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Mutual Mate Choice in the Deep
Snouted Pipefish *Syngnathus typhle*

BY

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Abstract

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This thesis integrates the fields of sexual selection, parental investment and sex role theory by investigating mutual mate choice and mate competition in the sex role reversed deep snouted pipefish *Syngnathus typhle* (Pisces: Syngnathidae) through a series of laboratory experiments. In *S. typhle*, the female transfers her eggs to the male's brood pouch where they are nourished and oxygenated for about a month, when the male gives birth to the independent fry.

Mate choice was found to be adaptive. Both sexes benefited from mating with preferred partners in terms of increased offspring viability and got larger, or faster growing, offspring when mating with large fish. Females were also shown to prefer males with thicker brood pouches. Thus, females, the more competitive sex, had multiple preferences. Both male and female choice behaviour was found to be flexible and influenced by available information on partner quality. In addition, males, but not females, copied the mate choice of others.

Both sexes were found to take their own quality in relation to surrounding competitors into account when deciding whether to display to potential partners. Male-male competition influenced both the mate choice of males and, potentially, overruled the mate choice of females. Males did not compete as intensely as females, nor did they use their sexual ornament in this context as females do. Rather, the ornament was used in interactions with females, and males that displayed more received more eggs.

The findings in this thesis emphasise the importance of not viewing mate choice and competition as opposite behaviours, but rather to apply a dynamic approach in mate choice studies, integrating choice and competition in both sexes.

Keywords: Sexual selection, mutual mate choice, mate competition, sex role reversal, parental investment

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This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Sandvik Maria, Rosenqvist Gunilla, Berglund Anders. (2000). Male and female mate choice affects offspring quality in a sex-role-reversed pipefish. *Proceedings of the Royal Society (London) Series B* 267: 2151-2155
- II Widemo Maria S., Widemo Fredrik. Plasticity in pipefish preferences: competitive ability and mate availability modulate mate choice in both sexes. (Submitted)
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- IV Widemo Maria S., Viio Tanja. Mate choice in the more competitive sex: female pipefish prefer males with thicker brood pouches. (Submitted)
- V Berglund Anders, Widemo Maria S., Rosenqvist G. Sex role reversal revisited: choosy females and competitive males in a pipefish. (Manuscript)

To Fredrik and Andreas

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INTRODUCTION

Sexual selection was introduced by Darwin (1859, 1871) as an explanation for extravagant male characters that by necessity must confer a disadvantage to the bearer in the struggle for survival. The evolution of these traits "*depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction*" (Darwin 1871). The existence of these traits was not a problem if the advantage, in terms of increased reproductive success, outweighed the viability cost of the trait. Darwin envisaged two processes that could lead to the evolution of secondary sex characters:

"There are many other structures and instincts which must have been developed through sexual selection- such as the weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals- their courage and pugnacity- their ornaments of many kinds- their organs for producing vocal or instrumental music- and their glands for emitting odours; most of these latter structures serving only to allure or excite the female." (Darwin 1871)

The two processes of sexual selection, competition over mates and mate choice did not in Darwin's view constitute a dichotomy: both sexes could exhibit mate choice and competition, but usually it was males that competed and females that chose a mate. After 1871, male-male competition over mates became accepted as an explanation for how extravagant male traits have evolved, but the topic of female choice was neglected for a long time (Cronin 1991). With the notable exception of the work of Fisher (1915, 1930), it was not until the sixties that these ideas became a topic for study and debate. Then came the first models describing how an allele representing a female preference for a certain type or size of a male trait could spread and how the male trait would grow over evolutionary time until all the males carried a large trait. These early models and later refinements (e.g. Fisher 1915, 1930; O'Donald 1962, 1967; Lande 1980, 1981; Kirkpatrick 1982; Seger 1985), while simplified and perhaps unrealistic in many ways, identified both important assumptions and illuminated problems that are still under debate today. A second type of models are often called indicator models as they assume that the male trait in question is an indicator of the male's quality or viability, (e.g. Williams 1966; Trivers 1972; Emlen 1973; reviewed in Pomiankowski 1988) where a female choosing a viable male will have offspring inheriting his "good" genes. These two classes of models still represent the core ideas of evolution of preferences and traits sexually

selected through mate choice (Andersson 1994). Perhaps unfortunately, these two "schools" of models have been treated as mutually exclusive explanations to the evolution of a trait, while in principle it does not matter whether the selective advantage to the chooser is in terms of increased viability or attractiveness of offspring. Interestingly, much of the debate in the past and today is about whether "Fisherian" or "good genes"- mechanisms is most prevalent in nature. However, the simplest scenario for the evolution of preferences is when the chooser benefits directly from its preference, in terms of access to resources that can be utilised for current or future reproduction (e.g. Heywood 1989; Hoelzer 1989). Considering the vast number of studies of mate choice, it is surprising how few have experimentally investigated direct fitness effects on the offspring resulting from mate choice. Moreover, conclusions regarding benefits gained are ambiguous (references in Møller and Alatalo 1999) and the interaction between mate choice and competition is poorly understood (Qvarnström and Forsgren 1998). Most evidence of adaptive mate choice stems from positive correlations between male popularity among females and some male trait (Andersson 1994).

Parental Investment

An important concept when studying mate choice is parental investment, i.e. the extent to which parental care of offspring increases offspring fitness, but also reduces the parent's future reproductive value. Parental investment is an additional way to ensure the spread of one's genes, besides obtaining as many matings as possible, or securing matings with the best available partner. Parental care, i.e. assisting the offspring during the early stages of its life, should evolve when the benefit of investment in existing young exceeds that of obtaining a new mating partner. In mammals, it is usually females that care, in birds, biparental care is the prevailing mode, and in fish, paternal care is most common among those ca 30 % of fish families containing species which care. The reasons for the prevailing male care in fish are probably twofold. Fish, in contrast to birds and mammals, have indeterminate growth. Females may therefore have a lot to gain from not caring for young but instead allocate resources to growth and in turn produce more eggs in the future, as body size correlates positively with egg production. There is thus a selection pressure on females to allocate resources to growth instead of care. As sperm is cheaper to produce than eggs, males are not energetically constrained in gamete production like

females. Furthermore, males often do not reduce their attractiveness to females when taking on the parental burden: typically, male care consists of nest building and egg guarding, and caring for one hundred or one thousand eggs may not differ much in cost to the male. Actually, to a female, a male who is already guarding eggs may be even more attractive than a male without eggs, as her own eggs experience lower risk of predation in a nest containing other eggs, e.g. through the dilution effect. (Perrone and Zaret 1979; references in Clutton-Brock and Godfray 1991 and in Sargent 1997). Thus, male care can be a sexually selected trait in fish. Usually males care for the eggs while females invest directly in the egg, a pattern potentially promoting the evolution of mate choice behaviours and mate competition in both sexes.

Sex Roles

"In various classes of animals a few exceptional cases occur, in which the female in stead of the male has acquired well pronounced sexually secondary characters, such as brighter colours, greater size, strength or pugnacity." (Darwin 1871).

The most common sex role pattern in nature is males competing over access to females and females being selective in choice of mate. Indeed, this pattern is so common that it has defined the sex roles: sex roles are conventional when males constitute the more intensely competing sex (Clutton-Brock and Vincent 1991). The main reason for this is that in most species, males have the higher potential reproductive rate (PRR), with the consequence that the operational sex ratio (OSR: the instantaneous proportion of males willing to mate to females willing to mate) becomes biased towards an excess of males (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). The male surplus causes competition among the males, and male reproductive success is hence determined mainly by the number of copulations performed. Female reproductive success, on the other hand, mainly depends on access to resources required to produce offspring and on the male's quality (genetic, or, when applicable, his ability to provide resources).

Sex role reversal may result if males for some reason have a parental investment so heavy that it lowers the male PRR to under that of females. Then, males limit female reproductive success, and females may compete over males. Sex role reversal is not a common phenomenon but sex role reversed species serve as especially good candidates for testing the generality of sexual selection models (Williams 1966).

Mate Choice

Although extensively studied, defining "mate choice" is not straightforward. Wiley and Poston (1996) suggested "any behaviour reducing the number of potential mates" as a definition. They further subdivided the concept into direct and indirect mate choice, where direct mate choice results from a match between a female's preferences and the attributes of a male. In contrast, indirect mate choice can be defined as the various ways females may set the stage for or encourage male-male competition, except for directly choosing particular males. Like direct mate choice, indirect mate choice may result in non-random mating and a genetic correlation between preference and ornament. The distinction between direct and indirect mate choice certainly broadens the perspective on sexual selection, demonstrating how competition for mates in one sex is inseparable from the conditions for competition set by the other sex. Indirect mate choice may lead to the evolution of the same kinds of traits as may evolve through the much more studied direct mate choice. Although being a useful tool to grasp how competition for mates and choice of mate are intimately linked, a more universally used definition, closer to the direct type of mate choice, is applied in this thesis.

"It may be suggested that in some cases a double process of selection has been carried on; the males having selected the more attractive females, and the latter the more attractive males. This process however, though it might lead to the modification of both sexes, would not make the one sex different from the other, unless indeed their taste for the beautiful differed; but this is a supposition too improbable in the case of any animal, excepting man, to be worth considering." Darwin (1871).

Mating preferences may be viewed as being composed of an individual's preference function(s), sampling tactic and choosiness (Widemo and Sæther 1999). Here, the preference function describes the strength of response to any size of stimuli and choosiness reflects the investment in mate choice, e.g. in terms of time and energy. Preference functions may be broken down further into "innate predispositions" and "reference templates". Templates may be continuously updated during the mating season. The strength of mating preferences may, at least in part, be influenced by competitive abilities in species where individuals of the same sex compete over attractive partners. Here, individuals of low competitive ability may benefit from being less choosy, at least when population density is high, if they are unlikely to succeed in mating with an attractive partner without being disrupted. In

species with mutual mate choice, things become even more complex as individuals also must take their own attractiveness into account when predicting the outcome of mate choice. Similar to the case of preference functions, continuously updated information about the abilities and attractiveness of competitors present may act as a reference template for assessing own competitive ability and attractiveness to the opposite sex.

Mutual Mate Choice

"In the converse and much rarer case of the males selecting particular females, it is plain that those which were the most vigorous and had conquered others, would have the freest choice; and it is almost certain that they would select vigorous as well as attractive females. Such pairs would have an advantage in rearing offspring, more especially if the male had the power to defend the female during the pairing-season, as occurs with some of the higher animals, or aided in providing for the young. The same principles would apply if both sexes mutually preferred and selected certain individuals of the opposite sex; supposing that they selected not only the more attractive, but likewise the more vigorous individuals." (Darwin 1871)

Although Darwin (1871) raised the idea of mutual mate preferences, the subject has received very little attention until recently. Usually, mate choice is considered a process where members of one sex (females) are choosing while members of the other sex are competing to be chosen. Parker (1983) pointed out that both females' and males' parental relative investment and quality as mates should be considered when making predictions regarding a solution of the sexual conflict over mating, and which sex should be more choosy. This view has been further developed in a series of models (Kirkpatrick, Price and Arnold 1990; Real 1991; Noe and Hammerstein 1994; Deutsch and Reynolds 1995; Johnstone, Reynolds and Deutsch 1996; Johnstone 1997; Bergstrom and Real 2000). Empirical studies where mutual preferences are simultaneously investigated are scarce (Côte and Hunte 1989; Jones and Hunter 1993; Kraak and Bakker 1998) as are empirical studies of the relative impact on individual fitness from female and male choice (Sandvik, Rosenqvist and Berglund 2000; Kolm 2002). One feature distinguishing the outcome of mutual choice models from single-chooser models is their prediction of assortative mating (Bergstrom and Real 2000). Mutual choice models identify and incorporate a sexual conflict: in single sex choice models the conflict of interest over matings lies between members of the same sex (e.g. over access to partners) while in mutual choice models, when one introduces

individual preferences, a conflict of interest arises between sexes as well (Bergstrom and Real 2000).

Plasticity in Mate Choice Behaviours

As a tool for identifying various mechanisms influencing decision making in mate choice, I view mate choice as a dynamic, mutual process, influenced by several factors that can be largely grouped as "intrinsic" and "extrinsic". The intrinsic factors are features of the choosing individual, where some are under control of the individual and can be adjusted according to circumstances, while others are fixed. Decision making in mate choice behaviours may be influenced by both environmental, social and motivational factors. Every individual has a given genetic setup which includes its inherited preferences as well as its ability to discriminate between stimuli, which may be constrained, for example through constraints in the sensory system or due to a limited memory capacity. Further, the resource status, condition or own quality of the individual will influence both an individual's motivation and its possibilities to be choosy. The social factors influencing mate choice can further be divided into within-sex competition and opposite sex quality distribution and level of choosiness of that sex.

Animals need not necessarily evaluate the quality of prospective partners themselves, but may obtain information from observing other individuals' decisions in mate choice. Mate choice copying has been suggested to be a tactic to reduce mate assessment costs and may influence individual mating decisions (e.g. Gibson, Bradbury and Vehrencamp 1991; Dugatkin 1992; Dugatkin and Godin 1993; but see also Brooks 1996; Lafleur, Lozano and Sclafani 1997), and may have consequences for the evolution of male traits as well as for female fitness (Losey et al. 1986; Wade and Pruett-Jones 1990; Gibson and Hoglund 1992; Kirkpatrick and Dugatkin 1994) in species with female choice.

Model Species and Methods

The deep snouted pipefish (*Syngnathus typhle*) inhabits meadows of eelgrass (*Zostera marina*) along the European coast. It has a life span of 2-3 years. In *S. typhle*, and a few other pipefish species, sex roles are reversed: females ready to mate are in excess, and they compete for males (Berglund, Rosenqvist and Svensson 1989). After a courtship dance, the female transfers her eggs to the male's brood pouch, where they

are fertilised. The male broods the offspring in a brood pouch formed by two skin folds along the tail which merge during pregnancy and a placenta-like structure develops. Males are pregnant for about one month and give birth to free swimming juveniles. Offspring are provided with energy and oxygen, and the long male pregnancy lowers the potential reproductive rate of males below that of females (Berglund et al. 1989; Berglund and Rosenqvist 1990). Temperature may modify but not reverse this sex difference (Ahnesjö 1995). Since females are faster reproducers than males the operational sex ratio becomes skewed towards females (Berglund and Rosenqvist 1993; Vincent, Ahnesjö and Berglund 1994).

Choosiness in males is a plastic trait that can be modified by predation threat, decreasing or disappearing in the presence of a predator (Berglund 1993; Fuller and Berglund 1996). The operational sex ratio also affects choosiness, and males are less discriminating when the sex ratio is experimentally skewed towards males (Berglund 1994). Furthermore, males are less likely to reject females under low encounter rates (Berglund 1995). In nature male *S. typhle* actively choose among and reject females, whereas females display vigorously, often in groups in a lek-like fashion (Vincent, Ahnesjö and Berglund 1994; Vincent, Berglund and Ahnesjö 1995).

Female pipefish compete for males, and males are choosy (Berglund 1991; Rosenqvist 1990). In females, both number of eggs and egg size correlate positively with female body size. Male body size is positively correlated with number of offspring, size of offspring and energy provided per offspring during brooding (Berglund, Rosenqvist and Svensson 1986). Females display a sexual signal, which they can activate at will, a zigzag pattern along the side of their body. The signal is used both in female-female encounters and as a way of courting the male. The surplus of sexually receptive females allows males to be choosy when mating. When given a choice, males prefer larger over small females, and more ornamented and dominant females over less so. Both males and females benefit from mating with a large partner: on average, larger females produce larger eggs, which in turn give rise to larger offspring. Larger males inevitably have larger pouches and can receive relatively more of a female's eggs, compared to a smaller male. In addition, larger males can invest more in each individual embryo (reviewed in Berglund and Rosenqvist, in press).

All papers in this thesis are based on experiments performed at Kristineberg Marine Research Station, Fiskebäckskil. The fish were collected by trawling with a

small trawl (ca 1x1m opening, mesh size 4 mm) pulled by boat over eelgrass meadows. Catching usually begun before, or at the very beginning of the mating season, before males had received eggs. The animals were brought into the laboratory and the sexes kept in separate tanks until experiment started. They were fed live *Artemia* mixed with frozen mysids *ad libitum*, and the occasional catch of small crustaceans when this could be obtained. All fish were released back into the wild after the experiments, when possible.

The aims of this thesis

The aims of this thesis can largely be summarised as exploring various factors or mechanisms that influence mate choice. The deep snouted pipefish is a well studied species, which means that much basic information (like, for example, the costs of reproduction to both sexes, as well as an estimate of quality of both sexes) necessary to understand complex mate choice is already known, and we can now focus on disentangling more subtle mechanisms and the interactions between these. I wanted to explore mutual choice in *S. typhle*, and have focussed on female choice, as male choice is firmly documented and explored. Particularly, I wanted to find out how choosy females are compared to males, and whether female choice is complex in the sense of being adjustable to circumstances and based on several male traits.

Further, I wanted to study the benefits of mate choice to the choosing individual, and whether the benefits differ depending on which sex is choosing. Finally, the outcome of choice, i.e., who gets to mate with whom, is discussed, and, in relation to that, male-male competition and male ornamentation is explored. Thus, I focus on incorporating the previously largely overlooked impact from choice in the sex predicted to be less choosy, and competition in the sex predicted to be less competitive, on the observed mating pattern.

RESULTS AND DISCUSSION.

Mate Choice is Mutual and Adaptive

Male choice in the deep snouted pipefish has been documented on a number of occasions (see introduction). In paper I, we tested the effect of male and female choice on offspring fitness correlates by setting up mate choice trials where males or females could choose between two potential mates. Choosing individuals were mated with either their preferred or non-preferred partner. Two fitness correlates were measured in the resulting offspring: growth during the first week after birth, and the ability to escape a common predator (a small sea anemone, *Sagartiogeton viduatus*).

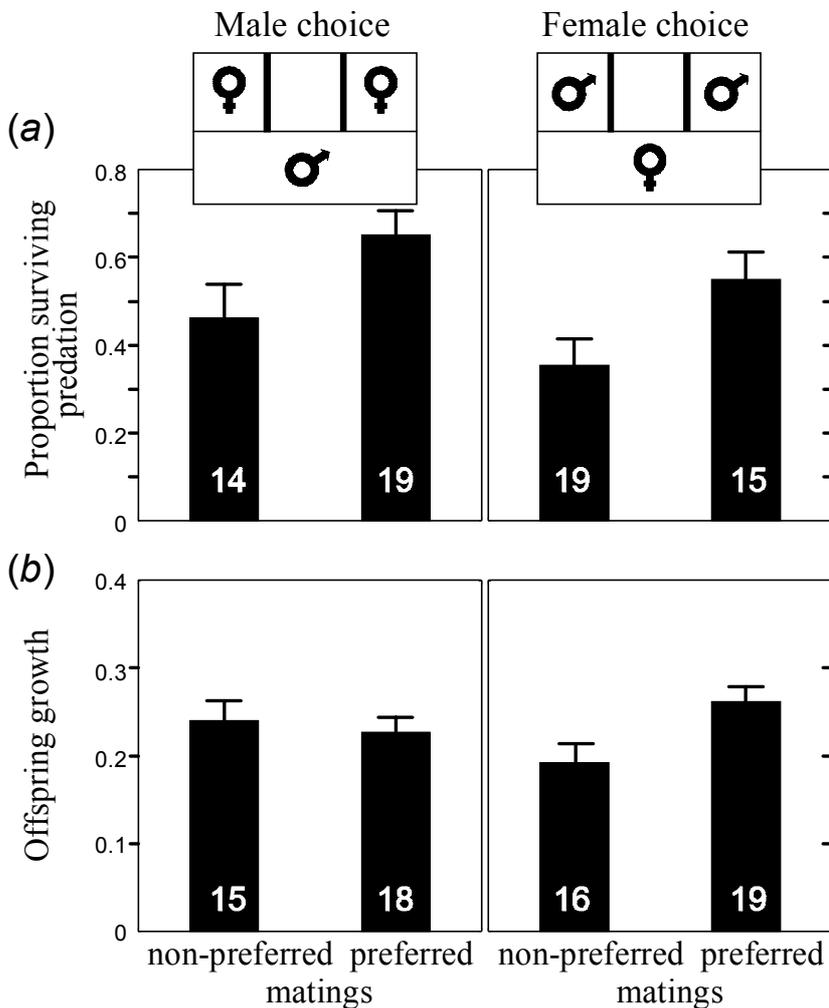


Figure 1. The effects of mate choice on offspring. Data were pooled across years and total sample sizes are shown on the columns. Bars are standard errors. (a) Offspring performance in the survival experiment, corrected for the effect of father's length. ANCOVA: sex $F_{1,61} = 1.72$, $p = 0.19$; preference $F_{1,61} = 5.74$, $p = 0.019$; sex*preference $F_{1,61} = 0.005$, $p = 0.9$; covariate: fathers length $F_{1,61} = 18.57$, $p < 0.001$. (b) Differences in growth between broods resulting from matings with preferred and non-preferred partners. See Table 2 for statistical analyses.

We found that parents allowed to mate with the partner of their choice produced offspring better at avoiding predation, both in male and female choice trials (Figure 1), as compared to parents mated to non-preferred mates. Results were similar also after correcting for the effect of father's length on offspring performance (Table 1).

Table 1. Results from multiple regressions with offspring birth length, growth and survival (proportion offspring escaping anemone predation) as dependent variables. (Regression models: birth length: $F_{3, 64} = 9.37, p = 0.00003$; growth: $F_{5, 61} = 5.61, p = 0.0003$; escape from anemones: $F_{4, 56} = 6.15, p = 0.0004$).

Independent variable	β , birth length	β , growth	β , survival
father's length	0.05	0.14	0.37*
Mother's length	0.40***	0.10	0.19
brood pouch fullness ¹	-0.02	-0.048	-0.17
fry birth length		-0.29*	0.08
Temperature ²		0.56***	

¹ proportion of brood pouch filled with eggs after mating.

² average water temperature during the growth period (day 0-7) of each brood.

β , partial correlation coefficient.

*: $p < 0.05$; ***: $p < 0.001$

Table 2. Results from analyses of variance with offspring growth from day 0 to day 7 as dependent variable.

	Factor	d.f. effect	d.f. error	F	P
<i>(a) both sexes</i>	Sex	1	63	0.27	0.60
	Preference	1	63	2.22	0.14
	Year	1	63	26.30	0.000003
	Sex*Preference	1	63	5.56	0.022
<i>(b) males only</i>	Preference	1	29	0.13	0.73
	Year	1	29	15.15	0.0005
	Preference*year	1	29	0.14	0.71
<i>Females only</i>	Preference	1	31	4.75	0.037
	Year	1	31	10.62	0.0027
	Preference*year	1	31	0.16	0.69

(a) Sex, preference and year were entered as factors in the three-way ANOVA model. Non-significant interactions were removed from the model (backward selection).

(b) Since there was a significant interaction between sex and preference in a, the sexes were analysed separately in two-way ANOVAs.

Female Choice and Multiple Preferences

In the same experiment, females, but not males, preferred mates conferring a higher offspring growth rate (Figure 1b, Table 2). Female length was positively correlated with offspring birth length, but not with offspring growth or survival (Table 1). Larger males produced better survivors but not larger young or faster growing young (Table 1).

In an early experiment on this species, Berglund et al. (1986) found that one trait females considered when choosing a mate was the males' length, preferring larger over smaller males. In paper **I**, we did not detect such a preference, but the experiment was not designed to test it as the two males in each replicate were not selected to differ in length. Nevertheless, female choice had an effect on offspring performance, so females must have evaluated males by some other cue(s). One potential cue in female choice is the male brood pouch. During the courtship dance some males repeatedly shake their brood pouch in front of the female (pers. obs) as if demonstrating it to the female. In paper **IV**, we tested whether females preferred males with thicker pouches. One female chose between two males, differing "only" in brood pouch thickness. Females were observed more often in front of the male with the thicker pouch (t-test for dependent samples, $t = 2.3$, $N = 30$, $P = 0.03$; Figure 2).

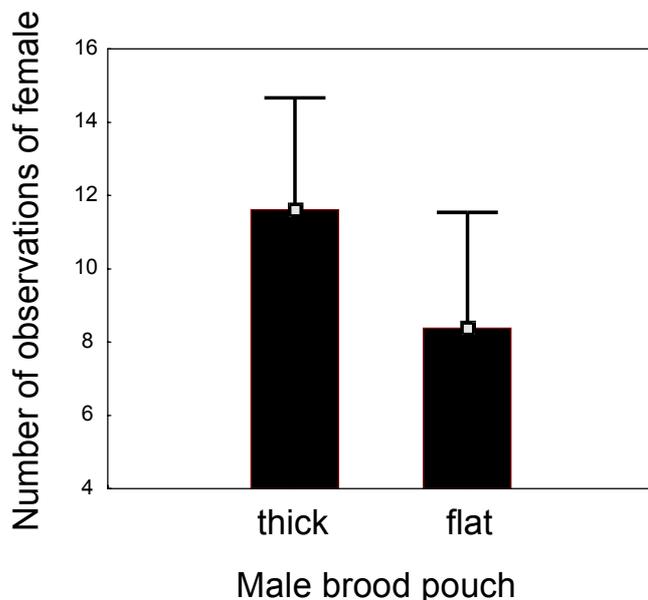


Figure 2. In the mate choice experiment, females were observed more often in front of the male with the thicker pouch than in front of the male with the flatter pouch. Points are means and whiskers are SE.

It has been argued in studies of male preferences in species with conventional sex roles, that the male preference found has evolved simply as a correlated response to selection on female preferences (e.g. Lande and Arnold 1985; Hill 1993). One way to exclude this explanation would be to study a trait found in only one sex. In the present study, we investigated a trait found exclusively in males; thus the preference is probably unique to females and has arisen in females.

In paper V, female choice was investigated further, and again, females were found to be choosy. This time, males were matched for both size and pouch thickness within each replicate, but still, females made a choice according to our criterion (more than 70% of the time spent before one particular male) in 59 out of 73 trials (Table 3). Thus, females prefer large males (Berglund et al. 1986), males with thicker brood pouches (paper IV), and the results from paper I and V suggest that at least one more cue is involved in female choice. Thus, females, the more competitive and presumed "least-choosy" sex in this species, have multiple preferences.

Table 3. A comparison between the male (Berglund and Rosenqvist 1991) and the female choice (paper V) experiments. (The focal fish is the choosing fish in front; the object fish are the two chosen same-sex fish as depicted in Figure 3). Both experiments had two parts: first a fish was allowed to choose between two enclosed partners, then partitionings were removed and the three were allowed to interact.

Variable	Male choice exp.: no. of replicates where occurring		Female choice exp.: no. of replicates where occurring		χ^2	P
	Yes	No	Yes	No		
mate choice by focal fish ¹	16	14	59	14	4.81	0.03
dances by focal fish ¹	22	8	1	72	63.5	<0.001
display by focal fish ¹	27	3	3	70	76	<0.001
object ornament display ²	30	0	12	56	58	<0.001
object intrasexual competition ²	30	0	30	38	27.4	<0.001
the object fish chosen as enclosed also successful when free	19	7	21	16	1.75	0.2
Intrasexual competition between object fish in replicates where one of them were chosen as enclosed but later unsuccessful when free	7	0	9	7	-	0.057 (Fishers exact two- tailed P)

¹when chooser and mates were enclosed

²when all fish were free to interact.

The Relative Choosiness of the Two Sexes

In paper **I**, the experiment covered a total of 358 mate choice replicates. In the 171 male choice trials, 90 males performed a choice while 81 did not, and the corresponding numbers in the 187 female choice trials were 110 and 77. Here, choice was defined as being observed in front of one particular mate more than 60% of the observations (the design included three compartments of which two contained mates; Figure 1). Here, females performed mate choice as often as males ($X^2= 1.39$, $df= 1$, $P= 0.24$). In the female choice experiment described in paper **V**, females exercised mate choice according to our criterion (more than 70% of the time spent before one particular male; Figure 3) in 59 out of 73 replicates. Compared to the corresponding male choice experiment (Berglund and Rosenqvist 2001), this is a higher proportion of choosing individuals, judged by the same 70% criterion: only 16 out of 30 males performed such a choice ($X^2= 4.81$, $P= 0.03$).

The experimental design in paper **II** was different: after capture, the fish were held in single-sex tanks for at least 12 days. Then they were released into aquaria in groups of three of the same sex. From each of these aquaria, a group could see into a different aquarium containing six members of the opposite sex. The six were either all large (Large treatment) or all small (Small treatment). The three focal fish differed in length, and each individual was classified as small, medium or large within its group. After 48 hours, the focal fish were moved into separate aquaria, provided with a small partner, and sexual behaviours were observed for five hours.

We found an effect of sex on whether or not the focal fish displayed during the first hour of observation, when comparing the Large and the Small treatment. Interestingly, while in general being more eager to court, females were as negative as males when presented with a partner of lower quality than expected.

Table 4. Partial associations between sex, treatment, relative size and whether focal fish displayed to partner fish during the 1st hour for treatments Small and Large.

Design variable	d.f.	χ^2	p
Sex	1	5.38	0.020*
Treatment ‘Small’ vs. ‘Large’	1	24.44	0.000001***
Relative Size	2	3.89	0.142
Sex*Treatment	1	0.58	0.444
Sex*Relative Size	2	2.32	0.127
Treatment*Relative Size	2	9.22	0.01*

*Design variables in final model: Treatment+Treatment*Relative Size+ Sex*
Fit between final model and data: $\chi^2= 3.71$, $df= 5$, $p= 0.59$

Thus, in the laboratory, females appear to perform mate choice as least as often as males in the absence of competition from other females.

Plasticity in Choice and the Effects of Information

In paper II and V, the influence from the chooser's own quality on its mating decision was tested. Potentially, an individual's own size, as well as its size in relation to conspecifics, may be important to consider when investing in mate choice. In paper V, we found that more small than large females performed a choice ($X^2= 5.17$, $P= 0.02$; Figure 3). Small males did not display any ornament and ornament use in males seemed to be a signal to females only.

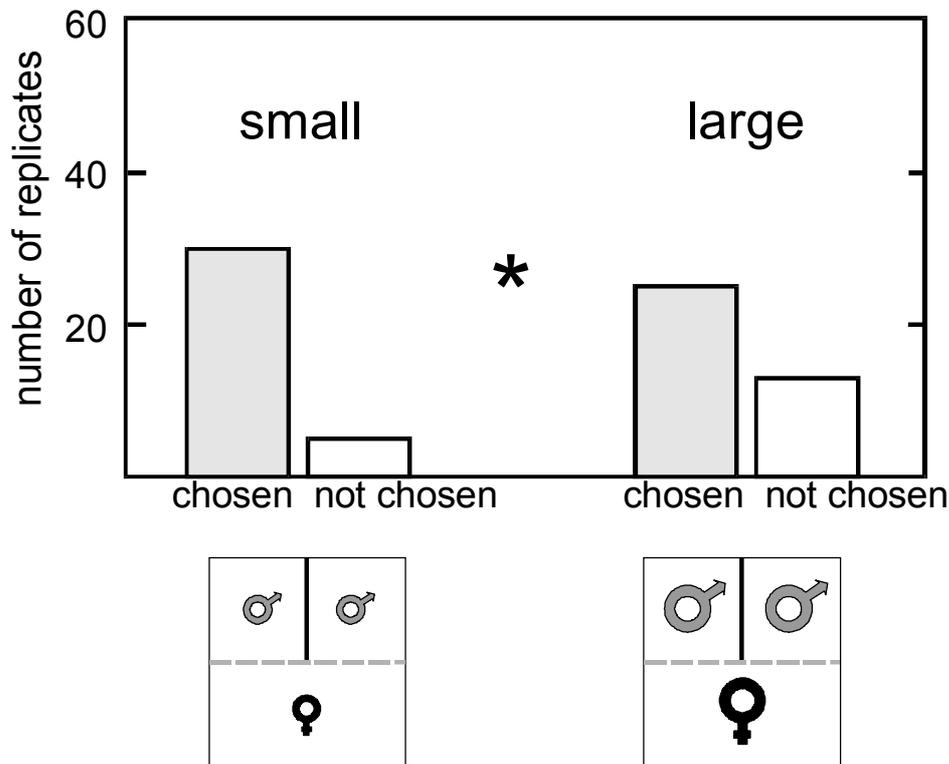


Figure 3. Number of choices and rejections of enclosed males. *:P= 0.02

In paper II, both male and female focal fish' size class influenced both the proportion of treatments where display occurred (Table 4; Figure 4) and the time from experiment start to the first display (Table 5).

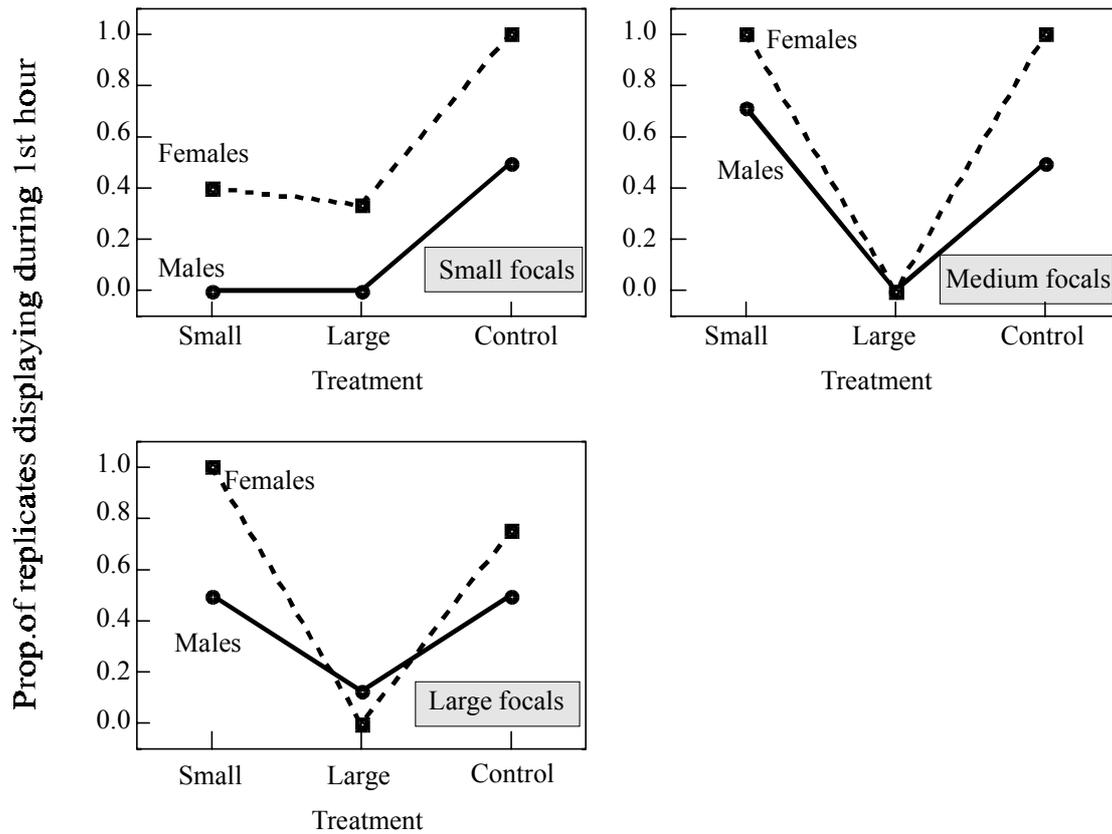


Figure 4. Proportion of replicates where focal fish displayed during the first hour of observations, split by treatment and relative size of the focal fish within replicates.

Small fish appeared to be subdued by their conspecifics and did not display early in the observed time window, but the effect disappeared as the experiment progressed.

Table 5. Effects of sex, treatment and relative size on time to first display among displaying fish in treatments Small and Large during the first three hours of the experiment.

Factor	d.f.	LL	χ^2	p
Sex	1	--74.06	5.29	0.021*
Treatment, 'Small' vs. 'Large'	1	-74.60	6.37	0.011*
Relative Size	2	--71.89	0.94	0.623
Sex*Treatment	1	-71.94	1.06	0.303
Sex*Relative Size	2	-71.59	0.35	0.841
Treatment*Relative Size	2	-76.19	9.54	0.008**
Sex*Treatment*Relative Size	2	-72.16	1.49	0.475

In paper II, we also tested whether the information on mate quality influenced decision making. Both males and females were found to be influenced in their decision of whether or not to mate with a given partner, by what level of quality of partners they had previously observed. Fish which had seen small individuals of the opposite sex were quicker to engage in courtship compared to fish that had seen large stimulus fish and then got a small partner (Figure 4; Table 4 and 5).

Accessing Information by Copying the Mate Choice of Others

I tested whether males and females used information from other individuals' mate choice in their own choice of mate (Paper III). A focal individual was allowed to choose between two "object" fish (matched for traits known to influence mate choice), one of which was seemingly preferred by others (Figure 5). The illusion was obtained by adding "model" fish that on one side of the aquarium could see and display to the object fish and the other could not.

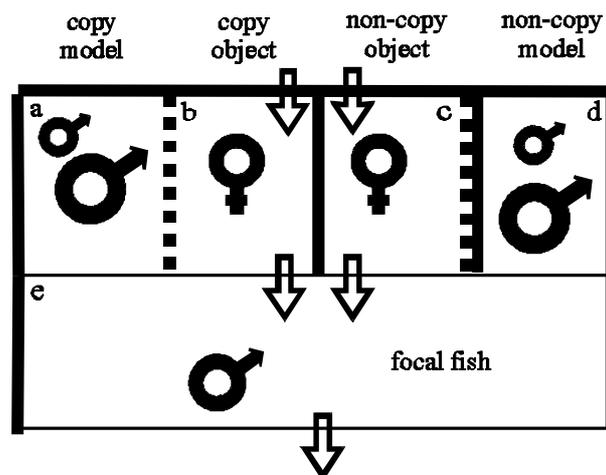


Figure 5. Mate choice aquarium seen from above. Thin lines are transparent walls, dotted lines are one-way mirrors and thicker lines are opaque walls. Arrows indicate water in- and outlet, allowing the focal fish to use potential olfactory cues in addition to visual cues. Model fish were placed in compartment a and d, object fish in b and c, and focal fish in compartment e.

Focal males displayed significantly more often in the 'copy' half of the aquarium: these displays were exclusively directed to the object females, and significantly more often to the 'copy' object female than the 'non-copy' object female (Figure 6; Table 6).

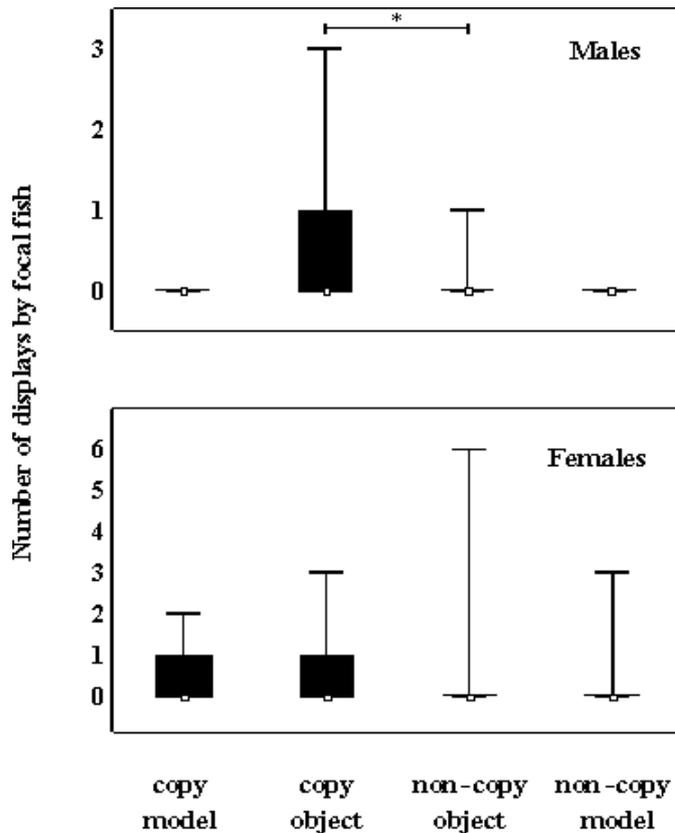


Figure 6. Focal fish sexual displays in front of model and object fish. Points are medians, boxes are 25-75 percentiles and whiskers are min-max. *: $P < 0.05$; see text and Table 6 for statistics.

Females, on the other hand, showed no preference for the 'copy' object male over the 'non-copy' object male in terms of position or display (Figure 6) in the 'copy' vs. 'non-copy' side of the aquarium (Wilcoxon matched pairs test, $N=22$, $Z=0.49$, $P=0.62$), or in front of the 'copy' vs. 'non-copy' object male (Table 6, Figure 6).

Table 6. Generalized linear mixed model assuming a Poisson distribution of errors. Replicate (sex) was entered as random effect and sex and treatment as fixed effects in the model.

Random effect	Focal fish position in front of object				Focal fish display in front of object			
	var \pm SE		Z		var \pm SE		Z	
Replicate (sex)	0.00		-		1.13 \pm 0.41		2.71	
Fixed effects	d. f. effect	d. f. error	F	p	d. f. effect	d. f. error	F	P
Treatment	1	43	1.61	0.211	1	43	3.83	0.056
Sex	1	43	0.00	0.976	1	43	2.99	0.091
Treatment*Sex	1	43	0.15	0.701	1	43	8.24	0.006

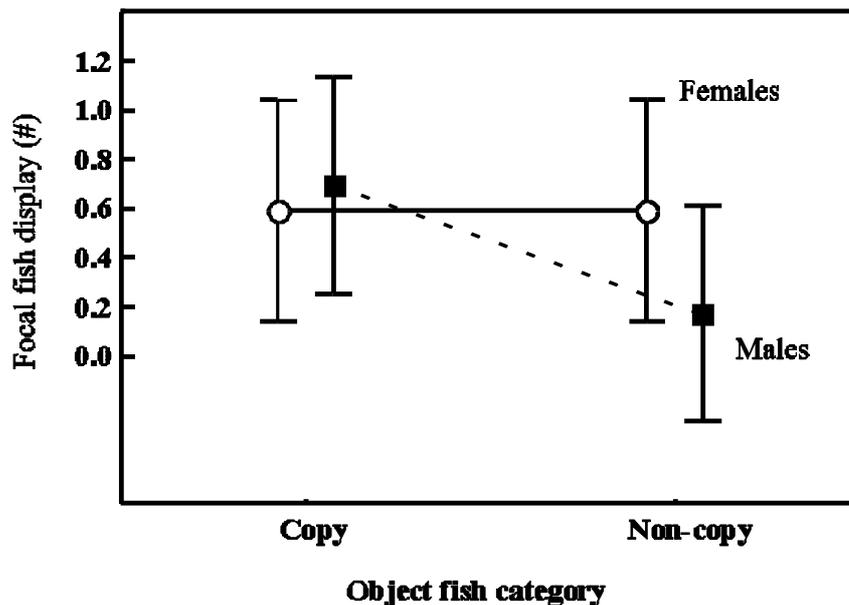


Figure 7. Males but not females display more in front of the 'copy' object fish. Points are means, vertical bars denote 0.95 confidence intervals. See Table 6 for statistics.

Competition Over Mates

In this pipefish, females compete intensely over mates (see references in introduction), a result confirmed in paper V, where females were found to compete significantly more often than males under the same circumstances (Table 3). Females compete by chasing each other and displaying their temporal ornament towards each other, whereas males were found to display towards females only and never during male-male competition. The reluctance to display in small fish of both sexes in paper II, was ascribed to the impact of competition for larger members of the same sex.

The Outcome of Mate Choice: Who Mates With Whom?

All the mechanisms described above thus influence, under certain circumstances and in one or both sexes the decision making process in mate choice. But the most important question, from a sexual selection point of view, remains: who mates with whom? The results presented here can be seen as an attempt to identify factors that must be taken into account when predicting mating patterns and the resulting selection pressures. In paper V, we found that female choice not always translated into female mating success, but was probably overridden by male choice or male-male

competition or both (Table 3). In paper **II**, there was no direct association between sex, treatment or relative size and whether the focal fish mated or not (all partial $\chi^2 < 0.96$, all $p > 0.14$), but there was a highly significant association between display and matings obtained, when the binary factor ‘Display in 5 hrs?’ was added to the same models. Although suggestive, this study only begins to investigate the relative importance of mate choice and competition in both sexes to the actual mating pattern.

A note of caution is appropriate, as all these results stem from studies in the laboratory. In order to disentangle the mechanisms in mate choice, manipulations must be done, preferably in controlled environments. However, this inevitably narrows the possibilities for interpretations regarding the ultimate goal of this research: what goes on in nature. The next step should thus be to see if the results from this thesis are valid also under natural conditions. This work should at least give some indications of what observations to expect in a population of pipefish in an eelgrass meadow on the Swedish west coast.

CONCLUSIONS

To summarise, the results presented in this thesis demonstrate that male and female choice was adaptive. Mate choice was a plastic or adjustable behaviour in both sexes, although it did not always vary in the same way in both sexes. Factors that influenced mate choice were the chooser's own quality and competitive ability in relation to same-sex competitors, the perceived quality of available mates and, in males, even the mate choice of other males. Male ornamentation seemed to serve as an inter-sexual signal, in contrast to the female ornament, which was used in both inter- and intra-sexual encounters. Mutual mate choice prevailed, as did mutual mating competition. Due to the above mentioned factors, the mate choice of an individual did not always result in mating, illustrating the need to take both sexes' behaviours during competition and choice into account to understand mate choice and predict the evolution of sexually selected traits. Also, this thesis demonstrates the danger of focussing on one single trait or preference, as valuable information then is lost: e.g., in paper **I**, we did not detect any preference for any measured trait, nevertheless, strong preferences and an effect on offspring quality was found.

In light of the above, the whole sex role concept may be worth reconsidering. It is not wrong in itself, but the terminology and the way it is commonly used tends to

contrast choice and competition for mate as opposite, mutually exclusive, entities. Mating is an individual decision, and individuals differ in quality, in attractiveness and in competitive ability. What determines the optimal degree of choosiness and competition for an individual is not only a question of the sex of that individual, but rather the total investment in reproduction that it can make, and the relative costs and benefits associated with the respective behaviours. In "investment in reproduction", investment in gametes and the basic sex difference is included, but it constitutes only a part. Both choosiness and competitiveness of an individual is influenced by the individual's own quality, particularly in relation to others of the same sex, as well as the distribution of quality of the opposite sex. However, the relationship between competition and choosiness within an individual is not straightforward. Both competitiveness and choosiness depends on the resources invested in each and is limited by the total amount of resources an individual can obtain. Still, the two do not necessarily trade off, so that if an individual invests more in the one, it must reduce the other. For example, an individual increasing its investment in competition will often be perceived by the opposite sex as more attractive, which means that this individual can afford to be more choosy without investing more in mate choice. Hence, the term "the least choosy sex" (generally used for males, and we have used it for *S. typhle* females), seems inappropriate considering the data presented here.

Are pipefish uniquely mutual, complex and plastic in mate choice? I believe not. For example, more and more research projects have reported that males do not mate indiscriminately, and that females compete with each other. Particularly in species with relatively equal investment in offspring from both sexes, mutual choice is expected, as quality variation within each sex and perturbations in their relative investment come to play a larger role. Further, investment in reproduction may cover more than parental investment, and even in species where one sex does not care for young, investment in competition may be high and it may pay off to allocate resources in relation to the quality of the opposite sex. Thus, I believe that mutual mate choice and competition will be reported from many more species.

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Thank you, Anders Berglund, for taking me on as a student back in the last millennium. I have very much appreciated having you as a supervisor. You have been supportive, enthusiastic and inspiring, and I have learnt a lot from you. I have also appreciated that you have let me pursue my own ideas and projects, although you should perhaps have stopped me before I blew that third field season on that catastrophe-experiment that never worked...well, looks like I managed to put together a thesis without that data after all. Thank you also for much fun and laughter during long gourmet dinners with good and plenty wine and lively nonsense discussions.

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P.S. Does anyone know if the magpie's tail is sexually or naturally selected????

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