

# Behavioral responses of a sex-role reversed pipefish to a gradient of perceived predation risk

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Conspicuous behaviors such as courtship and mating often make animals susceptible to predation. When perceiving themselves at an elevated level of risk, animals frequently reduce conspicuous behaviors in trade-off for a decrease in probability of being preyed upon. In the present study, we used two experiments to examine the effect of perceived predation risk from cod (*Gadus morhua*) on nonreproductive and reproductive behaviors in the sex-role reversed pipefish (*Syngnathus typhle*). In the first experiment, no differences due to predation risk were detected in the nonreproductive behaviors of either males or females. In the second experiment, predation risk had significant effects on reproductive behaviors. Pipefish were allowed to court and copulate at four different predation levels. We created predation levels differing in perceived predation risk by controlling the number of sensory modes through which pipefish could detect the presence of a cod. As predation risk increased, pipefish copulated and courted less frequently, swam alone (displayed and searched for conspecifics) less often, and waited longer before commencing courtship. These changes in behavior minimized the amount of time spent above the eelgrass and presumably reduced conspicuousness to visual predators. Pipefish also copulated after a smaller amount of courtship as predation risk increased, indicating that they may trade information concerning mate quality for a reduction in predation risk. No differences were found in any response variable between males and females. The role of operational sex ratios and intersexual competition in determining which sex assumes greater costs in mate acquisition is questioned. *Key words:* courtship, information gathering, mate acquisition, pipefish, predation, reproductive behavior, Syngnathidae, trade-off. [*Behav Ecol* 7:69–75 (1996)]

The behaviors required to avoid predation often conflict with the demands of mating behaviors (Endler, 1978, 1991, 1992; Lima and Dill, 1990; Magurran and Nowak, 1991; Sih, 1987). Communication between males and females favors unambiguous signals and signaling behavior which in the wrong context may act as a location cue to predators (Endler, 1992, 1993; Gwynne, 1987; Ryan, 1985). The manner in which animals balance crypsis versus signaling often yields insightful information about the amount of predation risk an individual will tolerate in relation to the importance of a given activity (Abrahams and Dill, 1989). Animals with flexible behaviors provide particularly interesting examples as one individual may generate a multitude of responses to different situations reflecting the actual trade-off function between predation risk and mating activities. For example, a comparison of two goby species found that the black goby (*Gobius niger*) reduced mating activities in response to predation risk presumably to wait and reproduce in the next season, while the sand goby (*Pomatoschistus minutus*), a species with only one reproductive event, disregarded predation risk (Magnhagen, 1990). In the presence of predators, male guppies (*Poecilia reticulata*) perform fewer sigmoid displays and revert to using forced, sneaky copulation attempts (Magurran and Seghers, 1990). Male signal blennies (*Emblemaria hypacanthus*) court females less vigorously and spend more time in shelter when under predation risk (Hastings, 1991). Both the semiaquatic bug (*Microvelia sustrina*; Sih, 1988) and the water strider (*Gerris remigis*; Sih et al., 1990) reduce mating activities in the presence of predators. The examples are numerous and indicate the importance of perception and response to predation.

Predation may also be important in structuring male and female roles in mating systems. In many systems, one sex (often the male) experiences increased predation as a result of either mate search and/or mate attraction (Endler, 1992; Lima and Dill, 1990; Sih, 1987). Male three-spined sticklebacks (*Gasterosteus aculeatus*) in breeding color are twice as likely to be preyed upon by trout as are males in nonbreeding color (Moodie, 1972). The mating call of male Tungara frogs (*Physalaemus pustulosus*) is used as a location cue by predatory bats and, hence, raises male predation risks (Ryan, 1985). Although the effects of predation on the evolution of male/female mate acquisition tactics has not received extensive theoretical consideration, the general trend is to assume that males incur higher predation risks as a result of high competition for mates (Andersson, 1994; Burk, 1982; Magnhagen, 1991; Trivers, 1972). In sex-role reversed species where females are expected to experience similar selection to males of conventional species, the opposite trend is predicted (Rosenqvist, 1993). Females should experience higher risk than males in mate acquisition due to predominant female competition for mates.

In the present study, we examine the effect of exposure to a predator on nonreproductive and reproductive behaviors using the sex-role reversed pipefish *Syngnathus typhle* (L.). We investigate male and female use of their natural substrate, eelgrass *Zostera marina* (L.), under various predation levels. Specifically, we address the following questions: How does predation risk affect pipefish use of their natural habitat outside of reproduction? How does predation risk affect mating behaviors and related decision making processes? Do males and females differ in their response to predation risk?

## Natural history of the pipefish, *Syngnathus typhle*

*Syngnathus typhle* inhabit eelgrass (*Z. marina*) from mid-Norway and the southern Baltic Sea southwards to Gibraltar and

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into the Mediterranean (Wheeler, 1992). Outside of reproductive activities, *S. typhle* appear very cryptic within eelgrass, at least to human observers. Individuals align themselves vertically within the eelgrass where their body colors closely approximate the surrounding substrate (Vincent et al., in press). Mate seeking and courtship behaviors disturb the resemblance between pipefish and their background rendering them conspicuous. Males swim horizontally above the eelgrass looking for females. In contrast, females bob vertically, emerging from the eelgrass in order to attract males. A lengthy and ritualized mutual dance always precedes copulation. The dance includes wriggling and shaking movements as well as rising above the eelgrass (Fiedler, 1954). The dance terminates with the female transferring her eggs to the male's brood pouch by means of a small ovipositor while the couple ascends. Thereafter the male, assuming a stiff S-shaped posture, fertilizes the eggs (Fiedler, 1954). Males may brood eggs from one or several females, and a female may, within a short time span, transfer eggs to several males (Berglund et al., 1988). Males provide offspring with nutrients and oxygen during pregnancy (Berglund et al., 1986b; Fiedler, 1954; Haresign and Schumway, 1981). The pregnancy ends with the young fish leaving the pouch, thereafter leading independent lives. The adult sex ratio is equal in nature (Berglund et al., 1986a,b), but the operational sex ratio (which counts only animals ready to mate) is mostly female biased (Berglund and Rosenqvist, 1993; Vincent et al., 1994).

## METHODS

Pipefish were collected from shallow (0.5–6.0 m) eelgrass meadows in the Gullmar Fjord on the Swedish west coast (58°15'N, 11°28'E) in May 1994. Fish were caught using a small beam trawl (2 mm mesh size) pulled by a boat. All fish were caught before the onset of the breeding season. Sexually mature males and females were kept in separate aquaria to assure that individuals would be reproductively active. Stock aquaria contained plastic plants and continuously renewed sea water (temperature, salinity, and light regime following natural conditions). Fishes were fed ad libitum with brine shrimps (*Artemia*), small wild-caught crustaceans, and frozen mysids.

### Microhabitat use in nonreproducing pipefish

We examined the effect of predation risk on *S. typhle* habitat preferences by placing individuals of one sex in habitat choice tanks containing cod (*G. morhua*), a natural predator. By using members of one sex, we reduced the possibility of reproductive behaviors influencing fish location within the tanks. Habitat choice tanks were created by planting live eelgrass in areas of high and low density in large, outdoor tanks (1.8 × 2.6 m, water depth 0.7 m). High density was greater than 10 times that of low. We planted six tanks in total.

Each tank also contained a small glass aquarium (25 × 48 cm) located along one side and centered between the high and low density areas. This aquarium contained a medium-size cod (220–340 mm) during predation treatments and was empty for control treatments. Cod are known from their stomach contents to occasionally eat pipefish (personal observation). Water inlet hoses ran directly into the cod aquaria forcing all incoming water to pass through it before flowing out into the tank. This allowed pipefish to detect olfactory in addition to visual cues during predation treatments. We used random numbers to assign predation and control treatments arbitrarily among the tanks before each trial.

For each experimental trial, we placed six sets of five individuals of one sex in the tanks at 0900 h. Cod were measured

and placed in the appropriate aquaria. Pipefish were given 2 h to acclimate. We recorded the number of individuals located in high and low density at 1100 h, 1500 h, and 1900 h. At 1900 h, we removed the pipefish and cod from the tanks. Water ran through the tanks continuously during the night, presumably eliminating cod odors. This experiment was conducted from 24 May through 4 June.

We also investigated the effects of predation risk on *S. typhle* tendencies to position themselves above the eelgrass. We placed glass bottles in the corners of the tanks and attached a string to the bottlenecks creating a visual marker around the perimeter of the tanks at a height of 18 to 20 cm which was in rough accordance with eelgrass height. We recorded whether individuals were above or within the eelgrass during tank checks. This experiment ran from 27 May through 4 June.

We calculated the proportion of individuals located in high versus low density areas and the proportion of individuals located above versus within the eelgrass in each tank throughout each day. An arcsine transformation was used for all proportions. Analysis of variance was conducted using treatment, sex, and treatment × sex as the sources of variance. All test probabilities are two-tailed.

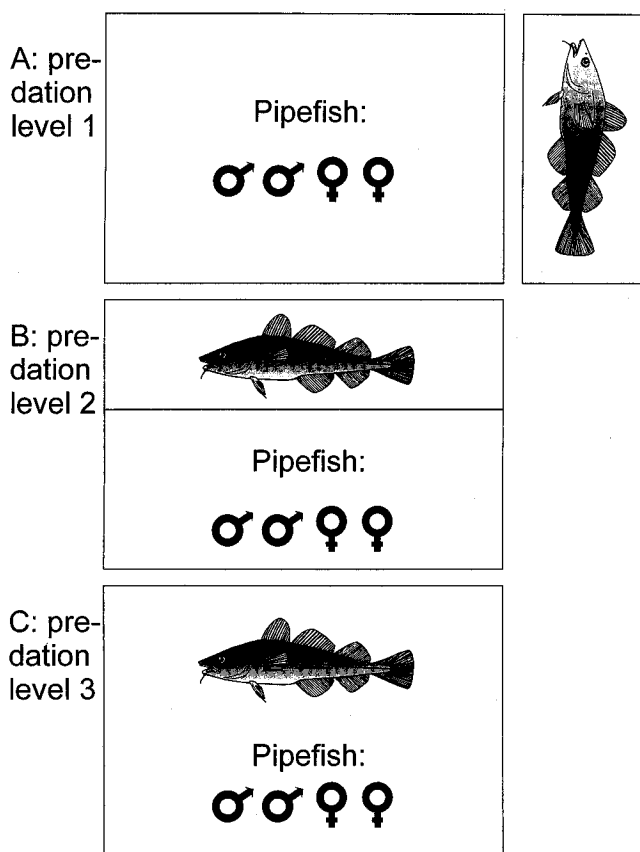
### Microhabitat use during courtship

In order to examine the effect of predation risk on microhabitat use during courtship, we placed males and females in aquaria planted with natural eelgrass and varied predation level by manipulating perceived predation risk. This was done using three different aquarium setups to control the number of sensory modes (i.e., visual, olfactory, and tactile) through which pipefish received signals indicating the presence of a predator. Below, we describe the experimental designs in order of increasing predation level. All controls were lumped and assigned predation level 0. We found no significant differences between control treatments for any response variable (Mann-Whitney *U* tests,  $p > .10$ ). The experiment ran from 26 May through 20 June.

*Predation level 1.* We planted two large glass aquaria (91 × 61 cm, water depth 0.5 m) with natural eelgrass. A smaller aquarium (48 × 38 cm) was situated outside at the end of each large aquarium. The small aquarium contained a cod during predation treatments and was empty for controls (Figure 1a). We conducted an equal number of control and experimental treatments. This design provided pipefish with limited visual and no olfactory or tactile signals from the predator. We used two males and two females per trial, each trial lasting from 1000 h to 2000 h, with a total of five replicates.

*Predation level 2.* We increased perceived predation risk by placing a glass barrier lengthwise through the large aquarium and then placing the cod in the back compartment of the aquarium (Figure 1b). This increased the perceived predation risk by providing greater visual access to the cod and allowing olfactory cues to operate. Again, control treatments simply consisted of a trial with no predator. Experimental trials were identical to the trial used in predation level 1. We ran 14 replicates of the experimental and control treatments, but discarded one control treatment from analysis due to the aberrant, tail-up swimming of one pipefish.

*Predation level 3.* We removed the glass barriers and placed the cod and pipefish in the same tank (Figure 1c). This increased perceived predation risk because the pipefish could also sense hydrodynamic (movement) cues. Cod were fed an excess of small gobies and shrimp in order to reduce actual predation on experimental pipefish. However, two males and one female disappeared, and one individual was wounded from an obvious predatory attack over the course of this ex-



**Figure 1**  
 Experimental setups for predation levels 1, 2, and 3. Control setups were identical but with no predator. In predation level 2, the glass pane was placed so that the back compartment was 25 × 91 cm and the front compartment was 36 × 91 cm.

periment. These were excluded from the analysis. Trials were identical to those conducted at predation level 1 and 2. No controls were conducted as they were identical to the controls used in predation level 1. Ten replicates were performed.

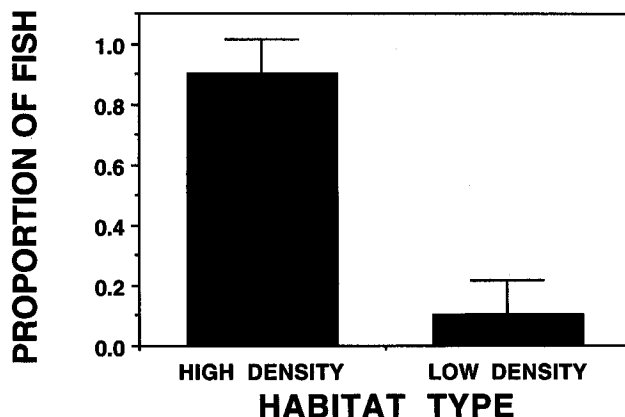
In all three experiments, we recorded pipefish behaviors for 10 h using time-lapse video cameras (1 s record/5 s pause). Intense light (100 W spots) was used for the entire 10 h in addition to natural light from windows.

Videotapes were analyzed for the number of copulations, time spent swimming above the eelgrass alone, and time spent swimming above the eelgrass in courting groups by both males and females. Pipefish were defined as swimming in courting groups when fish were observed simultaneously bobbing up and down while facing one another in close proximity. Courting groups always contained at least one male and one female. All of these behaviors take longer than the time between video time-lapse frames. From these videos, we also measured time until the first courting group appeared, total time spent above the eelgrass as single individuals, total time spent in courting groups, and the ratio of total time spent in courting groups per copulation. We derived multiple and, where appropriate for biological reasons, partial correlation coefficients between predation level and response variables. All test probabilities are two-tailed and have undergone a Bonferroni adjustment where appropriate.

## RESULTS

### Microhabitat use in nonreproducing pipefish

Pipefish preferred areas of dense eelgrass. Thus, fish were most often found in areas of high density substrate (Figure 2,



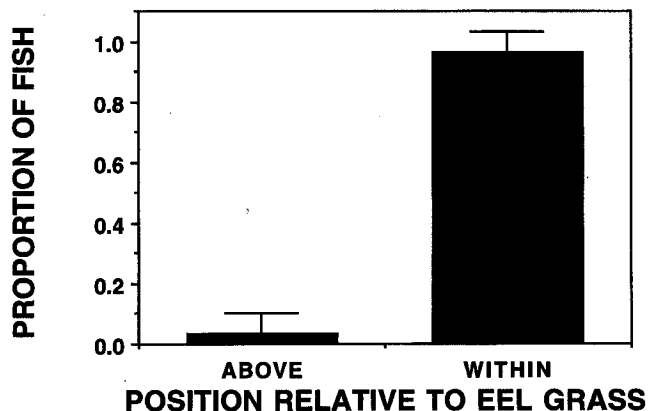
**Figure 2**  
 Mean proportion of individuals found in high and low density eelgrass,  $n = 27$ . Bars represent standard deviations.

paired  $t$  tests between the arcsine transformed proportions of individuals in high versus low density substrate,  $t = 21.9$ ,  $df = 60$ ,  $p < .01$ ). However, neither sex nor treatment (predator versus no predator) affected fish location within habitat choice tanks (ANOVA,  $p > .25$  for all variance sources, power  $> 0.71$  for sex, power  $> 0.89$  for treatment, power  $> 0.52$  for sex × treatment).

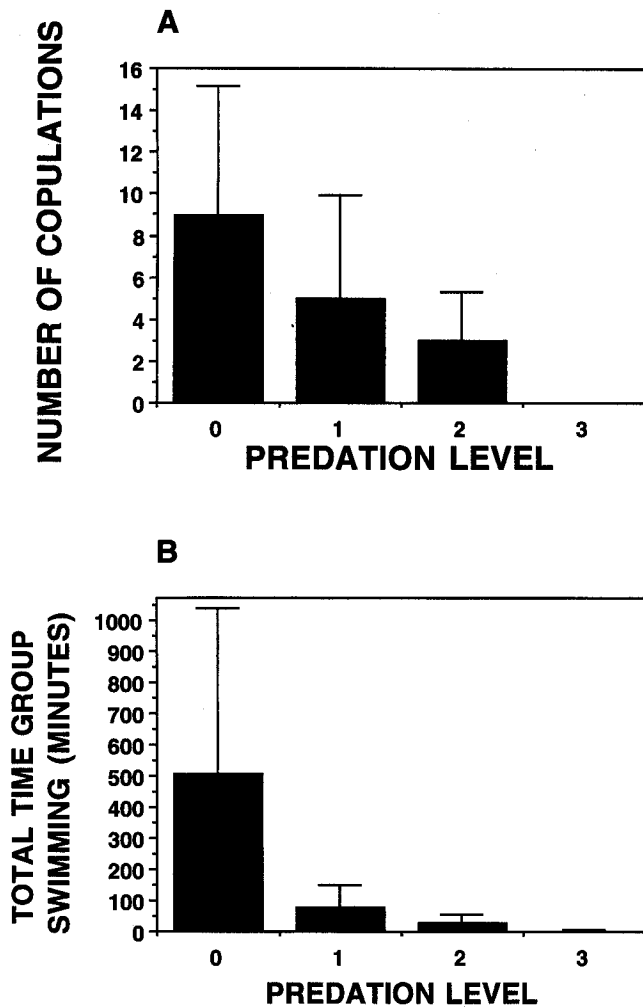
A similar result was found for pipefish tendencies to emerge from eelgrass. Pipefish preferred to be located within the substrate (Figure 3, paired  $t$  tests between the arcsine transformed proportions of individuals located above versus within the vegetation,  $t = 31.5$ ,  $df = 44$ ,  $p < .01$ ). No significant differences in pipefish vertical position existed among predation treatments or sex (ANOVA,  $p > .3$  for all variance sources, power  $> 0.89$  for both sex and treatment, power  $> 0.64$  for sex × treatment).

### Microhabitat use during courtship

None of the measured response variables was normally distributed warranting the use of nonparametric statistical tests (Kolmogorov-Smirnov one sample test using standard normal distribution,  $p < .01$  in all cases). Wilcoxon signed ranks test indicated no significant differences between males and females in time spent in courting groups or time spent single



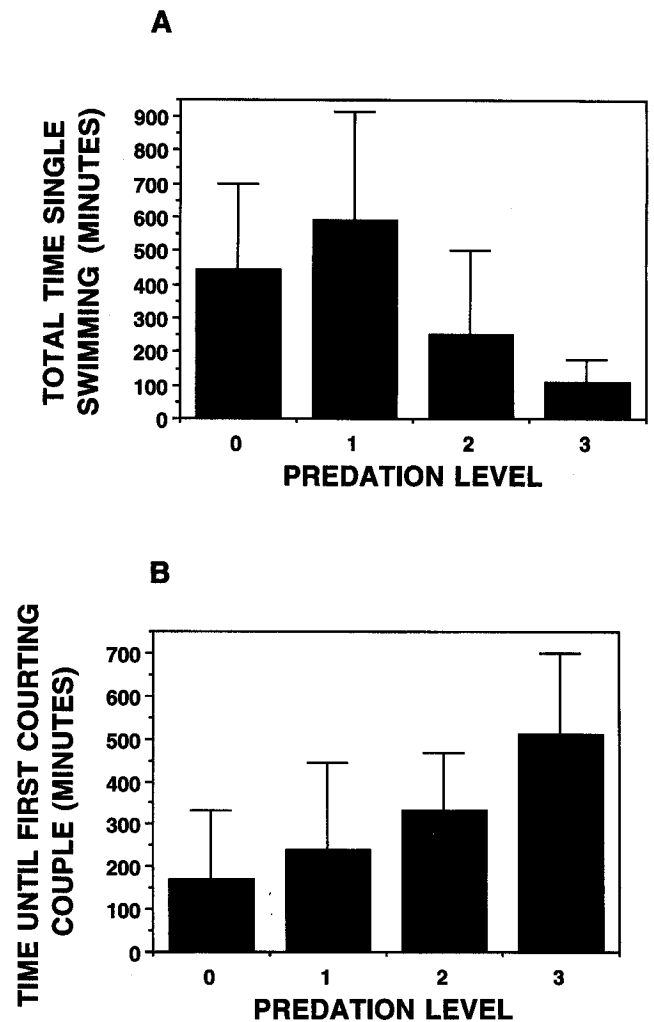
**Figure 3**  
 Mean proportion of individuals found above and within the eelgrass,  $n = 22$ . Bars are standard deviations.



**Figure 4**  
(A) Mean number of copulations per experimental trial in relation to predation level. (B) Mean total time spent swimming above the eelgrass in courting groups per experimental trial in relation to predation level. Bars represent standard deviations. See text for further details.

swimming ( $z = 1.47$ ,  $p = 0.14$ , power  $> 0.95$ , and  $z = 0.55$ ,  $p = 0.58$ , power  $> 0.66$  respectively). For the remainder of these results, we do not distinguish between sexes and only consider total time spent above the eelgrass in courting groups and total time spent alone above the eelgrass.

Pipefish copulated less frequently and spent less time above the eelgrass in courting groups as predation level increased (Figure 4a,b; Kendall rank-order correlation coefficient  $T = -0.590$ ,  $p < .01$ ,  $T = -0.673$ ,  $p < .01$  respectively). However, as copulations never occur without prior group dancing, these two variables were strongly intercorrelated (Kendall partial rank-order correlation coefficient,  $T = 0.417$ ,  $p < .01$ ), making it necessary to discern whether one of these variables caused an indirect correlation of the other with predation level. Kendall partial rank-order correlation coefficients between predation level and the number of copulations controlling for total time spent in courting groups, and between predation level and the total time spent in courting groups controlling for the number of copulations, showed that both variables were directly and negatively affected by predation level ( $T = -0.275$ ,  $p < .05$ ,  $T = -0.292$ ,  $p < .01$ ). Therefore, both variables were directly affected by predation level.



**Figure 5**  
(A) Average amount of time spent swimming above the eelgrass alone in relation to predation level. (B) Average amount of time until the first courting couple appeared in relation to predation level. Bars represent standard deviations. See text for further details.

The amount of time spent single swimming decreased and the time until the first courting group appeared increased as predation level increased (Figure 5a,b;  $T = -0.454$ ,  $p < .01$ ,  $T = 0.523$ ,  $p < .01$  respectively). Although males search and females display (forms of single swimming) roughly until courtship begins, the total time spent single swimming and the time until first courtship were not significantly intercorrelated with each other ( $T = -0.0218$ ,  $p > .10$ ).

The ratio of total time spent in courting groups per copulation also decreased significantly with predation level ( $T = -0.537$ ,  $p < .01$ ,  $n = 30$ ). This correlation coefficient had no values at predation level 3, as no copulations occurred. The ratio did not differ significantly between predation levels 1 and 2 (Mann-Whitney  $U = 10.0$ ,  $p > .10$ ).

The experimental setup for predation level 2 required that pipefish be placed in a smaller area than that used in predation levels 1 and 3, creating differences in fish density between the two experimental setups (Figure 1). Because density and encounter rate can potentially influence reproductive behaviors (Crowley et al., 1991; Real, 1990; Shelly and Bailey, 1992), we examined the effect of area on pipefish behaviors by comparing control treatments between predation levels 1 and 2.

conventional, generally low or noninvesting males (Fitzpatrick et al., 1995). Undoubtedly, however, the operational sex ratio influences the opportunity for selection on behavior similarly in both sexes (in this case, the surplus sex being the one to generally display and assume predation risk).

In actuality, the determinants of display, search, and subsequent predation risk most likely involve more factors than OSR as females in some species with male-biased OSRs have been found to suffer higher predation costs in association with mate search and display than do males (Forsgren and Magnhagen, 1993; Wing, 1988). Evolutionarily stable strategy (ESS) models show that a strategy in which one sex invests heavily in offspring and assumes high predation risks during mate search can be evolutionarily stable (Hammerstein and Parker, 1987). Our finding here emphasizes that the question of which factors determine which sex experiences costs in mate acquisition has not been solved and possibly has been overlooked (Magurran and Nowak, 1991; Rosenqvist and Berglund, 1992).

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