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Mate quality influences multiple maternity in the sex-role-reversed pipefish *Syngnathus typhle*

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In the pipefish *Syngnathus typhle*, pregnant males provide all parental care. Females are able to produce more eggs than males can brood, and consequently females compete more intensely for mates than do males, a phenomenon defined as sex-role reversal. As the genetic mating system influences the operation of sexual selection, we investigate variation in one phenotypic component of mate quality, female body size, as a possible proximate influence on mating system variation in *S. typhle*. Breeding trials were employed, each consisting of a single receptive male with four adult females. In each replicate, a focal male was paired either with a set of small or with a set of large females. Males were allowed to mate freely, and after several weeks of brood development, maternity of the progeny was resolved using three microsatellite loci. Males with access either to small or to large females successfully mated with a mean of 2.1 or 1.3 females, respectively, a significant difference. Results indicate that variation in female size can affect the mating system and thereby influence sexual selection in pipefish. Thus, the high rate of multiple mating by *S. typhle* males in the wild may be explained in part by the extensive size variation in naturally occurring, sexually mature females.

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Numerous factors may affect the strength and direction of sexual selection (Andersson 1994). Operational sex ratios (Emlen and Oring 1977), relative parental investments (Trivers 1972), potential reproductive rates of the sexes (Clutton-Brock and Parker 1992), mating systems (Oakes 1992, Webster 1992, Winqvist and Lemon 1994), life-history constraints (Partridge and Endler 1987), and other factors interact to influence intra- and intersexual selection. The genetic mating system, which recently has received renewed attention with the introduction of DNA-based parentage analysis, long has been appreciated as an important factor in sexual selection (Darwin 1871, Andersson 1994). In species with conventional sex roles, polygynous species tend to expe-

rience a greater gender-based asymmetry in sexual selection than monogamous species (Andersson 1994). Similarly, in sex-role-reversed species, sexual selection on females appears to be stronger in more polyandrous species (Jehl and Murray 1986, Jones and Avise 1997a, b). Because the mating system is causally related to sexual selection, a logical goal is to assess proximate factors shaping the mating system.

One such factor is variation in the phenotypic quality of mates, which in addition to impacting sexual selection directly (by promoting competition for high quality mates in monogamous as well as in polygamous species; Andersson 1994) also may have indirect effects via the genetic mating system. In some species, females

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paired to low quality mates are more likely to seek extra-pair copulations (Houtman 1992, Kempnaers et al. 1992), or to switch mates (Lifjeld and Slagsvold 1988, Orell et al. 1994, Otter and Ratcliffe 1996, Triefenbach and Itzkowitz 1998). In such cases, variation in male quality can promote genetic polygamy, presumably enhancing the opportunity for sexual selection. Variation in quality need not be genetically determined to affect the sexual selection process, since there may be direct, non-genetic benefits to mating with a high quality mate (e.g., nuptial gifts, better parental care).

The pipefish *Syngnathus typhle* offers a model system to investigate sexual selection in a sex-role-reversed species. Sex-role reversal is defined here as the situation in which competition for mates is more intense among females than among males (Vincent et al. 1992), so in sex-role-reversed species, sexual selection acts more strongly on females, and secondary sexual traits typically evolve in females rather than in males. Sex-role-reversed taxa provide opportunities to test predictions of a sexual selection theory that was derived primarily from observations of organisms with conventional sex roles (Darwin 1871, Williams 1975). In *S. typhle*, the phenomenon of male pregnancy appears to be largely responsible for the evolution of sex-role reversal, as this reduces the male's capacity to rear eggs below the female's capacity to produce them (Svensson 1988, Berglund et al. 1989, Berglund and Rosenqvist 1990). During copulation, the female transfers eggs to a pouch on the ventral surface of the male where they are fertilized internally. A female's investment in progeny is complete after egg transfer, but a male carries offspring for several weeks, providing nutrients, aeration, osmoregulation, and protection for his developing brood (Haresign and Shumway 1981, Berglund et al. 1986a).

Field and laboratory studies have documented a high rate of multiple mating by males in *S. typhle* (Berglund et al. 1988, Jones et al. 1999a). A recent genetic assessment of maternity found that 90% of *S. typhle* males mated multiply, with an average of 3.1 females contributing to a male's brood (Jones et al. 1999a). The males of other studied species of pipefishes and seahorses have substantially fewer mates per mating episode (Jones and Avise 1997a, b, Jones et al. 1998). Why males of *S. typhle* mate with so many females remains an open question. We know that males prefer to mate with larger females (Berglund et al. 1986b), so the mate choice effects of female size have been resolved (i.e., when small and large females are present, males choose larger females). However, the factors that influence the number of times a male will mate have not been investigated, even though this aspect of the mating system can dramatically alter the intensity of sexual selection. Our goal, therefore, was to investigate the influence of female size (which is already known to affect male mating decisions) on the propensity of males to mate multiply in *S. typhle*.

Methods

Experimental design

Adult *S. typhle* were collected from Gullmar Fjord on the Swedish west coast by a small beam trawl (2 mm mesh) pulled behind a boat through meadows of shallow eelgrass (*Zostera*). During two weeks in May (just before the mating period) 1996, adult females as well as males with well-developed but empty pouches were collected. The mating status of males is ascertained readily because the brood pouch is transparent and eggs are visible when present.

Mating trials were carried out from 15 to 22 June 1996 in 225-l barrels equipped with plastic eelgrass. Salinity, temperature, and light regime followed natural conditions. For each experimental trial, a male was placed in a barrel with four females until his pouch was filled completely (a few males failed to mate within 24 h and were released). All males that received eggs in the first 24 h had full pouches within 69 h. Immediately after each trial, females were frozen for DNA analysis, and pregnant males were transferred to small tanks to allow brood development.

The experiment consisted of two treatments based on female size: large (L) and small (S). In the L treatments, mean female standard length was 221.0 mm (range = 197–265 mm) whereas in the S treatments mean female length was 156.4 mm (range = 121–182 mm). Ten trials of each treatment were completed successfully. At the end of the experiment, the lengths (and widths) of females were recorded. Width was measured as the distance from dorsal to ventral surface at the deepest part of the abdomen. Females also were dissected to check for the presence of ripe ova.

Maternity analysis

Three microsatellite loci (*typh04*, *typh16*, and *typh18*) previously identified from *S. typhle* were used for the maternity analysis. Primer sequences and assay conditions are described elsewhere (Jones et al. 1999a). Pregnant males were kept alive for 16 to 21 d, allowing sufficient brood development for microsatellite assay, after which they were frozen with brood pouches intact. Embryos were dissected from the brood pouch and their positions mapped as in Jones and Avise (1997b). For six males, the entire brood was analyzed (Table 1). Inspection of the spatial arrangement of maternity within these broods (as well as the broods of 30 field-collected pregnant males; Jones et al. 1999a) demonstrated that embryos are arranged spatially by maternity within each pouch. Thus, for the remaining 14 broods, we sampled every third embryo and interpolated to estimate the total contribution from each female (Table 1).

For each embryo, maternity was assigned by exclusion. In 571 embryos (98%), two loci (*typh04* and *typh16*) were sufficient to exclude all but one of the four potential mothers. For the remaining nine embryos, an additional locus (*typh18*) was necessary for maternity assignment.

Results

Maternity assessment

The three microsatellite loci were sufficiently variable to resolve unambiguously the parentage of all 580 embryos typed. Non-amplifying (null) alleles, deduced in progeny arrays by non-Mendelian appearance of gel bands, can be a complication in parentage studies. However, no null alleles were present in our sample. Mutations also can be a concern for parentage analysis based on microsatellite markers. A total of five *de novo* mutations were observed at the loci *typh04* (3) and *typh16* (2). These mutations did not compromise the parentage analysis, however, because maternity of the

mutant embryos was assigned on the basis of other loci. A description of observed mutations in a much larger sample of families is presented elsewhere (Jones et al. 1999b).

In *S. typhle*, eggs are deposited through an opening at the top of the brood pouch. Thus, embryos from the first female are found at the pouch bottom, with eggs from later-mating females stacked successively on top. Our maternity analysis recovered the expected spatial structure of embryos within each pouch. Table 1 lists for each male the number of embryos mothered by each of his successive mates.

Male mating behavior

Males in the S-treatment tanks mated successfully with 2.1 females on average, significantly more than the mean of 1.3 females per male in the L treatment (Table 1, Fig. 1). This difference in the number of mates is probably not a consequence of mean differences in male phenotype because males in the two treatments did not differ significantly in length or numbers of

Table 1. Summary of the males used in the two treatments and results of the maternity analysis. The bottom row shows the *P*-value resulting from a *t*-test of the means in the L versus S treatments for each column (H_0 = no difference).

Male I.D.	Length (mm)	No. of embryos	Undev. eggs	Embryos assayed	No. of mates	No. embryos per mate (1st → last)
Large-female treatment:						
L44	161	64	9	24	1	64
L59	126	23	7	23	1	23
L60	145	62	5	25	1	62
L98	143	46	24	17	2	26, 20
L108	140	50	2	18	1	50
L116	131	39	14	14	1	39
L117	146	85	3	29	1	85
L132	139	70	4	24	2	26, 44
L187	140	66	1	66	2	57, 9
L190	130	31	7	31	1	31
mean	140.1	53.6	7.6	27.1	1.3	41.2
std.dev.	9.9	19.2	6.9	14.6	0.5	21.6
Small-female treatment:						
S22	137	50	2	50	2	47, 3
S43	148	74	4	74	3	35, 37, 2
S45	148	50	6	10	2	35, 15 ^a
S68	135	46	11	16	2	32, 14
S69	122	35	6	13	1	35
S70	123	31	13	12	3	17, 9, 5
S118	159	116	3	40	3	56, 21, 39
S141	130	64	15	22	1	64
S166	115	50	17	50	2	15, 24, 6, 5 ^b
S213	126	62	17	22	2	52, 10
mean	134.3	57.8	9.4	30.9	2.1	25.1
std.dev.	13.9	24.2	5.9	21.5	0.7	18.4
<i>P</i> -value	0.30	0.65	0.54	0.65	0.01	0.03

^a S45's pouch was damaged during transport to the molecular lab, resulting in a randomization of embryo order. Two females mated with S45, but the spatial arrangement of their embryos in the pouch is not known.

^b S166 received eggs from only two females, but the spatial arrangement of embryos in his brood pouch suggested that he had mated at least four times, alternating between the two mates.

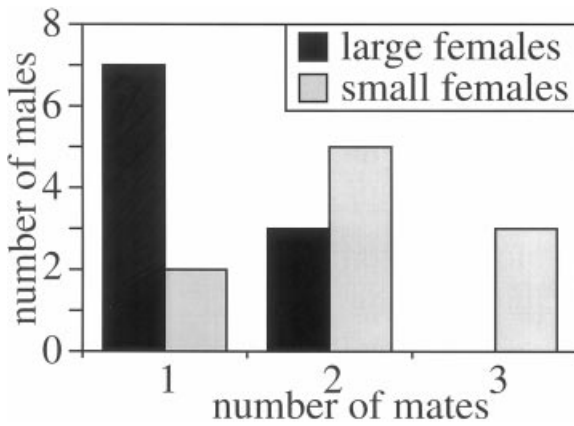


Fig. 1. Mating outcomes, based on genetic maternity analysis, for *S. typhle* in the large-female (presumably high quality) and small-female (low quality) experimental treatments.

embryos in the brood pouch (Table 1). Also, similar numbers of eggs per male were assayed in both treatments.

The males' pouches also contained from 1 to 24 eggs each that appeared to have undergone no development. These could represent unfertilized eggs or embryos arrested early in development. Males did not differ by treatment with respect to numbers of these undeveloped products (Table 1).

Female mating success

At the completion of the mating trials, dissections indicated that 79 of the 80 females contained ripe eggs, suggesting that females could have continued mating given additional receptive mates. The one female containing no eggs, present in the S treatment, probably was sexually immature.

The maternity data yielded the number of healthy embryos contributed by each female. Successful L females mothered a mean of 41.2 embryos per copulation, compared to 25.1 for the S females, a significant difference (Table 1). This difference is related to the fact that males in the S treatments had more mates than those in the L treatments, yet approximately the same amount of total brood space was involved.

S. typhle is sex-role reversed, so we might expect mating competition among females to be intense, especially with the skewed sex ratios experimentally employed. Thus, we also looked for correlations between female phenotype and reproductive success within each treatment. A linear model for categorical data (procedure CATMOD in SAS) was used to determine if female size rank within a barrel predicted successful mating. No significant effects were detected for either female length ($P = 0.14$) or width ($P = 0.25$). This may reflect inade-

quate statistical power to detect significant differences given our sample sizes, or too narrow a range of female phenotypic differences within treatments.

Discussion

The genetic parentage analysis clearly indicated that males mated more often in the presence of consistently small (S treatment) as opposed to large (L treatment) females. Since the brood pouches of all males appeared to be filled to capacity, a necessary consequence was that males in the S treatment received fewer eggs per copulation than those in the L treatment. Using a different experimental design, Berglund et al. (1986b) previously showed that male *S. typhle* prefer to mate with longer females. Our results complement such observations and further suggest that such behavioral tendencies can translate into different mating patterns as a function of the size availability of females. In natural populations of *S. typhle*, sexually mature females vary dramatically in size. Thus, one explanation for the high rate of multiple mating observed by male *S. typhle* in the field may be related to the extensive size variation in the standing crop of available mating partners.

One concern for laboratory-based studies is that the experimental conditions may not mimic the natural setting. In particular, the sex ratio may have an important influence on the sexual selection process. The dynamics of the operational sex ratio (OSR) of pipefish in nature are complex. The absolute adult sex ratio is near unity, but the OSR varies during the breeding season (Vincent et al. 1994). At the beginning of the season, the OSR is nearly 1:1, but as brood pouches are filled fewer receptive males are available and the OSR becomes increasingly female biased (Vincent et al. 1994). By the end of the initial mating phase, numerous gravid females are available to mate with each remaining receptive male. Thus, our use of four females per male simulates an OSR that naturally occurs as the breeding season progresses.

Potential causes of the behavioral response

Current results indicate that female size is one (of perhaps many; Burley 1981) phenotypic guide to female quality affecting the genetic mating system. However, to interpret these results in terms of adaptive mating strategies of the sexes requires additional knowledge of *S. typhle* mating behavior. A key unanswered question is whether males or females normally control the number of eggs transferred per copulation. In *S. typhle*, the mating participants are in physical contact only briefly, when the female's "penis" is inserted into the male's pouch (Ahnesjö 1992). Presumably, either partner could terminate egg transfer at any time.

If males control copulation, which seems likely as they are more choosy when selecting a partner than females (Berglund and Rosenqvist 1993), at least three hypotheses might explain our findings. First, a male may tend to accept fewer eggs from small females in light of the possibility that his next mate may be larger. Thus, the male is assured of some progeny while reserving additional brood space for a larger female that might appear later. Larger females produce larger eggs (Berglund et al. 1986a) that give rise to larger offspring (Ahnesjö 1992), which may explain this choice.

A second hypothesis based on male control of copulation is that males may mate with multiple small females to compensate for an inability to assess accurately the relative genetic quality of smaller females. In the wild, the size distribution of *S. typhle* females typically is bimodal, with distinct peaks of smaller and larger females representing one-year-olds and two-year-olds, respectively (Berglund and Rosenqvist 1990). In our study, most S females were probably one year of age whereas L females were two or more years old. Genetically superior females may grow faster on average or have enhanced survival such that a male's assessment of genetic quality in a mate might be more secure for older, larger females. To guard against receiving an entire brood from a female of low genetic quality, a male in the presence of only small females might seek additional mates. We are suggesting not that larger females necessarily are of higher genetic quality than smaller females, but that a male's ability to assess genetic quality may be a function of female age.

A third possibility is that males may assess female quality during courtship and copulation. A male may initiate courtship with a small female only to detect that she is of low quality. The male may terminate the mating after only a few eggs are received, leaving brood space for eggs from additional females. In some bird species, females apparently assess male quality through copulation (Lens et al. 1997), but such behavior has not been addressed in *S. typhle*.

A complementary suite of explanations could be invoked to explain our results if the observed patterns resulted instead from female control of mating (see Berglund et al. 1986b for evidence of female choice in *S. typhle*). For any of several reasons analogous to those listed above, perhaps females in this species are predisposed genetically to seek a "bet-hedging" strategy wherein they typically lay eggs in the pouches of multiple males, particularly when males are common and the quality of those males is difficult to assess. Larger female pipefish carry more eggs and on average probably transfer more eggs per copulation (Berglund et al. 1986b). If all female *S. typhle* are disposed to mate with multiple males and each female is inclined to place into each male some relatively constant fraction of her total egg supply, then larger females would on average fill more of a male's brood pouch.

Another possibility is that a small female might contain too few ripe eggs to fill a male's pouch. We cannot rule out this possibility conclusively, but at least two lines of evidence suggest that females were not simply depleted of eggs. First, dissections at the conclusion of the experiment revealed that virtually all small (as well as large) females still contained apparently ripe eggs. Female pipefish continuously ripen eggs, but new eggs could not have been ripened during the short time frame of our experiment (A. Berglund pers. obs.). Any ripe eggs present in the females upon dissection should have been available for transfer to a willing male. Second, in one case (S166) the male mated with two females, but the embryos were arranged in the brood pouch in a pattern indicating that he received the eggs in at least four copulations, alternating between the two females. In this case at least, a severe depletion of eggs in these females evidently was not the exclusive cause of the observed mating pattern.

Mate quality and sexual selection

The salient finding of the current experiment is that male pipefish had more mates in the exclusive presence of small females. If similar processes are at work in wild populations of *S. typhle*, then variation in mate-size availability may be one underlying factor shaping the genetic mating system. At least some populations of this species are polygynandrous, with both males and females mating multiple times in the course of a single male pregnancy (Berglund et al. 1988, Jones et al. 1999a). The presence of large numbers of small females in a local population may contribute to this mating system by promoting multiple mating by males. In species with sex-role reversal, such multiple mating by males actually may operate so as to decrease the strength of any gender-related asymmetry in sexual selection relative to what might be expected in more polyandrous syngnathid species (Jones and Avise 1997b).

Current results extend, to a sex-role-reversed species, previous studies that examined the consequences of variation in presumed mate quality in species with conventional sex roles (Lifjeld and Slagsvold 1988, Houtman 1992, Kempnaers et al. 1992, Orell et al. 1994, Otter and Ratcliffe 1996, Triefenbach and Itzkowitz 1998). Many factors influence animal mating behaviors and thereby the operation of sexual selection, but among these must be included mate availability with respect to phenotypic attributes associated with mate quality or attractiveness.

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