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Sex role reversal in a pipefish: female ornaments as amplifying handicaps

Anders Berglund

Berglund, A., Uppsala University, Deptartment of Animal Ecology, Norbyvägen 18d, SE-752 36 Uppsala, Sweden

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The reasons for sex role reversal in the pipefish *Syngnathus typhle* are reviewed. In this species, females compete for males, which are choosier than females. Before mating, females display a sexual ornament, a cross-wise striped pattern along their body sides. This ornament is here shown to be an amplifier that facilitates for males to tell females of different sizes apart (males prefer larger females). When students were asked to compare bar sizes, where bars differed in "ornamentation", accuracy in estimating size was highest with "heavy ornamented" as compared with "intermediate" or "not ornamented" bars. Moreover, bar size was more accurately judged with crosswise than with lengthwise striped bars, explaining why stripes run cross- rather than lengthwise in females. The ornament is probably costly (it reduces crypsis and may be socially provocative), and it is also attractive to males. Thus, the ornament is best described as an amplifying handicap.

1. Introduction

In this paper, I will review the reasons to why females in the pipefish *Syngnathus typhle*, rather than males, are ornamented, i.e., why *S. typhle* is sex role reversed. I will concentrate on the function of the female ornament for mate choice and its relation to body size, the latter an important determinator of female reproductive success (Berglund *et al.* 1986a). Moreover, I will present new data on a special function of this ornament, which is that of an amplifier facilitating for males to tell females of different size apart.

2. Pipefish paternal care

In all species within the Syngnathidae (pipefishes and seahorses), the male cares for the offspring either by attaching the female's eggs directly to his belly or by rearing them in a brood pouch (as in *S. typhle*). In promiscuous species with a brood pouch (such as *S. typhle*), a male can receive eggs from several females (Berglund *et al.* 1988), and a female may give eggs to several males. Within the brood pouch the offspring are provided with oxygen and nutrients via a placenta-like structure (Haresign & Schumway 1981, Berglund *et al.*

1986b, H. D. Masonjones, pers. comm.). Pregnancy, which lasts for three to eight weeks depending on water temperature, is terminated by live birth. After that the offspring lead completely independent lives. All pipefishes and seahorses are slow moving cryptic predators on small motile prey.

3. Sex role reversal in pipefish

Sexual selection (i.e., differences in reproductive success, caused by competition over mates; Andersson 1994) usually operates stronger in males than in females. As a result, males usually possess more elaborate secondary sexual characters than do females (Darwin 1871). The main reason for this is that in most species males can reproduce faster than females when the number of mates is not limiting. Consequently, this higher potential reproductive rate in males enables them to remate faster than females, and biases the operational sex ratio towards a male excess (Clutton-Brock & Vincent 1991, Clutton-Brock & Parker 1992, Kvarnemo & Ahnesjö 1996, Parker & Simmons 1996). The operational sex ratio is the proportion of males willing to mate to females willing to mate at a given time and place. The resource in short supply, namely females, then causes competition among the males, and traits increasing competitive success, so-called sexually selected traits, may evolve in males. Hence, mainly the number of copulations performed determines male reproductive success. 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). Females hence may have good reasons to be choosy in selecting a partner.

In a few species sex roles are reversed: females ready to mate are in excess, and hence they compete for the resource now in short supply, the males. Such unusual operational sex ratios can be caused by higher potential reproductive rates in females than in males, that is, when females are faster reproducers than males. This was the case in *Syngnathus typhle*, where the form and extent of male parental care decreased the relative potential reproductive rates of males below that of females (Berglund *et al.* 1989). This in turn influenced the operational sex ratio so that willing females were in excess, which in its turn caused males to be choosier and females more competitive. Consequently, females should be under stronger pressure from sexual selection than males, and we expect females rather than males to evolve behaviours and structures that aid them in mating competition.

Female *S. typhle* compete for males mainly through dominance hierarchies: overt aggression is difficult to observe in these slow-moving, joint-jawed and toothless fishes, but large females may interfere with and substantially decrease reproduction in small ones. Females with an ample supply of males produced fewer and smaller eggs if the saw an enclosed, larger (i.e., dominant) female, as compared to females seeing an equal-sized enclosed female. By largely giving up reproduction the dominated females instead grew better, indeed as rapidly as females not reproducing at all (Fig. 1; Rosenqvist 1990, Berglund 1991). By forfeiting current reproduction these females can come back at a larger, more competitive, body size next summer. As winter survival seems high (Berglund 1991), this life history decision makes good sense.

Competition may also take more direct forms. In nature, male *S. typhle* actively choose among and reject some females, while females vigorously display, often in temporary groups in a lek-like fashion. Males typically swim within the eelgrass, searching out groups of females who display by swimming up and down well above the eelgrass. Once such a displaying female group is found males may or may not dance, and perhaps subsequently mate, with a particular, often large, female (Vincent *et al.* 1994, 1995). Females actively compete for matings during such group displays, and at least large females try to herd other females off from the male (Vincent *et al.* 1995).

Thus, body size is an important trait in these pipefish. In fact, in experiments both males and females preferred to mate with a large partner if given a choice. They both enjoy direct advantages from doing so: a large female produces larger eggs than does a small, so males benefit from receiving these larger, energy-rich eggs. Females benefit by receiving the better paternal care a large male can provide, compared to what a small male

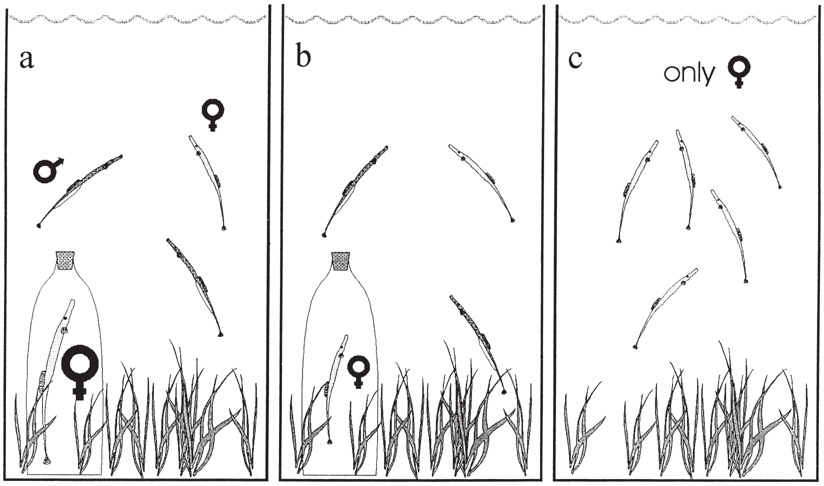

Fig. 1. Female *Syngnathus typhle* seeing an enclosed female larger than themselves (a) produced fewer and smaller eggs than females seeing an enclosed equal-sized female (b). Instead, they grew faster, indeed as fast as females not reproducing at all (c). Hence, a large female can dominate a small by suppressing the small female's reproduction. However, the small female may be able to partially compensate this by allocating resources away from present reproduction into growth. By doing so she may come back next year as a larger and more attractive and fecund female, compared to if she had not given up the present reproductive event (after Berglund 1991).

can offer (Berglund *et al.* 1986a, Rosenqvist 1990). These experiments were staged so as to provide the focal animals with a choice of partners, and given this opportunity to choose both sexes did so. However, males were choosier than females, as we may predict if predominantly females compete over males. When provided with a less attractive (i.e., small) partner, males were slower to copulate, copulated fewer times, and accepted fewer eggs, compared to females mating with a less attractive mate. Thus, males were reluctant to mate while females readily reproduced with low-quality partners (Berglund & Rosenqvist 1993).

Choosiness is a plastic male trait in *S. typhle*, which can be modified by for instance predation threat. The nuptial dance as well as the copulation largely occurs above the protective eelgrass vegetation these animals normally dwell within, so for the male to choose which female to favour and then dance and copulate with her are potentially risky behaviours. Consequently, choosiness disappeared in the presence of a predator, which in effect decreased the time spent dancing and also decreased the number of copulations. However, the number of eggs transferred per copulation increased, so males were filled to capacity as quick and safe as possible, but with eggs from a more random set of females (Berglund 1993). Moreover, the level of predation experienced by the males affected risk-taking: a predator only seen had less effect than a predator both seen and smelt, which in turn had less effect than a predator both seen, smelt and felt in the water (Fuller & Berglund 1996). In an extremely cryptic and slow-moving animal like *S. typhle* it makes good sense to be risk-sensitive: it is probably a most hazardous endeavour to leave the vegetation to reproduce. Therefore, by reducing the level of choosiness and consequently mate quickly and indiscriminately, males may in effect reduce predation risk.

Male choosiness is also modified by the operational sex ratio: choosiness disappeared completely under male excess (Berglund 1994). Furthermore, choosiness is affected by mate encounter rate: choosiness disappeared under low encounter rates, i.e., when mates were hard to find (Berglund 1995).

In nature, the adult sex ratio is about equal in *S. typhle* (Berglund & Rosenqvist 1993), i.e., an average female gets access to one male. From the pattern of competition and choosiness described above we may predict that female potential reproductive rate should exceed the male rate. In this population this boils down to the question "can a female fill more than one male during the time a male pregnancy lasts?" If so, females are faster than males and we have an egg surplus at hand in our pipefish population. In a simple experiment designed to answer this question a female was provided with an excess of males, and, indeed, more than one male was filled during an average pregnancy span (in fact, on average two males were filled; Berglund *et al.* 1989, Berglund & Rosenqvist 1993).

So why are females faster reproducers than males, causing an excess of reproducing females and creating competition among them? Obviously the high level of paternal care may have something to do with this, but is it a higher energy investment from males than from females into offspring that is the heart of the matter? No: males did not invest more energy in offspring than females. When the female's energetic contribution (i.e., the egg) was compared to the male's energy investment in offspring during his pregnancy, it turned out that the sexes supplied about the same amount of energy to each offspring (Berglund *et al.* 1986b). Thus, a lower energetic investment on the part of the female could not explain sex role reversal in this species. Instead, the long male pregnancy and the limited space for eggs within the male's brood pouch lowered his potential reproductive rate below that of females (Fig. 2; Berglund *et al.* 1989, Berglund & Rosenqvist 1990). High temperatures may lessen but not reverse this sex difference. As temperature rises, the male pregnancy shortens, but female egg production remains more or less the same. However, the point where males become faster than females at processing eggs is never reached (Ahnesjö 1995), at least not with the temperature regime at our latitudes.

Note that paternal care *per se* does not cause sex role reversal: the majority of caring fish species has exclusive paternal care, but sex roles are typically not reversed. This is so because the usual form of care is guarding and fanning, something that allows the male to accept several clutches and does not depress his potential reproductive rate below that of the females. Moreover, not even the extreme form of paternal care found in pipefishes and seahorses does necessarily cause sex role reversal. Seahorses typically have conventional sex roles (Vincent *et al.* 1992, Vincent 1994). As seahorses seem to be strictly monogamous (Vincent & Sadler 1995), the only time mating competition is likely to occur is at the onset of the breeding season. At this time, males have empty pouches while females need time to mature eggs. Thus, males can potentially reproduce faster than can females, and sex roles become conventional (Vincent *et al.* 1992).

So female *S. typhle* are faster reproducers than males and the operational sex ratio becomes skewed towards a female excess, because the faster sex will by necessity be ready to remate sooner than the slower sex, and will hence outnumber the slower sex. Accordingly, the operational sex ratio in field samples was typically female biased (Berglund & Rosenqvist 1993, Vincent *et al.* 1994). Studies corroborating these findings in other species are now beginning to emerge (e.g., Kvarnemo 1994, 1996, Balshine-Earn & McAndrew 1995, Simmons 1995, Wootton *et al.* 1995, Kvarnemo & Ahnesjö 1996, Mitani *et al.* 1996, Balshine-Earn 1996, Wiklund *et al.* 1998, Okuda 1999, Pröhl & Hödl 1999), so the use of operational sex ratios to predict mating competition is gaining increasing support.

4. Female ornaments

Does sexual selection act on sex role reversed females in the same way as on males of "traditional" species, producing the same type of secondary sexual characters? Not necessarily: females always invest energy and cytoplasm in the egg, whereas males produce a much less costly gamete. In many species, males pass nothing but genes on to their offspring. Such males may have to suffer a reduction in condition and/or survival due to the development and maintenance of sexual characters. Females and brood-caring males, who both invest substantial amounts of energy into offspring, always face yet another cost: a reduction in egg number, egg quality and/or parental investment, because resources are taken from reproduction to that character (Fitzpatrick *et al.* 1996). Females that invest in sexual ornaments do this at the expense of their reproductive potential (fewer or smaller eggs), and males that choose such ornamented females may lower their own reproductive success by doing so. In non-investing males, the sexual selection process will be constrained and finally brought to an end by counter-acting natural selection in terms of increased mortality or decreased condition imposed by the ornament (or the weapon). Females and investing

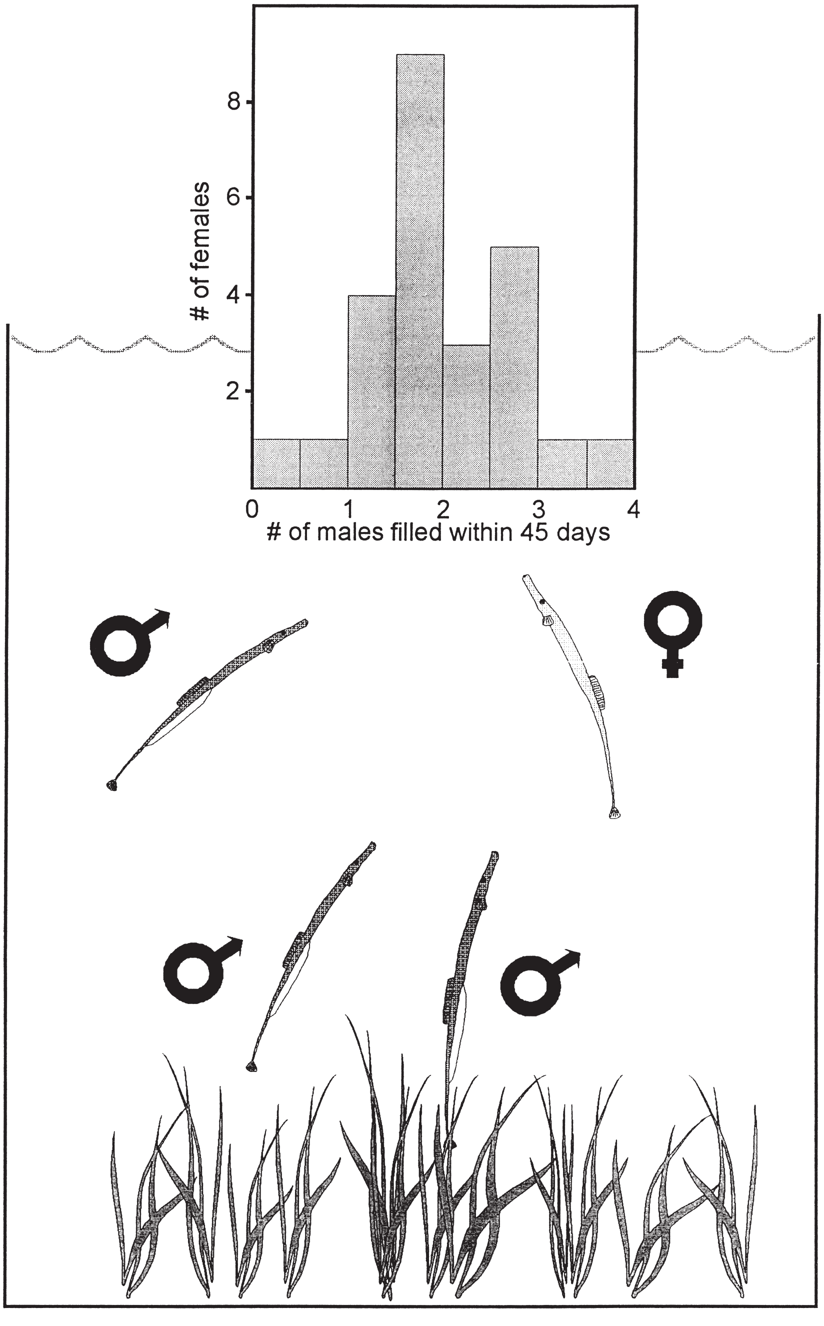

Fig. 2. Female *Syngnathus typhle* could fill on average two males during an average male pregnancy when provided with an excess of mates. This means that, at an even adult sex ratio, the female potential reproductive rate is twice that of males (after Berglund *et al.* 1989).

males suffer yet a constraint on ornament evolution: mating advantages accruing thanks to the ornament must compensate not only condition but also costs to potential fecundity in terms of a reduction in egg and/or parental care quantity or quality.

Such fecundity costs of sexual selection have hitherto gone unrecognised, and sexual selection has incorrectly been assumed to operate similarly in both sexes, producing the evolution of similar characters. Certainly, the operational sex ratio at mating influences the opportunity for selection in much the same way in both sexes, the surplus sex being selected. However, the costs associated with this selection may constrain the evolution of sexual characters to a higher extent in females and investing males, as compared to non-investing males.

The sexually selected female character should, however, in addition be energetically cheap also be an honest quality indicator (i.e., low quality females shall not be able to produce the character) that males somehow benefit from by choosing. If the character is not honest, that is, if also low quality females can display it, then males will benefit from not paying attention to it, as nothing is to be gained by selecting mates expressing this signal. Males not paying attention thus free themselves from the costs associated with being choosy. Hence, females need to be honest to attract attention, and honesty requires that the signal is costly (i.e., is a handicap), but, on the other hand, the signal should not seriously compromise the reproductive potential of the female. How can this be solved? In principle, three kinds of signals may do the trick:

1. Body size in fishes can serve as an example of the first kind of "signal", which strictly speaking is not a signal at all, as it primarily has not evolved to change the behaviour of others. Still, the information in body size can be of use, and we call this informative trait a cue (Hasson 1997) or a revealing indicator (Iwasa *et al.* 1991, Johnstone 1995). Note, however, that the difference between a signal and a cue needs not be clear-cut: body size may have been modified to actually signal dominance or attractiveness, and is hence, at least in part, also a signal. For instance, in *S. typhle* males prefer larger females with more and larger eggs (Berglund *et al.* 1986b). Large eggs give rise to high quality offspring (Ahnesjö 1992a, 1992b). Large females also dominate smaller ones, as a result gaining a reproductive advantage (Berglund 1991). Characters like body size, where an allocation to the character also is an allocation to reproduction, should be important cues/signals in sex role reversed species. This cue is difficult to fake convincingly, and does not compromise fecundity; on the contrary, it actually correlates with fecundity.
2. Energetically "cheap" but honest characters are conceivable if, for instance, different components of the resource in question are used for the character and for reproduction, respectively. An example may be when colour pigments in the food are used to produce sexual colourings, while the energetic bulk of the food goes into reproduction. Such a signal, honest by design and sometimes called an "index" (Hasson 1997, 1999, Taylor *et al.* 1999) cannot be faked, as its expression depends on the level of food intake, and thus honestly signals nutritional status. On the other hand, as most of the energy in the food goes to reproduction, not to the pigment, the energetic cost of the pigment may be small. The blue colour in females of the pipefish *N. ophidion*, a sexual signal actually preferred by males (Berglund *et al.* 1986a), may be an example. Alternatively, the two allocations can be partitioned in time, so that the production of the ornament does not interfere with the production of eggs or offspring care.
3. Signals may be costly in terms of something else than energy. For instance, colour patches signalling dominance ("status badges") may serve as honest signals carrying not an energetic but a social cost, applying to cheaters only. A cheater faces the cost when it encounters an opponent with a similar-size badge, and has to prove its worth in a real encounter, which the cheater of course is bound to lose. Therefore, status badges are honest (Boake & Capranica 1982, Järvi & Bakken 1984, Studd & Robertson 1985, Møller 1987b, Jones 1990). For example, in cases when a badge was experimentally exaggerated, male birds often suffered badly in real contests (Rohwer 1977, Rohwer & Rohwer 1978, Watson & Parr 1981, Møller 1987a, 1988). Status signals can also increase disease susceptibility by reducing immunocompetence as a consequence of elevated testosterone levels (Zuk *et al.* 1990, Owens & Hartley 1991). In several birds, fights occur most frequently between individuals of similar badge size (Balph *et al.* 1979, Møller 1987a, Maynard-Smith & Harper 1988). Maynard-Smith & Harper (1988) concluded from a model that honest communication is evolutionarily stable even if the badge is cheap, provided that a dishonest signaller pays the full cost of a contest. A dishonest mutant can invade the population only if he can escape from contests with a more aggressive opponent without fighting (but *see* Johnstone & Norris 1993).

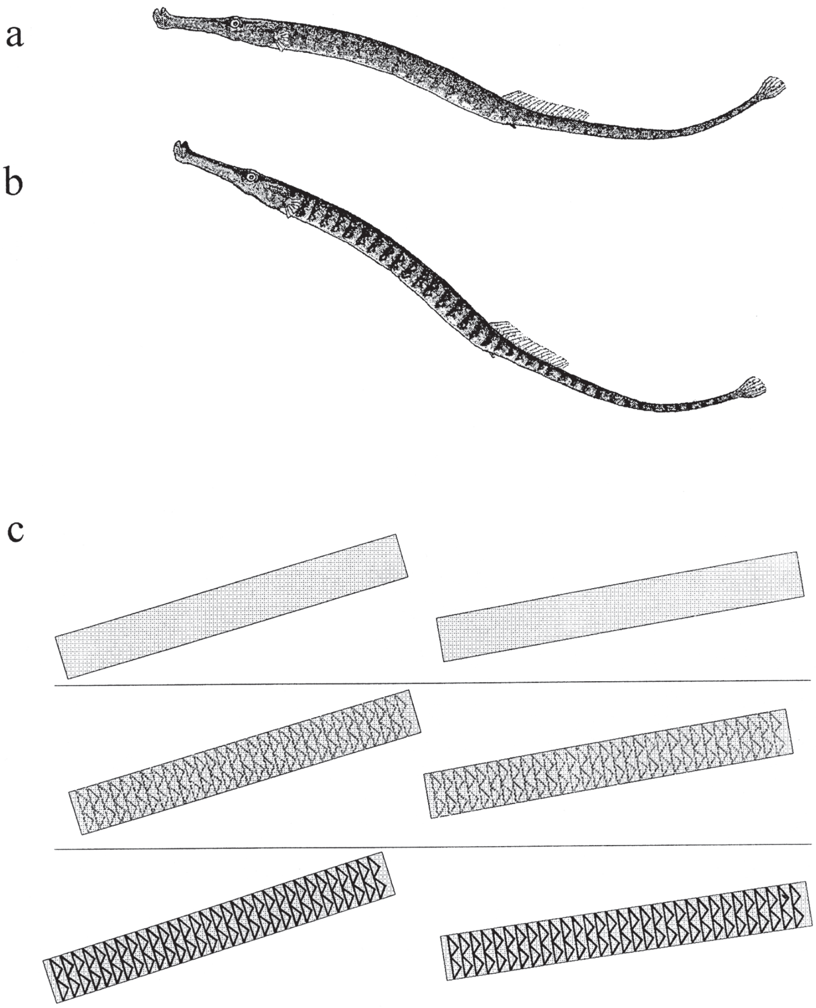

Fig. 3. During the mating period female *Syngnathus typhle* may increase the contrast of their ordinary, vaguely striped pattern (a) enormously by blackening the dark parts (b). This is seen only during the nuptial dance shortly before mating, or in female-female displays with no males present or with males nearby but not dancing with any particular female. The ornament can be flashed or extinguished in less than a minute (Berglund *et al.* 1997, Bernet *et al.* 1998). The bars mimicking pipefish with three different degrees of ornamentation (c) were used to let students estimate which in a pair of same-patterned bars was larger.

5. Female ornaments in *S. typhle*

The typical colour pattern in fish is a darker dorsal than ventral side, which may improve crypsis (Schliwa 1986). This pattern occurs also in *S. typhle*. The natural variation in colour in both female and male *S. typhle* is high, ranging from light green over grey and brown to nearly black. The different colours closely match the varying colours of the eelgrass, and may pale slowly over time. Besides the variation in colour, different colour patterns exist both in males and females: fish range from dull (uniformly coloured with little contrast) to a contrasted pattern with darker "stripes" looking like the letter B (Fig. 3). Females may during the breeding period suddenly increase their contrast enormously by blackening the B stripes (Fig. 3), here called "displaying the ornament". This only happens during the nuptial dance shortly before mating (Fiedler 1954), or in female-female displays with no males present or with males nearby but not dancing with any particular female (Vincent *et al.* 1994, 1995; A. Berglund's own observation). The ornament can be displayed or extinguished in less than a minute (A. Berglund's own observation). The ornament is thus a sexual signal simply formed by increasing the contrast of the pre-existing striped pattern (Fig. 3). This pre-existing pattern is "permanent" in the sense that it takes weeks to change its contrast, whereas stripes can be darkened temporarily in less than a minute. The maximum contrast of the permanent pattern never approaches anything like that of the ornament. Most likely all females can display the ornament, but they differ in their propensity to do so.

6. Amplifiers

An amplifier increases the resolution power of a signal, i.e., it makes differences between two signals easier to detect (Hasson 1989, 1990, 1991, 1997, 1999). Thus, the term "amplifier" is somewhat unfortunate in that the amplifier does not necessarily boost the signal or make it look stronger than it really is, it just improves readability. In other words, the amplifier acts on and enhances discrimination, rather than the perception of the signal itself.

If a sexually selected signal is an honest quality indicator, the claim is that an amplifier acting on this signal is honest by necessity and need not be costly in itself: low quality animals should not benefit from signalling their low quality more clearly (Hasson 1989). Moreover, the amplifier need not be attractive in itself, only the signal it amplifies. However, as the signal receiver obviously perceives the amplifier, the amplifier may evolve into becoming attractive. Low quality animals may be "forced" into displaying the amplifier, as not doing so may even more clearly signal low quality. Also, most amplifiers may increase conspicuousness both to competitors and predators, thus making the amplifier costly. Therefore, amplifiers may evolve to be costly, condition-dependent quality signals themselves, being attractive to potential mates. If so, they can be termed "amplifying handicaps" (Hasson 1990, 1997, Fitzpatrick 1998). Tail markings in birds may for instance be such amplifying handicaps, indicating feather quality more clearly (Fitzpatrick 1998).

Currently, no signal has been unambiguously demonstrated to actually function as an amplifier that indeed improves discrimination, but speculations to this end abound (e.g., Hasson 1991, Bradbury & Vehrencamp 1998, Taylor *et al.* 1999). Moreover, there are no empirical demonstrations of whether amplifiers are "pure", cost-free and unattractive signals, or costly and attractive. In this paper, I report on an amplifier in the sex-role reversed pipefish *Syngnathus typhle* L., namely the female ornament described above. I will demonstrate that it actually increases the accuracy of body size estimates (at least if pipefish see things the way humans do), i.e., it facilitates for the receiver of the information to tell differently sized females apart. As a consequence, this will facilitate for males to distinguish females carrying many and large eggs, as these properties both correlate positively with female size. Note that the stripes in female pipefish thus serve at least two purposes: they clarify size information (the amplifier function) and convey information about attractiveness (the ornament function). I also report on possible costs and attractive powers associated with the amplifier that makes it an amplifying handicap.

7. Do female ornaments facilitate size judgement?

7.1. Material and methods

To investigate whether the display of the striped pipefish pattern facilitates size judgement, I let undergraduate students judge by eye which of two bars (rectangles simulating pipefish) were longer (or higher) than the other. The bars (Fig. 3) had three different patterns: uniformly grey, grey with dark grey stripes, or grey with solid black stripes. Stripes mimicked the "B" pattern in real pipefish. The two bars in each comparison had the same pattern but differed in size, either length or width, by 2.5%. The entire bar, including stripes, was stretched by this amount in a computer drawing program (CorelDraw 7), so number of stripes did not differ between bars. 21 undergraduate students (10 males, 11 females) were asked to judge 2 pairs of each of the three patterns. The two bars in a pair were placed beside one another at different odd angles (Fig. 3). Bars were approximately 80 × 10 mm. Ample time was given for the judgement. Students were not aware of the purpose behind the investigation prior to testing. The test was repeated on 18 more undergraduate students (11 males and 7 females). A wrong choice was scored as 0, a correct as 1. The maximum score within each pattern category was 2, so a score of 1 was expected by chance only.

To investigate why pipefish are cross- rather than length-wise striped I repeated the test on 25 new undergraduate students (14 males and 11 fe-

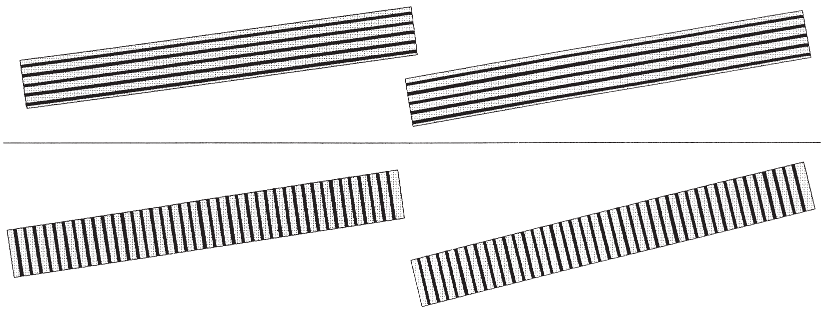

Fig. 4. To investigate why pipefish are cross- rather than length-wise striped students were asked to tell size differences between a pair of cross- or a pair of length-wise striped bars.

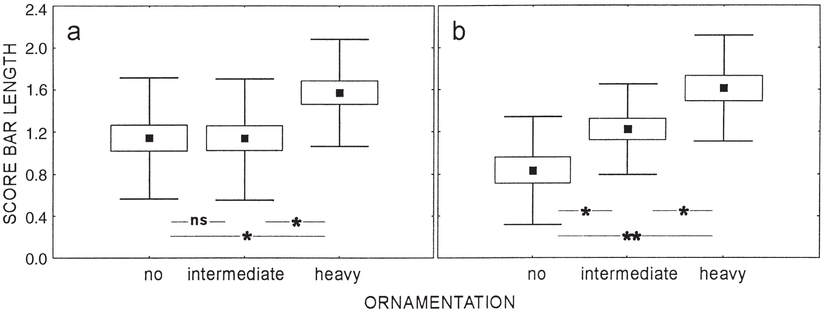

Fig. 5. It was easier for students to determine which bar was longer if the bars were more heavily striped. This was done in two independent test runs (a and b; a: Friedman repeated measurement ANOVA, $\chi^2 = 9.35$, df = 2, $n = 21$, $p = 0.009$; b: $\chi^2 = 17.6$, df = 2, $n = 18$, $p = 0.0001$). Test scores could range between 0 and 2, with 1 being what is expected from a pure guess. The figure shows the average scores (black squares) with S.E. boxes and S.D. bars drawn (* = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$, determined from Wilcoxon matched pairs tests).

males), but with only two patterns, black length- or cross-stripes on a grey bottom (Fig. 4). Each student judged 3 pairs of each of the two patterns. Scoring was similar as above, yielding a range of 0–3 with a score of 1.5 expected by chance only.

No student participated more than once in any study. Reported *p*-values are two-tailed.

7.2. Results

7.2.1. Ornament strength

It was easier to tell bar size apart when the ornament strength increased, also when the investigation was repeated with new students (Fig. 5). For bar length, students did no better than pure guessing at no or intermediate ornamentation (a 95% confidence interval overlapped the score expected from pure guessing), while at full ornamentation students did better than guessing (non-overlapping 99% confidence interval). In the repeat test students now did better also at intermediate ornamentation (95%), otherwise results were similar. Regarding bar height, non-ornamented bars produced guesses, whereas intermediate or full ornaments enabled students to do better than that. Intermediate ornamentation actually tended to work best, and even significantly so in the first test round (Fig. 6).

Sexes did not differ in estimate accuracy (Mann-Whitney *U*-tests, $p > 0.6$ in both test rounds and for both length and height), so they were pooled in the other analyses.

7.2.2. Cross- or lengthwise ornamentation

Regarding bar length the way stripes went did not matter for the accuracy of size estimates, but height differences were more easily discerned if bars were cross-wise striped (Fig. 7), like real pipefish are. In all cases students did better than pure guesswork (non-overlapping 95% confidence intervals).

Sexes did not differ in estimate accuracy (Mann-Whitney *U*-tests, $p > 0.8$), so they were pooled in the other analyses.

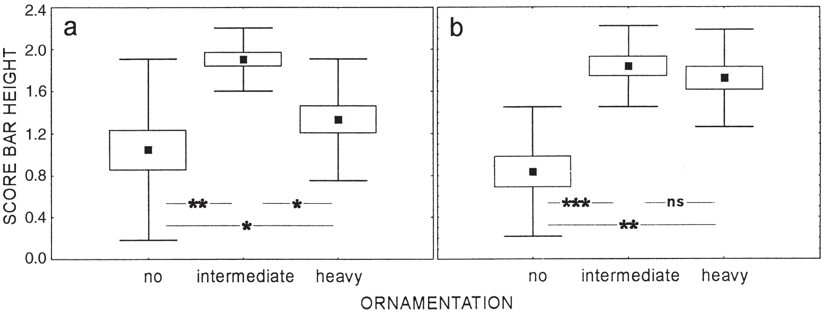

Fig. 6. It was easier for students to determine which bar was higher if the bars were intermediate or heavily striped, as concluded from two independent test runs (a and b; a: Friedman repeated measurement ANOVA, $\chi^2 = 15.2$, df = 2, $n = 21$, $p = 0.0005$; b: $\chi^2 = 21.7$, df = 2, $n = 18$, $p = 0.00002$). Test scores could range between 0 and 2, with 1 being what is expected from a pure guess. The figure shows the average scores (black squares) with S.E. boxes and S.D. bars drawn (* = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$, determined from Wilcoxon matched pairs tests).

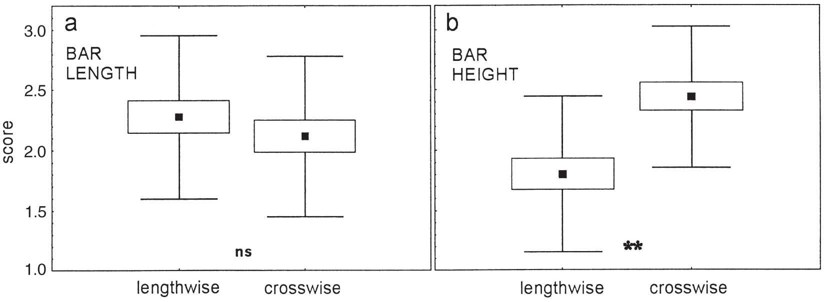

Fig. 7. — a: It was not easier for students to determine which bar was longer if the bars were cross- rather than length-wise striped (Wilcoxon matched pairs test, $n = 25$, $T = 13.5$, $p = 0.3$). — b: Height was easier to estimate on cross- than on length-wise striped bars (Wilcoxon matched pairs test, $n = 25$, $T = 0.00$, $p < 0.01$). Test scores could range between 0 and 3, with 1.5 being what is expected from a pure guess. The figure shows the average scores (black squares) with S.E. boxes and S.D. bars drawn.

8. Discussion

If pipefish see the world anywhere near the way students do (recall Section 7), the female ornament is an amplifier of body size, facilitating for males to tell females differing slightly in size apart. Moreover, the way stripes run (across the body) seems to be no arbitrary, Fisherian trait (which, indeed, is not expected in males or females providing direct benefits to their offspring; Fitzpatrick *et al.* 1996). Actually, cross-stripes facilitated for males to estimate female size: telling small differences in body height (but not body length) apart was easier this way than with length-wise stripes. Body height may actually be more important than body length to males, as the former measure correlates more strongly with female fecundity (unpublished field data from 20–28.5.1995, partial correlation analysis with the effects of female body length and height on number of eggs ($n = 53$); length: $\beta = 0.119$, $p = 0.5$ and height: $\beta = 0.40$, $p < 0.05$).

A cloth designer may come up with another explanation to the cross-wise stripes, as such are known to make bodies look fatter. If so, the signal can be termed deceptive, and all females are “cheaters”. However, the “fattening” quality of the signal should apply equally to all females, regardless of body height, so this quality of the signal would not aid males in their choice of partner.

Pipefish have good vision and hunt by eye (Fiedler 1954), and the chromatophore-regulated melanin-based ornament ought to pose no problem with possible UV-vision in pipefish; the assumption of enough similarity between human and pipefish vision for ornament perception seems reasonable. However, in the wild the ornament also interacts with female movements and the flickering rate of ambient light. Whether these interactions blur or further strengthen the amplifying nature of the ornament is unknown, but at least to human observers females look extremely conspicuous while moving up and down above the eelgrass meadows in the sun-flicker, in fact more conspicuous than when standing still in uniform light.

Thus, the ornament actually functions as an amplifier. Is it a cost-free and in itself unattractive amplifier? No; the signal has some possible costs and is also attractive in itself to males.

8.1. Costs

In an experiment no energetic costs were found for the ornament (Berglund *et al.* 1997): well-fed as well as starved females displayed the ornament to the same degree, so at least short-term nutritional status does not affect this signal. However, in the presence of a predator (a cod) females became more reluctant to display the ornament than in a predator-free setting (Bernet *et al.* 1998). This suggests that the ornament decreases crypsis (quite apparently this is so to the human eye), and to avoid predation females refrain from displaying it. Thus, a predation cost seems likely. We are currently analysing experiments designed to investigate if the amplifier is a status badge, signalling dominance to other females independent of body size. Preliminary observations indeed suggest that this is so. If so, the cost would apply to females cheating the signal in encounters with truly dominant females displaying a similar-size signal. The idea that amplifiers can be cost-free therefore seems to gain no support from the pipefish data: survival and social costs most likely intervene to turn the amplifier into an amplifying handicap.

8.2. Attractiveness

In experiments, the ornament reliably predicted female mating success: ornamented females attracted more males, danced more and sooner, mated more and sooner and produced and transferred more eggs than did non-ornamented females. Ornamentation also accurately predicted female quality (egg numbers). Males utilising ornamentation as a cue in their mate choice may hence be able to perform their choice more quickly, reducing the time spent on potentially dangerous mate search (Berglund *et al.* 1997, Bernet *et al.* 1998). The ornament is attractive in itself: an experiment where females were manipulated (painted) to differ in ornamentation but not in behaviour (females were sedated and moved by a motor) confirmed that males prefer the ornament independent of female display (Berglund and Rosenqvist, in prep.). Thus, the idea that amplifiers can be neutral in mate choice was not confirmed by the pipefish data: the amplifier was highly attractive to the choosy sex, and hence is an ornament as well as an amplifier.

So do "pure", cost-free, unattractive amplifiers exist at all? Theory, especially empirical verification, is still in its infancy in this field. In pipefish, clearly low quality (i.e., small) females would not benefit from faking (displaying) the ornament, as that would only more clearly reveal their small body size to males and other females. However, the fact that large females always would benefit from signalling as clearly as possible their size, both to males and to other females, makes me believe that amplifiers easily evolve into genuine quality signals with associated costs. High quality females would benefit from revealing their large body size, and hence dominance, to other females by displaying the amplifier, which then in effect takes on the function of a status badge. If males then use this signal of dominance to assess female size more accurately and/or more rapidly, they would benefit by diminishing their costs of mate choice. Hence, the amplifier would be under sexual selection from both female-female competition and male mate choice, and we can expect it to evolve as an "armament/ornament" sexual trait (*see* Berglund *et al.* 1996) with associated costs.

In conclusion, the type of amplifier found in the pipefish *S. typhle*, with probable costs and an attraction power, may be widespread among animals; however, whether amplifying handicaps is the rule and "pure" amplifiers the exception awaits exploration.

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References

Ahnesjö, I. 1992a: Consequences of male brood care; weight and number of newborn in a sex-role reversed pipefish. — *Func. Ecol.* 6: 274–281.

Ahnesjö, I. 1992b: Fewer newborn result in superior juveniles in the paternally brooding pipefish *Syngnathus typhle*. — *J. Fish Biol.* 41B: 53–63.

Ahnesjö, I. 1995: Temperature affects male and female potential reproductive rates differently in the sex-role reversed pipefish, *Syngnathus typhle*. — *Behav. Ecol. Sociobiol.* 6: 229–233.

Andersson, M. B. 1994: *Sexual selection.* — Princeton Univ. Press, Princeton.

Balph, M. H., Balph, D. F. & Romesburg, H. C. 1979: Social status signalling in winter flocking bird: an examination of current hypothesis. — *Auk* 96: 78–93.

Balshine-Earn, S. 1996: Reproductive rates, operational sex ratios and mate choice in St. Peter's fish. — *Behav. Ecol. Sociobiol.* 39: 107–116.

Balshine-Earn, S. & McAndrew, B. J. 1995: Sex-role reversal in the black-chinned tilapia, *Sarotherodon melanotheron* (Ruppel) (Cichlidae). — *Behaviour* 132: 862–874.

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. 1994: The operational sex ratio influences choosiness in a pipefish. — *Behav. Ecol.* 5: 254–258.

Berglund, A. 1995: Many mates make male pipefishes choosy. — *Behaviour* 132: 213–218.

Berglund, A., Bisazza, A. & Pilastro, A. 1996: Armaments and ornaments: an evolutionary explanation of traits of dual utility. — *Biol. J. Linn. Soc.* 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. & Bernet, P. 1997: Ornamentation predicts reproductive success in female pipefish. — *Behav. Ecol. Sociobiol.* 40: 145–150.

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. — *Marine 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.

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.

Boake, C. R. B. & Capranica, R. R. 1982: Aggressive signal in "Courtship" chirp of a gregarious cricket. — *Science* 218: 580–582.

Bradbury, J. W. & Vehrencamp, S. L. 1998: *Principles of animal communication.* — Sinauer Associates, Sunderland, Mass.

Clutton-Brock, T. H. & Parker, G. A. 1992: Potential reproductive rates and the operation of sexual selection. — *Q. Rev. Biol.* 67: 437–455.

Clutton-Brock, T. H. & Vincent, A. 1991: Sexual selection and the potential reproductive rates of males and females. — *Nature* 351: 58–60.

Darwin, C. 1871: *The descent of man and selection in relation to sex.* — Murray, London.

Fiedler, K. 1954: Vergleichende Verhaltensstudien an Seenadeln, Schlangennadeln und Seepferdchen (Syngnathidae). — *Z. Tierpsychol.* 11: 358–416.

Fitzpatrick, S. 1998: Birds' tails as signaling devices: markings, shape, length, and feather quality. — *Am. Nat.* 151: 157–173.

Fitzpatrick, S., Berglund, A. & Rosenqvist, G. 1996: Ornaments or offspring: costs to reproductive success restrict sexual selection processes. — *Biol. J. Linn. Soc.* 55: 251–260.

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.

Haresign, T. W. & Schumway, S. E. 1981: Permeability of the marsupium of the pipefish *Syngnathus fuscus* to [^{14}C]-alpha amino isobutyric acid. — *Comp. Biochem. Physiol.* 69A: 603–604.

Hasson, O. 1989: Amplifiers and the handicap principle in sexual selection: A different emphasis. — *Proc. R. Soc. Lond. B Biol.* 235: 383–406.

Hasson, O. 1990: The role of amplifiers in sexual selection: an integration of the amplifying and the Fisherian mechanisms. — *Evolutionary Ecology* 4: 277–289.

Hasson, O. 1991: Sexual displays as amplifiers: Practical examples with an emphasis on feather decorations. — *Behav. Ecol.* 2: 189–197.

Hasson, O. 1997: Towards a general theory of biological signaling. — *J. Theor. Biol.* 185: 139–156.

Hasson, O. 1999: Knowledge, information, biases and signal assemblages. — In: Espmark, Y., Amundsen, T. & Rosenqvist, G. (ed.), *Animal signals. Signalling and signal design in animal communication*: 107–124. Tapir publishers, Trondheim, Norway.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991: The evolution of costly mate preferences II. The "handicap" principle. — *Evolution* 45: 1431–1442.

Järvi, T. & Bakken, M. A. 1984: The function of the variation in the breast stripe of the great tit (*Parus major*). — *Anim. Behav.* 32: 590–596.

Johnstone, R. A. 1995: Sexual selection, honest advertisment and the handicap principle: reviewing the evidence. — *Biol. Rev*. 70: 1–65.

Johnstone, R. A. & Norris, K. 1993: Badges of status and the cost of aggression. — *Behav. Ecol. Sociobiol.* 32: 127–134.

Jones, I. L. 1990: Plumage variability functions for status signalling in least auklets. — *Anim. Behav.* 39: 967–975.

Kvarnemo, C. 1994: Temperature differentially affects male and female reproductive rates in the sand goby: consequences for the operational sex ratio. — *Proc. R. Soc. Lond. B Biol.* 256: 151–156.

Kvarnemo, C. 1996: Temperature affects operational sex ratio and intensity of male-male competition: An experimental study of sand gobies, *Pomatoschistus minutus*. — *Behav. Ecol.* 7: 208–212.

Kvarnemo, C. & Ahnesjö, I. 1996: The dynamics of operational sex ratios and competition for mates. — *Trends Ecol. Evol.* 11: 404–408.

Maynard-Smith, J. & Harper, D. G. C. 1988: The evolution of aggression: can selection generate variability? — *Philos. Trans. R. Soc. Lond. Biol.* 319: 557–570.

Mitani, J. C., Gros, L. J. & Richards, A. F. 1996: Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. — *Am. Nat.* 147: 966–980.

Møller, A. P. 1987a: Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. — *Anim. Behav.* 35: 1637–1644.

Møller, A. P. 1987b: Social control of deception among status signalling house sparrows *Passer domesticus*. — *Behav. Ecol. Sociobiol.* 20: 307–311.

Møller, A. P. 1988: Badge size in the house sparrow *Passer domesticus*. Effects of intra- and intersexual selection. — *Behav. Ecol. Sociobiol.* 22: 373–378.

Okuda, N. 1999: Sex roles are not always reversed when the potential reproductive rate is higher in females. — *Am. Nat.* 153: 540–548.

Owens, I. P. F. & Hartley, I. R. 1991: “Trojan sparrows”: evolutionary consequences of dishonest invasion for the badges-of-status model. — *Am. Nat.* 138: 1187–1205.

Parker, G. A. & Simmons, L. W. 1996: Parental investment and the control of sexual selection: predicting the direction of sexual competition. — *Proc. R. Soc. Lond. B Biol.* 263: 315–321.

Pröhl, H. & Hödl, W. 1999: Parental investment, potential reproductive rates, and mating system in the strawberry dart-poison frog, *Dendrobates pumilio*. — *Behav. Ecol. Sociobiol.* 46: 215–220.

Rohwer, S. 1977: Status signaling in Harris sparrows: some experiments in deception. — *Behaviour* 61: 107–129.

Rohwer, S. & Rohwer, F. C. 1978: Status signalling in Harri’s sparrows: experimental deceptions achieved. — *Anim. Behav.* 26: 1012–1022.

Rosenqvist, G. 1990: *Mate choice and sexual selection in two species of sex-role revered pipefish (Syngnathidae)*. — Ph.D. Thesis, Uppsala.

Schliwa, M. 1986: Pigment cells. — In: Hahn-Matoltsy, R. (ed.), *Biology of the integument of vertebrates*: 56–77. Springer-Verlag, Berlin.

Simmons, L. W. 1995: Relative parental expenditure, potential reproductive rates, and the control of sexual selection in katydids. — *Am. Nat.* 145: 797–808.

Studd, M. V. & Robertson, R. J. 1985: Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). — *Anim. Behav.* 33: 1102–1113.

Taylor, P. W., Hasson, O. & Clark, D. L. 2000: Body postures and patterns as amplifiers of physical condition. — *Proc. R. Soc. Lond. B Biol.* Vol. 267. [In press].

Vincent, A., Ahnesjö, I., Berglund, A. & Rosenqvist, G. 1992: Pipefishes and sea-horses: Are they all sex role reversed? — *Trends Ecol. Evol.* 7: 237–241.

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. — *Env. Biol. Fishes* 44: 347–361.

Vincent, A. C. J. 1994: Seahorses exhibit conventional sex roles in mating competition, despite male pregnancy. — *Behaviour* 128: 135–151.

Vincent, A. C. J. & Sadler, L. M. 1995: Faithful pair bonds in wild seahorses, Hippocampus whitei. — *Anim. Behav.* 50: 1557–1569.

Watson, A. & Parr, R. 1981: Hormone implants affecting territory size and aggressive and sexual behaviour in red grouse. — *Ornis Scand.* 12: 55–61.

Wiklund, C., Kaitala, A. & Wedell, N. 1998: Decoupling of reproductive rates and parental expenditure in a polyandrous butterfly. — *Behav. Ecol.* 9: 20–25.

Wootton, R. J., Fletcher, D. A., Smith, C. & Whoriskey, F. G. 1995: A review of reproductive rates in sticklebacks in relation to parental expenditure and operational sex ratios. — *Behaviour* 132: 915–933.

Zuk, M., Johnson, K., Thornhill, R. & Ligon, J. D. 1990: Parasites and male ornaments in free-ranging and captive red jungle fowl. — *Behaviour* 114: 232–248.