Do male two-spotted gobies prefer large fecund females?

Christophe Pélabon, Åsa A. Borg, Jens Bjelvenmark, Elisabet Forsgren, Iain Barber, and Trond Amundsen

Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway, Department of Marine Ecology, Göteborg University, Sweden, and Institute of Biological Sciences, University of Wales Aberystwyth, UK

A male mating preference for large females may be expected when female size is correlated with fecundity. We tested for such a preference in a fish, the two-spotted goby (Gobiusculus flavescens, Gobiidae), for which a male preference for colorful females has been demonstrated. We offered males a choice between two stimulus females of different size, controlling for female color and stage of egg maturation. We also analyzed the relationship between size and fecundity (total number of eggs in the clutch) by allowing females of different size to spawn in a controlled environment. Female length explained 37% of the variation in fecundity, but males showed only a weak preference for large females. We compared the coefficient of variation (CV) in fecundity between female two-spotted gobies and other fish species for which male preferences for large females have been reported. The CV in fecundity in the two-spotted goby was among the lowest. We suggest that the low variation limits the potential fecundity benefit to be gained by a male selecting females on the basis of size alone. Our study emphasizes the importance of the variation in partner quality for the direction and the strength of mate preferences, as suggested by theoretical models. Key words: coefficient of variation, fecundity, mate choice, size, two-spotted goby. [Behav Ecol 14:787–792 (2003)]

In conventional theory of sex roles, males are described as being nonselective of mating partners, maximizing their reproductive success by increasing the number rather than the quality of mates. Females are described as being highly selective, maximizing their fitness by selecting high quality mates (Andersson, 1994; Trivers, 1972). However, theoretical approaches have repeatedly suggested the occurrence of mutual mate choice, opening the possibility of mate selection by males even in species with conventional sex roles (Bergstrom and Real, 2000; Clutton-Brock and Parker, 1992; Johnstone et al., 1996; Kokko and Johnstone, 2002; Kokko and Monaghan, 2000; Parker, 1983; Parker and Simmons, 1996; Real, 1991). Theory suggests that the level of variation in mate quality strongly affects the benefits associated with mate choice (Clutton-Brock and Parker, 1992; Parker, 1983; Real, 1991), whereas the costs are affected by the operational sex ratio (OSR, Emlen and Oring, 1977), the potential reproductive rate (Clutton-Brock and Parker, 1992), predation (Forsgren, 1992), individual condition (Bakker et al., 1999), and loss of future mating opportunities (Johnstone et al., 1996; Owens and Thompson, 1994).

Variation in fecundity as a source of differences in quality among females could drive the evolution of male mating preferences even in species with conventional sex roles (Andersson, 1994). Males are expected to prefer larger females in taxa in which female fecundity is related to body size. Males may also show a mating preference for female size because size may reflect some underlying genetic quality such as growth rate (Reynolds and Gross, 1992). In species in which larval survival, male reproductive success, and female reproductive output depend on growth rate and size at maturity, a mating preference for large individuals may be expected.

Studies have demonstrated male preferences for large females in insects, reptiles, amphibians, and fishes (Andersson, 1994). In fish, the preferences reported are generally strong, and a male mating preference for large females appears typical. However, only a few studies report data both on male mating preferences for large females and on the relationship between fecundity and female size (see Itzkowitz et al., 1998; Kraak and Bakker, 1998).

In the present study, we tested whether male two-spotted gobies (Gobiusculus flavescens) prefer large females to smaller ones. Observations in the wild, on the studied population, suggest a change in the OSR during the reproductive season, with a strong female bias toward the end of the season (Forsgren E, Amundsen T, Borg AA, and Bjelvenmark J, unpublished data). Therefore, late in the season, males may have ample opportunity to choose among mating partners. Female two-spotted gobies develop yellow-orange bellies during breeding. Controlled mate choice experiments have revealed a strong male preference for more colorful females (Amundsen and Forsgren, 2001). In these experiments, female size was standardized, and it remains unknown whether males also prefer to mate with larger, and presumably more fecund, females. By using the same protocol as in the study of male preference for female color (Amundsen and Forsgren, 2001), we performed a mate choice experiment in which males were given a choice between two stimulus females of different size. We also examined the relationship between fecundity and female body size.

METHODS

The study was conducted at Kristineberg Marine Research Station on the west coast of Sweden (58°15' N, 11°27' E). Analyses of female fecundity in relation to body size were based on spawnings obtained from 20 June–16 July 2000, and from 21 June–14 July 2001. Mate choice trials were conducted from 20 June–15 July 2001.
Studie species

The two spotted goby is a small (35–55-mm-long) fish inhabiting shallow waters along rocky shores of the Baltic and European Atlantic coasts (Miller, 1986). During a single breeding season (from May–August in our study area), males acquire and defend nest sites in empty bivalves or crevices in the algal vegetation, e.g., between Laminaria fronds (Gordon 1983, personal observation). Males attract females to their nests with courtship displays. After spawning, the female leaves the nest, and exclusively, the male provides parental care, fanning and cleaning the eggs for a period of 1–3 weeks depending on water temperature (Bjelkenmark and Forsgren, 2003; Skolbeckken and Ute-Palm, 2001). The two-spotted goby exhibits sexual size dimorphism, with males on average slightly larger than females (male: total length mean ± SE = 47.0 ± 0.48 mm, n = 56; female: total length mean = 45.6 ± 0.16 mm, n = 210; random sample from May–July 2001). Both males and females display sexual ornamentation during the breeding season. Males have highly developed dorsal fins with iridescent blue markings, as well as iridescent blue spots along the body flanks. Females develop conspicuous yellow-orange bellies during breeding (Amundsen and Forsgren, 2001: Figure 1).

General procedures

Two-spotted gobies were hand-netted by a snorkeler in waters adjacent to the research station. Males and females were held separately according to date and place of capture. Storage aquaria had a constant water supply with nonfiltered seawater (intake at 7-m depth) at ambient sea temperature. Food (freshly hatched Artemia nauplii) was provided daily ad libitum. Fish used in the experiment were held for an average period of 4 days (range = 1–6) for females and 2 days (range = 1–7) for males. All males used in the experiment were 41.5 mm or larger. Fish were returned to the fjord after completion of trials, except for 15 males dissected for parasite analysis (Pélabon C, Barber I, and Amundsen T, unpublished data). All fish used in both studies were weighed (to the nearest 0.01 g) and measured (total length, to the nearest 0.5 mm).

Female size and fecundity

During two consecutive breeding seasons, females of different sizes were allowed to reside with a nest-holding male under controlled conditions. Females were taken randomly in relation to their size. Each female was placed with a male into an aquarium (30 × 25 × 30 cm). Each aquarium was provided with a nest site (halved clay flowerpot 6 cm in diameter), gravel, artificial vegetation, and a permanent water flow. The room and the water temperature were kept constant (to the nearest 0.01 g) and measured (total length, to the nearest 0.5 mm). Eggs were spawned. This renders the possibility for females to vary their clutch size according to some aspects of the male or the environment unlikely.

Mate choice trials

Test tanks (75 × 30 × 30 cm) were divided into three compartments of similar size (each 25 cm long) by transparent Plexiglas partitions perforated to allow water flow. Each compartment was provided with fine gravel on the bottom and one artificial plant to mimic a natural environment. The central (male) compartment was provided with an artificial nest, a PVC tube, 8 cm long and 1 cm in diameter. Males were introduced to the central compartment the day before the trial, to allow time for acclimatization, including occupation of the artificial nest. The two side compartments were hidden from the male by opaque removable partitions. Two females of similar belly coloration (see below) but different size (mean total length ± SE, large: = 47.9 ± 0.18 mm; small: mean ± SE = 43.0 ± 0.16 mm; mean difference ± SE = 4.94 ± 0.11 mm; range = 3.5–9.0 mm) were introduced to the two side compartments a few hours before the trial (median = 3.25 h; range = 2:05–11:20). The size difference between stimulus females corresponded to about twice the SD of the mean female length recorded on a random sample of 210 females captured at the same period. Fish were weighed and measured just before introducing them into the test tank. Trials were started by the removal of the opaque partitions when all fish were swimming in the water column.

Each trial lasted 20 min. During this period, we continually recorded courtship behavior patterns of males and females. We also scan-sampled the position and the activity (swimming, resting on the bottom/glass/algae, or in the nest) of the fish every 20 s. We recorded three different male courtship behaviors: (1) fin displays (the erection of the fins when approaching the female), (2) shivers (lateral shivering movements of the body when oriented parallel to a nearby female) and (3) leads (swimming away from the female compartment with undulating fin and body movements; in the wild, typically used when leading a female to the nest). Male association with each female was assessed from the time spent within a response zone less than 5 cm from the female compartment while the female was simultaneously present on the other side less than 5 cm from the Plexiglas partition.

Matching stimulus females for roundness and redness

We selected stimulus females of similar roundness (defined by the residuals of the regression of the mass, \( Y \) over the length, \( X \), after log-transformation of both). The allometric relationship between length and mass did not differ between small and large stimulus females (ANCOVA, interaction effect: \( F_{1,168} = 0.13, p = .72 \), category [large versus small] effect: \( F_{1,168} = 0.12, p = .73 \)). Because males prefer more colorful females (Amundsen and Forsgren, 2001), we also matched stimulus females for belly coloration in order to avoid a confounding effect of female color on male preferences for female size. To match pairs of females for belly coloration, females were first allowed to swim next to each other and matched by eye, by at least three observers. This procedure was later confirmed by photographing the females (after the trials) and quantifying the color of the bellies from digital images. Two digital pictures (one of each side) were taken of each female following a standardized photographic protocol. Analysis of the belly coloration was made by using Adobe Photoshop 5.0. By using the red-green-blue color model, we calculated the “red index” (\( R_0 \)) of the female ornament. The colored area of the female belly was first selected using the

\[ Y = 44.1 \pm 0.25 \text{ (from those that did not spawn)} \]

\[ t = 7.09, df = 213, p = .43 \]

\[ \text{Inspection of gonads after spawning on several females (Pélabon C, personal observation)} \]

\[ \text{revealed that all mature} \]

\[ \text{eggs were spawned. This renders the possibility for females to vary their clutch size according to some aspects of the male or the environment unlikely.} \]

\[ \text{Mate choice trials} \]

\[ \text{Test tanks (75 × 30 × 30 cm) were divided into three compartments of similar size (each 25 cm long) by transparent} \]

\[ \text{Plexiglas partitions perforated to allow water flow. Each} \]

\[ \text{compartment was provided with fine gravel on the bottom and one artificial plant to mimic a natural environment. The} \]

\[ \text{central (male) compartment was provided with an artificial} \]

\[ \text{nest, a PVC tube, 8 cm long and 1 cm in diameter. Males were} \]

\[ \text{introduced to the central compartment the day before the} \]

\[ \text{trial, to allow time for acclimatization, including occupation of the} \]

\[ \text{artificial nest. The two side compartments were hidden from the} \]

\[ \text{male by opaque removable partitions. Two females of similar} \]

\[ \text{belly coloration (see below) but different size (mean total length ± SE, large: = 47.9 ± 0.18 mm; small: mean ± SE = 43.0 ± 0.16 mm; mean difference ± SE = 4.94 ± 0.11 mm; range = 3.5–9.0 mm) were introduced to the} \]

\[ \text{two side compartments a few hours before the trial (median = 3.25 h; range = 2:05–11:20). The size difference between} \]

\[ \text{stimulus females corresponded to about twice the SD of the} \]

\[ \text{mean female length recorded on a random sample of 210} \]

\[ \text{females captured at the same period. Fish were weighed and} \]

\[ \text{measured just before introducing them into the test tank.} \]

\[ \text{T} \]

\[ \text{rials were started by the removal of the opaque partitions when all fish were swimming in the water column.} \]

\[ \text{Each trial lasted 20 min. During this period, we continually} \]

\[ \text{recorded courtship behavior patterns of males and females.} \]

\[ \text{We also scan-sampled the position and the activity (swimming, resting on the bottom/glass/algae, or in the nest) of the fish} \]

\[ \text{every 20 s. We recorded three different male courtship} \]

\[ \text{behaviors: (1) fin displays (the erection of the fins when} \]

\[ \text{approaching the female), (2) shivers (lateral shivering} \]

\[ \text{movements of the body when oriented parallel to a nearby} \]

\[ \text{female) and (3) leads (swimming away from the female} \]

\[ \text{compartment with undulating fin and body movements; in the wild, typically used when leading a female to the nest).} \]

\[ \text{Male association with each female was assessed from the} \]

\[ \text{time spent within a response zone less than 5 cm from the} \]

\[ \text{female compartment while the female was simultaneously present on the other side less than 5 cm from the} \]

\[ \text{Plexiglas partition.} \]

\[ \text{Matching stimulus females for roundness and redness} \]

\[ \text{We selected stimulus females of similar roundness (defined by the residuals of the regression of the mass, Y over the length, X, after log-transformation of both). The allometric relationship between length and mass did not differ between small and large stimulus females (ANCOVA, interaction effect: F_{1,168} = 0.13, p = .72 category [large versus small] effect: F_{1,168} = 0.12, p = .73). Because males prefer more colorful females (Amundsen and Forsgren, 2001), we also matched stimulus females for belly coloration in order to avoid a confounding effect of female color on male preferences for female size. To match pairs of females for belly coloration, females were first allowed to swim next to each other and matched by eye, by at least three observers. This procedure was later confirmed by photographing the females (after the trials) and quantifying the color of the bellies from digital images. Two digital pictures (one of each side) were taken of each female following a standardized photographic protocol. Analysis of the belly coloration was made by using Adobe Photoshop 5.0. By using the red-green-blue color model, we calculated the “red index” (R0) of the female ornament. The colored area of the female belly was first selected using the} \]
"magic wand" option. The RI of this selected area was subsequently obtained by dividing the mean of the red component by the sum of the red, green, and blue component means given by the software (Braithwaite and Barber, 2000; Frischknecht, 1993; Villafuerte and Negro, 1998). Repeatability (Lessells and Boag, 1987) of the method, estimated by photographing each of 18 females twice at approximately 90-min intervals, was high ($R = .82$). This suggests that our protocol for color analysis was sufficiently reliable to capture potential differences in "redness" among stimulus females used in the experiment.

There was no difference in RI between small and large stimulus females ($t_{test} = 0.11$, $n = 82$, $p = .91$), and RI of pairs of stimulus females was correlated ($r = .24$, $p = .03$, $n = 82$), confirming our ability to match females for their belly coloration.

Statistical analysis

We inferred a male’s preference for large females from the proportion of time spent together with the largest female, and from the proportion of courtship displays directed towards her. Both the difference in quality between stimulus females and the absolute quality of a female (here, absolute size) may affect courtship intensity as well as male preferences. Therefore, we tested for the relationships between courtship intensity (total number of courtship displays to both females) and the absolute size of the largest stimulus female, and we analyzed the relationships between male preferences and the difference in size between stimulus females. Because behavioral variables tended to be over-dispersed and not normally distributed, we used nonparametric statistics when needed. Proportions of courtship display directed towards the largest female were arcsine-square root transformed.

RESULTS

Female size and fecundity

The average clutch size was 1368 eggs (SE = 40.30; range = 672–2101). Clutch size increased significantly with female length ($F_{1,70} = 40.59$, $p < .001$) (Figure 1). The significant effect of year revealed by ANCOVA ($F_{1,70} = 8.32$, $p = .005$) resulted from a minor but significant difference in female length ($F_{1,205} = 17.33$, $p < .001$), but not in clutch size ($F_{1,73} = 0.23$, $p = .64$), between years. Taking both years into account by using a partial correlation controlling for year, there was a strong correlation between female length and fecundity ($r_{Year} = .61$, $n = 70$, $p < .001$, $r^2 = .37$).

Male preference for large females

Males spent on average 56% (SE = 2%) of the time in the response zones. Of the total time spent in association with either female, about 57% was spent with the larger, which is only marginally significantly different from the 50% expected if no discrimination occurs (Table 1). Fin displays represented 72% of the total displays, whereas shivers and leads represented 17% and 11%, respectively. The proportion of fin displays directed toward the large female was significantly higher than expected in the absence of any preference, whereas no significant preference was detected for shivers and leads (Table 1). Most of the behaviors, except leads, showed a similar pattern of preference, with a mean proportion of display directed toward the large female of close to 57% (Table 1). For a comparison with the study of Amundsen and Forsgren (2001) on male preferences for colorful females, we pooled shivers and leads. The proportion of shivers + leads directed toward the large female was not significantly different from 50% (Table 1). Therefore, males only showed a weak preference for large females.
Neither the total number of displays (fins + shivers + leads) nor the proportion of displays directed toward the large female increased when the size of the large stimulus female increased (total number of display: $r_s = -.06$; fin display $r_s = .07$; shiver: $r_s = .21$; lead: $r_s = -.01$, all $p > .28$). Similarly, the proportion of displays directed toward the large female did not increase when the difference in length between the two stimulus females increased (fin display: $r_s = .13$; shiver: $r_s = .29$; lead: $r_s = .13$; all: $p > .28$). Finally, we found no evidence of assortative preference for size. The preference displayed by small males (less than median length) was similar to the preference displayed by large males (more than median length, all tests: $1 < p < .76$).

**DISCUSSION**

Variation in female size in two-spotted gobies explains 37% of the variation in clutch size. However, the preference for large females displayed by males in the present study was weak. This result is in contrast to a preference displayed by males for female coloration in the same population demonstrated by using the same experimental protocol. In that study, more than 80% of the male displays were directed toward the most colorful females (Amundsen and Forsgren, 2001). According to theoretical models, the direction and strength of mating preferences will be affected by variation in quality among mating partners perceived by the choosers (Parker, 1983). In this study, two factors may affect the variation in female quality as perceived by the males. First, because the trait used is not fecundity itself, male assessment of the variation in fecundity among females can be impaired by a weak correlation between the relevant trait, here, size and fecundity. Second, if the quality-related trait in question shows little variation among females, there is less to be gained by a male from being selective.

**Male assessment of fecundity variation among females**

If the strength of the correlation between size and fecundity can affect the male mating preference for large females, a positive relationship is expected across populations or species between the strength of the male mating preference and the correlation between size and fecundity. We reviewed data for species for which there was information on both male preferences for female size and size-fecundity relationships (Table 2). In three-spined sticklebacks (Gasterosteus aculeatus), Kraak and Bakker (1998) reported a male mating preference for large females that was close to the preference observed in the present study. However, the relationship between length and fecundity was much stronger than in our experiment (Table 2). In the beaugregory damselfish (Stegastes leucostictus), the mean proportion of displays directed toward large females was high (Table 2). However, the relationship between size and fecundity, inferred from the relationship between ovarian dry mass and length, was not stronger than that observed in the two-spotted goby (Table 2). Several other studies that report a preference for large females did not allow calculation of the strength of the male mating preference in a way comparable to the present study. In general, the coefficient of determination ($r^2$) of the relationships between length and fecundity for these species were not much different from that for two-spotted gobies. This suggests that the relationship between length and fecundity in female two-spotted gobies is not weaker than for many species in which a male preference for large females has been detected.

**Male preference and variation in female fecundity**

The potential benefits associated with mating preferences depend on variation in quality among mating partners (Parker, 1983). In mate choice trials, one might not expect a strong mating preference if the difference between choice options is not sufficient. However, a positive relationship is expected between the strength of the male mating preference and the amplitude of the difference between stimuli (Nutall and Keenleyside, 1993; Ptacek and Travis, 1997; Sargent et al., 1986). The size difference between the two stimulus females was considerable in the present study (range: 3.5–9.0 mm; mean = 4.94 mm, more than 10% of the total length). In terms of fecundity, this represented an expected average difference in clutch size of about 350 eggs (about 30% increase on average from “small” to “large”). Therefore, we believe that the weak male preference for the large females in two-spotted gobies does not result from an insufficient difference in fecundity between stimulus females used in our experiment. In addition, we did not find any increase in the strength of the male mating preference for the larger female as the difference in size between the two stimulus females increased.

If, in a natural population, there were little variation in a specific female quality, owing, e.g., to the life history of the species, selection for male preferences in relation to that

---

**Table 1**

<table>
<thead>
<tr>
<th>Courtship behavior</th>
<th>Proportion with the larger female</th>
<th>Preference for large versus small female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (SE)</td>
<td>T (df)</td>
</tr>
<tr>
<td>Time in response zone</td>
<td>0.57 (0.036)</td>
<td>1.84 (54)</td>
</tr>
<tr>
<td>Fin display</td>
<td>0.58 (0.038)</td>
<td>2.06 (32)</td>
</tr>
<tr>
<td>Shiver</td>
<td>0.57 (0.002)</td>
<td>0.891 (36)</td>
</tr>
<tr>
<td>Lead</td>
<td>0.51 (0.076)</td>
<td>-0.244 (26)</td>
</tr>
<tr>
<td>Lead + shiver</td>
<td>0.55 (0.062)</td>
<td>0.536 (37)</td>
</tr>
</tbody>
</table>

Proportions of time spent close to, and courtship behaviors directed toward, the larger of two stimulus females were tested by using one-sample $t$ test against no preference (50%), after transformation ([arcsine($P$)]\(^{0.5}$). The number of trials showing a preference for either the large or the small females was tested by using a binomial test. Differences in sample sizes are owing to differences in the numbers of males displaying each behavior.

* Proportion of time in the response zone (RZ) with the large female/(proportion of time in the RZ with small female + proportion of time in the RZ with large female).
Table 2
Male mate preference, length-fecundity correlation, and variation in fecundity in fish species in which male preferences for large female has been observed

<table>
<thead>
<tr>
<th>Fish species</th>
<th>Male preference for large female</th>
<th>Reference for male mating preference</th>
<th>CV for fecundity</th>
<th>Length versus fecundity correlation (r)</th>
<th>Reference for female fecundity</th>
<th>Paternal care</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beaugregory damselfish,</td>
<td>0.85</td>
<td>Itzkowitz et al., 1998 (Table 1)</td>
<td>0.72</td>
<td>.54b</td>
<td>Itzkowitz et al., 1998</td>
<td>Nest</td>
</tr>
<tr>
<td>Stegastes leucostictus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Redlip blenny,</td>
<td>Yes</td>
<td>Côte and Hunte, 1989</td>
<td>0.62</td>
<td>.73</td>
<td>Côte and Hunte, 1989 (calculated from Figure 3)</td>
<td>Nest</td>
</tr>
<tr>
<td>Ophiodon atlanticus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Two-spotted goby,</td>
<td>0.57</td>
<td>the present study</td>
<td>0.26</td>
<td>.61</td>
<td>the present study</td>
<td>Nest</td>
</tr>
<tr>
<td>Gobiusculus flavescens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand goby,</td>
<td>0.53–0.57</td>
<td>Kvarnemo and Forsgren, 2000 (Figure 1)</td>
<td>0.23</td>
<td>.63</td>
<td>Kvarnemo, 1994, 1997 Forsgren Ë, unpublished data</td>
<td>Nest</td>
</tr>
<tr>
<td>Pomatoschistus minutus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sailfin molly,</td>
<td>Yes</td>
<td>Ptacek and Travis, 1997</td>
<td>0.45</td>
<td>NA</td>
<td>Trexler, 1997 (calculated from Figure 3)</td>
<td>No</td>
</tr>
<tr>
<td>Poecilia latipinna</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sockeye salmon,</td>
<td>Yes</td>
<td>Foote, 1988</td>
<td>0.16</td>
<td>.59d</td>
<td>Manzer and Miki, 1986 (calculated from Table 2)</td>
<td>No</td>
</tr>
<tr>
<td>Oncorhynchus nerka</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Three-spined sticklebacks,</td>
<td>0.61</td>
<td>Kraak and Bakker, 1998 (Figure 3a)</td>
<td>0.37</td>
<td>.87</td>
<td>Kraak and Bakker, 1998 (calculated from Figure 2a)</td>
<td>Nest</td>
</tr>
<tr>
<td>Gasterosteus aculeatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pipefish,</td>
<td>Yes</td>
<td>Berglund et al., 1986</td>
<td>0.37</td>
<td>.76</td>
<td>Berglund et al., 1986 (calculated from Figure 1)</td>
<td>Yes</td>
</tr>
<tr>
<td>Syngnathus typhle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Brood pouch</td>
<td></td>
</tr>
</tbody>
</table>

Fecundity has been calculated from the number of eggs per clutch except when mentioned differently.

a Proportion of either time spent with or displays toward large female (when available).
b Inferred from the relationship between length and ovary dry mass.
c Based on the number of neonates for South Carolina females raised on high food level (Trexler, 1997).
d Based on the average for four different populations (Great Central, Sproat, Henderson, and Hobiton; see Manzer and Miki, 1986) and three age classes. These populations have been chosen as the closest in latitude to the one studied by Foote (1988).

Aspect of quality would be weak. We reviewed variation in female fecundity for fish species for which male preferences for large females have been studied (Table 2). In this review, the CV in female fecundity in two-spotted gobies is one of the lowest. Therefore, the potential benefits associated with a mating preference for female size seem limited in two-spotted gobies. Interestingly, the lowest CV in fecundity noted among species with paternal care is shown by the sand goby (Pomatoschistus minutus), for which a similarly weak male mating preference for large females has been reported (Kvarnemo and Forsgren, 2000). Both of these goby species normally live for only 1 year, rendering variation in female size much less than in species that may live for several years and reproduce repeatedly. This suggests that in taxa with indeterminate growth, selection on males to discriminate between females on the basis of their length should be weaker in species in which all reproductive individuals are basically the same age. Surprisingly, male preference for female size has also been documented in the sockeye salmon, Oncorhynchus nerka, in which the lowest CV in female fecundity was found (Table 2). However, salmon females compete for the spawning site, with larger females gaining better sites (Sargent et al. 1986). Therefore, additional fitness components may be associated with the male preference for female size.

The average clutch size of the two-spotted goby was 1368 eggs, and only 5% of females lay clutches larger than 1850 eggs. Observations from the field suggest that natural nests contain on average about the equivalent of three typical clutches (Amundsen T, Bjelvenmark J, Forsgren E, and Svensson A, unpublished data). Therefore, because of possible space (in the nest) or energetic (paternal care) constraints on the total number of eggs a male can care for and the low variation in female fecundity, the increase in reproductive success associated with selection based solely on female body size will be limited. Even when the OSR is strongly female biased, net benefits associated with a selection on female size should rapidly be overtaken by the benefits associated with less selective matings for at least two reasons. First, if males are not selective, the interval between successive matings should be shorter. Consequently, the development of the different clutches in the nest should be more synchronized, and the period of paternal care decreased. Second, females may vary in other sources of quality than fecundity. If clutch qualities such as hatching success or offspring survival are more variable among females than is fecundity, and are not correlated with the latter, a preference for female size would not be expected. It is worth noting here that no relationship between egg size and clutch size has been found in the two-spotted goby (Pélabon C, Amundsen T, and Forsgren E, unpublished data), suggesting that clutch size is not related to possible clutch size determined by egg size. If female belly coloration reflects clutch quality in the two-spotted goby, mating with colorful females might increase male fitness more than mating with large females, which would explain why the male
preference for female coloration is stronger than for female size. Alternatively, if female quality is unpredictable from her phenotype, selection should favor males that mate with several females instead of with a smaller number of highly fecund females. Indeed, when two tactics lead to an equal mean fitness, selection should, under certain conditions, favor the one with the lowest variance (Philippi and Seger, 1989; Slatkin, 1974), which in this case would be a tactic that maximizes the number of females spawning.

In conclusion, the present study supports theoretical models of mating preference that emphasize the importance of variation in quality among mating partners in determining the direction and strength of choosiness (Johnstone et al., 1996; Kvarnemo and Simmons, 1999; Parker, 1983). It also suggests that in species which live only for one year, and in which males care for clutches laid by several females, variation in female fecundity is typically too small to select for male discrimination on the basis of female size.

We thank Kris Fiche, Henrik Pärn, Bob Wootton, and two anonymous referees for valuable comments on earlier drafts of this article. We also thank Katja Nagel for the invaluable help, comments, and friendship provided during fieldwork. I. Kvarnemo kindly sent us data on sand goby. The study was financially supported by the MARE program of the Research Council of Norway, the EU Transnational Access to Research Infrastructures program at Kristineberg, the Swedish Natural Sciences Research Council, the Swedish King Carl XVI Gustaf’s anniversary fund, the Norwegian Academy of Science, and Natural Environment Research Council (UK).

REFERENCES