

Male mate choice selects for female coloration in a fish

Trond Amundsen** and Elisabet Forsgren*

*Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway; and **Department of Marine Ecology, Göteborg University, Kristineberg Marine Research Station, S-450 34 Fiskebäckskil, Sweden

Communicated by Gordon H. Orians, University of Washington, Seattle, WA, August 20, 2001 (received for review October 25, 2000)

Although sexual selection theory has proved successful in explaining a wide array of male ornaments, the function of ornaments occurring in females is largely unknown. Traditionally, female ornaments have been considered nonfunctional, being merely a genetically correlated response to selection for male ornamentation. However, this hypothesis is only relevant to species in which the ornament is basically the same in the two sexes. Alternatively, female ornaments may be influenced by selection acting directly on the females, either through female–female competition or male choice. We tested the latter hypothesis in mate-choice experiments with two-spotted gobies (*Gobiusculus flavescens*). In this small marine fish, females have bright yellow-orange bellies during the breeding season, a conspicuous trait that is not present in males. We conducted two aquarium experiments to test whether males preferred to mate with more colorful females. In the first experiment, males had a choice between two females that varied in natural coloration (and belly roundness). In the second experiment, we manipulated belly coloration and kept roundness constant. Males spent more time with colorful than with drab females in both experiments and also performed far more courtship displays toward colorful females. Our study provides experimental evidence that males prefer ornamented females in a fish that is not sex-role reversed, supporting the hypothesis that female ornamentation is sexually selected.

It is now well established that males of a variety of animal species have evolved their beautiful decorations through sexual selection. Much less is known of the reasons why females of some species express a similar extravaganza. Traditionally, ornaments occurring in females have been considered as mere by-products of selection on the males (1, 2). However, theory suggests that showy female traits can be selected through female–female competition (3, 4) or male mate choice (5–8). The idea that female showiness is subject to direct selection is corroborated by comparative evidence demonstrating frequent evolutionary changes in female plumage among birds (9–11). Despite this fact, empirical studies addressing social and sexual selection in females are either scarce or completely lacking in most major taxa. The present study tests whether male choice may select for female coloration in fishes, a taxon in which conspicuous female traits are widespread (12, 13).

Recent studies on birds suggest that male choice can select for female ornaments (14–18). In most other taxa, including fish, female ornaments are almost unstudied and the evolutionary reasons for female beauty largely unknown. This fact is somewhat surprising, considering that, in fish, male choice for large or fecund females seems to be widespread (12, 19–22). Although females of many fish species display beautiful colors, only a few studies have attempted to test whether male fishes also prefer ornamented females. In three-spined (*Gasterosteus aculeatus*) and brook (*Culaea inconstans*) sticklebacks, males prefer females with nuptial coloration over females lacking indices of their reproductive state (23, 24). Female nuptial coloration in these and other species has been interpreted as a signal of readiness to spawn that has evolved because it facilitates efficient mating and reduces male harassment of females that are not in a reproductive state (23, 24). This scenario does not explain the evolution

of color characteristics whose expression may vary among reproductive females. To our knowledge, the idea that males discriminate between fecund females on the basis of color so far has received support only in sex-role-reversed pipefishes. In the pipefish *Nerophis ophidion*, males prefer to mate with females having more extensive areas of blue coloration (25) and also prefer females with larger ventral skinfolds (26). In *Syngnathus typhle*, females with a highly contrasting bar pattern were preferred by males (27). These results suggest that female ornamental traits are sexually selected in pipefishes. However, because of their reversed sex roles, male choice in pipefish is functionally analogous to female choice in species with conventional sex roles. Conventional sex roles (males being the more competitive sex) are, by far, the predominating pattern in fishes. In such species, no previous study has demonstrated that males prefer more ornamented females when given a choice between females that are ready to spawn. The only extant study conducted in such a system—on convict cichlids (*Cichlasoma nigrofasciatum*)—revealed no male preference for females with more bright ventral coloration (28). We report here experiments on two-spotted gobies (*Gobiusculus flavescens*), a species in which males are clearly competitive. Our results demonstrate a function of female coloration in male mate choice, suggesting that the female ornament is a product of sexual selection.

Methods

The study was conducted at Kristineberg Marine Research Station on the Swedish west coast (58° 15' N, 11° 27' E) during 18 June–24 July 1998.

Model Species. The two-spotted goby is a small (4–5 cm) fish inhabiting shallow waters along rocky shores. It is a semipelagic shoaling species (29), but males take up and solitarily defend nest sites in the algal vegetation (e.g., empty mussels *Mytilus edulis*, or crevices in the holdfasts of kelps *Laminaria* spp.) (ref. 30; unpublished data). Males attract females to their nests with a courtship display. During spawning, the eggs are attached to the nest in a single layer and are fertilized by the male immediately after laying. Several females may spawn in the nest of a single male (30). The male cares for the eggs for a period of 1–3 weeks, depending on water temperature, until hatching (31–33). Paternal care includes defense against predators, fanning (oxygenating) and cleaning the eggs. Both males and females normally live for only 1 year (34), but may reproduce several times during a season (in our study area, from May until late July).

Male two-spotted gobies are somewhat larger than females (unpublished data) and have conspicuous iridescent-blue spots and fin patterns during breeding. Females have only a very pale version of the male ornament but develop colorful yellow-orange

See commentary on page 12857.

*To whom reprint requests should be addressed. E-mail: trond.amundsen@chembio.ntnu.no.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.



Fig. 1. Mutual courtship display of two-spotted gobies *Gobiusculus flavescens*. The female (Upper) displays her colorful belly by bending the body toward the male (photo by E.F.).

bellies during breeding (Fig. 1). Female belly coloration is carotenoid-based. It is caused mainly by the pigmented eggs being visible through the skin, but is also caused by orange-red pigment spots in the abdominal skin. Basically, coloration extends over the whole egg-carrying part of the belly. Thus, variation between females in the extension of belly coloration largely reflects female size (and to some extent roundness) and is thus trivial. The focus of this study is to understand the mating consequences of individual variation in color quality among mature females, varying from a pale yellow-orange to a bright orange appearance. Generally, rounder females (with more developed eggs) are more colorful than less round ones, but there is also significant variation in color between equally round females. Females of other goby species in the same area lack belly coloration and have a cryptic appearance. Both male and female two-spotted gobies may court opposite-sex individuals (Fig. 1). Male courtship typically takes the form of swimming rapidly toward a female, followed by a lateral display with the colorful dorsal fins erect. This behavior is usually followed by a leading display in which the male swims toward the nest (sometimes entering) in a particular undulating manner, beating his tail. Sometimes this behavior entices the female to follow the male into the nest, after which spawning may or may not follow. Females court males by approaching them at close range and bending their bodies to expose their colorful bellies to the maximal extent.

Observations in the wild suggest that the operational sex ratio changes dramatically over the season, from being male-biased at the start to becoming strongly female-biased by the end of the season. At this stage, a male may be surrounded by several females courting him at the same time (E.F., T.A., Å. Borg, and J. Bjelvenmark, unpublished data). The apparent surplus of reproductive females late in the season provides an opportunity for males to be selective in mate choice. For females, the scarcity of nest-holding males likely makes it hard to find nests for spawning. In this situation, female attractiveness potentially has a large impact on female spawning success, and, hence, on overall reproductive success.

Males and females were captured by hand-netting in the algal zone (depth ≤ 1 m) at various islands nearby the station. They were brought immediately to the station, separated by sex, and

kept in storage aquaria until use in experiments. The aquaria had a constant water supply (from an intake of shallow-depth water) and were fed once daily with *Artemia* larvae *ad libitum*. The aquaria were supplied with gravel and artificial algae to simulate a natural environment. Total fish length was measured to the nearest mm, and wet body mass was recorded to the accuracy of 0.01 g with a Mettler balance.

Experiment 1: Natural Color Variation. Mate preference trials ($n = 15$) were conducted in three-compartment aquaria (60 liters, $74 \times 23 \times 35$ cm), with a male placed in the center and the two females placed to the left and right of the male. The compartments were separated by transparent Plexiglas dividers that were perforated to allow water transport. Water was piped into the aquarium in the center (male) compartment (length 25.0 cm), with outlets of similar flow from the two female compartments (each of length 24.5 cm). The two females were of similar length but differed markedly in belly coloration (Fig. 2a; colorful 41.33 ± 1.80 mm, drab 41.27 ± 1.67 mm; paired $t = 0.32$, $df = 14$, $P = 0.75$). Female placement to the right and left was randomized, so that the colorful female appeared a similar number of times to the left (7) and the right (8) of the male. All three compartments were supplied with gravel and one artificial algae each. The male compartment was supplied with a PVC tube (length = 80 mm, inner diameter = 14 mm) that was placed centrally at the bottom so that it could be used as a nest.

First, we placed the male into the central compartment, and allowed ample time for him to establish ownership of the nest tube (4–256 hr, median = 72 hr). Thereafter, we introduced the females (one colorful and one drab) into the adjacent compartments. Females usually acclimatized very swiftly to the new aquarium. Once the females appeared to swim undisturbed in their compartments, and the male was out of the nest tube (1–16 min, median = 2 min after female introduction), we recorded the interest shown by the male in the two females for the next 30 min. We recorded two parameters indicative of male mate preferences: (i) the time spent in association with each of the two females and (ii) sexual displays directed at the females. Association was quantified by scan-sampling the position of the male every 30 s. If the (head of the) male was within a zone ≤ 5 cm from any of the female compartments (indicated on the aquar-

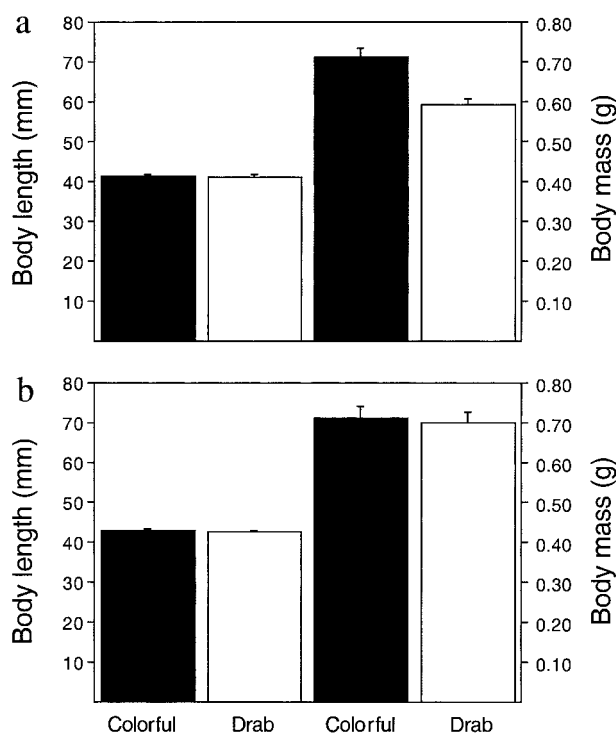


Fig. 2. Characteristics of females participating in experiments aimed to test male preference for female coloration in two-spotted gobies. (a) Natural color variation: males were exposed to two females of the same total length but varying in natural coloration. Because female color is related to roundness, colorful and drab females differed somewhat in wet-body mass in this experiment. (b) Color manipulation: males were exposed to two females that were very similar in total length and wet-body mass; their belly coloration had been manipulated to become drab and colorful, respectively. (Bars = means + 1 SE.)

ium with a permanent marker) he was considered to be in association with that particular female. If positioned elsewhere in the compartment, he was considered to show no preference. Male displays were basically of two kinds: (i) lateral shivers, in which the male swims close to the female with fins erect, shivering his body, and (ii) lead displays, in which the male swims from the female to the nest with exaggerated, undulating fin and body movements, in the same way as males in a natural setting may entice females to inspect their nest. Sometimes this lead display included entering the nest. A few lead displays were not clearly directed; the male swam in the same particular manner as in a typical lead, but not down to the nest. Males often erected their fins when close to females. However, because fins may be erect for reasons other than display, we conservatively excluded this behavior when quantifying courtship. Courtship was continuously recorded throughout observation sessions. The observed (and recorded) male courtship displays were identical to those performed by males when courting females in the wild. Extensive field observations confirm that the recorded displays do not occur in nonmating contexts in the wild. Hence, the recorded displays clearly reflect male sexual interest in the female. The only difference between the experimental (captive) and a natural setting was that females could not follow the courting males in captivity, and, thus, were constrained from spawning.

To check for any differences in female behavior, we also recorded the position of the females every 30 s and displays by the females if such occurred. In several trials, one or both females laid down on the bottom for extensive periods, sometimes digging into the gravel so as to hide, probably indicating a lack of acclimatization to the experimental setting (two-spotted

gobies are normally not bottom-dwelling). Such trials were not used in any analyses. Likewise, we did not include trials in which the male showed no interest in either female.

Because there is a relationship between coloration and belly roundness, colorful females of this experiment were on average somewhat heavier (hence rounder) than drab females (Fig. 2a; colorful, 0.71 ± 0.09 g; drab, 0.59 ± 0.06 g; paired $t = 6.01$; $df = 14$; $P < 0.001$).

Experiment 2: Color Manipulation. To control for the potentially confounding relationship between female color and roundness, we performed an experiment in which female color was manipulated ($n = 16$). We selected pairs of females of medium coloration and of similar length and wet-body mass (Fig. 2b); hence, we were also selecting for similar roundness. One of the pair members was randomly assigned to a color-enhancement treatment; the other was used as a control. Color was enhanced by means of a permanent marker (color RY 16 “Apricot”, Copic) that very closely resembled the color of the most colorful females. Color was enhanced uniformly over the part of the abdomen that is naturally more or less colorful (caused mainly by egg color). Control fish were treated equally, but with a colorless marker (color 0 “Colourless Blender”, Copic). Similarity between the colored marker and natural egg coloration of the most colorful females was confirmed spectrometrically (S. Andersson, Göteborg Univ., Göteborg, Sweden). The color of individual fish, including those in the experiments, could not be reliably quantified spectrometrically, mainly because of the glossiness of the belly.

After randomization, there was no difference in wet-body mass between treatments (colorful, 0.71 ± 0.11 g; drab, 0.70 ± 0.10 g; paired $t = 1.26$; $df = 15$; $P = 0.23$). However, chance produced a minute difference in length between colorful (43.00 ± 2.07 mm) and drab (42.63 ± 2.00 mm) females (paired $t = 2.42$; $df = 15$; $P = 0.029$). The average difference in length of 0.37 mm is well within measurement error, and it is highly unlikely that this difference could influence mate preferences. Still, we tested whether results would be the same if we excluded cases in which colorful females were longer (by 1 mm or more). Including only trials in which colorful females were either as long as or shorter than drab ones produced the same preference patterns and did not affect the statistical significance of the tests. Actually, the results were even stronger with this subset of data. For reasons of brevity, we only report results for the full data set.

Experimental procedures were almost identical to those described for experiment 1, including acclimatization of test fish, protocol for behavioral observations, and criteria for inclusion of trials. However, based on experience from experiment 1, we decided to scan sample behavior every 20 s (instead of every 30 s) and to conduct each trial over only 15 min (i.e., a total of 45 scans/trial). Males stayed alone in the aquaria for 1–52 hr (median = 24 hr) before females were introduced, and observational recordings started 1–18 min (median = 1 min) after female introduction. The colorful female was placed in the left compartment nine times and in the right compartment seven times (determined at random).

All fish (both experiments) were released into their natural habitat after completion of the trials.

Because male responses to the two females are not completely independent, we tested the preference (proportion of time/displays) for the colorful female vs. an expectation of no preference (50% with each) with a one-sample test. Proportions were arcsine transformed before testing. Means are reported ± 1 SD.

Results

Experiment 1: Natural Color Variation. Males spent $45.4 \pm 11.6\%$ of the time in the two zones close to the females. Thirteen of 15

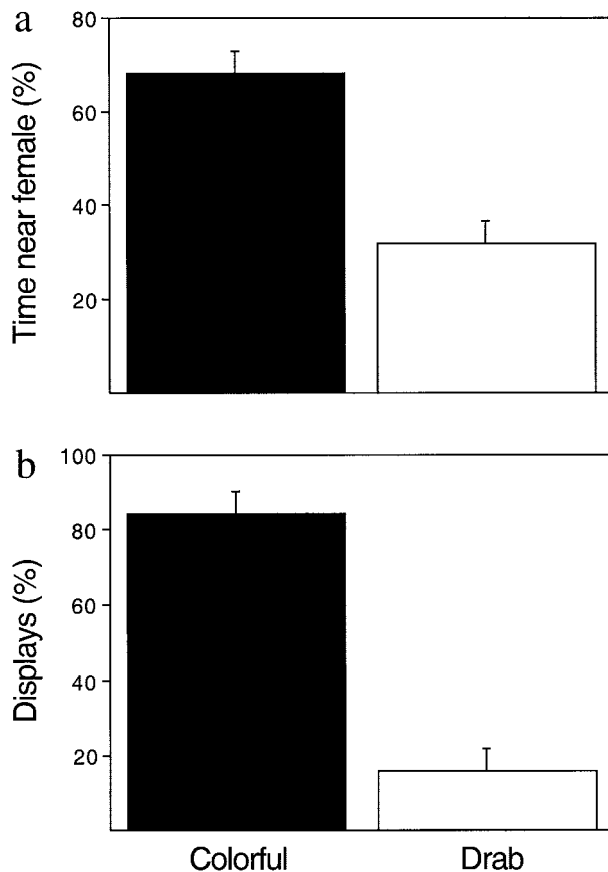


Fig. 3. Preferences of male two-spotted gobies for females varying in natural coloration. (a) Percentage of time spent in association with colorful and drab females ($n = 15$). (b) Percentage of displays directed toward colorful and drab females ($n = 10$). (Bars = means + 1 SE.)

males spent more time with the colorful than with the drab female (binomial $P = 0.007$). On average, males associated approximately twice as much with the colorful as with the drab female (Fig. 3a; $t = 3.84$; $df = 14$; $P = 0.002$). Males performed 89.6 ± 112.6 (range 0–298) displays per hr toward females. Including only those males that displayed toward females ($n = 10$), we observed on average 59.4 ± 64.1 shivers per hr and 75.0 ± 74.7 lead displays per hr (of which 17.6% involved nest entering). All of these males directed more courtship displays toward the colorful than the drab female (binomial $P = 0.002$). The number of displays directed at the colorful female was more than five times higher than for the drab one (Fig. 3b; $t = 4.93$; $df = 9$; $P = 0.001$). There was no difference between colorful and drab females in the time spent swimming ≤ 5 cm from the male compartment (colorful, $76.4 \pm 26.0\%$; drab, $77.2 \pm 31.6\%$; Wilcoxon signed-ranks test, $Z = -0.18$; $P = 0.86$). Female courtship displays occurred in four trials only, preventing further analysis.

Experiment 2: Color Manipulation. Results from the color manipulation experiment were very similar to those of experiment 1. Males spent $43.1 \pm 21.5\%$ of the time ≤ 5 cm from the female compartments. Fourteen of 16 males spent more time with the experimental (colored) than with the control (sham treated, i.e. drab) female (binomial $P = 0.004$). As for experiment 1, males spent on average more than twice as much time in association with the colorful than with the drab female (Fig. 4a; $t = 3.68$; $df = 15$; $P = 0.002$). Males performed 26.8 ± 53.8 (range 0–204) displays per hr toward females. Including only those males that

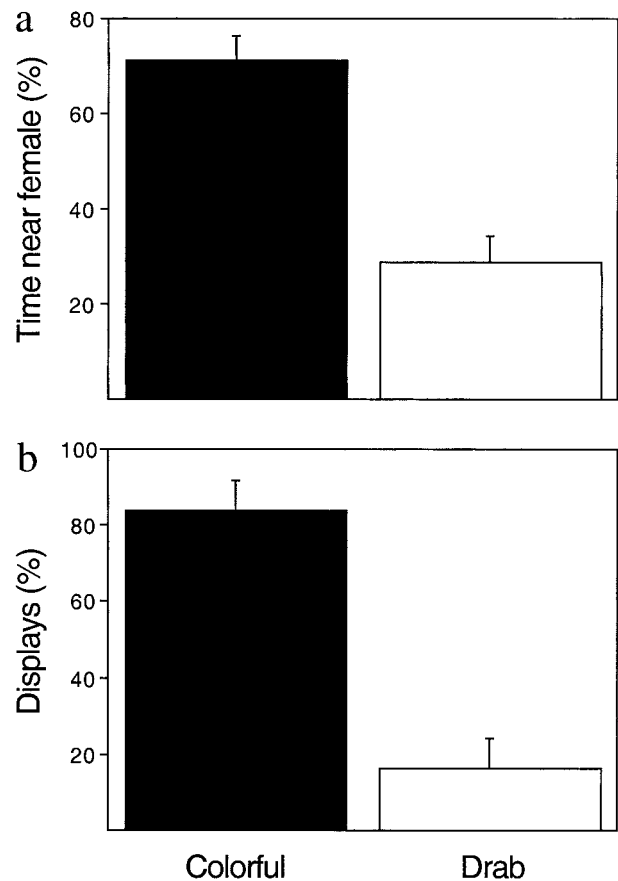


Fig. 4. Preferences of male two-spotted gobies for females varying in experimentally manipulated coloration. (a) Percentage of time spent in association with colorful and drab females ($n = 16$). (b) Percentage of displays directed toward colorful and drab females ($n = 8$). (Bars = means + 1 SE.)

displayed toward females ($n = 8$), we observed on average 39.6 ± 40.4 shivers per hr and 14.0 ± 32.3 lead displays per hr. Of these eight males, six displayed more often to the colorful than to the drab female (binomial $P = 0.29$). The mean number of displays directed at the colorful female was about five times higher than for the drab female (Fig. 4b; $t = 3.95$; $df = 7$; $P = 0.006$). There was no difference between the female treatments in time spent swimming ≤ 5 cm from the male compartment (colorful, $69.9 \pm 28.1\%$; drab, $69.7 \pm 29.4\%$; Wilcoxon signed-ranks test, $z = -0.28$; $P = 0.78$). Female courtship displays did not occur in any trial.

Discussion

Our study demonstrates conclusively a male preference for orange belly coloration in female two-spotted gobies. When confronted with two females differing in natural coloration (experiment 1), males associated more with and displayed more to colorful females. Experiment 2, in which female belly color was manipulated, revealed that the male color preference was not confounded by differences in female belly roundness. These results demonstrate male choice based on variation in color among ripe females in a fish that is not sex-role reversed. They suggest that the colorful belly of female two-spotted gobies has evolved, at least partly, as a response to male mate choice.

In terms of association and sexual display, the strength of the male preference was strikingly similar in the nonmanipulative (experiment 1) and manipulative (experiment 2) parts of the study (Figs. 3 and 4). At first sight, this observation might be

taken to suggest that female roundness is not so important in male mate choice of two-spotted gobies, in contrast to several other fish studies that have reported preferences for larger or more fecund females (12, 19–22). However, males may pay attention to roundness when exposed to several females of similar belly coloration, or when the contrast in roundness is considerable. The importance of female roundness could be disentangled by future experiments equalizing coloration in females of varying roundness.

Why are male two-spotted gobies so sensitive to female belly coloration? One possibility is that belly coloration acts as an amplifier (35) of female fecundity. To a human observer, the orange belly of an ornamented female is a highly conspicuous trait, with a high contrast to the fish body and to the habitat background. By adding color to an already round belly filled with mature eggs, females may facilitate male evaluation of fecundity. But why are not all mature females equally colorful? If the amplifying trait is costly to develop, it may at the same time be informative of female quality. Female belly coloration is mainly caused by variation in egg color (which can be seen through the skin), and, to a lesser extent, by pigment spots in the skin. Two-spotted gobies obtain carotenoids through their crustacean-dominated diet (e.g., ref. 36). It has been suggested that carotenoids act as honest indicators of individual quality in a diverse set of organisms (37–42). It remains to be demonstrated which aspects of quality, if any, might be signaled through bright carotenoid-based coloration in female two-spotted gobies.

Preference functions demonstrated under controlled captive conditions need not reflect realized mate choice in the wild (43). In general, males are assumed to be rather indiscriminate, being selected to fertilize as many females (or eggs) as possible. However, male choosiness should be expected if females vary in quality, the operational sex ratio (OSR) is female biased (6, 44–46), or there is a limit to the number of females/eggs that can be fertilized. Similar to many other littoral fishes, two-spotted goby males provide uniparental care. Eggs are deposited in cavity-like nest sites defended by the males. Obviously, there is a limit to the number of eggs that can be efficiently cared for and protected by a single male, and nest architecture often imposes a constraint on the number of eggs that can be deposited. Still, an average nest-holding male can care for the eggs of at least 2–3 females at the same time. Hence, a strongly female-biased sex ratio is probably required to favor male choosiness. As mentioned in *Methods*, such a strong bias seems to occur late in the breeding season. At that time, advertising males are very scarce, whereas mature females are abundant, thus allowing males to be choosy. The seasonal change in sex ratio seems to be accompanied by changes in mating competition and courtship by males and females (E.F., T.A., Å. Borg, and J. Bjelvenmark, unpublished data). It is noteworthy that, despite the equally strong bias in interest in colorful females in both experiments, the average frequency of male courtship displays was lower in the second than in the first experiment. This difference is most likely related to the fact that, whereas both experiments were performed late in the season, experiment 2 was made after completion of experiment 1, i.e., toward the very end of the breeding season. At this very late stage, males may become less active in courtship for at least two reasons: (i) the extremely female-biased OSR prevailing makes courtship less important because females are now very eager to mate with available males; and (ii) the males are more exhausted—two-spotted gobies live for only 1 year, and adults typically die shortly after their last breeding. A de-

cline in male courtship frequency over the season also occurs in the wild (E.F., T.A., Å. Borg, and J. Bjelvenmark, unpublished observations).

It remains to be demonstrated what benefits males may gain from being choosy. In a situation where a male may easily have several females to lay eggs in his nest, the number of eggs deposited by each female may not significantly influence male fitness. More likely, male reproductive success may be influenced by factors (phenotypic or genetic) related to the viability of eggs or offspring. Recent evidence suggests that egg carotenoids reduce oxidative stress and, hence, are indicative of egg quality (47). Studies of farmed fish species indicate that carotenoids, especially astaxanthin, are important for egg and larval quality (48, 49). Future research may reveal whether female coloration in two-spotted gobies reflects egg size, egg viability, or offspring posthatching viability. Intriguingly, in Arctic charr *Salvelinus alpinus* a relationship seems to exist between female color and indices of immune capacity (50). Studies of relationships between ornamentation, parasites and immune parameters in females are very few and should be encouraged.

The demonstrated male preference for female coloration does not preclude a function of female ornamentation in contest competition among females. Indeed, signals indicative of female competitive ability may be expected in social species such as shoaling fish and flock-living birds (3, 4), although competitive interactions in such systems are often subtle. Field observations suggest, however, that female belly coloration is much more often displayed toward males than females (E.F., T.A., Å. Borg, and J. Bjelvenmark, unpublished observations). Still, the potential of female coloration in social competition calls for investigation.

Female conspicuous morphological traits (“ornaments”) are widespread in fish and other taxa (12, 17, 18), perhaps more so than what is reflected in many textbooks. In some species, females are showy and indistinguishable from males (e.g., butterflyfishes); in others they carry ornaments that are different from those of the males (this study) or similar but less well developed (e.g., many salmonids). Females may be even more strikingly colored than males, as seen in several wrasses. Female coloration is most commonly caused by pigments or structural colors in the skin, but may sometimes also reflect egg color (as in two-spotted gobies). Yellow to red egg and skin colors typically are results of carotenoids ingested and modified. However, the basis of structural colors is less well understood. Only few studies have addressed the functional significance of the diversity of showy female traits, but a function has often been found when sought for (refs. 23–28, and this study). Interestingly, among sticklebacks, female nuptial coloration seems to have originated before male ornamentation (51). Science has now provided us with a reasonably good understanding of male showiness. We suggest that more attention should be directed at the largely unstudied phenomenon of female “beauty” in fish and other animals.

We thank Sylve Robertsson for constructing excellent field equipment, Iain Barber, Jens Bjelvenmark, and Åsa Borg for assistance in catching fish, and Staffan Anderson for assistance with spectrometric analyses. Anders Berglund, Gordon H. Orians, Ben Sheldon, and two anonymous reviewers provided valuable comments on a previous draft. The study was financially supported by grants from the Swedish Natural Science Research Council (to E.F.) and the European Union Large Scale Facilities Program at Kristineberg (to T.A.).

1. Lande, R. (1980) *Evolution (Lawrence, Kans.)* **34**, 292–305.
2. Lande, R. (1987) in *Sexual Selection: Testing the Alternatives*, eds. Bradbury, J. W. & Andersson, M. B. (Wiley, New York), pp. 83–95.
3. West-Eberhard, M. J. (1979) *Proc. Amer. Phil. Soc.* **123**, 222–234.
4. West-Eberhard, M. J. (1983) *Q. Rev. Biol.* **55**, 155–183.

5. Burley, N. (1977) *Proc. Natl. Acad. Sci. USA* **74**, 3476–3479.
6. Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. (1996) *Evolution (Lawrence, Kans.)* **50**, 1382–1391.
7. Owens, I. P. F. & Thompson, D. B. A. (1994) *Proc. R. Soc. London Ser. B* **258**, 93–99.

8. Kokko, H. & Monaghan, P. (2001) *Ecol. Lett.* **4**, 159–165.
9. Irwin, R. E. (1994) *Am. Nat.* **144**, 890–907.
10. Peterson, A. T. (1996) *Bull. Brit. Orn. Club* **116**, 156–172.
11. Burns, K. J. (1998) *Evolution (Lawrence, Kans.)* **52**, 1219–1224.
12. Turner, G. F. (1993) in *Behaviour of Teleost Fishes*, ed. Pitcher, T. J. (Chapman & Hall, London), pp. 307–331.
13. Marshall, N. J. (2000) in *Animal Signals*, eds. Espmark, Y., Amundsen, T. & Rosenqvist, G. (Tapir Academic, Trondheim, Norway), pp. 83–120.
14. Jones, I. L. & Hunter, F. M. (1993) *Nature (London)* **362**, 238–239.
15. Amundsen, T., Forsgren, E. & Hansen, L. T. T. (1997) *Proc. R. Soc. London Ser. B* **264**, 1579–1586.
16. Jones, I. L. & Hunter, F. M. (1999) *Anim. Behav.* **57**, 521–528.
17. Amundsen, T. (2000) *Trends Ecol. Evol.* **15**, 149–155.
18. Amundsen, T. (2000) in *Animal Signals*, eds. Espmark, Y., Amundsen, T. & Rosenqvist, G. (Tapir Academic, Trondheim, Norway), pp. 133–154.
19. Andersson, M. (1994) *Sexual Selection* (Princeton Univ. Press, Princeton).
20. Sargent, R. C., Gross, M. R. & van den Berghe, E. P. (1986) *Anim. Behav.* **34**, 545–550.
21. Bisazza, A., Marconato, A. & Marin, G. (1989) *Ethology* **83**, 335–343.
22. Kraak, S. B. M. & Bakker, T. C. M. (1998) *Anim. Behav.* **56**, 859–866.
23. Rowland, W. J., Baube, C. L. & Horan, T. T. (1991) *Anim. Behav.* **42**, 243–249.
24. McLennan, D. A. (1995) *Anim. Behav.* **50**, 213–221.
25. Berglund, A., Rosenqvist, G. & Svensson, I. (1986) *Behav. Ecol. Sociobiol.* **19**, 301–307.
26. Rosenqvist, G. (1990) *Anim. Behav.* **39**, 1110–1115.
27. Berglund, A. & Rosenqvist, G. (2001) *Anim. Behav.* **61**, 345–350.
28. Beeching, S. C., Gross, S. H., Bretz, H. S. & Hariatis, E. (1998) *Anim. Behav.* **56**, 1021–1026.
29. Svensson, P. A., Barber, I. & Forsgren, E. (2000) *J. Fish Biol.* **56**, 1477–1487.
30. Gordon, J. C. D. (1983) *Ophelia* **22**, 173–183.
31. Collins, S. P. (1981) *Proc. R. Irish Acad.* **81b**, 63–87.
32. Utne, A. C. W. (1995) Ph.D. thesis (Univ. of Bergen, Bergen, Norway).
33. Bjelvenmark, J. (1998) M.S. thesis (Göteborg Univ., Göteborg, Sweden).
34. Johnsen, S. (1945) *Bergen Museums Årbok, Naturvitenskapelig rekke* **4**, 30–49.
35. Hasson, O. (1989) *Proc. R. Soc. London Ser. B* **235**, 383–406.
36. Berg, J. (1979) *Mar. Biol. (Berlin)* **50**, 263–273.
37. Milinski, M. & Bakker, T. C. M. (1990) *Nature (London)* **344**, 330–333.
38. Hill, G. E. (1991) *Nature (London)* **350**, 337–339.
39. Houde, A. E. & Torio, A. J. (1992) *Behav. Ecol.* **3**, 346–351.
40. Olson, V. A. & Owens, I. P. F. (1998) *Trends Ecol. Evol.* **13**, 510–514.
41. von Schantz, T., Bensch, S., Grahm, M., Hasselquist, D. & Wittzell, H. (1999) *Proc. R. Soc. London Ser. B* **266**, 1–12.
42. Møller, A. P., Biard, C., Blount, J. D., Houston, D. C., Ninni, P., Saino, N. & Surai, P. F. (2000) *Avian and Poultry Biol. Rev.* **11**, 137–159.
43. Widemo, F. & Sæther, S. A. (1999) *Trends Ecol. Evol.* **14**, 26–31.
44. Emlen, S. T. & Oring, L. W. (1977) *Science* **197**, 215–223.
45. Parker, G. A. (1983) in *Mate Choice*, ed. Bateson, P. (Cambridge Univ. Press, Cambridge, U.K.), pp. 141–166.
46. Parker, G. A. & Simmons, L. W. (1996) *Proc. R. Soc. London Ser. B* **263**, 315–321.
47. Blount, J. D., Houston, D. C. & Møller, A. P. (2000) *Trends Ecol. Evol.* **15**, 47–49.
48. Verakunpiriya, V., Mushiake, K., Kawano, K. & Watanabe, T. (1997) *Fish. Sci.* **63**, 816–823.
49. Petterson, A. & Lignell, Å. (1999) *Ambio* **28**, 43–47.
50. Skarstein, F. & Folstad, I. (1996) *Oikos* **76**, 359–367.
51. McLennan, D. A. (1996) *Syst. Biol.* **45**, 261–277.