STICKLEBACK MALES, ESPECIALLY LARGE AND RED ONES, ARE MORE LIKELY TO NEST CONCEALED IN MACROPHYTES

by

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Summary

Previous studies have shown (1) that stickleback males enjoy increased mating success when their nest is concealed, (2) that males reduce their courtship in the face of predation risk to a lesser extent when their nest is concealed, and (3) that eggs in concealed nests have higher hatching chances. Here we test the prediction that male sticklebacks prefer to establish a territory at a site with a macrophyte under which they can conceal their nest. We planted macrophytes at half of the potential nest sites at two depths, in a section of a channel in which sticklebacks naturally occur. Subsequently, we found significantly more nests with eggs at the sites concealed by macrophytes than at the control sites, suggesting that wild sticklebacks preferred to build their nests at sites that offer concealment. At the shallow depth, males occupying a site with a macrophyte were larger and redder than males at control sites, but not at the deeper level. This suggests that males of higher competitive ability and greater conspicuousness were more likely to settle at shallow sites where predation risk by the grey heron is high.

Keywords: three-spined stickleback, *Gasterosteus aculeatus*, nest site choice, nest concealment, competition, predation risk, large size, red coloration.

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Introduction

Over the past few decades, female mate choice has been demonstrated to be widespread in diverse species across many taxa. Traditionally, female mate choice has been invoked to explain the evolution of extravagant male traits by sexual selection (Darwin, 1871; Andersson, 1994). Relatively few studies consider the possibility that females choose characteristics of the territory that a potential mate defends, at least in fish (Sargent, 1982; Thompson, 1986; Hastings, 1988a, b; Warner, 1988; Kraak *et al.*, 1999a). Certain aspects of a territory may be associated with direct fitness benefits to a female. For example, if the female or her young have to feed within the territory, it is important for a female to assess the quality of the resources held within the territory. Similarly, if territories vary in the degree to which they offer protection, from predators or any other detrimental agent, to the female or her young, a female should assess this aspect of the territory. If certain territories enhance offspring survival more than others, females and males should have the same territory preferences. If the availability of these good quality territories is limiting, males will compete for them, resulting in a correlation between male competitive ability and territory quality. Females may then either base their choice on male competitive quality, or directly on territory quality, depending on what is the most reliable correlate of offspring survival.

Fishes with male parental care for eggs in a nest provide a suitable system for investigating these issues. An example of such fishes is the three-spined stickleback *Gasterosteus aculeatus*, where the male defends a territory in which he builds a nest. The female oviposits her eggs in the nest and leaves them to the care of the male. Nest sites may vary in how well the female is protected from disturbances and predation during oviposition. And, most importantly, nest sites may differ in how well the eggs are protected, resulting in variation in the chances of survival to independence of the offspring. Stickleback males have to oxygenate their eggs by fanning, and defend them against egg predators, which are often cannibalistic conspecifics (FitzGerald, 1991). The male himself may also be safer in some types of territory than in others, and if a caring male is preyed upon, his offspring will certainly fall victim to egg predators.

Kraak *et al.* (1999a) found in a field study that males and their nests were less likely to disappear when they were concealed by a macrophyte. A study in wading pools (Sargent & Gebler, 1980) showed that male sticklebacks at concealed nests suffered fewer intrusions and devoted more time to fanning, resulting in higher hatching rates. Male sticklebacks with nests concealed by macrophytes also received more eggs (Kraak *et al.*, 1999a), implying more mates, than males with exposed nests. Apparently females found hidden nests attractive oviposition sites, probably because the survival chances of their offspring were higher in those nests.

Since males are more likely to breed successfully, i.e. have higher mating success and higher hatching success, when they have a concealed nest, one might expect that males prefer to settle and build their nest at sites where they can conceal their nest, *e.g.* under a macrophyte. If macrophytes are rare, one might also expect that males compete for these sites, and that males with traits that are associated with high competitive ability are more likely to defend such a site, *e.g.* bigger males. Furthermore, conspicuous males might be more prone to predation by visual predators, or to nest destruction by conspecifics that are attracted to the nest by visual cues. In that case males with brighter breeding coloration have more to gain from choosing sites where they can hide themselves and their nest.

In the present study we address two questions. Do male sticklebacks prefer to settle and build a nest at a site with a macrophyte? And, are males with certain traits more likely to have their nest at a site concealed by a macrophyte?

Methods

We performed our study in June and July 1997, at the same site as our previous studies (Kraak *et al.*, 1997, 1999a, b), at Roche (near Montreux, Switzerland, 46°26′N, 6°55′E) in the drainage system of the Rhone near Lake Geneva. Our study site was restricted to a stretch (of about 90 m length) of a small channel. The channel is boarded with blocks of concrete, 35 cm by 60 cm, along the sloping walls, and it has a wooden boarded floor. Sticklebacks nest in cutouts that exist in one corner of each concrete plate, or under the boards that line the concrete slopes at the bottom. Macrophytes, mainly small-leafed *Berula erecta*, occur in the channel sparsely, and even more so at shallow depths. These plants are not used by sticklebacks as nesting material. The most common predator of fish at Roche is the grey heron *Ardea cinerea*. Male sticklebacks nesting at or near the bottom are out of reach of this predator; shallower nest sites are at risk. During parental duties on a nest which is concealed under a macrophyte, stickleback males are visually hidden from this predator, and from conspecifics.

For the experiment we chose two stretches of channel without any vegetation, and at which there were no nesting males at the start of the experiment. These stretches had lengths of 8.2 m (stretch A) and 9.9 m (stretch B). These stretches contained 54 and 48 potential nesting sites respectively, considering only the cutouts of the concrete plates. We ignored nesting sites under the wooden boards at the bottom, because it was unpracticable to systematically check for nests there; only 3 males were suspected to have nests there throughout the experimental period. Half of the potential sites on each stretch were located on the northern sloping wall and the other half on the south. Furthermore, on both stretches, on both the north and the south, half of the sites were near the bottom (level 1) and the other half 35 cm higher up on the slope (level 2; the vertical distance between the levels was about 25 cm). These latter sites were about 10 to 45 cm below the water surface, depending on ambient water level which fluctuated due to weather conditions. We randomly assigned a macrophyte to half of the potential nesting sites, in such a way that at each level (1 and 2), on each side (north and south), on each stretch (A and B) equal numbers of nesting sites would be with and without plant. This way we assigned 51 sites with a macrophyte and 51 comparable sites without a macrophyte. We collected plant material (*Berula erecta*) from a wider channel into which our smaller channel drained. We tied the material together with wire into bundles, and attached the bundles onto hairpins, which we stuck between the blocks of concrete. A plant bundle was placed upstream of each assigned potential nest site, in such a way that the cutout, viewed from all sides, was visually hidden under the plant material. We spent 6 days a week at the study site, and replaced a macrophyte bundle as soon as we noticed its disappearance (due to the strong current plant bundles were sometimes flushed away). At least twice per week we checked each potential nest site and recorded whether a nest was present and whether it contained eggs. We checked the latter, wearing a diving mask, by carefully touching the nest.

For the second question we considered the whole study site including the stretches mentioned above. We caught each male nest owner with a dip-net, and put him in a bucket of water from the channel. Within one minute after catching we photographed the anterior half of the ventral side of the fish (one slide) and one randomly chosen lateral side (two slides, sometimes one slide) in a standardized way (described in Bakker & Mundwiler, 1994). We later analyzed the male breeding colors on the slides with a densitometer (X-Rite 310 Photographic Densitometer). The optical densities of red (R, filter 700 nm), green (G, filter 546.1 nm), and blue (B, filter 435.8 nm) were measured at 10 defined points (0.5 mm diameter) in the red throat region, and at 6 defined points in the iris of the eye (on each of the two slides, hence 12 points in total). From these measurements we calculated for each male a red index for the throat and blue and green indices for the eyes (for details see Bakker & Mundwiler, 1994; Kraak *et al.*, 1999a, b; see also Frischknecht, 1993). The red index of reproductively active males in a typical population (Wohlensee, Switzerland, Bakker & Mundwiler, 1994) ranged from 0.738 to 0.884. After photographing the fish we measured the standard length and the weight of the fish. Their condition factor was calculated as weight divided by standard length to the third power. All fishes were marked by clipping the first and/or the second dorsal spine, and/or one of the ventral spines. By a combination of these markings and standard length we were able to indentify individuals, and thereby control for pseudoreplication. Each male was returned to his site.

Statistical analyses

We analysed frequency data with binomial tests, or, in the case of contingency tables, with chi-square tests. We tested for differences in trait values between different sets of males with t-tests, and we used Pearson's r to test for correlations among traits.

Results

In the course of 54 days we detected 65 different nests with eggs within our experimental stretches. Of these nests, 53 were at sites with a macrophyte, and 12 were at sites without a macrophyte (binomial test, with the probability to settle at a site without macrophyte assumed to be 50%: $p \ll 0.00001$; the assumption of a probability of 50% of settling at a site without macrophyte is conservative because this probability increases as more and more of the sites with macrophyte become unavailable). These 65 nests were built by at least 50 different males: 41 males were caught from a site with a macrophyte and 9 from a site without macrophyte (binomial test performed on nests with different known nest owner only: $p < 0.00001$). Of the 53 nests with a macrophyte, 34 were at shallow sites and 19 at deep sites, and of the 12 nests without macrophyte, 4 were at shallow sites and 8 at deep sites ($\chi^2 = 3.8, p = 0.051$). Some sites were used more than once in succession, creating some non-independence in the dataset. We therefore also analysed the data using the sites themselves (instead of the nests) as statistical units. Thirty-three different sites with a macrophyte (of 51 available) were used for these 53 nests, whereas 9 different sites without macrophyte (of 51 available) were used for these 12 nests ($\chi^2 = 23.3$, $p \ll 0.00001$). Since some of these sites might have been occupied by the same male at different times, we cannot exclude a small degree of pseudoreplication. However, since minimally 50 different males were involved (see above) we believe that this highly statistically significant result is robust. Hence, sites with a macrophyte were much more likely to be used by a stickleback male for a nest, and this bias tended to be stronger at the shallow depth. All above results are from analyses of the data from the two stretches pooled; similar patterns emerge within the two streches (results that are significant in the pooled dataset are also significant in each of the two datasets separately).

We succeeded in catching 66 males from their nests at the study site. Fifty of these males were caught from the nests in the experimental stretches mentioned above: 41 from a nest with macrophyte, and 9 from a nest without a macrophyte. The other 16 males were caught from nests without a macrophyte outside the experimental stretches. Note that all sites without a macrophyte were unmanipulated sites, irrespective of whether they were within the experimental stretches mentioned above or not. One additional

TABLE 1. *Mean trait values (SD, N) of males at sites with and without macrophyte*

Trait	Macrophyte	All males	Deep males	Shallow males
red throat index	present	0.84 (0.03, 39)	0.83 (0.03, 15)	0.84 (0.03, 24)*
	absent	0.83 (0.04, 25)	0.84 (0.04, 17)	0.81 (0.03, 8)
green eye index	present	0.70 (0.01, 39)	0.71 (0.01, 15)	0.70 (0.01, 24)
	absent	0.70 (0.01, 25)	0.70 (0.01, 17)	0.71 (0.02, 8)
blue eye index	present	0.69 (0.01, 39)	0.68 (0.01, 15)	0.69 (0.01, 24)
	absent	0.69 (0.01, 25)	0.69 (0.02, 17)	0.68 (0.01, 8)
standard length in mm	present	49.6 (4.4, 41)	48.0 (3.6, 15)	50.4 (4.5, 26)**
	absent	47.4 (9.5, 25)	48.1 (11.5, 17)	46.1 (2.3, 8)
condition in mg × cm^{-3}	present	17.24 (0.93, 41)	17.47 (1.00, 15)	17.10 (0.88, 26)
	absent	17.39 (1.12, 25)	17.14 (1.09, 17)	17.92 (1.07, 8)

Student's t-test: $^{*}p < 0.05$, $^{**}p < 0.01$, all other $p > 0.1$; p-values are after Bonferroni correction for 5 tests. Two males were not photographed.

male was caught from a nest site with a macrophyte naturally growing there. This male is left out of the analyses, so that we compare 41 males that settled at a (manipulated) macrophyte site with 25 males that settled at an (unmanipulated) no-macrophyte site. The two groups of males did not differ in any of the traits we measured (Table 1, third column). However, if we separate the males according to the depth of their nest, an interesting picture emerges. Among males settled at the bottom, males with and without a macrophyte again did not differ (Table 1, fourth column). On the other hand, among the males that settled at a shallower depth, within reach of the predatory grey heron, the males nesting under macrophytes were redder and larger (Table 1, fifth column). Among the males at shallow sites, red throat intensity and body size were strongly correlated (Pearson's $r = 0.73$, $p \ll 0.001$); no other significant correlations existed between males' traits at these or the deeper sites. Overall, there were no differences between males settled at different depths (t-tests, all $p > 0.35$). Among the total of 66 males there are at most two males that contributed twice to the dataset (as inferred from same clipped spine markings and similar body length); however, they might possibly be different individuals. Removing them from the dataset did not alter our conclusions.

Discussion

First of all we need to justify why we chose to score male nest site preference as presence of nest with eggs. The objection to this criterion is, that it can be influenced as well by female preferences (for nest site and/or male) and such risks as nest raiding. We chose to use presence of nest with eggs, because only of those nests we could be sure that they actually were completed nests, and not an abandoned or unfinished nest or a clump of nesting material. Moreover, if we observed a nest without eggs over *e.g.* three days in succession at the same site, we could not know whether this represented one nest or three different successive nests. Nests with eggs did not pose this problem because if a nest contained *e.g.* three day old embryos the nest must have been in place already for three days. Finally, of nests without eggs we could not reliably determine the owner, because in our population males did not guard their nests very well yet when empty. Sometimes we found more than one different male associated with a particular empty nest(-like) structure in quick succesion; this was not the case when the nest contained eggs. However, if we consider all observations of nest(-like) structures (with and without eggs), which form a dataset consisting of unreliable and non-independent data points, we find that out of 314 observations 245 were at a site with a macrophyte and 69 at a site without. This ratio is similar to the one we found for nests with eggs only, and deviates so much from an expectation of 1:1 ($\chi^2 = 98.6, p < 10^{-22}$) that we believe our results regarding male nest site preference are robust. Since we could not catch owners of nests without eggs, we can not check for robustness in a similar way regarding the male traits. We have to take this into account when interpreting the results.

Our field experiment revealed a clear preference of male three-spined sticklebacks for concealed nest sites, which tends to be more pronounced at shallow depths. In sticklebacks, this is the first time that such a preference was experimentally assessed in the field. Our results agree with experimental laboratory studies (Hagen, 1967; Kynard, 1979; Sargent & Gebler, 1980; Cleveland, 1994), and with correlational field data (Hagen, 1967; Black & Wootton, 1970; Moodie, 1972; Kynard, 1978; FitzGerald, 1983; Mori, 1993). It is likely that this preference exists due to benefits of concealed nest sites either for the males themselves, for their embryos in their nest, or for their offspring after hatching. The evidence so far points to an increased reproductive success of males with concealed nests due to a greater mating success (Sargent & Gebler, 1980; Sargent, 1982; Candolin & Voigt, 1998; Guderley & Guevara, 1998; Kraak *et al.*, 1999a, b) and/or greater paternal success as measured by the smaller likelihood of nest abandonment before completion of the parental cycle (Moodie, 1972; Kynard, 1978; Mori, 1993; FitzGerald, 1993; Kraak *et al.*, 1999a), or higher hatching rates (Sargent & Gebler, 1980). A further advantage of concealed nests is better defense against sneakers (Sargent & Gebler, 1980; Sargent, 1982) but too much concealment could also promote the opposite (Mori, 1995).

One of the factors that may influence nest-site choice is predation risk. Recently, Candolin & Voigt (1998) experimentally showed that the visual presence of a predator made more males build their nest close to vegetation. Such a predator-induced nest-site choice is also known for other fishes, for instance *Gobiomorphus breviceps* (Hamilton, 1998). In our study, males that nested closer to the water surface tended to choose relatively more often nest sites that were concealed than males that nested at deeper levels. Males at the shallow sites were probably more liable to predation by the grey heron, the main stickleback predator in the channel. In another study of the same population, more exposed nests disappeared at shallow levels than at deeper levels before the completion of the parental cycle (Kraak *et al.*, 1999a).

Another factor that influences nest-site choice in sticklebacks is male-male competition. When the availability of nest sites is limited or when nest sites differ in quality, one expects males with high competitive abilities to be at an advantage. In several fish species, larger males are better competitors for nest sites (*e.g.* Bisazza & Marconato, 1988; further examples in Turner, 1993). In sticklebacks, redder and larger males are better competitors for territories (Bakker & Sevenster, 1983; Rowland, 1989; Bakker, 1994; Baube, 1997). However, there is a scarcity of data on traits associated with males that outcompeted other males for concealed nest sites. In Kynard's (1979) experiments, males with different numbers of lateral plates differed in their competitive abilities when competing for a limited number of concealed nest sites. In Sargent & Gebler's (1980) study, better competitors were not larger but other traits were not scored. In a previous field study of the same population, males with concealed nests did not differ in color traits or body size from males with more exposed nests (Kraak *et al.*, 1999a). Field studies of FitzGerald (1993), Mori (1995), and Guderley & Guevara (1998) suggested that redder males, or males with more skin carotenoids, nest at more concealed sites. In the present study, we found that males at concealed nest sites were redder and larger suggesting that these males might have outcompeted other males. Differences between males nesting at concealed sites and those nesting at more exposed sites were most pronounced at the shallow level. The shallow level may be attractive for nest building to males, provided that they are protected against predators: water velocity in the channel is high (up to 45 cm/s) and water temperature is low (maximum 14°C), but are less extreme at the more shallow level (Bakker *et al.*, unpubl. study). Lower current velocity and higher water temperature may reduce energetic costs of the male's activities and may be beneficial to his hatched offspring, which concentrate near the water surface. Furthermore, fewer sticklebacks pass the nest sites per unit of time at the shallow level (Kraak *et al.*, 1999a), thus reducing disturbances during courting, mating and caring at the shallow level. Mating opportunities did not seem to be affected: males nesting at the shallow level would go down to court passing females as often as males at the deep level would (S.B.M. Kraak, unpubl. data).

The differences in traits between males that nest at shallow sites that differ in concealment may thus be explained by differences in competitive abilities of males with a common nest site preference. This explanation requires that attractive nest sites were limiting. The difference with our previous study, in which no associations between male traits and nest concealment were found, is that in the present study we manipulated nest site concealment. Concealed nest sites are normally very rare at shallow levels in the channel, but in the present study half of the available nest sites were made concealed by placing macrophytes at potential sites that were randomly assigned. Not all concealed sites were used, suggesting that they were not limiting in the present study. This argues against different competitive abilities as an explanation for the observed results. However, the unused concealed sites may have been unattractive for reasons that we are unaware of. In that case, males may have competed for a limited number of attractive concealed sites.

An alternative explanation for the observed results is that males with different traits have different nest site preferences. Such variation in nest site preferences in sticklebacks with respect to concealment is suggested by variation in nest site choice in the absence of competitors (van Iersel, 1958; van den Assem, 1967; Hagen, 1967; Jenni *et al.*, 1969; Jenni, 1972; Candolin & Voigt, 1998). The benefits of concealed nests are likely to be different for males that differ in the intensity of red breeding coloration; redder males are probably more conspicuous to visual predators, and also to nest raids by conspecifics if these use visual cues. Greater vulnerability of redder males to predation was suggested in a previous study of the same population because males at exposed nest sites tended to be redder at the deeper level where the predation risk is lower than those at the shallow level were (Bakker *et al.*, unpubl. study). Red males have a potentially high mating success, because females find red males attractive (Bakker & Mundwiler, 1994), but if they have to reduce their courtship because of predation risk (Candolin & Voigt, 1998) they might not be able to actually exploit this advantage. Redder males, with their greater vulnerability to predation, may therefore gain more from having a concealed nest, and this may have resulted in them being more likely to occupy these sites.

An interesting alternative explanation is that males adjusted their expression of red coloration after nest site choice, according to the riskiness of their chosen site. We consider this unlikely, because we have no indications that males adjust the expression of their red coloration, and because male red coloration before breeding generally correlates well with male red coloration after having built a nest in an aquarium (T.C.M. Bakker, unpubl. data), implying that (relative) male red coloration is already largely determined before nest site choice. Furthermore, Guderley & Guevara (1998) found that males at concealed nests had more skin carotenoids; it is unlikely that males can adjust the level of skin carotenoids so quickly following the choice of a nest site.

Finally we must consider the possibility that our finding that males at concealed nest sites were redder and larger might be restricted to nests with eggs, as was mentioned at the start of the discussion. Maybe all males were equally likely to settle at sites with macrophytes, but female choice differed between concealed and unconcealed sites, for example perhaps females preferred duller or smaller males among those whose nest was not concealed. Or perhaps non-concealed nests were less likely to be raided when the owner was dull or small.

The results of the present study shed some light upon the discrepancy between field and laboratory findings with respect to the impact of intensity of red breeding coloration in sexual selection in this population (Kraak *et al.*, 1999a). The absence of a greater reproductive success of redder males in the field (Kraak *et al.*, 1999a) may be due to the lack of concealed nest sites in the channel close to the water surface. Greater reproductive success of redder males may be found in other parts of the water system where shallow concealed nest sites are not limited. The ecological context in which a population occurs, such as the local abundance of macrophytes and predators, may thus determine the direction and intensity of sexual selection.

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