

An intimidating ornament in a female pipefish

Anders Berglund^a and Gunilla Rosenqvist^b

^aDepartment of Ecology and Evolution/Animal Ecology, Norbyvägen 18d, SE-752 36 Uppsala, Sweden, and ^bDepartment of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

A sexually selected signal may serve a dual function being both attractive to mates and deterring rivals. Presently, there are few unambiguous demonstrations of an ornament functioning in both a mate choice and mate competition context and none regarding female ornaments. We have shown earlier that a temporary ornament, a striped pattern, in a sex-role reversed female pipefish, *Syngnathus typhle*, attracts males. Here we show that this ornament also intimidates rival females: in one experiment a male could interact with either 1 or 2 females. Latency until copulation was longer when 2, rather than 1, females were present. Moreover, when 2 females were present, competition lasted longer and time until mating took place increased when females displayed their ornaments more equally. In another experiment, a focal female could see 1 stimulus female and 1 stimulus male, the latter 2 being unaware of each other. The ornament of the stimulus female was manipulated, either strengthened by being painted black or left unaltered by being sham-painted. As a result, focal females experiencing black-painted stimulus females decreased courtship as well as competitive activities compared with focal females seeing sham-painted females. Moreover, focal females seeing black-painted females displayed less of their own ornament compared with controls. This decrease was due to a decrease in display toward males rather than to stimulus females. Thus, this female ornament indeed has a dual function, attracting mates and deterring rivals. In addition, the social costs invoked by this intimidating effect on rivals may help to maintain signal honesty. *Key words*: mating competition, ornament, pipefish, sex-role reversal, status badge, *Syngnathus typhle*. [*Behav Ecol* 20:54–59 (2009)]

INTRODUCTION

Traditionally, sexual selection has been viewed as taking place during mate choice and during competition over mates (Andersson 1994; Kokko et al. 2003). A particular sexually selected signal may be used both to evaluate a potential mate and a potential competitor (Berglund et al. 1996) if it signals overall quality and interest toward both mates and competitors. However, numerous exceptions to this dual function of sexually selected traits exist (Qvarnström and Forsgren 1998), for example, in insects (Moore AJ and Moore PJ 1999; Sih et al. 2002; Candolin 2004), in fish (Forsgren 1997; Kangas and Lindström 2001; Wong 2004), in a salamander (Howard et al. 1997), in a lizard (Lopez et al. 2002), and in birds (Lancot et al. 1998; Leitao and Riebel 2003). There are numerous explanations for the evolution of a signal with conflicting functions in both intra- and intersexual selections. For example, a trade-off between time devoted to attractive parental care and mating competition may exist, or care can maybe not be convincingly signaled through the same trait as competitive strength. Moreover, if different types of information are being signaled to mates and rivals, then the costs that ensure signal honesty may be different (e.g., muscles to fight off competitors vs. immunocompetence to attract partners). If so, one signal may not honestly signal the 2 different pieces of information unless there is overlap in the nature of the costs.

Unfortunately, however, there are few unambiguous demonstrations of whether a particular signal has a dual or conflicting function (but see Mateos 1998; Tarof et al. 2005; Allen and Levinton 2007; Griggio et al. 2007; Mougeot et al. 2007). If only natural variation in ornament expression is used in experiments, results may be suggestive but perhaps not conclu-

sive. This is because a number of other traits, including behavior, may be correlated with ornament expression. Whether the ornament or any of the correlated traits is the target of selection is often difficult to disentangle. Ideally, studies of ornament function should involve signal manipulations while keeping other traits, including behavior, constant. To our knowledge, very few such studies exist. It has been demonstrated in crested auklets that head crests on dummies function to be attractive both to male and female partners (Jones and Hunter 1993), whereas being deterring to male (but not female) competitors (Jones and Hunter 1999). In a sex-role reversed pipefish, *Syngnathus typhle*, we have previously demonstrated that a female ornament, a striped pattern, was attractive to males by manipulating the ornament while controlling other traits, including behavior (Berglund and Rosenqvist 2001b). Moreover, males can also display this ornament, and females were attracted to it (Berglund et al. 2005). So far, however, we have no unambiguous demonstration of the ornament's function in mating competition, although the effects of display, including ornament display, during such competition are known (Vincent et al. 1994; Berglund and Rosenqvist 2001a; Berglund et al. 2005).

The pipefish, *S. typhle*

In pipefish, a lengthy and ritualized mutual dance precedes copulation. Females transfer eggs to a brood pouch under the male's tail, where they subsequently are fertilized. Embryos are brooded in the pouch until birth several weeks later (Berglund et al. 1986a, 1986b). Thus, males enjoy 100% paternity confidence (Jones et al. 1999). Males as well as females may mate with multiple partners (Berglund et al. 1988; Jones et al. 2000). The male pregnancy ends with the young fish leaving the pouch, thereafter leading independent lives. The adult sex ratio is roughly equal in our study populations (Berglund et al. 1986a, 1986b). *Syngnathus typhle* is sex-role reversed: males are typically more choosy than females, and females compete more intensely than males for access to

Address correspondence to A. Berglund. E-mail: anders.berglund@ebc.uu.se.

Received 25 March 2008; revised 24 July 2008; accepted 6 August 2008.

© 2008 The Authors

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/2.0/uk/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

mates. This is due to the fact that the number of females willing to mate typically outnumber males willing to mate in nature, that is, males are the limiting sex and the operational sex ratio is therefore female biased (Emlen and Oring 1977; Berglund et al. 1989; Berglund and Rosenqvist 1990, 1993, 2003; Vincent et al. 1994; Berglund 2000). Nevertheless, both sexes engage in choice and mating competition to varying degrees (Berglund et al. 2005). Furthermore, females form reproductive dominance hierarchies, where dominant, that is, larger, females suppress reproduction in subdominants (Berglund 1991). In nature, this is done as females display in groups in a lek-like fashion (Vincent et al. 1994).

The temporary ornament in *S. typhle* is displayed during female–female interactions, from females to males and from males to females, but rarely between males (Berglund et al. 2005). It consists of a striped pattern resembling a row of capital B's along the fish's flanks (Fiedler 1954). Displaying the ornament is a rapid process, with full presentation occurring within less than a minute. Females as well as males find the ornament attractive in partners (Berglund and Rosenqvist 2001b; Berglund et al. 2005). Female–female competition promotes ornament display (Bernet et al. 1998), and males use the information provided during such interactions in their mate choice (Berglund and Rosenqvist 2001a). These pipefish are extremely cryptic, resembling the eelgrass they inhabit in color, shape, and movements (Vincent et al. 1994). Displaying the ornament is costly, not in terms of energy (Berglund et al. 1997) but in terms of lost crypsis, and indeed, females under predation threat display less (Bernet et al. 1998). During female–female interactions, females receiving the display reduced their subsequent performance in courtship (Berglund and Rosenqvist 2001a), suggesting a social cost to female–female interactions that involve this ornament display.

The aim of this study is to investigate this social cost by demonstrating that ornament display in females intimidates rival females, that is, reduces the courting and competing activities of the receiver. This will, to our knowledge, be the first such demonstration. We employed 2 experiments: in the first, with naturally displaying females, a male was confined with either 1 or 2 females, a simple way to introduce the effect of female–female competition. Secondly, we subjected a focal female to one potential competitor, another female, and one potential mate, a male. We manipulated the ornament of the competitor by painting or sham-painting her to determine whether the focal female's courtship activities and competitiveness were influenced by ornament “display” in the rival.

METHODS

Catching and housing the fish

We caught pipefish in shallow eelgrass meadows in the Gullmar Fjord at the Swedish west coast (58°15' N, 11°28' E) just prior to the breeding season. This allowed us to catch males without eggs in their brood pouches. We housed sexually mature males and females in separate tanks. Stock tanks contained plastic plants (resembling eelgrass) and continuously renewed seawater (temperature, salinity, and light regime following field conditions). The fish were fed live brine shrimps (*Artemia*), small, wild-caught crustaceans, and frozen mysids ad lib twice daily.

Experiment 1: naturally displaying females

We ran this experiment from May 26 until June 11, 1998. A male was placed with either 1 or 2 females in a 120-L aquarium (measuring 40 × 50 × 60 [height] cm). The aquaria were continuously provided with seawater. Temperature and light con-

ditions followed natural conditions. We planted fresh eelgrass in beach sand in the aquaria to provide shelter. Fish were not fed during trials (in nature, fish do not feed during courtship (Berglund A, Rosenqvist G, personal observation), and the trials were too short in duration to cause any harm to the fish). One single female and one paired female treatment ran in parallel each day, and each trial lasting for 8 h. Replicates where males received no eggs were excluded from the analysis as fish in these may not have been reproductively active, leaving 14 replicates of each treatment. Females did not differ in body length, neither between treatments (mean ± standard deviation: paired females 198.1 ± 14.7 mm [$n = 28$] and single females 196.6 ± 13.1 mm [$n = 14$]; Student's t -test, $t_{40} = 0.537$, $P = 0.6$) nor within pairs in the paired female treatment (the female to the left compared with the one to the right, 197.6 ± 15.8 mm and 198.5 ± 14.2 mm; $t_{26} = 0.151$, $P = 0.9$). Females in a pair were picked to differ in color so we could tell them apart. We have earlier shown that color is not a criterion used by males when choosing a partner (Berglund and Rosenqvist 2001a, 2001b). Males did not differ in length between treatments (males in the single female treatment were 181.6 ± 15.3 mm and in the paired female treatment 183.1 ± 13.3 mm; Student's t -test, $t_{26} = 0.264$, $P = 0.8$). Males were, however, smaller than females (males 182.4 ± 14.1 mm and females 197.2 ± 14.1 mm; Student's t -test, $t_{68} = 4.33$, $P < 0.001$), reflecting natural size differences in our field populations this year. New males and females were used in each trial and set free afterwards. Numbers of eggs in males were counted after gently removing them from the brood pouch.

Each trial was video filmed using 2 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 24-h time-lapse mode (which employs 1/8th of normal tape speed). Intense light (a 100-W spot and a 20-W luminescent lamp placed ½ m above each aquarium) was used during filming, in addition to natural light from windows. Video tapes were analyzed using the Observer 4.0 software. The following behaviors were scored: whether a female was dancing with the male or, in the paired female treatment, competing with each other and whether they displayed their ornaments or not. A female was recorded as dancing when she swam up and down in synchrony with the male, both in close proximity facing one another. We considered the females to be competing when they pursued each other for more than a minute (see Berglund and Rosenqvist 2001a, 2001b; Berglund et al. 2005 for details). Copulations were also recorded. The Observer software keeps track of numbers, duration, and latency of these behaviors with a precision of less than a second, which is a sufficient accuracy for these slow-moving fishes. Video scoring was done by assistants naive to the object of the experiment.

Experiment 2: painted and sham-painted females

We ran this experiment, where ornament display was manipulated, from May 27 until June 8, 1999. A focal female was placed in the front half of a 120-L aquarium (same as above). In each of 2 rear compartments, either a male or a stimulus female was placed. The 2 latter animals could not see each other, but the focal female could see both stimulus animals (Figure 1). In addition, the focal female could smell both the male and the stimulus female as water flowed in her direction. Two treatments were employed, in one, the ornamented treatment, the focal female was painted with cross stripes where the ornament naturally occurs with a Copic™ felt pen “black,” in the other, the nonornamented treatment, she was painted in the same way with a Copic™ felt pen “blender” for a colorless

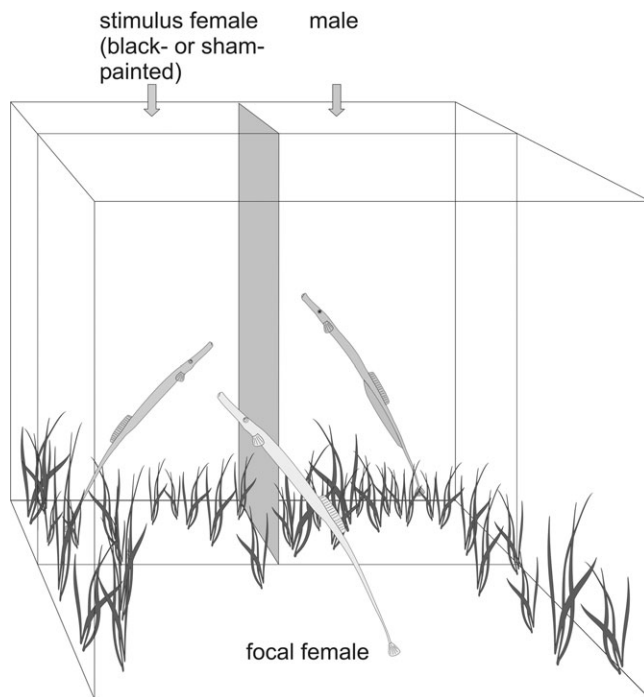


Figure 1
Experiment 2: the painted and sham-painted female experimental design.

control. We have no reason to suspect that the focal fish would recognize painted individuals as odd or strange as we have shown earlier that males prefer females that have been painted with black cross stripes (Berglund and Rosenqvist 2001b).

The aquaria were provided as described above with water, light, and eelgrass, and no food was provided. One ornamented and one nonornamented treatment (with 12 replicates of each) ran in parallel each morning, with females and males assigned randomly to either treatment. The rear fish were randomly placed with the male either to the left or to the right. We attempted to use females that were similar in their standard length within each replicate (mean \pm standard deviation: focal females 226.3 ± 20.7 mm and stimulus females 225.8 ± 20.5 mm; paired t -test, $t_{23} = 0.386$, $P = 0.7$). Focal females in the ornamented treatment did not differ in body length from focal females in the nonornamented treatment (226.8 ± 16.5 mm and 225.8 ± 24.9 mm, respectively; Student's t -test, $t_{22} = 0.1$, $P = 0.9$). The same was true for the stimulus females (226.2 ± 16.7 mm and 225.4 ± 24.6 mm, in the ornamented and nonornamented trials, respectively; $t_{22} = 0.1$, $P = 0.9$) and the males (208.7 ± 19.9 mm and 206.8 ± 21.8 mm, in the ornamented and nonornamented trials, respectively; $t_{22} = 0.2$, $P = 0.8$). Females were larger than males (2-way analysis of variance: $F_{1,68} = 12.6$ and $P = 0.001$ for sex differences and $F_{1,68} = 0.08$ and $P = 0.8$ for treatment differences, with no significant interaction, $F_{1,68} = 0.009$, $P = 0.9$). Again, this reflects natural size differences between males and females in our study population this year. New males and females were used in each trial.

Each trial lasted 6 h, giving the fish sufficient time to interact, with the entire period being video filmed using the same technique, lighting, and software as above. We scored whether the focal female was closest to the stimulus female or the male, whether she was dancing with the male or competing with the stimulus female and whether she displayed the ornament or

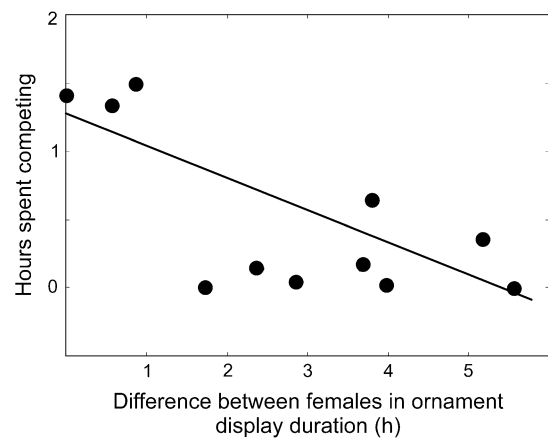


Figure 2
Experiment 1: naturally displaying females. When 1 male interacted with 2 females, time spent competing was shorter when 1 female naturally displayed her ornament markedly longer than the other ($r = -0.714$, $P = 0.014$, $n = 11$).

not and to whom. Dancing and competing were scored as above. Behaviors in the 2 stimulus animals were scored as resting or swimming. In trials where no dancing or competition occurred, females were assigned a latency value of 6 h for initiating dancing and competition, respectively (i.e., the maximum time possible within a trial). This is a conservative assignment, being the first time they could have danced or copulated had the trial been continued. Videos were also here scored by assistants naive to the purpose of the experiment.

Statistical probabilities reported are 2-tailed. Nonparametric tests were used whenever assumptions for parametric tests could not be met. Number of replicates analyzed are sometimes lower than actually ran due to problems with playing back a few video films.

RESULTS

Experiment 1: naturally displaying females

Total dancing time per female tended to be shorter with 2 rather than 1 females present (0.39 ± 0.61 h and 0.78 ± 0.58 h, respectively; Student's t -test, $t_{38} = 1.99$, $P = 0.053$), and the number of copulations per female was also lower with 2 females present (2.96 ± 2.86 and 5.93 ± 3.79 , respectively; Student's t -test, $t_{38} = 2.79$, $P = 0.008$). Latency until dancing as well as duration of, or latency until, ornament display did not differ between treatments (all P values > 0.16). However, latency until the first copulation took place was longer when 2 females were present as compared with when the male was alone with 1 female (3.81 ± 1.46 h and 2.01 ± 1.27 h, respectively; Student's t -test, $t_{25} = 3.33$, $P = 0.003$).

Looking only at the treatment with 2 females present, the smaller the difference between the 2 females in ornament display duration the longer they competed (Figure 2). Moreover, the first copulation took place later if females displayed their ornaments more equally (Figure 3).

Experiment 2: painted and sham-painted females

Focal females from the black- and sham-painted treatments did not differ in total time spent in front of the stimulus female, and consequently, they did not differ in total time spent before the male either (Table 1). Behaviors restricted to mating, however, differed: when seeing a sham-painted as compared with a black-painted female, focal females danced sooner,

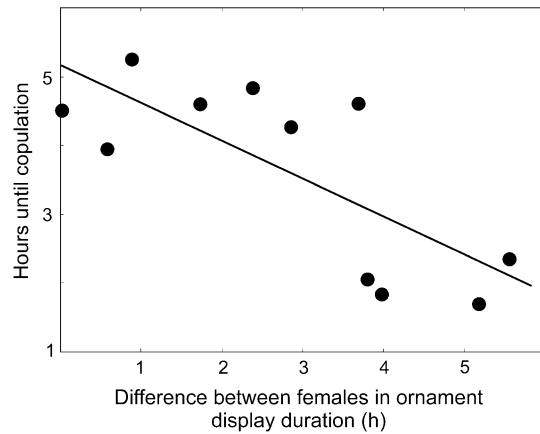


Figure 3
 Experiment 1: naturally displaying females. When 1 male interacted with 2 females, copulation occurred sooner when 1 female naturally displayed her ornament markedly longer than the other ($r = -0.749$, $P = 0.008$, $n = 11$).

more frequently, and for a longer total duration with their stimulus males (Table 1 and Figure 4a). Moreover, focal females competed sooner, more frequently, and for a longer total duration with nonornamented stimulus females than with stimulus females painted with black stripes (Table 1 and Figure 4b). The focal females displayed their own ornaments in response to both the male and the stimulus female. In the nonornamented treatment, they displayed in total more frequently and for a longer total duration than in the ornamented treatment. However, latency until displaying the ornament did not differ significantly between treatments (Table 1). Differences between treatments were more due to changes in display toward males than toward females: when separating ornament display by focal females toward males from display toward stimulus females, focal females seeing a sham-painted as compared with a black-painted female displayed more often, sooner, and for longer toward their males,

whereas such display differences toward stimulus females did not reach significance (Table 1).

Ornamented and nonornamented stimulus females did not differ in activity: total swimming duration was 226 ± 118 min and 154 ± 160 min, respectively, with $t_{22} = 1.27$, $P = 0.22$.

DISCUSSION

Observing a highly ornamented female competitor evidently affected a female’s own courtship and her willingness to engage in competition: she reduced both, as evident from experiments using either a natural or a manipulated ornament display. This behavior has been suggested in theoretical models (Fawcett and Johnstone 2003; Härdling and Kokko 2005). Thus, the experiment with painted females demonstrated that the ornamental stripes, although being attractive to mates, also intimidate females in 3 ways: first, the females subjected to heavy ornament display in rivals decreased their courtship toward males by displaying less of their ornament. They did not display significantly less to black-painted as compared with sham-painted females, however, but the actual differences ran in this direction (Table 1). A low n -value due to many replicates lacking any display at all toward females as well as a large variation between individuals make us hesitant to conclude much regarding intrasexual ornament display. Interestingly, observing a black-painted female obviously had a larger effect on ornament display toward potential mates rather than on display toward the black-painted female herself. Second, focal females observing a black-painted compared with sham-painted females also performed less actual courtship (dancing activities) with the male. Third, focal females engaged less in competition, here scored as pursuit, with the heavily ornamented female. All these findings were corroborated by the experiment using naturally displaying females, although that experiment on its own cannot conclusively tell that the ornament display is the causative agent. An alternative interpretation of these results is that the black-painted female was perceived as odd and not worth displaying at. However, we have shown earlier that males prefer females that have been painted with black stripes over sham-painted females (Berglund and Rosenqvist 2001b), and it seems unlikely that male and

Table 1
 Experiment 2: the painted and sham-painted females

Behavior	Treatment (mean \pm standard deviation)		U	P
	Ornamented	Not ornamented		
Total time spent before male (minutes)	219 \pm 107	189 \pm 135	64	0.7
Number of dances with male	0.67 \pm 1.50	3.25 \pm 3.82	37	0.04
Latency until the first dance (minutes)	345 \pm 43	290 \pm 75	37	0.04
Total dance duration (minutes)	2.4 \pm 7.6	30.6 \pm 85.2	37	0.04
Number of competitive events with stimulus female	0.58 \pm 1.38	4.83 \pm 7.21	32	0.02
Latency until first competitive event (minutes)	337 \pm 57	249 \pm 112	35	0.03
Total duration of competitive events (minutes)	1.7 \pm 4.6	13.2 \pm 21.6	35	0.03
Number of ornament displays	0.5 \pm 1.0	2.5 \pm 2.7	36	0.04
Number of ornament displays to males	0.17 \pm 0.39	1.33 \pm 1.30	31	0.02
Number of ornament displays to stimulus females	0.33 \pm 0.65	1.17 \pm 1.59	50	0.20
Latency until first ornament display (minutes)	314 \pm 97	232 \pm 118	41	0.07
Latency until first display (minutes) to males	343 \pm 40	275 \pm 90	35	0.03
Latency until first display (minutes) to stimulus females	314 \pm 97	232 \pm 118	53	0.27
Total duration of ornament display (minutes)	3.5 \pm 9.2	43 \pm 60	38	0.0496
Total display duration (minutes) before males	1.8 \pm 5.3	17 \pm 21	33	0.02
Total display duration (minutes) before stimulus females	1.7 \pm 4.0	26 \pm 42	50	0.20

Focal female behaviors in the ornamented and nonornamented treatments. $n = 12$ in each treatment, and statistical probabilities derive from Mann–Whitney’s U -test.

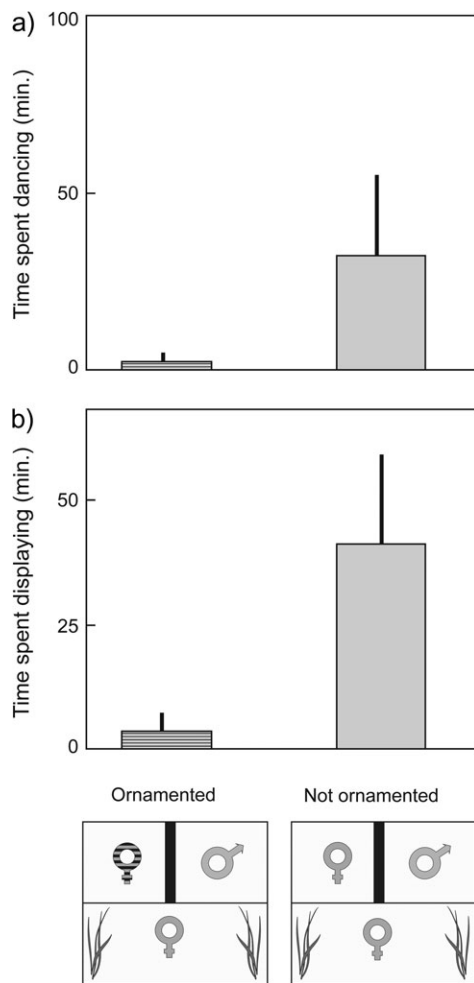


Figure 4
Experiment 2: the painted and sham-painted females. (a) The total time focal females spent dancing with males in the presence of an ornamented and a nonornamented female and (b) the total time focal females spent competing with ornamented or nonornamented females. Mean and standard error values are shown.

female perception of the painted stripes differ. Moreover, this also shows that lightning conditions were appropriate for stripe perception.

In the painted female experiment, we did not control the behavior of the stimulus female, which may have had 1 of 2 consequences: either the ornamented stimulus female was unaware of the experimental increase in her status, in which case our demonstration of the function of the ornament holds, or she perceived her status increase and changed her behavior accordingly. In the latter case, it is possible that the intimidation effect on the focal female was, at least in part, due to some additional dominant behavior in the stimulus female rather than to the ornament itself. However, even in this case, we still claim that the ornament manipulation caused the intimidation, albeit indirectly via behavioral changes in the manipulated female. Still, we suggest that the latter explanation is unlikely, as activity, measured as total swimming time, did not differ between ornamented and nonornamented stimulus females. If the ornamented stimulus female perceived the raise in her status and changed her behavior, this should be manifested as a higher activity.

Displaying the ornament may be socially costly to a female if it provokes socially dominant females. In our experiment with

painted females, the artificially increased ornament display inhibited competition in the focal females. However, in a natural situation a displaying, dominant female may escalate rather than submit to a displaying rival. If so, the contest (and any associated courtship with the nearby male) may be substantially prolonged and copulation latency increased, just as found here in the experiment with naturally displaying females. Moreover, this finding is corroborated by field observations (Vincent et al. 1995). This mating delay may, in turn, be costly in terms of lost mating or feeding opportunities (Berglund et al. 2006) or in terms of increased predation pressure as intrasexual conflicts make the contestants more conspicuous and/or less vigilant (Berglund 1993; Fuller and Berglund 1996). Consequently, signal honesty in this pipefish may be maintained by signal costs in terms of increased predation risk (Bernet et al. 1998) and by being socially intimidating and thereby costly (this study). Such costs may effectively decrease the possibilities for subordinate females to “trick” males by displaying the ornament dishonestly (reviewed in Andersson 1994), that is, the ornament effectively functions as a status badge (Berglund et al. 1996). Our results also provide a mechanism for how female dominance is achieved: dominant females are able to reduce the reproduction of subdominants (Berglund 1991), and this effect may well be mediated, at least in part, via ornament display.

Evidently one and the same signal can be used both to attract mates and deter rivals, something demonstrated here as well as by others (e.g., Mateos 1998; Tarof et al. 2005; Allen and Levinton 2007; Griggio et al. 2007; Mougeot et al. 2007). However, as mentioned earlier, numerous exceptions to this dual function of sexually selected traits exist. The question now becomes, when can a particular signal function in both contexts and when can it not? We propose that when the same commodity, such as condition or health, increases both competitive ability and attractiveness, and the exercise of competition does not substantially reduce the potential for advertising attractiveness, then one and the same signal may have a dual function. If the choosing individual benefits from its choice in terms of direct benefits, and competition and the provisioning of such direct benefits do not take place simultaneously or otherwise trade off, we expect dual signals to evolve. If indirect benefits are involved, duality may evolve even more readily, as the trade-off between time devoted to competition and time devoted to attracting mates may be even more relaxed; indeed, the choosing sex may be attracted by mates successful in competition. Conversely, we expect separate signals to evolve as deterrents and attractants, respectively, when one activity bears on the other. This may happen when different commodities are involved, such as muscle mass in competition but offspring feeding ability in mate attraction, or when signal design is incompatible, such as long-distance signaling to competitors but short-distance signaling to mates, or when time devoted to one activity trades off with time devoted to the other, such as time spent in contest with rivals versus time devoted to parental care (Qvarnström and Forsgren 1998). In short, effort devoted to mating competition and mate attraction must be viewed as any life-history traits, and possible trade-offs hence influence signal evolution. Alternatively, separate (or multiple) signals may be used toward mates and competitors to increase signal strength, signal redundancy, or signal efficiency. Such signals need not be independent of each other, however: one may, for instance, act as an amplifier on the other (e.g., Berglund 2000). Altogether, understanding the context promoting signaling via one or more signals is vital for our understanding of how sexually selected signals evolve and how they are designed.

In summary, we have demonstrated that a female signal intimidates rival females in this sex-role reversed pipefish.

Females experiencing an experimentally increased display from an apparently dominant rival reduced their levels of courtship as well as competition. Thus, this signal has a dual function, serving to attract mates and deter rivals, both of which increase the reproductive success of the displayer. We suggest that one main cost associated with display that may maintain signal honesty is provoked aggression from rivals. This effect then has the additional function of intimidating poor-quality individuals from competitively courting nearby males.

FUNDING

Swedish Research Council (A.B.) and the Norwegian Research Council (G.R.).

Many thanks to Anna Billing for field assistance, to Ronny Höglund and Arnt Narve Bordal for help with the video analysis, and to Ingrid Ahnesjö, Anna Billing, Anahita Kazeem, Sarah Robinson-Wolrath, and Jonathan Wright for valuable comments on earlier drafts. The work was carried out at Kristineberg Marine Research Station.

REFERENCES

- Allen BJ, Levinton JS. 2007. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Funct Ecol*. 21:154–161.
- Andersson MB. 1994. *Sexual selection*. Princeton: Princeton University Press.
- Berglund A. 1991. Egg competition in a sex-role reversed pipefish: subdominant females trade reproduction for growth. *Evolution*. 45:770–774.
- Berglund A. 1993. Risky sex: male pipefishes mate at random in the presence of a predator. *Anim Behav*. 46:169–175.
- Berglund A. 2000. Sex role reversal in a pipefish: female ornaments as amplifying handicaps. *Ann Zool Fenn*. 37:1–13.
- Berglund A, Bisazza A, Pilastro A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc Lond*. 58:385–399.
- Berglund A, Rosenqvist G. 1990. Male limitation of female reproductive success in a pipefish: effects of body size differences. *Behav Ecol Sociobiol*. 27:129–133.
- Berglund A, Rosenqvist G. 1993. Selective males and ardent females in pipefishes. *Behav Ecol Sociobiol*. 32:331–336.
- Berglund A, Rosenqvist G. 2001a. Male pipefish prefer dominant over attractive females. *Behav Ecol*. 12:402–406.
- Berglund A, Rosenqvist G. 2001b. Male pipefish prefer ornamented females. *Anim Behav*. 61:345–350.
- Berglund A, Rosenqvist G. 2003. Sex role reversal in pipefish. *Adv Study Behav*. 32:131–167.
- Berglund A, Rosenqvist G, Bernet P. 1997. Ornamentation predicts reproductive success in female pipefish. *Behav Ecol Sociobiol*. 40:145–150.
- Berglund A, Rosenqvist G, Robinson-Wolrath S. 2006. Food or sex—males and females in a sex role reversed pipefish have different interests. *Behav Ecol Sociobiol*. 60:281–287.
- Berglund A, Rosenqvist G, Svensson I. 1986a. Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). *Behav Ecol Sociobiol*. 19:301–307.
- Berglund A, Rosenqvist G, Svensson I. 1986b. Reversed sex roles and parental energy investment in zygotes of two pipefish (Syngnathidae) species. *Mar Ecol Prog Ser*. 29:209–215.
- Berglund A, Rosenqvist G, Svensson I. 1988. Multiple matings and paternal brood care in the pipefish *Syngnathus typhle*. *Oikos*. 51:184–188.
- Berglund A, Rosenqvist G, Svensson I. 1989. Reproductive success of females limited by males in two pipefish species. *Am Nat*. 133:506–516.
- Berglund A, Widemo MS, Rosenqvist G. 2005. Sex-role reversal revisited: choosy females and ornamented, competitive males in a pipefish. *Behav Ecol*. 16:649–655.
- Bernet P, Rosenqvist G, Berglund A. 1998. Female-female competition affects female ornamentation in the sex-role reversed pipefish *Syngnathus typhle*. *Behaviour*. 135:535–550.
- Candolin U. 2004. Opposing selection on a sexually dimorphic trait through female choice and male competition in a water boatman. *Evolution*. 58:1861–1864.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*. 197:215–223.
- Fawcett TW, Johnstone RA. 2003. Mate choice in the face of costly competition. *Behav Ecol*. 14:771–779.
- Fiedler K. 1954. Vergleichende Verhaltensstudien an Seenadeln, Schlängelnadeln und Seepferdchen (Syngnathidae). *Z Tierpsychol*. 11:358–416.
- Forsgren E. 1997. Female sand gobies prefer good fathers over dominant males. *Proc R Soc Lond B Biol Sci*. 264:1283–1286.
- Fuller R, Berglund A. 1996. Behavioral responses of a sex-role reversed pipefish to a gradient of perceived predation risk. *Behav Ecol*. 7:69–75.
- Griggio M, Serra L, Licheri D, Monti A, Pilastro A. 2007. Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behav Ecol Sociobiol*. 61:423–433.
- Hårdling R, Kokko H. 2005. The evolution of prudent choice. *Evol Ecol Res*. 7:697–715.
- Howard RD, Moorman RS, Whiteman HH. 1997. Differential effects of mate competition and mate choice on eastern tiger salamanders. *Anim Behav*. 53:1345–1356.
- Jones AG, Rosenqvist G, Berglund A, Avise JC. 1999. The genetic mating system of a sex-role-reversed pipefish (*Syngnathus typhle*): a molecular inquiry. *Behav Ecol Sociobiol*. 46:357–365.
- Jones AG, Rosenqvist G, Berglund A, Avise JC. 2000. Mate quality influences multiple maternity in the sex-role-reversed pipefish *Syngnathus typhle*. *Oikos*. 90:321–326.
- Jones IL, Hunter FM. 1993. Mutual sexual selection in a monogamous seabird. *Nature*. 362:238–239.
- Jones IL, Hunter FM. 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Anim Behav*. 57:521–528.
- Kangas N, Lindström K. 2001. Male interactions and female mate choice in the sand goby, *Pomatoschistus minutus*. *Anim Behav*. 61:425–430.
- Kokko H, Brooks R, Jennions MD, Morley J. 2003. The evolution of mate choice and mating biases. *Proc R Soc Lond B Biol Sci*. 270:653–664.
- Lancot RB, Weatherhead PJ, Kempnaers B, Scribner KT. 1998. Male traits, mating tactics and reproductive success in the buff-breasted sandpiper, *Tryngites subruficollis*. *Anim Behav*. 56:419–432.
- Leitao A, Riebel K. 2003. Are good ornaments bad armaments? Male chaffinch perception of songs with varying flourish length. *Anim Behav*. 66:161–167.
- Lopez P, Munoz A, Martin J. 2002. Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. *Behav Ecol Sociobiol*. 52:342–347.
- Mateos C. 1998. Sexual selection in the ring-necked pheasant: a review. *Ethol Ecol Evol*. 10:313–332.
- Moore AJ, Moore PJ. 1999. Balancing sexual selection through opposing mate choice and male competition. *Proc R Soc Lond B Biol Sci*. 266:711–716.
- Mougeot F, Rez Rodriguez LP, Martinez Padilla J, Leckie F, Redpath SM. 2007. Parasites, testosterone and honest carotenoid-based signalling of health. *Funct Ecol*. 21:886–898.
- Qvarnström A, Forsgren E. 1998. Should females prefer dominant males? *Trends Ecol Evol*. 13:498–501.
- Sih A, Lauer M, Krupa JJ. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. *Anim Behav*. 63:1079–1089.
- Tarof SA, Dunn PO, Whittingham LA. 2005. Dual functions of a melanin-based ornament in the common yellowthroat. *Proc R Soc Lond B Biol Sci*. 272:1121–1127.
- Vincent A, Ahnesjö I, Berglund A. 1994. Operational sex ratios and behavioural sex differences in a pipefish population. *Behav Ecol Sociobiol*. 34:435–442.
- Vincent A, Berglund A, Ahnesjö I. 1995. Reproductive ecology of five pipefish species in one eelgrass meadow. *Environ Biol Fishes*. 44:347–361.
- Wong BBM. 2004. Superior fighters make mediocre fathers in the Pacific blue-eye fish. *Anim Behav*. 67:583–590.