Sex-role reversal revisited: choosy females and ornamented, competitive males in a pipefish

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In the pipefish Syngnathus typhle sex roles are reversed, that is, females compete more intensely than males over mates. However, competition over mates among individuals of one sex does not necessarily prevent members of that same sex from being choosy, and choosiness in the other sex does not prevent competition within it. In an experiment we allowed a female pipefish to choose freely between two males, after which we released the males and let the three interact. Comparisons with earlier results show that both sexes courted partners and competed with conspecifics. However, females courted more often than did males, and courtship was more frequent in treatments involving large individuals than in treatments with small individuals. Males competed among themselves for access to mates but for a shorter duration than females in the same situation. Males displayed an ornament towards females but not to males during mating competition. Females, however, used their ornament in both contexts. Females did not always mate with the male of their previously made choice, which we interpret as females being constrained by male-male competition, male motivation to mate, or both. Thus, in this sex-role reversed species, mate choice in the more competitive sex may be circumvented and even overruled by mate competition and mating willingness in the least competitive sex. Hence, sex roles should not be considered as sexes being either choosy or competitive but rather that males and females may exhibit different combinations of choice and competition. Key words: mate choice, mate competition, mutual mate choice, pipefish, sex-role reversal, Syngnathus typhle. [Behav Ecol 16:649–655 (2005)]

Mate choice and competition over mates are well-studied processes causing sexual selection (Andersson, 1994). Usually, males compete among themselves over access to females, which are in short supply due to their lower potential reproductive rate. The lower rate by females arises from their heavier investment in young (Clutton-Brock and Parker, 1992; Clutton-Brock and Vincent, 1991; Kvarnemo and Ahnesjö, 1996; Parker and Simmons, 1996; Reynolds, 1996; Trivers, 1972). Females are typically more choosy than males when selecting a mate from the pool of available partners. This is the most common sex-specific pattern of reproduction, that is, “conventional” sex roles. In some species, however, the pattern for various reasons is the opposite: the parental investment has evolved to burden males more than females, decreasing male potential reproductive rate below that of females. These species have reversed sex roles, where females compete more intensely over mates (Berglund et al., 1989; Clutton-Brock and Vincent, 1991; Vincent et al., 1992) and typically males choose partners. One such species is the deep-snouted pipefish, Syngnathus typhle L.

In nature, sex roles may commonly be less straightforward: it is well known that females in many species with conventional sex roles, while being choosy, may very well also compete with other females over males or mating status. For instance, in pied flycatchers and great tits, females may compete with other females to remain monogamously mated (Breijeragen and Slagsvold, 1988; Slagsvold, 1993). In the blue tit, a female-biased sex ratio may cause severe competition for breeding opportunities among females (Kempenaars, 1994).

In Dunnocks, females may use song to compete for males (Langmore and Davies, 1997), and in the alpine accentor, females attract males by song (Langmore et al., 1996). Furthermore, in red-winged blackbirds female-female aggression may ensure paternal investment (Yasukawa and Searcy, 1981), and in lekking topis, female compete over central males (Bro-Jorgensen, 2002). Consequently, females may show adaptations aiding in such competition, such as various displays (e.g., Amundsen, 2000; Langmore, 1998). Moreover males, while still being the more competitive sex, may also be choosy when given the opportunity (e.g., Andersson, 1994). Furthermore, sex roles may change over the season in response to changes in mating competition (Forsgren et al., 2004; Gwynne, 1990). However, even if conventional sex roles thus may be somewhat modified, there is yet no demonstration of such modifications in species with reversed sex roles. Are the forces producing sex-role reversal so strong that such modifications do not exist?

Mutual mate choice is expected to occur in species where potential reproductive rates of the two sexes are more similar (Owens and Thompson, 1994) and mutual choice may have consequences for selection pressures on both males and females (Bergstrom and Real, 2000; Deutsch and Reynolds, 1995; Johnstone, 1997; Johnstone et al., 1996; Kirkpatrick et al., 1990; Noe and Hammerstein, 1994; Parker, 1983; Real, 1991). Mutual mate choice has been demonstrated in several species (e.g., Jones and Hunter, 1993; Kolm, 2002; Krasa and Bakker, 1998; Sandvik et al., 2000), but the extent to which the preferences of a particular individual are constrained by its partner’s preferences, and how these shapes actual matings, may vary substantially (e.g., Widemo and Saether, 1999). Individual behaviors may be governed by factors beyond the individual’s control, such as by competition from others, and sometimes an individual may even be forced to act in conflict with its own interest due to competition from others. For example, in the alpine accentor, females attract males by song (Langmore et al., 1996). Furthermore, in red-winged blackbirds female-female aggression may ensure paternal investment (Yasukawa and Searcy, 1981), and in lekking topis, female compete over central males (Bro-Jorgensen, 2002). Consequently, females may show adaptations aiding in such competition, such as various displays (e.g., Amundsen, 2000; Langmore, 1998). Moreover males, while still being the more competitive sex, may also be choosy when given the opportunity (e.g., Andersson, 1994). Furthermore, sex roles may change over the season in response to changes in mating competition (Forsgren et al., 2004; Gwynne, 1990). However, even if conventional sex roles thus may be somewhat modified, there is yet no demonstration of such modifications in species with reversed sex roles. Are the forces producing sex-role reversal so strong that such modifications do not exist?

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to, for instance, manipulation by the other sex. By possessing flexible decision rules that may change over time depending on circumstances, costs of such imposed constraints may be decreased (Qvarnström and Forsgren, 1998). For example, individuals in good condition may be better competitors and are able to pursue their interest to a larger extent than low-quality individuals.

In the deep-snouted pipefish, females compete intensely over mates (Berglund and Rosenqvist, 2001b; Vincent et al., 1994), but, provided with a choice between two potential mates, they are also choosy, preferring larger over smaller males (Berglund et al., 1986) and males with thicker brood pouches over males with flat pouches (Widemo and Vïo T, unpublished data). Furthermore, males, while preferring larger over smaller (Berglund et al., 1986), dominant over subordinate (Berglund and Rosenqvist, 2001b), ornamented over less ornamented (Berglund and Rosenqvist, 2001a; Berglund et al., 1997; Bernet et al., 1998), and parasite-free over parasitized females (Rosenqvist and Johansson, 1995; Mazzi, 2004), may display the same sexual ornament as females (Berglund, Widemo, and Rosenqvist, unpublished data). Moreover, mate choice decisions are adjustable to circumstances: male choice in *S. typhle* depends on predation risk (Berglund, 1993; Fuller and Berglund, 1996), the operational sex ratio (Berglund, 1994), partner encounter rate (Berglund, 1995), possibilities for copying mate choice (Widemo, in press), and competition from consensuals (Widemo and Widemo F, unpublished data). Both sexes benefit directly from mating with larger individuals of the opposite sex, so larger size means higher quality in terms of reproductive returns in both males and females of this species (Berglund et al., 1986; Sandvik et al., 2000).

In this paper, we report a study of male-male competition and female choice in a species with reversed sex roles. We did this by investigating mutual mate choice and mating competition in *S. typhle*. We looked at mate choice in “the least choosy sex” (i.e., females) and mating competition in “the least competitive sex” (i.e., males) and compared with earlier results on male choice and female-female competition to see if the modes of choice and competition differed between the sexes. We also investigated whether individual quality (here body size) affected choice and competition. For *S. typhle*, we predicted the following:

1. Female *S. typhle* will engage more in courtship than males: females willing to mate usually outnumber males willing to mate in nature (Berglund and Rosenqvist, 1993; Vincent et al., 1994), so females may have more to gain from courtship activities.

2. Males will compete for access to females but less so than females placed in the same situation: this prediction stems from the same logic as in (1) above.

3. Courtship will be more intense in treatments involving large individuals than in treatments involving small individuals: if courtship reveals individual quality, large individuals should be more eager to display their superior quality.

4. Large males will engage more in competition than small males: large individuals are usually stronger than small individuals and thus may have more to gain from competitive interactions.

Last, we explored whether individual preferences, as expressed in an unconstrained situation, actually resulted in mating. After females had chosen between two males in separate compartments, we released all three fish into the same compartment and recorded matings. A comparison with an earlier published, almost identical experiment on male choice allowed us to discuss differences between the sexes in this respect.

**METHODS**

We ran the female choice experiment two consecutive summers, from 20 May to 8 June in 2000 and from 26 May to 18 June in 2001. We caught the pipefish in shallow eelgrass meadows in the Gullmar Fjord at the Swedish west coast (58° 15’ N, 11° 28’ E) in May, before the breeding season. We kept sexually mature males and females in separate tanks (<50 individuals per 225-l tank). Stock tanks contained plastic plants and continuously renewed seawater (temperature, salinity, and light regime following natural conditions). The fish were fed live brine shrimps (*Artemia*), small, wild-caught crustaceans, and frozen mysids ad lib twice daily.

Each of 73 trials was run with 8 (or more) females choosing between two enclosed males during the first 4 h. After that, the enclosures were removed to allow male-male competition and actual mating to occur for the rest of the time. Enclosed males could not see or smell each other but both could see the female. The female could see and smell the two males as water flowed from the male compartments into the female compartment and then out of the aquarium. The experiment was video surveyed with two trials filmed simultaneously in 1204 aquaria (40 × 50 × 60 [height] cm). The aquaria were continuously provided with seawater. Temperature and light followed natural conditions. We planted fresh eelgrass (*Zostera marina L.*) in beach sand in the aquaria for shelter. Fish were not fed during trials. After each trial, we scored the degree to which the male’s brood pouch was filled with eggs and gently removed and counted them. After recovery, a quick process, males as well as females were released back into the wild. No mortality occurred during trials.

We matched males within each pair for standard length, number of parasites, and contrast (the vaguely striped “ground” pattern from which the ornament is formed, as estimated by eye on a five-grade scale, see Bernet et al. [1998] for details regarding ornament estimation in females; male ornaments are basically the same). We chose males deliberately to differ in overall color (green versus brown) so that we could recognize individuals. Brown males did not appear darker than green ones, so color did not interfere with our estimate of contrast or ornament display. New males and females were used in each replicate. We have previously shown that color does not affect male choice of females (Berglund and Rosenqvist, 2001a,b).

We ran two treatments, one involving only large fish and the other involving only small fish. In the large treatment, males measured (mean ± SD) 187.9 ± 18.0 mm in standard length (*N* = 76), and males in the small treatment measured 139.7 ± 9.9 mm (*N* = 70), a significant difference (*t* test, *t* = 19.8, *p* < .001). Paired males did not differ in size in either treatment (*t* tests, large treatment: *t* = 0.21, *p* = .8; small treatment: *t* = 0.37, *p* = .7). Neither number of parasites nor contrast differed between treatments or within male pairs (nonnormal distributions, Mann-Whitney *U* tests, all *p* > .1).

All males had fully developed brood pouches. For females, size in the large treatment was 223.9 ± 22.5 mm (*N* = 37) and 159.8 ± 16.2 mm (*N* = 34) in the small treatment, a significant difference (*t* = 13.6, *p* < .001). Females were larger than males (*p* < .001 in both treatments), reflecting the natural size differences in our field samples in these years. The number of parasites did not differ between females from the two treatments (Mann-Whitney *U* test, *p* > .5).

Video filming was done with Hitachi Hi-8 WM-H80E video cameras connected to Panasonic AG-6730 time-lapse super-VHS video recorders equipped with AG-IA670 time code generators-computer interfaces, using the 24H time-lapse mode (which employs one-eighth of normal tape speed). Intense light (a 100 W spot and a 20 W luminescent lamp
placed 0.5 m above each aquarium) was used during filming, in addition to natural light from windows. Video scoring was done by assistants naive to the purpose of the study. During video analysis we measured the time the female spent in front of each male’s compartment; the time the males and the female were resting, swimming, or dancing; and the time a male or a female displayed the ornament. After the partitions were removed, we also measured the time males spent competing (displaying the ornament towards the other male or chasing/being chased by him) and the number of copulations with the female. A male and a female were recorded as dancing when they simultaneously bobbed up and down in close proximity while facing one another. We considered males to be competing when they pursued each other in the aquarium for more than a minute. We used the Observer 4.1 software to measure the frequency, duration, and latency of all relevant behaviors with a precision of less than a second. In trials where no dancing or copulation occurred, males were assigned a value of 4 h latency for dancing and copulation, respectively, that is, the time a trial took.

During video analysis a few tapes could not be scored, so the N values reported may be lower than the total number of replicates. Statistical probabilities reported from these experiments are two tailed. Nonparametric tests were used whenever the assumptions of parametric tests were not met.

RESULTS
Mate choice
We tested for evidence that females showed preferences for particular males. If they did not, and distributed themselves randomly between the two compartments, then the difference in the time spent in front of the left side minus the time spent in front of the right would be normally distributed around a mean of zero. This was not the case; the distribution was significantly nonnormal (Kolmogorov-Smirnov test of normality, \( p < .01 \)). If females did exhibit preferences, then the distribution of differences should have been bimodal, with the absolute values of those differences consequently being normally distributed (see Rowe et al., 1997, for a similar case comparing fluctuating asymmetry with antisymmetry). The distribution of absolute values was not different from normal (Kolmogorov-Smirnov test of normality, \( p > .2 \)), indeed indicating a bimodal distribution. Thus, females did not distribute themselves randomly before the two males, most likely due to female choice for a particular male. However, preferred and rejected enclosed males neither differed in length or parasite number nor in number of eggs received, number or duration of dances, number of copulations, or ornament duration, whether they were from large or small treatment replicates (all \( p > .2 \)). Females spent 112 ± 78 min before green males and 129 ± 79 min before brown males, a nonsignificant difference (\( t_{144} = 1.25, \ p = .2 \)).

Courtship display
Within replicates, males displayed their ornament much less than did the female. While enclosed, females displayed on average for 2.6 ± 20 min to either male, whereas the total time of both males’ displays together was 0.2 ± 2.2 min (Wilcoxon matched-pairs test, \( T = 33, \ N = 146 \) in both groups, \( p = .002 \)). When set free, females displayed for 19.7 ± 1.1 min (\( N = 67 \)) and males for 0.5 ± 2.1 min (\( N = 136; \) Mann-Whitney \( U = 2779, \ p < .001 \)).

Large females were quicker to display their ornament than small females when free (latency 142 ± 96 min and 189 ± 89 min, respectively, \( k_{50} = 2.07, \ p = .04 \)) and also displayed it longer (duration 31.8 ± 44.8 min and 4.6 ± 9.7 min, respectively, Mann-Whitney \( U = 326, \ p = .002 \)). Large and small females did not differ in this respect when enclosed (both \( p > .25 \)). While enclosed, males rarely displayed their ornament to the female (4% of the cases, Figure 1a). When free, 18% of the males displayed their ornament (Table 1).

![Figure 1](https://academic.oup.com/beheco/article-abstract/16/3/649/190501)

**Figure 1** Number of replicates with (a) ornament displays (or no displays) by enclosed individuals to either potential partner in left: a previously made male choice experiment (Berglund and Rosenqvist, 2001a), using a similar design as in this study but letting a focal male choose between two object females, and right: the female choice experiment reported here (b) intrasexual aggression (or no aggression) in the form of chasing between free consensules in the male (left) and female (right) choice experiments. The difference between the male and the female choice experiment indicated as ***\( p < .001 \) \( \chi^2 \) tests.

Only large males displayed an ornament, never small ones. Moreover, display time by large males correlated with body length (Spearman rank correlation \( R_s = .26, \ N = 76, \ p = .03 \)). Large males who displayed their ornament quicker and for longer, both when enclosed and when free, received more eggs (enclosed males: egg number correlated with ornament
The number of replicates where specific events occurred is shown. The focal fish is the choosing fish in front, the object fish are the two

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Event</th>
<th>%</th>
<th>N</th>
<th>%</th>
<th>N</th>
<th>(\chi^2)</th>
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<tbody>
<tr>
<td>Enclosed part</td>
<td>Focal fish danced</td>
<td>73</td>
<td>30</td>
<td>1</td>
<td>73</td>
<td>63.5</td>
<td>&lt;.001</td>
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<tr>
<td></td>
<td>Focal fish displayed ornament</td>
<td>90</td>
<td>30</td>
<td>4</td>
<td>73</td>
<td>76</td>
<td>&lt;.001</td>
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<tr>
<td>Free part</td>
<td>Object fish displayed ornament</td>
<td>100</td>
<td>30</td>
<td>18</td>
<td>68</td>
<td>58</td>
<td>&lt;.001</td>
</tr>
<tr>
<td></td>
<td>Object fish competed</td>
<td>100</td>
<td>30</td>
<td>44</td>
<td>68</td>
<td>27.4</td>
<td>&lt;.001</td>
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<td></td>
<td>Object fish chosen when enclosed was also successful when free</td>
<td>73</td>
<td>26</td>
<td>57</td>
<td>37</td>
<td>1.75</td>
<td>.2</td>
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<td></td>
<td>Competition between object fish in replicates where one of them were chosen when enclosed but later unsuccessful when free</td>
<td>100</td>
<td>7</td>
<td>56</td>
<td>16</td>
<td>—</td>
<td>.057 (Fisher’s (p))</td>
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The number of replicates where specific events occurred is shown. The focal fish is the choosing fish in front, the object fish are the two chosen same-sex fish. A Fisher’s exact probability test was used where expected frequencies were too small to allow a chi-square test.

Mating competition

When the partitions in the aquaria were removed and all interactions between individuals were allowed, males who displayed their ornament directed their display only towards the female during courtship and not to the other male during male-male competition (except once for a few seconds only).

Males did not always compete directly when free to do so (chasing occurred in 44% of the replicates) (Figure 1b, Table 1). Large and small males did not differ in the duration of chases (large males: 7.1 ± 13.2 min (N = 38), small males: 11.3 ± 27.3 min (N = 30), Mann-Whitney \(U = 523, p = .6\)).

Mating success

The male preferred by the focal female while enclosed did not always succeed (i.e., get more dances or matings than the other male) when set free (Figure 2). Large and small treatments did not differ in this respect when counting replicates only (15 out of 24 chosen large males later succeeded, and 6 out of 13 small males; \(\chi^2 = 0.9, p = .3\)). However, a more powerful analysis reveals that the choice made by the enclosed females predicted which male she subsequently got to mate or dance with in the large but not in the small treatment (Figure 2). Enclosed males that were first chosen by the female and also successful when free tended to be larger than males first chosen but unsuccessful later on (176.5 ± 28.5 mm versus 164.0 ± 25.6 mm, \(t_{20} = 1.94, p = .057\)).

**DISCUSSION**

These and previous results (Berglund and Rosenqvist, 2001a) show that in the sex-role reversed pipefish, *S. typhle*, both sexes court as well as compete over mates. However, males compete less than females, and, while displaying an ornament towards females, males never use this signal in mating competition. Females, however, use their ornament in both contexts.

The female choice experiment reported here can be compared with an earlier male choice experiment (Berglund and Rosenqvist, 2001a), where male choice between two females and female-female competition was investigated. In the present female choice experiment only two things differed from the previous male choice experiment. First, in the present experiment we used two size classes of animals (small and large) instead of just one (large). Second, each trial lasted for only 4 + 4 instead of the 24 + 24 h (with scoring of behaviors during the first 10 + 10 h) used in the male choice experiment. There are two reasons for this difference: first, in the male choice experiment most behaviors occurred well within 4 h anyway, making the shorter time used here sufficient to capture the essentials. Second, when studying female choice and male mate competition in a sex-role-reversed species we expected a low frequency of behaviors, so we wanted to increase statistical power as much as possible by increasing the number of replicates. This was done partly by shortening each replicate. Data from the male choice experiment (Berglund and Rosenqvist, 2001a) have been reanalyzed to enable the comparisons made here. Here, we use the full 10 h of observations, but truncating observations to 4 h did not change results or statistical significances qualitatively.

**Female choice and male-male competition**

Females in the deep-snouted pipefish seemingly exercised mate choice, a result corroborating earlier studies (Berglund et al., 1986; Sandvik et al., 2000). Males also exercise mate choice as shown for instance in the previous male choice experiment (Berglund and Rosenqvist, 2001a). Moreover, the female and the male choice experiments together demonstrate that both sexes engaged in intrasexual competition over mates (Figure 1b, Table 1). Competition and choice within one sex cannot be assumed to be mutually exclusive activities. Regarding courtship in the form of ornament display, we predicted that females would court more intensely than males and that courtship would be more intense in treatments involving larger individuals, regardless of sex. All these predictions were confirmed, showing that ornament display may be more rewarding for females than for males and that this display may reveal individual quality. Still, females were, compared to males in the previous male choice experiment, relatively unsuccessful in getting their enclosed partners to dance or display the ornament (Table 1, Figure 1a), suggesting more reluctance towards mating in males. Further, we predicted that females would engage more in intrasexual competition than would males, again a prediction that was
ornament display in the female choice experiment (Figure 1b, Table 1). Moreover, males never displayed their ornament during male-male competition, whereas females frequently and readily displayed to the other female while competing (Berglund and Rosenqvist, 2001a). Again, competition may, just like courtship, be especially rewarding to the sex in excess, namely females, who consequently engage disproportionately in this activity. Last, we predicted that large males would compete more intensely than small. This, however, was not found: perhaps an equal-size opponent is provocative regardless of own absolute size.

In this experiment we could not identify any specific morphological trait used by females in their choice of male, as males were matched for morphological traits known to affect mate choice. This means that females, in addition to male size (Berglund et al., 1986) and brood pouch thickness (Widemo and Viitala, unpublished data), probably base their decision on male behaviors, such as ornament display (see below). Possible other candidates for a cue for female preferences are male odors (e.g., Olseñ et al., 1998).

Ornament display

We have documented male ornamental display in a sex-role reversed species. The male ornament may have evolved as a correlated response to selection for ornamentation in females as males prefer ornamented females (Berglund and Rosenqvist, 2001a). However, we have shown here that the male ornament had a function of its own. It was used as a signal towards females, and males who displayed more benefited from this by receiving more eggs, just like females in the previous male choice experiment achieved a higher mating success by displaying (Berglund and Rosenqvist, 2001a). We do not know precisely what males signal, but their willingness to mate or their quality are good candidates. Interestingly, males did not use their ornament in male-male competition, so the function of the ornament seems solely to be signaling to females.

With our fairly large sample size and an experiment designed to encourage male-male competition (males matched to try to obtain equal competitors and a 2:1 male-biased operational sex ratio), we should have been able to detect whether the ornament was used in male-male displays. Females, on the other hand, use their ornament for both purposes (Berglund and Rosenqvist, 2001a,b; Berglund et al., 1997). Why this sex difference in ornament use? Maybe the fact that males competed among themselves to a lesser degree than females (Table 1) can explain why they did not use their ornament in male-male competition: if competition over mates is not as important to males, there is no great benefit to a special signal in this context. We have previously shown that ornament display in males, although not costly in terms of energy (Berglund et al., 1997), actually was costly in terms of increased predator vulnerability (Bern et al., 1998) and by provoking other females (Berglund and Rosenqvist, 2001b, Berglund and Rosenqvist, unpublished data). Because the males do not display towards each other, the cost of the ornament to males may be limited to an increased predation risk during display towards females. Moreover, the benefits to males from male-male displays are probably lower than benefits to females from female-female displays. Males usually do not have to compete over females as the operational sex ratio generally is female biased (Berglund and Rosenqvist, 1993; Vincent et al., 1994). Thus, the possible benefits to males from intrasexual displays probably do not outweigh costs, restricting this particular signal to have only an intersexual function in males. Ornament display in females, on the other hand, exhibited the more common pattern of a combined intersexual-intrasexual function (e.g., Berglund et al., 1996). Still, males did compete over females by chasing each other, just like females do when competing over males (Figure 1b), but to a lesser extent than females.

Choice and mating success

Exhibiting a preference and actually succeeding in pursuing the mate choice may be two very different things. The extent to which females are able to pursue their interest in the wild is not known. The mere fact that females have preferences (Berglund and Rosenqvist, 1993; Berglund et al., 1986) and that these preferences are adaptive (Sandvik et al., 2000) suggests that at least some females can mate according to their choice.

Females in the female choice experiment sometimes showed a preference for one particular male and then danced or mated with the other when free to do so (Table 1). This was also the case in the previous male choice experiment, and the
two experiments did not differ in this respect (Table 1). Four possible explanations for the subsequent failure of previously chosen individuals exist. (1) Our choice estimate, physical proximity, did not accurately estimate actual choices in all cases, and individuals actually uninterested in choosing while enclosed were erroneously registered as having chosen a partner. If so, this would decrease the concordance between choice and mating. However, physical proximity has previously proved to accurately predict actual matings, at least in choice situations with partners of unequal size (e.g., Berglund, 1994). (2) The focal individual changed its mind when additional mate choice cues become available. We find this explanation less likely, although we cannot exclude it. Only tactile cues were added when object fish were released. The deep-snouted pipefish is a highly visually oriented species, and the setup used in this experiment has in previous studies proved to provide sufficient information for the chooser to make a reliable estimate of partner quality (e.g., Sandvik et al., 2000). (3) In the female choice experiment, the female was rejected by the male she preferred. This is more likely because males in this species are critical in their choice of mate (e.g., Berglund and Rosenqvist, 1993). In addition, everything else being equal, the probability that the female would fancy one out of the two potential partners is twice as high as the probability that this particular male would reciprocally accept this particular female as mate. If no intrasexual competition was observed between free fish, this would be the likely explanation. However, competition always occurred between the free females in the previous male choice experiment, and in the present female choice experiment this happened between the males in 44% of the cases. (4) Competition occurred and the chosen individual was outcompeted by its consensual. We see at least a tendency that males, but not females, rejected potential partners that previously preferred them and that female-female competition, but not the male-male equivalent, was important in determining mating success. In those replicates where preference while enclosed did not coincide with success when free, intrasexual competition when free was observed in 100% of the cases in the male and in 56% of the cases in the female choice experiments, a near-significant difference (Table 1). One indication supporting the competition hypothesis is that males who were preferred when enclosed and successful when free tended to be larger than males chosen at first but unsuccessful later on. There is no reason to expect a larger male of the two to be more interested in mating with a particular female (in fact, the smaller male should be more keen to mate as the female is relatively larger than himself), but we may indeed expect larger males to be stronger competitors. The two latter explanations certainly do not exclude one another.

The choice made by the enclosed females predicted which male she subsequently got to mate or dance with only in the large, but not the small, treatment (Figure 2), although this difference was not apparent when counting replicates only (Table 1). Thus, the choice of larger females had more profound subsequent effects than small females’ choices as the large females were better able to translate preferences into actual mating success. Most likely, small females courted any male and subsequently mated with whichever male was willing, producing little concordance between choice and actual mating, whereas large, choosy and attractive females could transform their choice into mating to a higher degree than could small females. A similar pattern was found in the previous male choice experiment, where fish sizes were similar to the large treatment here: females receiving more matings when set free had also received more male time while enclosed (recalculated data; Mann-Whitney U test, $p = .001$, $N = 60$). Sex roles

Clearly, males are competitive and females choosy in this pipefish species. Are then sex roles really reversed? These and previous results demonstrate that competition is more important and is signaled more clearly in females. The commonly used definition of sex roles only considers competition over mates (Vincent et al., 1992) and does not make predictions regarding mate choice in either sex. However, sex-role reversal is usually accompanied by a higher level of choosiness in the less competitive sex. What we point out is merely that competition and choice are not mutually exclusive behaviors: the predominantly competitive sex may well exhibit preferences and benefit from choice and vice versa, and adding this complexity definitely enhances our understanding of the process of sexual selection. This has been repeatedly demonstrated in species with conventional sex roles (e.g., Amundsen, 2000), but the fact that we have demonstrated the same complexity in a sex-role reversed species points to the generality of this pattern. Although males courted and competed less than females, these infrequent behaviors may still have had profound effects on actual mating outcomes: indeed, mating decisions by members of the more choosy sex (here, males) should be particularly relevant for, and influential on, female mating prospects.

To summarize, females seemed to exhibit preferences and perform mate choice. Males competed over females, but overall, males competed less than females in the same situation. Large males in competition over large females did not differ from small males in competition over small females. Apparently, female choice may sometimes be overruled by male behaviors. We cannot say whether male-male competition or male-mating reluctance determined who mates with whom in the cases where female choice was overruled. Males displayed the sexual ornament, but to a lesser extent than females. The function of the male ornament also differed from the female function: males used it solely to signal to females, whereas in females it has a dual function in both courtship and competition. Our experiment, taken together with our previous results, demonstrates that sex roles should not be considered as sexes being only choosy or only competitive but rather that males and females may end up with our previous results, demonstrates that sex roles should not be considered as sexes being only choosy or only competitive but rather that males and females may end up at different levels of choice and competition depending on the sex-specific costs and benefits involved. The level of choosiness and competitiveness exhibited by a particular individual hence depends not only on its sex but also on its competitive ability in relation to surrounding males and females.

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