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ARTICLES

Increased signalling effort when survival prospects decrease: male–male competition ensures honesty

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For signalling to be honest the handicap principle claims that signals must impose fitness costs so that only the best individuals can afford the most exaggerated signals. The cost of signalling in terms of reduced survival decreases, however, towards the end of an individual's lifetime, which can induce an increase in signalling effort as a terminal effort. I show for the three-spined stickleback, *Gasterosteus aculeatus*, that a decrease in survival prospects through impaired condition leads to an increase in red nuptial coloration that makes the signal less reliable as an indicator of male parental ability. Males in poor condition with a large signal sometimes cannibalized all the eggs they received, probably to start a new breeding cycle with a higher energy reserve. However, the inclusion of socially imposed costs of signalling through male–male competition during courtship increased the honesty of the signal, as some males in poor condition and of poor parental ability decreased their signal expression. Some cheaters still occurred, but the signalling system was honest on average. This implies that socially imposed costs are important in the maintenance of honest sexual signalling. Dishonesty may occur under favourable conditions when the cost of signalling is reduced. This emphasizes the importance of considering the environmental conditions experienced by individuals when investigating the evolution and maintenance of honest sexual signals.

One of the debated issues of sexual selection theory is the evolution and maintenance of honest sexual signals of mate quality. This is especially intriguing in species where there is no direct physical limitation on signal expression and individuals can decide how much to allocate to it. According to Zahavi's (1975) handicap principle, for signalling to be honest in these cases, it should be costly in terms of reduced survival or fecundity and the cost should increase with the expression of the signal. If individuals of high quality then experience lower costs, or higher benefits for a given level of signalling, the optimal balancing of costs and benefits of signalling should ensure that individuals of high quality develop more exaggerated signals than individuals of low quality (Grafen 1990a, b; Getty 1998).

For individuals that breed several times during their lifetime, signalling could thus be subjected to a life history trade-off between present and future signalling effort. This could lead to some individuals cheating if they invest proportionally more in present signalling and less in future signalling than others (Kokko 1998). This might be the case when individuals within a population differ in their future reproductive value. Individuals with a low prospect of survival might invest relatively more in present reproduction if they have the necessary resources than individuals with a higher future reproductive value. This possibility has been detected in the three-spined stickleback, *Gasterosteus aculeatus*, where food-deprived, poor-condition males develop more red carotenoid-based nuptial coloration than males in good condition (Hosking 1996; Baube 1997; Candolin 1999b). This is most likely due to poor-condition males having a lower probability of survival and future reproduction than males in good condition and therefore having less to lose from signalling at a high level. This possibility is further emphasized by the finding that an increased cost of signalling in terms of enhanced predation risk increases the difference in redness between males in good and poor condition, as males in poor condition reduce their red coloration less and take greater risks than males in good condition when exposed to predators (Candolin 1999b).

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I investigated whether an increased signalling effort in response to a decreased probability of survival decreases the honesty of signalling in relation to male parental ability, or if an increased signalling effort is accompanied by increased parental effort. Three-spined stickleback males care for their offspring alone and the parental ability of the male is crucial for reproductive success (Wootton 1976). I further investigated whether the inclusion of male–male competition and socially imposed costs of signalling (Maynard Smith & Harper 1988; Johnstone & Norris 1993) could make the signal a more reliable indicator of male parental ability. It is likely that signalling is restricted by several costs and the laboratory experiments mentioned above might not have included all the costs that are necessary for honest signalling to prevail. In particular, socially imposed costs of signalling may be important in the determination of signal expression, as red coloration functions both as a cue in female mate choice and as a threat signal in male interactions (Bakker & Sevenster 1983; Rowland 1994), and as males can quickly adjust their colour expression to the dominance status of other males (Candolin 1999a).

METHODS

I collected three-spined sticklebacks by fry traps from the littoral of the Baltic Sea in southern Finland near Tvärminne Zoological Station before the breeding season (late April) in 1998. The fish were housed in flow-through aquaria at 18°C under natural lighting conditions at a density of 10 fish per 125-litre aquarium. They were fed daily on frozen chironomid larvae. After at least 1 week of maintenance, I separated males from females on the basis of hints of nuptial coloration and randomly assigned the males to two feeding treatments. For 3 weeks, one group of males was food deprived, whereas the other was fed in excess twice a day on frozen chironomid larvae. All flow-through aquaria were cleaned daily so that the environmental conditions were the same in all aquaria. The lack of suitable nesting materials discouraged breeding behaviour. Sticklebacks do not usually feed during the 2–3-week parental phase and thus sustain food deprivation well (Wootton 1976). All food-deprived males were alive and healthy at the end of the 3 weeks and did not differ in behaviour from fed males. Females were fed frozen chironomid larvae ad libitum to ensure a constant supply of gravid females.

To determine the reliability of the red coloration as an indicator of male parental ability for condition-manipulated males in the presence and absence of male–male competition, I carried out two experiments with different males. In the first experiment, I determined the honesty of the red coloration as an indicator of male parental ability in the absence of male competition. An important source of egg mortality in the wild is cannibalism by the male (Whoriskey & FitzGerald 1994), and food-deprived males may cannibalize eggs and thus be poor parents. In the second experiment, I determined whether male interactions increase the honesty of the signal: I paired a food-deprived and a fed male and determined their red coloration first when separated from each other and then when interacting with each other and related their colour expression to their parental ability. The fish and surviving eggs were returned to the wild after the experiments. The research was approved by the Animal Care Committee of the University of Helsinki. Values reported are means ± SE. Statistical tests were two tailed.

Experiment 1: Single Males

I placed food-deprived and fed males into individual aquaria (45 × 35 cm and 30 cm high), each containing a nesting dish with sand, an artificial plant and algae for nest construction. Fed males had a higher condition factor (wet weight/(standard body length)^3) than food-deprived males (fed males: 1.29 ± 0.02; food-deprived males: 1.19 ± 0.03; t test: $t_{28}=3.05$, $P=0.005$) but did not differ in standard body length (fed males: 53.2 ± 0.6 mm; food-deprived males: 53.9 ± 0.7 mm; t test: $t_{28}=0.84$, $P=0.41$). The fish were not fed during the experiment. When a male had built a nest and entered the courtship phase, I showed him a dummy female in front of the aquarium. I used a dummy female to eliminate effects of female behaviour on male signal expression. After 5 min of female exposure, I dip-netted the male and photographed his left lateral side under standardized conditions in a large dark box containing a digital camera (Kodak DC 50; see Candolin 1999b for details). The photography procedure took less than 1 min and the male did not have time to fade as a result of handling stress. I returned the male to the aquarium immediately after photography and all males resumed normal behaviour within 1 min and showed no signs of distress or damage. To determine the extent and quality of the red coloration from the digital images, I used image analysis software (MCID-M4, Imaging Research Inc., Brock University, St Catharines, Ontario, Canada) to exclude observer biases. I selected areas that ranged in colour from yellow to red to purple (hue: 1–50 and 340–359; saturation: 0–0.631; intensity: 0.157–0.663), and recorded their size and mean colour quality. I used a tristimulus system constructed to fit the human eye, as colour vision of sticklebacks does not differ greatly from that of humans (reviewed by Frischknecht 1993; McKinnon 1995). I used both absolute and relative sizes (percentage of total lateral area) of the red areas in the analyses. However, the results were basically the same and only relative sizes are presented.

After photography, I added a female to the aquarium to spawn in the male's nest. The female was removed immediately after spawning. I determined the amount of eggs spawned both by recording female wet weight before and after spawning, and by weighing the eggs 3–4 h after spawning when the egg mass had hardened. To weigh the eggs, I lifted the nesting dish from the aquarium and carefully removed the egg mass with forceps and dried it on absorbent paper. I weighed the egg mass in a bowl of water and then returned it to the nest and to the aquarium. In all cases, the male accepted the nest and repaired the entrance and any other parts of the nest that had been damaged. This procedure has no significant influence on egg survival (Kraak et al. 1997). The two measures of egg mass, the change in female weight and the weight of the egg mass, were highly correlated (r_{28}=0.95, P<0.000). This, together with the fact that males were never observed eating eggs during the first few hours of parental care, indicates that males did not eat eggs to any significant extent during this time. I therefore used the weight of the egg mass in the analyses.

I then allowed the male to care for the eggs for 8 days until they were almost ready to hatch. I determined the percentage of the eggs that had survived for 8 days by removing dead and undeveloped eggs and weighing the remaining eggs as described above. Developed, healthy eggs are easily distinguished from dead eggs as the dark embryo moves inside the eggshell. Under the present conditions, the eggs would have hatched on day 9 or 10. The number of developed, healthy eggs present on day 8 agrees with the number of eggs actually hatching when a male is allowed to continue to care for the eggs until hatching (r^2=0.996, b=0.943, $F_{1,14}$=3102, P<0.001; unpublished data). The weight of an egg may change during development, but this should be the same over replicates and not confound the results. I tested 15 food-deprived and 15 fed males.

Experiment 2: Competing Males

I placed a fed and a food-deprived male of the same body size (± 1 mm) into an aquarium (70 × 45 cm and 30 cm high) divided by an opaque sheet into two male compartments. The partitioning sheet was fitted tightly to the aquarium so that water could not flow between the two male sections. The fed male had a higher condition factor than the food-deprived male (fed male: 1.28 ± 0.02; food-deprived male: 1.18 ± 0.03; paired t test: t_{17}=3.43, P=0.003). The fish were not fed during the experiment. To identify the males during the experiment, I cut the tip of one of the three large dorsal spines for both males so that one male had a blunt front spine and the other a blunt back spine (randomized among treatment groups). The spines are not innervated (Moyle & Cech 1988) and fish do not react when the spine is cut. The cutting procedure was done while the males were transferred from the holding tanks to the individual aquaria and did not appear to impose any extra stress on them, as fish that have been cut resume normal swimming behaviour as quickly as fish that have not been cut (personal observation). To ensure that both males were in the same breeding condition, I replaced the males with a new pair of males if one of them took more than a day longer than the other to complete a nest (two cases). When both males had completed a nest, I exposed them to a dummy female in front of the aquarium for 5 min and then photographed the males for red colour determination, as described above.

To investigate whether male interactions influence signal expression, I allowed the males to interact by replacing the partitioning sheet with a row of artificial vegetation. The males could then interact but still had a boundary between their territories. When introduced to each other the males often chased each other for a few minutes. One of the males then showed his subdominance by reducing his red coloration and by swimming away and avoiding any further contact with the other male. Very little direct interaction occurred after that. The males never injured each other. In all cases, both males continued to care for and defend their nest. After a day of interaction, I exposed the males to a dummy female and then dip-netted both males at the same time, with the help of an assistant, and photographed them for colour determination. I then separated the two males with the partitioning sheet and I allowed each male to spawn with a female. The females were size-matched so that both males would receive about the same amount of eggs. I determined the amount of eggs spawned by weighing them as described above. I then replaced the partitioning sheet with a row of vegetation and allowed the males to care for their eggs under interaction. The percentage of the eggs that survived to the hatching stage was determined as described above. I tested 18 pairs of males.

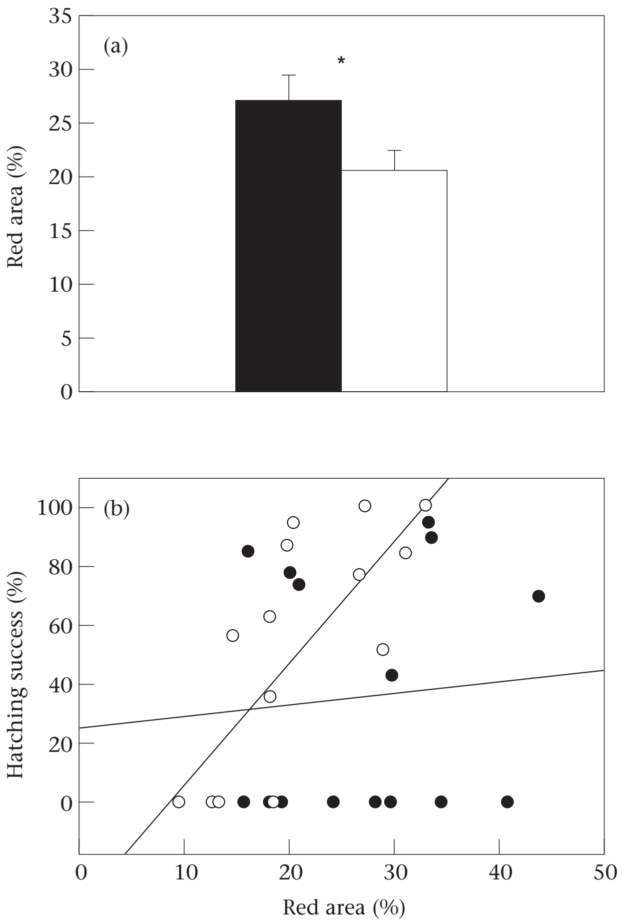

Figure 1. (a) Mean+SE red area of food-deprived (■) and fed males (□). Both N=15. * P<0.05. (b) Relationship between percentage red area and percentage hatching success for food-deprived (●; Y=24.7+0.4X) and fed males (○; Y=−34.9+4.1X).

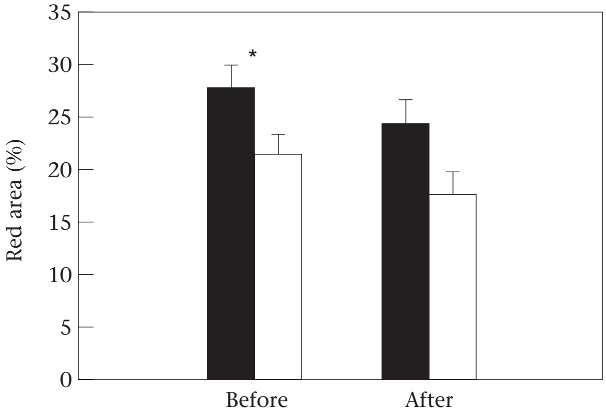

Figure 2. Percentage red area ($\bar{X}$+SE) of food-deprived (■) and fed males (□) before and after interaction with another male. All N=18. *P<0.05.

RESULTS

Single Males

Food-deprived males developed larger red areas than fed males (t test: t_{28}=2.20, P=0.036; Fig. 1a) but there was no difference in hatching success between the two groups (food-deprived males: 35.4 ± 10.5%; fed males: 49.7 ± 10.5%; t_{28}=0.97, P=0.34). The red areas did not reflect hatching success when the two groups were pooled (r^2=0.07, b=1.25, $F_{1,28}$=2.10, P=0.16; Fig. 1b). However, when they were analysed separately, hatching success depended on red area for fed males (r^2=0.52, $F_{1,13}$=14.3, P=0.002) but not for food-deprived males (r^2=0.01, $F_{1,13}$=0.10, P=0.76). The relationship between red area and hatching success consequently depended on food ration, as demonstrated by a significant interaction between red area and feeding treatment (ANCOVA: red area: $F_{1,20}$=6.75, P=0.015; food ration: $F_{1,20}$=1.96, P=0.17; red area × food ration: $F_{1,20}$=4.60, P=0.041). There was no difference in colour quality (hue, saturation and intensity) of the red areas between food-deprived and fed males (all t_{28}<0.95, P>0.45).

Competing Males

Food-deprived males on average developed larger red areas than fed males when the males were separated (t_{34}=2.14, P=0.040). After interaction, food-deprived males still tended to have larger red areas (paired t_{17}=1.78, P=0.093; Fig. 2), but the honesty of the signal had increased: the difference between the paired males in signal expression did not reflect their difference in hatching success before interaction (r^2=0.02, $F_{1,16}$=0.39, P=0.54; Fig. 3a) but it did after interaction (r^2=0.28, $F_{1,28}$=6.09, P=0.025; Fig. 3b). The increased honesty was due to some of the poor-condition males that did not rear any offspring to the hatching stage decreasing their red area under interaction. This was most likely due to male interactions, and not a time effect, as food-deprived and fed courting males maintain their red areas when kept singly and photographed on 2 successive days (Candolin 1999b).

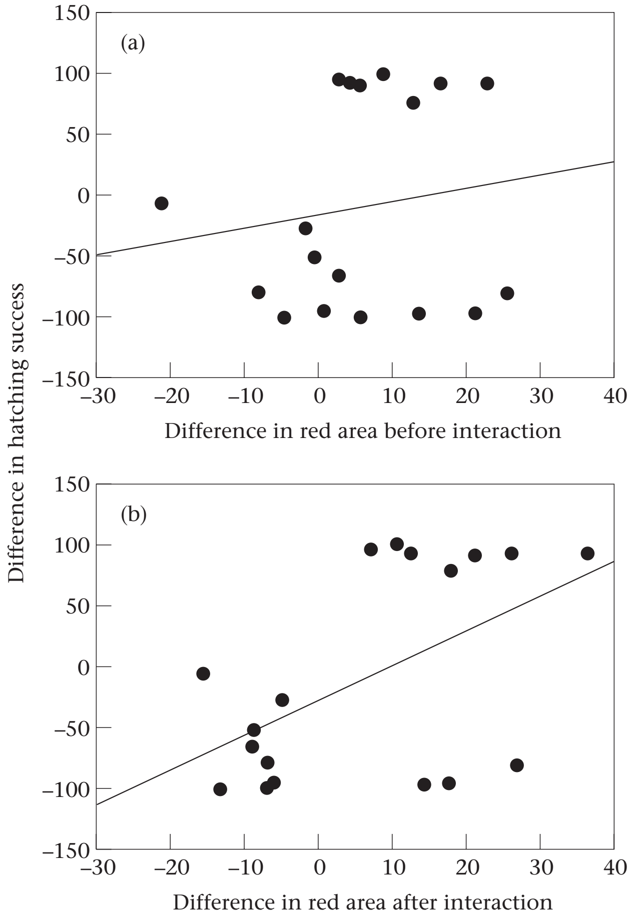

Figure 3. Relationship between the difference between the food-deprived and the fed male in hatching success (% hatched for food-deprived male−% hatched for fed male) and in red area (% red area of food-deprived male−% area of fed male) (a) before male interaction (Y=−15.10+1.34X) and (b) after male interaction (Y=−27.4+2.87X). Each point represents one male pair.

Figure 3 shows that the food-deprived males of low parental ability that decreased their red areas under interaction had usually had red areas of about the same size as the paired fed male before interaction. Food-deprived males that maintained their areas, on the other hand, had had much larger areas than the fed male. The slight overall decrease in red area under interaction (Fig. 2) was due to the male with the smaller area usually decreasing his area (from 20.4 ± 2.1 to 13.7 ± 1.4; paired t test: t_{17}=4.99, P<0.001), whereas the male with the larger area did not change (28.8 ± 1.9 and 28.4 ± 1.7; paired t test: t_{17}=0.28, P=0.78). Most of the food-deprived males that maintained their large red area under interaction also invested in parental care and reared most of their offspring to the hatching stage. Some, however, did cheat. On three occasions, the food-deprived male had the larger red area both when separated and when interacting, but did not rear any offspring to the hatching stage.

There was no difference in hue, saturation, or intensity of the red areas of food-deprived and fed males, either before (t test: all t_{34}<1.32, P>0.19) or after interaction (paired t test: all t_{17}<1.20, P>0.24). However, the male with the larger red area after interaction also had the more saturated red area (0.204 ± 0.004 compared to 0.183 ± 0.004; paired *t* test: t_{17}=3.73, P=0.002), but there was no difference in hue (t_{17}=0.44, P=0.66) or intensity of the red areas (t_{17}=0.05, P=0.96).

DISCUSSION

Food-deprived males developed larger red areas than fed males when courting a female in the absence of competitors. This is in line with earlier studies that have found poor condition to induce an increase in signalling effort (Hosking 1996; Baube 1997; Candolin 1999b). The higher signalling effort did not, however, correspond to a higher parental ability of the males. Several of the bright red males in poor condition cannibalized all the eggs that they received. The signal was consequently not an honest indicator of male parental ability for males in poor condition. This was probably due to food-deprived males with a low probability of surviving the present reproductive cycle benefiting from eating their eggs to start a new breeding cycle with higher energy reserves. They may initially invest more than good-condition males in signal expression because of lower costs to future survival and reproduction. After successful mating, the net benefit of eating the eggs may, however, be higher than the net benefit of caring for the eggs if the males do not have enough resources to survive the present parental phase. Cannibalism may then occur as an investment in future reproduction to increase the probability of surviving a future breeding cycle and maximize lifetime reproductive success (Rohwer 1978; Sargent 1992).

The inclusion of male–male competition in the experimental design increased the honesty of the signal so that the system became honest on average. Although the minimum level of honesty required for stability is not known in this system (it is a function of the costs and benefits of trust and deception, Johnstone & Grafen 1993), the increase in honesty should increase the benefit to the females of responding to the signal and thus increase the stability of the system. The increased honesty was due to some poor-condition males of low parental ability decreasing their colour expression when confronted with a male in good condition. These poor-condition males of poor parental ability might not have been able to pay the socially imposed cost of signalling, that is, the risk of a fight with a superior male, as it may consume more resources than they can afford or lead to serious injuries (Rohwer 1975; Maynard Smith & Harper 1988; Johnstone & Norris 1993). They may therefore have adjusted their red coloration to their dominance status and fighting ability. As dominance was correlated with parental ability, male interactions increased the honesty of the red coloration as a signal of male parental ability.

The food-deprived males that maintained their large red area under interaction usually managed to rear their offspring to the hatching stage. A high investment in signalling under competition was then associated with a high investment in parental care. This was probably due to signal expression under competition being expensive in relation to parental activities, such as defending the nest against other males and oxygenating the eggs. A high investment in signalling under competition would be a significant waste of time and resources if it did not lead to successful reproduction. A male that has invested a lot of resources in maintaining his large red area and signalling his dominance status under competition therefore also invests in parental care, if he still has the resources required.

Some males, however, did cheat after interaction. Three of the 18 food-deprived males with a larger red area than the fed male both before and after interaction did not rear any of their offspring to the hatching stage. These food-deprived, dominant males had most likely eaten their own eggs to increase their condition in order to start a new breeding cycle with larger energy reserves. They were consequently cheaters. However, their frequency was low, three out of 18 pairs. The system was thus honest on average under male interactions, which may be enough for the signalling system to be stable. Moreover, the frequency of cheaters may be even lower in the wild at the beginning of the season when the body condition of the males has not yet started to deteriorate from expensive breeding activities. It is likely that males resort to cheating in only exceptional cases, that is, when their resource level is too low to survive the parental phase, or when the probability of getting a new more rewarding egg clutch is high.

How general it is that male–male competition contributes to the maintenance of honest sexual signalling is not known. A few studies have shown that male–male competition influences signal intensity and that it can obscure or alter female mate preferences (Trail 1985; Zimmerer & Kallman 1988; Greenfield 1994; Morris et al. 1995; Galeotti et al. 1997; Petersson et al. 1999). Whether male–male competition hinders or facilitates adaptive female choice depends, however, on whether it increases the chances that females will mate with high-quality males. Since male dominance often reflects male phenotypic or genetic quality (Bisazza et al. 1989; Montgomerie & Thornhill 1989; Alatalo et al. 1991; but see Forsgren 1997), it seems probable that male–male competition should often be an important factor in mating systems with flexible signals of dual utility. This highlights the importance of considering the environmental conditions that males experience during signalling and to include several potential costs, including male–male interactions, when investigating the mechanisms that maintain honest sexual signalling.

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