

Stickleback distraction displays: sexual or foraging deception against egg cannibalism?

FREDERICK G. WHORISKEY

Department of Renewable Resources, Macdonald College of McGill University, 21,111 Lakeshore Rd., Ste-Anne-de-Bellevue, Quebec H9X 1C0, Canada

(Received 13 June 1990; initial acceptance 20 August 1990;
final acceptance 23 October 1990; MS. number: A5820)

Abstract. Three-spined stickleback, *Gasterosteus aculeatus*, males guarding nests containing eggs were tested for their use of distraction displays against all-male, all-female and mixed male and female conspecific intruder groups. Distraction displays were used against all groups, suggesting that the display is a foraging rather than a sexual deception. Most males used two different displays, with the most obvious being employed primarily when intruders were close to the nest. Males also buried their nests with sand to protect them. Groups with male members made more territorial intrusions and fought more with the residents than all-female groups. However, nest survival-to-hatching was better in mixed and all-male trials than all-female trials. Raiding caused most nest destructions, although suffocation following burying killed some eggs. The high nest survival-to-hatching in the all-male and mixed trials probably occurred because some male intruders established territories. This reduced the number of fish in raiding groups and resulted in joint attacks by several territorial fish on the remaining group members. Resident males could control the remaining fish with aggression. Males guarding nests without eggs also used distraction displays, but they did not bury their nests.

Distraction displays are conspicuous behaviour patterns that divert a predator's attention from nests, eggs or young to an adult guardian (Simmons 1955; Skutch 1955; Gochfeld 1984). The displays may be simple, involving a guardian showing itself and moving off with the predator following, or they may deceive the predator by providing false information about nest location or vulnerability of a guardian to capture (e.g. Gochfeld 1984). Distraction displays are used frequently by birds and occasionally by other vertebrates (Armstrong 1949a, b; Gochfeld 1984). Most reports describe motor patterns and speculate on a display's origins. Attention has also been focused on display efficiency and variation among populations (reviewed in Gochfeld 1984; see also Pederson & Steen 1985; Kalsi & Khera 1987; Hudson & Newborn 1990). However, Gochfeld (1984) commented that it was difficult to think of another problem where the 'ratio of anecdotal accounts to scientific study is so great'.

The three-spined stickleback, *Gasterosteus aculeatus*, is the only fish reported to use distraction displays (Whoriskey & FitzGerald 1985; Foster

1988; Ridgway & McPhail 1988). Its display is the only example, from any taxon, used to thwart intraspecific predation (egg cannibalism). Male sticklebacks provide uniparental care for nests and young (FitzGerald & Wootton 1986). During the breeding season, raiding conspecific groups composed of females, non-nesting males and occasional nesting males attack nests and consume eggs. When raiding groups are too large to be controlled by paternal aggression, male sticklebacks use distraction displays to attempt to decoy the group away from nests (Whoriskey & FitzGerald 1985; Foster 1988; Ridgway & McPhail 1988).

Interpretations and descriptions of the stickleback distraction display differ. Whoriskey & FitzGerald (1985) described it as 'fighting cannibalism with sex'. The terminal display of the courtship ritual is a 'show'. A male rolls on its side and pokes its snout into the nest, showing the female the entrance. At Isle Verte, Quebec, males threatened by raiding groups rolled on their sides, swam up into the water column and out of their territories, then poked their snouts onto the substrate. Raiding

fish that followed attacked the substrate at the point indicated by the male (Whoriskey & FitzGerald 1985). Females may raid nests to force males to start new reproductive cycles, thereby creating mating opportunities (FitzGerald & van Havre 1987). A show deception composed of courtship elements would target receptive females in raiding groups. The non-nesting and occasional nesting males that join raiding groups should not respond to a courtship-based display, but might follow females that have been decoyed away and are making rapid movements that signal the presence of food (e.g. Pitcher 1986).

Other authors working with different populations have suggested that the stickleback display is based on a foraging deception. Ridgway & McPhail (1988) described a 'spasmodic' distraction display, in which a stickleback male assumed a contorted 'U' or sigmoid posture, swam spasmodically along the bottom away from the nest, and finished by poking its snout into the substrate. These motions were interpreted as exaggerated feeding gestures. Males guarding eggs displayed, while those with empty nests did not. Foster (1988) examined the distraction displays of sticklebacks from sites with different risks of egg cannibalism. At a site with intense egg cannibalism, males used a conspicuous display. They swam out of their territories, sometimes tipped on their sides displaying nuptial coloration, and finished by aggressively rooting in the substrate, presumably mimicking feeding. Males with and without eggs in their nests displayed (Foster 1988). If these displays mimic the species foraging behaviour, then they should target both males and females.

In the laboratory, I presented all-male, all-female or mixed intruder groups of sticklebacks from Isle Verte to males guarding nests with eggs. I predicted that the distraction display was a sexual signal and that all-female groups would orient to and follow it, while all-male groups would not. If all-male groups were decoyed, then the alternative hypothesis that the display was a foraging deception would be accepted. Males guarding empty nests were presented with intruders to test whether the display was employed only when a male was guarding eggs. Finally, the danger posed to residents' nests by the different intruder groups was evaluated by monitoring resident nest fate until the nest was destroyed or the eggs hatched.

METHODS

Study Organism

Three-spined sticklebacks were seined at Isle Verte, Quebec, and transported in aerated containers to the laboratory. Fish were held in large (1000 litres) holding tanks and provided with an ad libitum mixture of freeze-dried and live (white worms, *Enchytraeus* sp.) food until used.

Protocol

Two males, selected at random, were introduced into a 20 cm deep wading pool measuring 1 m in diameter. The pool bottom was covered with a 2.5-cm layer of white silica sand, and short sections of thread served as nesting material. The first male to build a nest became an experimental subject, and the other was removed. A weighed, ripe female was added to the pool to spawn with the male. Following spawning, the female was removed and reweighed to determine the size of the egg mass in the nest. Females that did not actively court within 15 min were removed and a new female was provided. Spawning occurred in the morning, and trials were started the following afternoon.

The experimental treatments consisted of adding an intruder group to a pool containing a resident male, then quantifying the resident's use of and intruder's response to distraction displays. Intruder groups were comprised of: (1) 12 males (all-male), (2) 12 females (all-female) or (3) six males and six females (mixed). Twenty-four resident males were tested, eight each assigned at random to the three treatments. Weights of the egg masses defended and sizes of the resident males did not differ significantly among treatments (Kruskal-Wallis ANOVA, median weight of eggs defended = 1.15 g (range 0.90–1.46 g), $P > 0.28$; median male total length 7.3 cm (range 6.7–7.8 cm), $P > 0.35$). Different intruders were used in each of the 24 trials.

Behavioural Observations

Immediately after the introduction of intruders to a pool, a single 20-min observation was made. I recorded the following: the time it took for the resident to first orient to the intruder group, the time to the resident's first attack, the total number of resident attacks (bites and lunges), the number of attacks by intruders on the resident, and the

number of attacks on the nest. Resident nest-oriented behaviour patterns recorded were the number of times males bored into the nest (see Wootton 1976), number of fanning bouts (aeration of the eggs), and sand-biting. Sand-biting usually consists of males taking a mouthful of sand and spitting it back to the substrate (Wootton 1976). Males in these experiments used the behaviour to bury the nest in an apparent defence against cannibalism. I recorded the number of distraction displays performed, the distance of the closest intruder to the nest when the display was initiated, and intruder responses (orient or ignore) to the displays.

Following the observation period, I left the intruders and residents together until the nests were destroyed or the eggs hatched (8 days). I did this to determine which type of intruder group posed the greatest threat to resident male reproductive success, and to correlate the data obtained in the initial observations with male ability to hatch eggs. The dynamics of the unanticipated burying behaviour, which could contribute to resident reproductive success, were also quantified. Nest state was checked three times daily, at 0900, 1300 and 2000 hours. At each check, I noted the percentage of the nest surface that was covered with sand, and the number of other territorial and/or nesting males present in the pools (all-male and mixed groups only).

Males without Eggs

Six males guarding empty nests were tested to see whether they would employ the distraction display. All-male intruder groups were used, otherwise the protocol was as previously described.

Statistical Analysis

The small sample sizes (six to eight per treatment), made interpretation of tests for normality and homogeneity of variance problematic, so I used non-parametric statistics. Kruskal-Wallis ANOVAs, Spearman correlations (r_s), Wilcoxon-Mann-Whitney U -tests, and chi-squared tests were done with the STATGRAPHICS program (Statistical Graphics Corporation). Multiple comparisons of means after the ANOVAs were carried out following Conover (1980).

RESULTS

Intruder groups with male members were the most aggressive (Table I). Residents were attacked sig-

nificantly more often by all-male or mixed groups than by all-female groups. Residents suffered significantly more nest attacks from the all-male than the mixed or all-female groups. Some males from the all-male and mixed intruder groups began to defend areas within the pool during the 20-min observation. Many attacks on the resident came in disputes over the establishment of territories.

Resident aggression against intruders was high in all trials, however members of all-female groups were attacked significantly more often than members of other groups (Table I). Generally females fled without retaliating when attacked, thus some female intrusions could be managed with aggression. Residents facing all-male groups devoted less attention to nest care (significantly lower levels of boring) than did residents confronting all-female groups (Table I).

Two distinct distraction displays were noted. The first consisted of the fish positioning itself at an angle of about 45° to the substrate, and rooting vigorously therein, presumably mimicking foraging. Median values for the occurrence of rooting by residents confronted with all-male, all-female and mixed groups of intruders (4, 0 and 1, respectively) did not differ significantly (Kruskal-Wallis ANOVA, $P > 0.17$). The second display noted was the show. Median values for number of shows performed (4.5, 0.5 and 2 for all-male, all-female and mixed groups, respectively) also did not differ significantly between treatments (Kruskal-Wallis ANOVA, $P > 0.10$). However, the total number of distraction displays (sum of the rooting and show displays) differed significantly between groups (Kruskal-Wallis ANOVA, $P < 0.05$). More displays were used against all-male groups than all-female groups (Table I).

Of the 24 residents with eggs tested, 19 used some form of display, and 11 used both show and rooting (Table I). The choice of the distraction display employed depended on the distance of the intruding group from a male's nest, rather than group type. Shows occurred when intruders were close and the threat to nest survival presumably the greatest. Rooting was employed to steer away groups that were outside of but heading towards the territory. Median values (range in parentheses) of the distance of the closest intruder from the nest when the show and rooting displays respectively were initiated were 0 (0-45) and 80 cm (25-100) for all-male experiments, 10 (0-68) and 55 cm (40-100) for all-female experiments and 0 (0-50) and 60 cm

Table I. Median values of resident behaviour, and percentage of the resident males using a given distraction display, during the 20-min observations (range in parentheses)

	Intruder group		
	All male	All female	Mixed
Behaviour*			
Resident attacks	265 ^a (195-480)	362 ^b (286-474)	278 ^a (180-383)
Attacks on resident	10.5 ^a (1-20)	1.5 ^b (0-17)	18.5 ^a (6-66)
Attacks on nest	2.0 ^a (0-6)	0 ^b (0-1)	0.5 ^a (0-4)
Boring	5.5 ^a (3-12)	13.5 ^b (6-19)	7.5 ^{ab} (5-16)
Number of distraction displays used	6.0 ^a (3-29)	2.5 ^b (0-10)	3.0 ^{ab} (0-26)
Sandbiting	29 (8-80)	28 (1-62)	15 (0-41)
% Males tested using distraction displays†			
Rooting	75	38	63
Show	88	50	63
Some display	100	63	75

*Values in a row marked with a different superscript differ significantly from each other (Kruskal-Wallis ANOVA followed by a multiple comparison test).

†*N* = 8 in all cases. Some display: males using either show or rooting.

(25-100) for the mixed trials. The differences in distances between show and rooting were significant for all three treatments (Wilcoxon-Mann-Whitney *U*-test, *P* < 0.05, *N*₁ = *N*₂ = 8).

The displays were effective. In most cases where displays were observed, at least some of the fish in the intruder group focused their attention on and followed the male. The few instances where there was no response occurred soon after the intruders were introduced to a pool. The fish were probably still orienting to their new surroundings and hence were unreceptive. No nests were destroyed during the 20-min observations, and distractions successfully drew raiding groups out of several territories even after intruders had found and attacked the nest. However, there were no significant correlations between the total number of distractions used in the behaviour observation and a male's ability to ultimately hatch its eggs (all-male intruders, *r*_s = -0.28, *P* > 0.45; all-female intruders, *r*_s = 0.20, *P* > 0.90; mixed groups, *r*_s = -0.11, *P* > 0.76).

All resident males in the all-male and all-female trials, and seven of eight males facing mixed groups buried their nests as protection against cannibals.

There was no significant difference in the level of sandbiting of residents exposed to the different groups (Kruskal-Wallis ANOVA, *P* > 0.59, Table I). Residents frequently covered and uncovered their nests in the days following the behavioural observation, however there was no evident diurnal periodicity or long-term trend to the activity.

The number of nests that survived to hatching varied significantly between treatments. Five nests produced fry in the mixed group experiments, compared to three and none in the all-male and all-female intruder experiments, respectively. Nests that faced intruder groups containing males (pooled sample of all-male and mixed groups) had a significantly higher probability of hatching than those facing all-female groups (chi-squared test, *df* = 1, *P* < 0.05). No nest destructions were directly observed; however, the most likely cause was raiding. Stomachs of four intruder fish were analysed following the disappearance of six nests. There were eggs in the stomachs of the intruders in all cases, and resident males also ate eggs in five of six instances. The eggs in one nest in the all-female series had apparently asphyxiated. They were

undergoing normal incubation until the male built a volcano-like mound over the nest 6 days into the experiment. When the eggs failed to hatch on time, I opened the nest to find a strong odour of hydrogen sulphide and dead eggs.

Some males from the all-male or mixed intruder groups set up territories and/or nests in the pools during the 8-day observation period. No significant difference occurred in the number of additional fish nesting in all-male and mixed group intruder treatments (Wilcoxon–Mann–Whitney U -test, $P > 0.53$), so the data were pooled. The number of additional nesting or territorial males ranged from two to six (median = 4). There was no significant correlation ($r_s = -0.27$, $P > 0.31$) between the number of nesting or territorial males and the residents' ability to hatch their eggs.

Resident time to orientation to the intruders, time to first attack and number of fanning bouts did not differ significantly between the treatments (Kruskal–Wallis ANOVA, $P > 0.02$).

Similar to males guarding eggs, males with empty nests used distraction displays to defend their nests. Five of six males tested used the rooting display, and three of six used the show display. However, resident male behaviour to all-male intruders differed when I compared males guarding eggs ($N = 8$) with males with empty nests ($N = 6$). Males with eggs bored more (median of 5.5 (range 3–12) versus 1.0 (range 0–8) bouts, Wilcoxon–Mann–Whitney U -test $P < 0.05$) and sandbit more (median of 29 (range 8–80) versus 2 (range 0–17) bouts, Wilcoxon–Mann–Whitney U -test, $P < 0.05$) than males with empty nests.

DISCUSSION

Intruder groups with male members were the most aggressive to residents. Nest survival-to-hatching, however, was best in the all-male and mixed intruder trials. This appears contradictory. Soon after the introduction of groups with males, a burst of territorial activity occurred. If an intruder male gained a territory, it withdrew from the group. Up to six intruder males established territories and/or built nests during an experiment. Territorial defence also took up space in the pool, leaving a small 'neutral' area for occupation by the remaining intruders. Fish attempting to move out of the neutral zone usually transgressed two or more territory boundaries, and faced joint attacks from several males. Thus, the long-term nest raiding

danger in all-male and mixed group trials was reduced compared with all-female trials by two factors: decreases in intruder group size as males established territories, and by the joint attacks of intruders by territorial males if the remaining intruders moved out of the neutral area. Similar behavioural dynamics may occur at the field site from which these fish came. At Isle Verte the fish arrive in the tide pools and replace previous residents in synchronized pulses resulting from the timing of tidal flooding of the breeding site (Whoriskey et al. 1986). Males may settle their territorial disputes before any begin guarding eggs, establishing their 'alliances' and decreasing their risk of being raided.

Two different distraction displays were noted; each worked equally well against all intruder types. This refutes the hypothesis that the display is a sexual signal (Whoriskey & FitzGerald 1985), and both are probably best regarded as foraging deceptions. However, groups approaching but still relatively far from the nest were given a rooting display, whereas show was used when the intruders were close and the risk to the eggs presumably the greatest. The more conspicuous show may be better than rooting at focusing the attention of the intruders on a resident male. The show may be reserved for dangerously close intrusions because it is energetically more costly than rooting, although this suggestion needs testing.

It is not clear why the sticklebacks of Isle Verte, as well as those in Foster (1988), use distraction displays in defence of empty nests, while those studied by Ridgway & McPhail (1988) did not. A vast array of abundant nesting materials are available in most breeding habitats (Wootton 1976, 1984), thus it is unlikely that nesting materials would need to be defended. The divergent results could be a consequence of different methods: Ridgway & McPhail (1988) presented their intruders in a bottle, while the other studies used free-swimming intruders.

Twenty-four of 30 residents tested (all trials using males with or without eggs) used one of the two displays, while 14 of 30 used both. All males probably had both displays in their behavioural repertoire, but did not exhibit them because their nests were not sufficiently threatened by the intruder group. The widespread possession of the distraction displays by individuals from Isle Verte, and the presence of population-specific distraction displays in other populations (Foster 1988; Ridgway &

McPhail 1988; Foster & Ploch 1990) suggests that intraspecific egg predation has been a major evolutionary factor affecting three-spined sticklebacks. At Isle Verte, up to 100% of the stickleback nests present in a tidal pool have been destroyed by raiding groups (Whoriskey & FitzGerald 1987, unpublished data), and high rates of nest destruction have been recorded at other sites (Hyatt & Ringler 1989).

The egg-protection role of nest burying is indicated by the fact that virtually all males guarding nests with eggs buried their nests with sand in response to intruder groups, whereas males without eggs did not. Burying was done rapidly; many nests were completely covered within the initial 20-min behavioural observation period despite the time residents devoted to aggression and surveillance of the group. The sand cover could act as a mechanical barrier to the raiders. It could also help the nest blend in with the substrate, making it difficult for predators to detect. Parents that display must leave their nests, and covering them before moving away would seem to be an obvious defence. However, animals other than the stickleback apparently do not cover a nest before moving off to decoy a predator (e.g. Gochfeld 1984).

Nest burying was a dynamic process, and great inter-individual variability occurred in the way the nests were covered and uncovered. Burying may interfere with a male's ability to oxygenate his eggs, and the eggs in one experimental trial died apparently from asphyxiation after they were covered with a sand mound. However, eight males that buried their nests successfully hatched eggs, indicating that this interference can be compensated for, probably by increased fanning. Previous studies have shown that three-spined stickleback males generally open up the nest and/or increase their levels of fanning as the eggs age and their oxygen demand increases (see Wootton 1976; Reebbs et al. 1984). No such trends emerged from my data, perhaps because inter-individual differences in the perception of the risk of being raided occurred among males, and occluded any general trend. While burying was widespread in these experiments, I have never observed it at Isle Verte. The substrate type may dictate when nests can be buried. If the fine mud of the Isle Verte tidepools was placed on a nest, it could seal it, suffocating the eggs. Nest burying may be limited to populations breeding on coarse substrates (e.g. Vrat 1949; Kynard 1979).

Distraction displays are examples of manipulation via communication (see Dawkins & Krebs 1978). Sticklebacks from geographically widespread populations have developed one or more signals with which they manipulate raiding groups of conspecifics. However, animals that are being repeatedly manipulated should learn from the experience and cease to respond (e.g. Markl 1985). Foxes apparently learn to ignore bird distraction displays (Sonerud 1988). It remains to be determined whether these fish will do the same.

ACKNOWLEDGMENTS

The Natural Sciences and Engineering Research Council of Canada, and les Fonds pour le développement de Chercheurs et Aide à la Recherche provided financial support. I thank I. Jamieson for discussions and G. J. FitzGerald, S. Foster, M. Richardson and R. Titman for critically reading versions of this manuscript.

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