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ORIGINAL ARTICLE

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Fifteen-spined stickleback (*Spinachia spinachia*) females prefer males with more secretional threads in their nests: an honest-condition display by males

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Abstract In the fifteen-spined stickleback (*Spinachia spinachia*), the male alone builds a nest and provides care for the eggs until they hatch. The nest is made of filamentous algae held together with shiny secretional threads of a glycoprotein, here called tangspiggin. Tangspiggin is produced by transformed kidney cells. I investigated how tangspiggin production was related to food intake by giving males low or high food rations. Males in the high-food group produced significantly more tangspiggin than those in the low-food group. Since low food rations did not lead to a significant drop in resting metabolic rate (oxygen consumption), tangspiggin production appears to be one of the first energy-demanding processes to be dropped during food deprivation. Among males given equal food rations, females preferred to mate with those with elevated levels of tangspiggin in their nests. Tangspiggin threads may signal safety for the offspring by keeping the eggs within the nest and protecting them from egg predators. Moreover, the threads become less shiny with age, due to particle deposition, and older nests that may house older (more valuable) eggs are thereby well camouflaged. Tangspiggin provides an honest signal of male condition, acting as an extra-bodily ornament, signaling direct benefits to females or possibly also indirect benefits of "good genes" from a male who is a successful forager.

Keywords *Spinachia spinachia* · Secretion · Glycoprotein · Nest · Ornament · Female choice

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Introduction

Theoretically, dishonest signaling can occur only at a low frequency in animal populations (Dawkins and Guildford 1991; Johnstone and Grafen 1993; Johnstone 1994). Empirical support for dishonesty under natural conditions is scarce (Steger and Caldwell 1983; Backwell et al. 2000). The body of theoretical and empirical data suggests that signals must carry a cost for the display to be honest, so that only high-quality individuals can afford to develop conspicuous traits and armaments (Zahavi 1975, 1977; Kodric-Brown and Brown 1984; Berglund et al. 1996). Alternatively, individuals may be constrained to honesty, as is the case when bright ornaments provides an honest indicator of a male's resistance against parasites (Hamilton and Zuk 1982; Milinski and Bakker 1990; Møller 1990; Höglund et al. 1992; Lindström and Lundström 2000).

Females often prefer males that are better at rearing and/or defending their offspring (Keenleyside et al. 1985; Bisazza and Marconato 1988; Knapp and Kovach 1991; Côte and Hunte 1993; Wiegmann and Baylis 1995; Forsgren 1997; Östlund and Ahnesjö 1998). In species where the male provides parental care, an ornament may reflect his ability to do so (Hoelzer 1989; Wolf et al. 1997).

Earlier studies on the reproduction of the fifteen-spined stickleback showed that females are choosy with respect to both male traits (Östlund and Ahnesjö 1998) and nest characters (Östlund-Nilsson 2000), where nest construction announces safety from nest predators. Studies showing that the nest is an important cue for female choice in fish have focused on nest concealment (Sargent and Gebler 1980; Sargent 1982; Hastings 1988; Kraak et al. 1999), water depth (Kynard 1978), oxygen stress (Jones and Reynolds 1999), and nest size (Lindström 1992; Kvarnemo 1995), or indirectly on male-male competitive ability over nest sites (Lindström 1988; Bisazza et al. 1989; Magnhagen and Kvarnemo 1989; Marconato et al. 1989; Hoelzer 1990; Lindström 1992). Many studies have also found that egg content may also

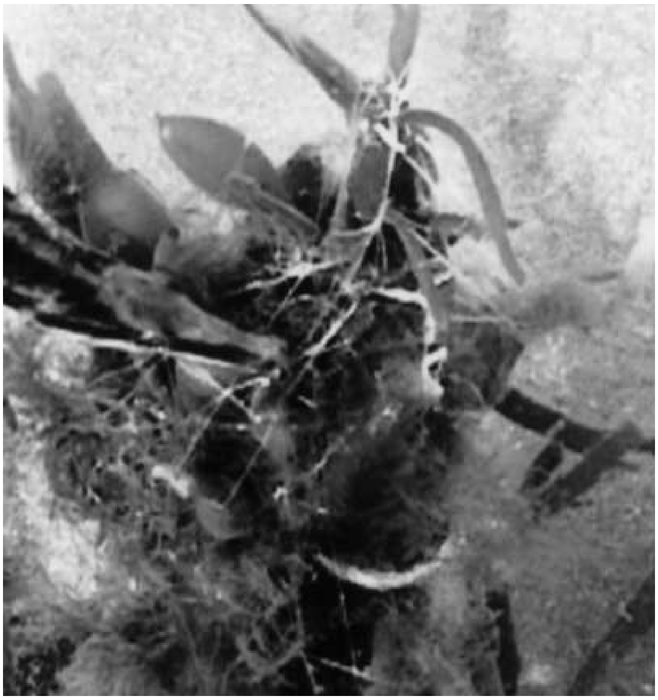

Fig. 1 The nest of the fifteen-spined stickleback is glued together by the male's secretional threads (tangspiggin) seen here as white threads

attract females (Ridley and Rechten 1981; Marconato and Bisazza 1986; Unger and Sargent 1988; Knapp and Sargent 1989; Sikkel 1989; Kraak and Videler 1991; Goldschmidt et al. 1993; Forsgren et al. 1996). However, there are no studies in the literature examing if the nest itself works as an honest extra-bodily ornament, reflecting male condition. Since parental duties are costly (for reviews see Clutton-Brock 1991; Smith and Wootton 1995), male condition is important for the quality of care.

In the fifteen-spined stickleback, the male alone builds a nest and rears the offspring. The nest is shaped and built of soft epiphytic red and green algae. These are attached to a macroalgae (usually *Ascophyllum nodosum* or *Fucus vesiculosus*) and glued together by conspicuous shiny secretional threads (Fig. 1).

The fifteen-spined stickleback is the largest species in the stickleback family (Gasterosteidae), and exhibits by far the greatest production of secretional threads (Hentschel 1979). These threads are made up by a protein synthesized in kidney tubuli cells, which during the breeding period transform into protein-secreting cells (Hentschel 1977, 1979; De Ruiter and Mein 1982). The protein is released from the cloaca as long (tens of centimeters), tough and sticky threads. The corresponding protein in the three-spined stickleback has recently been partially characterized and named spiggin (from the Swedish name for stickleback: spigg; Jakobsson et al. 1999). Spiggin is probably slightly different from the protein made by the fifteen-spined stickleback, since it does not form such long threads and mainly works as glue. Here, I call the secretional protein made by the fifteen-spined stickleback male tangspiggin (from the Swedish name for this species: tångspigg). Because it is a protein, it may be metabolically expensive to synthesize, and its synthesis may therefore be related to the food intake rate of the animal.

I hypothesize that the amount of tangspiggin produced by a male and attached to his nest function as an extra-bodily ornament that acts as an honest display of male condition to females. To test this hypothesis, I investigated the relationship of tangspiggin production to food intake and estimated how much of the male energy budget (measured in a respirometer as oxygen consumption) is spent on tangspiggin production. This was done in two groups of males, one given a low and one a high food ration. Moreover, in groups of males given equal amounts of food, I examined whether females prefer males with experimentally increased tangspiggin threads in their nests.

Methods

The study was carried out on a population of fifteen-spined sticklebacks at Klubban Biological Station on the west coast of Sweden, May–July 1999. The fish were caught early in May–June by snorkeling and trawling from a depth of 1–6 m, in *Fucus* or *Zostera* vegetation. Males were placed singly in 50-l aquaria [length×height×width (l×h×w)=0.4×0.5×0.25 m] and females were placed together (approximately ten per group) in 250-l (l×h×w=1.0×0.5×0.5 m) aquaria. All aquaria were continuously supplied with seawater (temperature 11–13°C), and all experiments were done at this temperature. In the statistical analysis, mean values are given as means±SD and probabilities are two-tailed. The data were checked for normality and percentages/proportions were arcsin√x-transformed. The data in experiment 1 and 2 did not meet the parametric assumptions of being drawn from an underlying normal distribution and so nonparametric analyses were employed and the data were corrected for ties.

Experiment 1: secretional production

Male pairs were matched to be as similar as possible from the start of the experiment in standard length (high food: 112±8 mm; low food: 112±9 mm; paired *t*-test: $n=17$, $t=0.43$, $P=0.67$) and wet mass (high food: 5.1±1.3 g; low food: 4.7±1.1 g; paired *t*-test: $n=17$, $t=1.70$, $P=0.10$). I randomly assigned one of the males within each pair to a high food ration and the other to a low food ration. I ran 17 male pairs for 12 days. The males in the low-food group were given food twice a day every 3rd day and the males in the high-food group were supplied with food twice every day. At each feeding, I gave the males live mysid shrimps (15–20 mm) and the tail of *Crangon crangon* shrimps (tail length: 10 mm). When fed, the fish were given two shrimps each and I checked that all males ate their food.

Each male was supplied with a plastic plant in which to attach the filamentous red algae for nest building. For each male, the same amount (10 ml compressed volume) of a mixture of two species of algae (*Polysiphonia fibrillosa* and *Ceramium rubrum*) was provided to exclude a possible effect of algal availability on tangspiggin production. On the 12th day, I collected all tangspiggin threads and nest material, including tangspiggin threads found on the bottom of the aquarium. There was no difference between the food groups in the dry mass of algae given for nest building (high food: 0.76±0.34 g; low food: 0.65±0.29 g, paired *t*-test: $n=12$, $t=0.19$, $P=0.85$). The aquaria were cleaned every 3rd day and occasional tangspiggin threads on the bottom were collected and added to the amount collected at the end. Water temperature did not differ between the males within each male pair (high food: 11.7±1.1°C; low food: 11.6±1.1°C; paired *t*-test: *n*=17, *t*=1.61, *P*=0.13).

Experiment 2: oxygen consumption and calculation of tangspiggin production cost

Here I used new males because I wanted to reduce the disturbance of the secretion production experiment. To estimate the portion of a male's resting metabolic rate devoted to production of tangspiggin, I measured the resting metabolic rate of individual males in a closed respirometer, as described by Nilsson (1996). The respirometer volume was 2.8 l, and the consumption of O_2 was registered with an O_2 electrode. The respirometer was filled with air-saturated seawater. After an initial period of exploratory activity (ca 15 min), the fish showed virtually no locomotory activity, resulting in a steady rate of O_2 consumption, which was registered for at least 1 h (air saturation of the water was never below 80%). Because of the large volume of water and the presence of other organisms, oxygen consumption could not be measured during nest building. Therefore, I considered measuring resting metabolic rate as the best option for assessing the energy budget of the fish. This value, however, excludes the cost of physical activity and food digestion but allows comparisons with other basal metabolic costs such as those of organ activity. The fish were not fed for 24 h prior to the measurements. The O_2 consumption of two groups of fish (high food, *n*=6; low food; *n*=5) having experienced the same 12 days of high and low food rations as fish in the previous experiment were examined.

To compare tangspiggin production costs with the resting metabolic rates, I calculated the tangspiggin production cost in terms of oxygen consumption. Assuming that tangspiggin has a similar amino acid composition and glycosylation degree as spiggin (Jakobsson et al. 1999), there are 9.0 mmol peptide bonds per gram dry mass of protein. By then making the standard assumptions that (1) each mole of peptide bond costs 5 mol ATP (Fuery et al. 1998) and (2) that one mole O_2 is required for producing 5 mol ATP (Hochachka and Somero 1984), the metabolic cost for making tangspiggin should be 9.0 mmol O_2/g dry mass.

This value is similar to the theoretical cost of 7.5 mmol O_2/g protein (for an average protein), and is similar to recent experimentally measured costs for protein synthesis in ectothermic vertebrates (see Fuery et al. 1998 for a review).

The mean values for resting oxygen consumption were used to calculate the cost of tangspiggin synthesis in these groups as a percentage of resting metabolic rate according to the formula:

$$100(\mathrm{Vp}\times a)/(\mathrm{Bw}\times \mathrm{VO_2})$$

where Vp is the rate of tangspiggin production (g protein/h), *a* is the cost of tangspiggin synthesis (9.0 mmol O_2/g protein), Bw is body wet mass (in kg), and VO_2 is the mean rate of resting O_2 consumption for a fish in the high or low food groups.

Experiment 3: female choice experiment

I used new males and females in this experiment, and the choice was made between paired males. Each male was given a plant of knotted wrack (*A. nodusum*) which was trimmed so that plants within pairs appeared the same in terms of branches and wet mass (38–40 g). Each part was attached to a stone for holdfast. As in the preceding experiment, all males were given 10 ml of a mixture of two species of algae (*P. fibrillosa* and *C. rubrum*) for nest building and were fed to satiation twice a day.

The males were matched in pairs for building experience, that is, both males in a male pair were allowed to build on a nest for the same number of days. This was either 12 or 4 days for both males, thereby producing nests differing in tangspiggin amount. To avoid a possible effect of female preference for genetically linked nest construction skills, I swapped nests among males. Thus, each male had to adopt another male's nest. Moreover, I gave the males within each pair nests that differed in the amount of tangspiggin content, so that one male was given a nest that had been built on for 12 days while the other male was given a nest that had only been built on for 4 days. Nest construction can be completed in 4 days; males in the field and laboratory have been found to reproduce in 2-day-old nests (personal observation).

Males within each pair were also matched for standard length (high-tangspiggin nests: 121±7 mm; low-tangspiggin nests: 125±8 mm; paired *t*-test: *n*=6 pairs, *t*=1.96, *P*=0.11) and male wet mass (high-tangspiggin nests: 5.6±1.1 g; low-tangspiggin nests: 6.0±1.2 g; paired *t*-test: *n*=6 pairs, *t*=1.14, *P*=0.31). When analyzing the dry mass of the nest contents after the experiment, I found that the nests of males provided with 12-day-old nests had three times as much tangspiggin (0.050±0.014 g) as those of males given 4-day-old nests (0.017±0.009 g; paired *t*-test: *n*=6 pairs, *t*=5.10, *P*=0.0039). However, no difference was found in the weight of red algae in 4- versus 12-day-old nests (0.81±0.20 vs 0.85±0.23 g, respectively; paired *t*-test: *n*=6 pairs, *t*=0.62, *P*=0.57).

After nest building, the males were transferred along with their adopted nests to the experimental aquaria. The aquaria were 40.5×70×60 cm (h×l×w) and an opaque screen to separate males was 45 cm long. All the experimental aquaria were constantly supplied with seawater and the experiments were conducted outdoors during daylight. In every second replicate, I placed the male with more tangspiggin in the left compartment. After the males had acclimatized overnight (normally long enough for them to accept their new nest) in their respective compartments, I leashed them by putting a 3-mm-wide cling wrap gently around the body, close to their pelvic fins. I then tied a thin fishing line (diameter=0.10 mm) to the cling wrap and attached the other end of the line to a small piece of cork which in turn was connected with the same type of line to the top of the adjacent aquarium wall (Östlund-Nilsson 2000). By leashing the males, I was able to exclude male-male interactions after I removed a transparent screen that separated the females from the males. Leashing stickleback males does not affect courtship or mating negatively (Östlund-Nilsson 2000; Östlund-Nilsson and Nilsson 2000).

After leashing the males, I placed a female in the female compartment. During the first 10 min of the experiment the transparent screen was kept down. During this time the female could acclimatize. I also made sure that she had visited both males before the transparent screen was removed. I observed the females until mating occurred.

Results

Experiment 1: secretional production

Males from the high-food treatment group produced significantly more tangspiggin (34.4±37.9 µg dry mass/h, maximum=169 µg dry mass/h, minimum=7.5 µg dry mass/h, *n*=16) than males from the low-food group (13.0±15.2 µg dry mass/h, maximum=39.9 µg dry mass/h, minimum=0.0 µg dry mass/h, *n*=15) during the 12-day period (Wilcoxon signed-rank test, *Z*=–2.97, *P*=0.0052; Fig. 2a). Moreover, the high-food group used a significantly larger proportion of their resting metabolic rate (7.4±8.1%, maximum=36%, minimum=1.6%, *n*=16) for tangspiggin production than the low-food group (2.8±3.3%, maximum=8.7%, minimum=0.0%, *n*=15) (paired *t*-test on transformed data; *t*=3.83, *P*=0.0021)

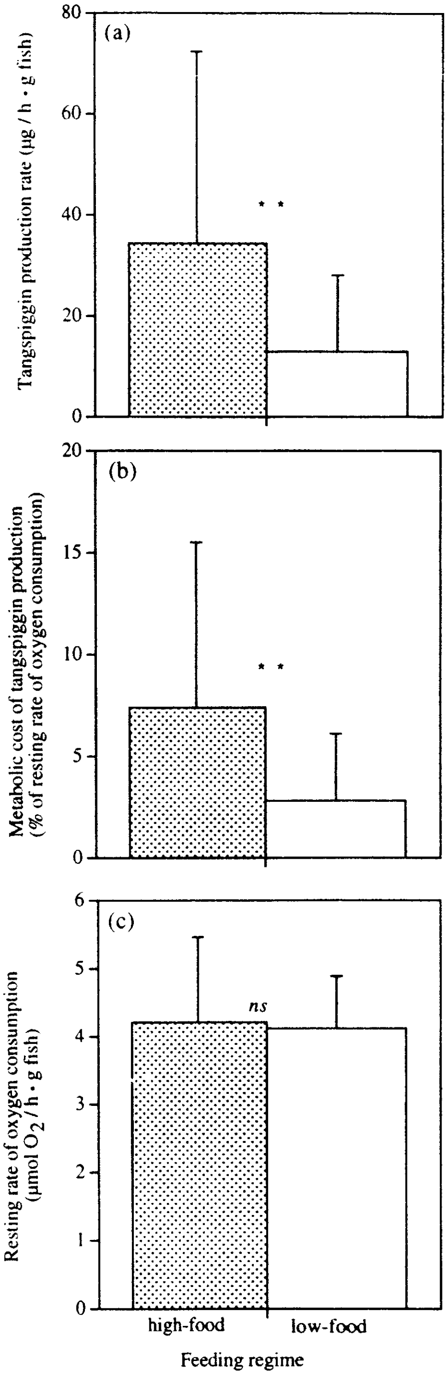

Fig. 2 **a** Well-fed males (*stippled bars*) produced significantly more (**P<0.05) tangspiggin than starved males (*open bars*). **b** Well-fed males (*stippled bars*) used a larger part of their resting metabolic rate for tangspiggin production than starved males (*open bars*) (**P<0.05). **c** The resting rates of O_2 consumption were virtually identical for well-fed (*stippled bars*) and starving (*open bars*) males (*ns* not significant)

Experiment 2: oxygen consumption and calculation of tangspiggin production cost

The resting rates of O_2 consumption for the high- and low-food groups were virtually identical, being 4.21±1.25 and 4.12±0.772 µmolO_2/h per gram wet mass, respectively (n=6 and n=5 for high and low food, respectively; Mann-Whitney U-test, Z=0.00, P>0.999; Fig. 2c). Thus, the amount of food given to the low-food group was not low enough to cause the metabolic depression typical of a starving animal (Blaxter 1989).

Experiment 3: female choice experiment

In the mate choice experiment, 6 out of 6 females chose to spawn with the males that had more tangspiggin in their nests (two-tailed binomial test: P=0.032). Mating occurred within 16 min (10.3±1.7 min). In all replicates, the female inspected both males and their nests before she mated.

Discussion

My results suggest that males with less tangspiggin in their nest suffer a substantial fitness cost in terms of lower reproductive success, given that females preferred to mate with males that had more tangspiggin in their nests. Earlier studies in the fifteen-spined stickleback showed that females not only base their choice on male characteristics but also on extra-bodily traits like a safe position of the nest (Östlund-Nilsson 2000). Tangspiggin threads may provide a strong visual stimulus for the females, being very shiny and bright, especially when recently produced.

The production of tangspiggin was related to food intake, and males from the high-food group used significantly more of their total resting metabolic rate to produce tangspiggin than did males given less food. Thus, tangspiggin synthesis is apparently so costly, or demands such a high level of nourishment, that it is one of the first processes to be suppressed during periods of food deprivation, before any substantial metabolic depression is seen (see Blaxter 1989). This indicates that males in poor condition would decrease tangspiggin production. Accordingly, tangspiggin could work as an honest signal for male condition in this species where the males provide females with direct benefits (Hoelzer 1989; Perrin 1995; Wolf et al. 1997). Individuals in the high-food group used on average 7.4% of their resting metabolic rate for tangspiggin production. This is a very substantial cost. The metabolic cost of the brain (one of the energetically most expensive organs in the body) is considered to be an important determinate of brain size, but animals typically devote only 2–8% of their resting metabolism to brain function (Mink et al. 1981; Nilsson 1999).

I deliberately manipulated one factor that has a large influence on an animal's condition, namely food intake. In the field, food intake is only one of several determinants of condition. However, the manipulation of food intake should reasonably mimic variation among males under natural conditions. Parental activities often shorten the time available to search for food (Magnhagen 1986;

Lindström and Hellström 1993; Marconato et al. 1993; Okuda and Yanagisawa 1996), and this can trigger filial cannibalism in fish (Marconato et al. 1993; Okuda and Yanagisawa 1996). Filial cannibalism has been reported in numerous fish species (Loiselle 1983; De Martini 1987; FitzGerald and van Havre 1987; Hoelzer 1988, 1992; Marconato and Bisazza 1988; Petersen and Marchetti 1989; Petersen 1990; Kraak 1996). Moreover, fanning activity is dependent on food intake (Townshend and Wootton 1985) and alone can reduce body fat and nonpolar lipids (FitzGerald et al. 1989; Coleman and Fischer 1991). Because both tangspiggin production and fanning activity (which is critically important for hatching success in this species; Östlund and Ahnesjö 1998) are physically demanding, females that choose males on the basis of a nest with more tangspiggin will ensure that the father is in a good nutritional state. Such males may provide better care for her offspring and engage in less filial cannibalism than males in poor condition with less tangspiggin. Furthermore, low amounts of tangspiggin presumably do not provide eggs with sufficient protection against potential egg predators.

While tangspiggin threads in newly built nests are very bright and shiny, with time they become less conspicuous due to overgrowth by clay particles. This transformation may actually have an important function, in that tangspiggin initially attracts females to newly built nests by being bright and shiny, functioning as a sexually selected ornament (Hoelzer 1989; Wolf et al. 1997). In older nests, where the tangspiggin threads are no longer so obvious, they still provide the benefits of keeping the eggs within the safety of the nest and probably reduce nest raiding by some egg predators, by reducing nest detectability.

An alternative interpretation of these results is that females prefer older over younger nests, i.e., that the age factor is more important than tangspiggin production rate. I find this unlikely because neither the males nor the females had any knowledge of the age of the nests in my experiments. Furthermore, the difference in age was minor, and except for tangspiggin content, the nests appeared identical (i.e., no difference in the quality of the filamentous algae and tangspiggin brightness). Moreover, female preference for older nests in the field would probably be selected against because older nests are duller, which would make them harder to find and thus increase the females' search costs.

Conclusion

The production of tangspiggin correlated with male food intake rate. Thus, the production of tangspiggin is probably favored by sexual selection as an honest signal of male condition. By choosing a male with a lot of tangspiggin in his nest, females may gain indirect benefits by obtaining "good genes" from a male who is a successful forager, or direct benefits, since such males are more likely to provide better care for the eggs.

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