacked the brighter red video image more than either the moderate or dull image, suggesting that the bright image aroused relatively more aggression than fear. Hence, the attack response to conspecific males appears to be context-dependent.

Barlow & Siri (1994) showed an effect of context other than that of encounter location. They found that dummy models of the gold morph of the Midas cichlid, *Cichlasoma nitrellum*, which dominates grey, white and black morphs in the laboratory, receive more attacks than grey, white, or black dummies when the dummies are presented ‘passively’ to the subject but not when the dummies are made to react to the subject’s own behaviour. Furthermore, the gold dummy is attacked more only when presented against a white or grey background but not against a black or gold background. That dominant colour morphs do not always evoke or inhibit attack in Midas cichlids or stickleback supports the claim that the response to, and possibly the function of, colour depends on the context of the encounter.

The effect of context can be readily explained by the dual-process model of agonistic behaviour (Rowland et al. 1995). This model is based on the
conflict hypothesis that ethologists (Tinbergen & van Iersel 1947; Tinbergen 1952; Morris 1956; Baerends 1975) originally proposed to explain the origin and evolution of displays. The conflict hypothesis maintains that organisms in which the mutually incompatible tendencies to attack and flee are equally activated are unlikely to express either behaviour pattern, but instead perform a threat display (Hinde 1981). We suggest that the context of an encounter modifies the behavioural response by influencing the motivational tendencies of the animal.

The dual-process model proposes that it is the interaction between internal processes (primarily aggression and fear) and external stimuli (e.g. the colour of the intruder and the site of the encounter) that determines attack response in male stickleback. That is, when a male is in his territory, his overall level of aggression is higher than when he is in a neutral area. Thus, even though brighter males are more likely to attack (Rowland 1984; McLennan & McPhail 1989), a defending male within its own territory should be selected to meet this challenge by quickly responding to bright intruders with appropriately high levels of aggression. When a male is outside his territory, however, bright opponents may activate fear more strongly than aggression and thereby prevent the former male from fully expressing attack behaviour. Hence, response to relative colour intensity would be expected to be context-dependent in male stickleback.

Our model of motivational processes underlying the agonistic behaviour of three-spined stickleback is consistent with the predictions made by Parker’s (1974) model of the evolution of fighting. If two males have equal resource-holding power but one male controls a resource (the territory owner) and the other is an intruder, then the territory owner would be expected to escalate if loss of the resource would lead to a larger fitness decrease for the territory owner than a fitness increase for the intruder (Parker 1974). Thus, the territory owner should be more likely than the intruder to escalate (attack) because the owner has already invested in the territory; in short, the costs are higher to obtain a new territory than to retain the present one. By contrast, the intruder must pay the initial investment costs before gaining any fitness benefits (Parker 1974). In three-spined stickleback, males without territories (i.e. males in neutral tanks) are less likely to attack because searching for an unoccupied territory may be less costly than fighting for one already occupied particularly if the owner (i.e. the video image male) is bright red and of a higher resource-holding power than the attacker. When males are on their own territories (i.e. in home tanks), however, they tend to defend their territory against all attackers with less regard for resource-holding power. Therefore, the dual-process model provides a mechanism by which individuals can adopt situation-specific fighting strategies.

This study illustrates the importance of the spatial location of an agonistic encounter in mediating the response of three-spined stickleback males to the nuptial coloration of rivals. Although we infer a change in the internal state of the male as a determinant of his response, the underlying physiological basis for this effect is unknown. Further research into the proximate mechanism of this context-induced motivational switch should provide additional insight into the control and evolution of territorial behaviour.

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