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Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae)

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Summary. In order to understand the causes of sexual dimorphism, mate choice and size-related fecundity were studied in two pipefish species, *Syngnathus typhle* and *Nerophis ophidion*. Sexual dimorphism is more pronounced in *N. ophidion*; females are larger, have sexual colourings, and are more active during courtship. In *S. typhle* the sexes are alike in all these respects. Males brood their offspring in both species. In *N. ophidion* fecundity was positively correlated with both body size and the amount of sexual colouring in females. In males no correlation between body size and fecundity, or between body size and embryo size existed. Predictably, in mate choice experiments with equal-sized females, males chose females with more extensive sexual colourings. We explain sexual dimorphism in this species as a consequence of both natural selection (fecundity increases with size in females but not in males) and sexual selection (males prefer larger females). We argue that sexual size dimorphism did not evolve by selection minimizing overlap in food niches between the sexes, because food production is high in the *Zostera* beds where the fishes live, and no size dimorphism was found in the sympatrically occurring *S. typhle*. Furthermore, in *N. ophidion* dimorphism is not greater in a particular mouth character than in overall body size. In *S. typhle* egg size and the average number of eggs transferred per spawning were positively correlated with female body size. Apparently more energy per offspring was provided by larger males than by smaller males, and larger males also carried more offspring. As predicted, large mates were preferred by both sexes in mate choice experiments. This is explicable in terms of both natural selection (fecundity increases with size in both sexes) and sexual selection (both sexes prefer large mates). As a consequence of selection acting in the same direction in both sexes, sexual dimorphism is absent in *S. typhle*.

Introduction

Sexual dimorphism may result from three basically different forces. First, natural selection acts on fecundity and may produce different patterns of size-specific fecundity in the two sexes. It is, for instance, common to many species that a larger size in females increases their fecundity, while the same may not be true in males (Tinkle et al. 1970; Wootton 1979; Tollestrup 1982). The second force is natural selection for reduced food competition between the sexes, so that, for instance, the larger sex exploits larger food items (Slatkin 1984; Temeles 1985). Third, sexual selection through mate competition and/or mate choice may result in sexual dimorphism (Trivers 1972; Halliday 1978; Wade and Arnold 1980; Lande 1981; Andersson 1982; Searcy 1982; Carothers 1984). By sexual selection we mean selection for an enhanced mate-acquiring ability.

When studying sexual selection it is important to distinguish between mate choice on the one hand and intrasexual competition for mates on the other (Wade and Arnold 1980; Halliday 1983; Bischoff et al. 1985). To demonstrate active mate choice, the following have to be shown (Halliday 1983): (1) a nonrandom mating pattern, (2) an active mate choice rather than intrasexual competition for mates and (3) the adaptiveness of mate choice. Adaptiveness can be shown either in a direct way if higher reproductive success in one sex results from choosy behaviour in that sex, or in an indirect way if mates of "higher genetic quality" are chosen. Usually females are the more discriminating sex, and female choice, in the above sense, has been suggested to operate in several fish species (Noble 1938; Downhower et al. 1983; Bischoff et al. 1985). A few studies demonstrating male choice in sex role-reversed species exist, for example, in mormon crickets (Gwynne 1981).

The aim of this study is to explain differences in sexual dimorphism in two sex role-reversed pipefish (Syngnathidae) species. This explanation will be in terms of various selective pressures posed by different mating patterns and size–specific fecundity relations in these two related, sympatric species. We will also investigate whether an intersexual niche divergence can account for sexual dimorphism by measuring dimorphism in an important foraging character (snout height).

Male pipefish nurse their offspring on the body surface or in a brood pouch and give birth to free swimming offspring (Rauther 1925; Fiedler 1954). Males furthermore provide their offspring with oxygen and nutrients. Epithelial structures suggesting this exist (Kronester-Frei 1975), a transfer of labeled amino acids has been documented (Haresign and Schumway 1981) and, finally, offspring decrease less in weight during pregnancy than would be predicted by their energy loss as calculated from their respiration rates (Berglund et al. 1986). Thus, in terms of reproductive investment, females contribute eggs, while males fertilize them and provide paternal care to the offspring. In several pipefish species, courtship behaviour consists of a complex nuptial dance prior to copulation (Gudger 1906; Fiedler 1954; Gronell 1984).

The two species, *Nerophis ophidion* (L.) and *Syngnathus typhle* L. (= *Siphonostoma typhle* Moreau 1881), differ in terms of sexual dimorphism in size, colour and courtship behaviour. In *N. ophidion* females are larger than males (Berglund et al. 1986), have a permanent sexual colouring consisting of several intensively blue stripes along the anterior part of the body, possess dorsoventral skin folds which enlarge the female's appearance and are more active in courtship (Fiedler 1954). In contrast, sexes are similar sized in *S. typhle* (Berglund et al. 1986), colouring is the same and the two sexes are equally active during courtship. Both species live in the same habitat, i.e. *Zostera marina* (L.) beds, where they feed on small mobile animals, but *S. typhle* is larger and is able to capture larger prey. Sex ratios are equal in both species (Berglund et al. 1986). *N. ophidion* males brood their young openly on the ventral side of their abdomen, whereas *S. typhle* males possess a brood pouch for this purpose. *N. ophidion* males receive their entire clutch from one female at one occasion, whereas *S. typhle* males copulate repeatedly with several females, and one female deposits eggs in several males (Berglund et al. in preparation).

Methods

Fishes were collected during spring and summer, 1983–1985, in the Gullmar Fjord on the Swedish west coast (58°15′N, 11°28′E). Sample sites were shallow (0.5–6 m) *Zostera marina* meadows. Animals were captured using a small beam trawl (mesh size 2 mm) pulled by a boat. Field samples were taken at least every third week from May to September, and fishes were killed in an MS 222 solution (metacaine; 3-aminobenzoic acid ethyl ester methanesulfonate) and kept frozen until measured. For both species, we recorded standard length, numbers and developmental stages of embryos, dry weight (60° C for at least 24 h) of body, eggs/embryos, and gonads, and approximate "fullness" of egg accommodation space in males. In our calculations of embryonal changes during male pregnancy, we employed (1) immature embryos, without visible eye spots, and (2) mature embryos, ready to hatch with no, or only a small, yolk sac. In *Nerophis ophidion* the snout height was measured on dried specimens to the nearest 0.1 mm. In *N. ophidion* females the area of blue sexual coloration was measured from camera obscura drawings or from photographs.

Respiration of *Syngnathus typhle* embryos was measured by the Winkler titration method, using between 23 and 173 embryos per bottle. Embryos were carefully removed from the male prior to respirometry, and respiration was measured over a 4-h period in oxygen saturated, filtrated seawater (18°–19° C, 32.0‰–33.8‰). For further description see Berglund et al. (1986).

The pipefish used in the experiments were kept in aquaria where temperature (11°–18° C) and salinity (21‰–29‰) equalled field conditions. They were fed with *Artemia* and freshly caught small crustaceans.

Female egg output per spawning in *S. typhle* was measured in the lab, from 1 June–31 July 1985. This information cannot be obtained from field samples because eggs mature continuously and females spawn repeatedly. Six tanks were used, each holding approximately 1.5 m^3 of continuously renewed seawater (12°–17° C, 21‰–29‰). Each tank contained three smaller cylindrical cages (diameter 0.3 m). Both tank and cages were equipped with artificial *Zostera*.

Five to six males of different sizes, with well-developed brood pouches, were put into the tank outside the cages, and one male was put in each cage. Four females were then introduced, one in each cage and one outside. Females were transferred between cages and the outside every 24 h. This experimental design enabled the females to mate repeatedly and occasionally to exert mate choice. The number of eggs deposited in males per spawning event was counted every 24 h. Hence, even if several spawning events with the same male were to occur during this period of time, they were counted as one spawning only.

In the mate choice experiments, one sex could choose between two mates. These experiments were performed in 1984 and 1985. In *N. ophidion* only male choice between two females was studied. The females did not differ in length, but in the area of blue coloration. Eleven replicates were run. In *S. typhle*, male choice between different-sized females and female choice between different-sized males were studied. Size was measured as standard length.

In *S. typhle* two female-excess treatments were run: one with all fishes free swimming (26 replicates) and the other with

Table 1. Correlation matrix for area of blue colour, body length and body dry weight in *Nerophis ophidion* females ($n=12$) in 1984

		Blue area	Length	Body weight
Number of mature eggs	$r=$	0.762	0.723	0.677
	$P<$	0.004	0.008	0.016
Blue area	$r=$		0.797	0.808
	$P<$		0.002	0.002
Length	$r=$			0.936
	$P<$			0.001

females in 5 l plastic bag enclosures to prevent female–female interactions (15 replicates). Eighteen replicates were run of the male-excess treatment. Each experimental bout lasted for no more than 14 days. The female receiving the most nuptial dances or copulation attempts during the observation periods was considered preferred. The nuptial dance may last for several hours in this species, and partners were not rejected once a pair had formed. Similarly, the male receiving the first egg batch was considered preferred in the male-excess experiment.

The mate choice experiments were performed in 125 l aquaria with recirculating seawater (18° C, 22.5‰–25.0‰). A natural light period was used. Each aquarium had sand and two artificial *Zostera* plants. Food was provided during the experimental bouts.

All statistical tests used are two-tailed, unless otherwise stated.

Results

Nerophis ophidion

The number of mature eggs in females sampled in 1984 was positively correlated to the area of blue colour, as well as to body length and body weight (Table 1). In 1983, the number of mature eggs was correlated to female weight ($r=0.528$, $n=19$, $P<0.02$), but we have no colour measurements from this year.

In males there was no correlation between male body weight and the number of embryos brooded (1983 $r=0.154$, $n=18$; 1984 $r=0.296$, $n=25$). Furthermore, there was no correlation between male weight and the average weight of one eyeless (immature, without developed eyes) embryo (1983 $r=0.062$, $n=19$; 1984 $r=0.059$, $n=18$).

Given these results, we predicted that in mate choice experiments where body size is held constant, more blue, i.e. more fecund, females would be preferred by males. In agreement with this expectation, males chose the female with the largest blue coloration in all 11 replicates (one-tailed binomial test, $P=0.001$). There was no significant difference in body length between females of different colouring used in these experiments (Student's t-test, $t=0.094$, $df=20$). Aggressive or hostile female – female interactions were never observed, and females seemingly remained indifferent to each other.

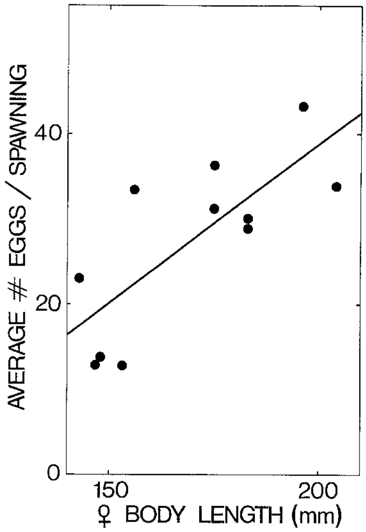

Fig. 1. Average number of eggs transferred from female to male *Syngnathus typhle* per spawning as a function of female body length

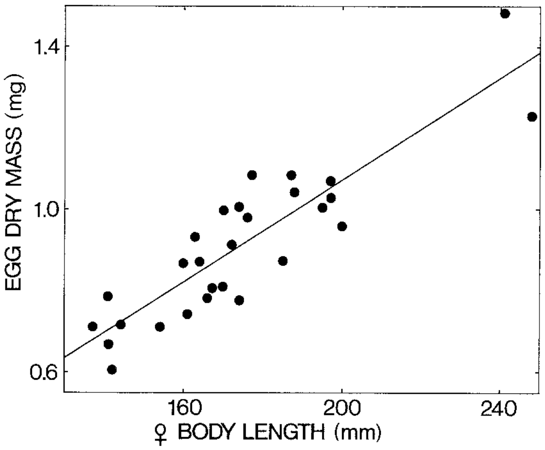

Fig. 2. The mass of one egg in female *Syngnathus typhle* as a function of body length

Snout height was positively correlated to body weight in both males ($r=0.564$, $n=61$, $P<0.001$) and females ($r=0.858$, $n=43$, $P<0.001$). To see whether males and females have the same snout height for a given body weight, we compared regressions of snout height vs body weight for the two sexes (1984 field samples) and found no significant differences in slope ($F_{1,100}=0.48$) or intercept (adjusted means; $F_{1,101}=0.98$).

Syngnathus typhle

A positive correlation between female length and average number of eggs transferred per spawning

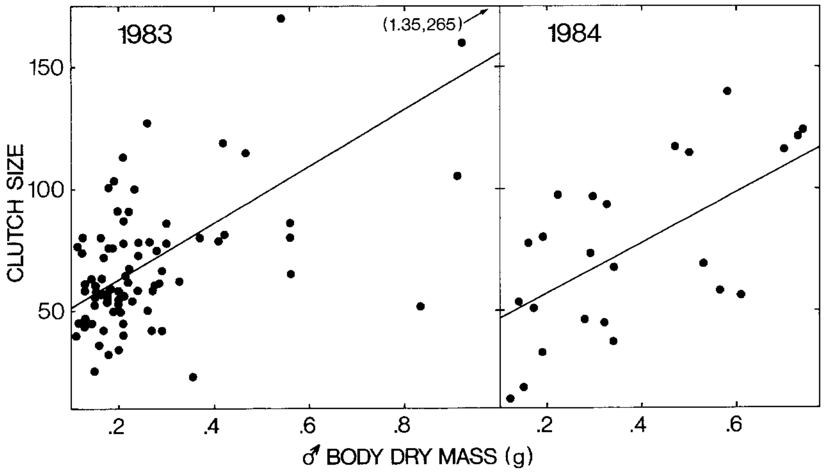

Fig. 3. Clutch size, i.e. numbers of offspring in the brood pouch, in male *Syngnathus typhle* as a function of male body mass in field samples from 2 years. Within brackets numerical x,y values are shown for a data point lying outside the graph

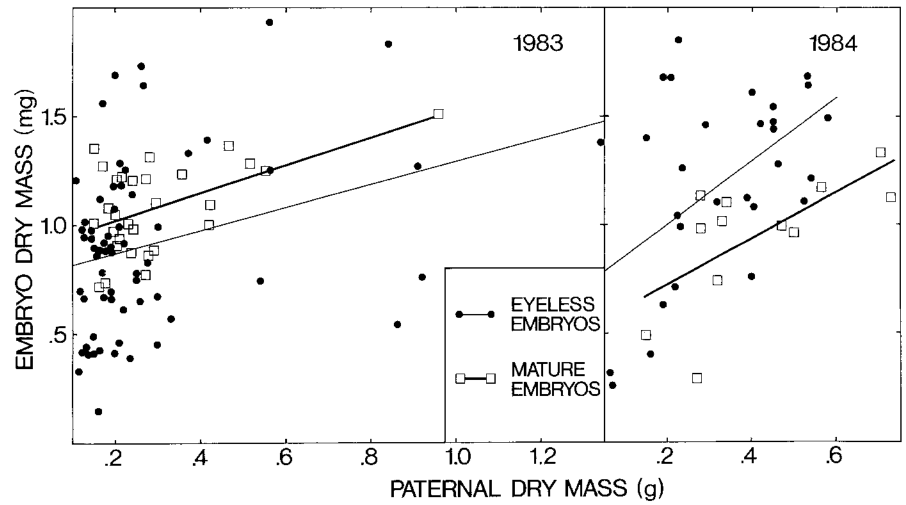

Fig. 4. The mass of an embryo at two developmental stages in a male *Syngnathus typhle* brood pouch as a function of male mass in field samples from 2 years

(one female usually spawned with several males) was observed in the egg-output experiment ($r = 0.767$, $n = 11$, $P < 0.01$; Fig. 1). The average weight of one egg was also positively correlated to female length ($r = 0.879$, $n = 28$, $P < 0.001$; Fig. 2).

In field samples there was a positive correlation between male body weight and clutch size (i.e. number of offspring that the male pouch can accommodate) in both 1983 ($r = 0.728$, $n = 76$, $P < 0.001$) and 1984 ($r = 0.599$, $n = 24$, $P < 0.002$; Fig. 3). Furthermore, large males carried larger embryos than small males (Fig. 4): the regression of average embryo weight on male weight was significant in both 1983 (eyeless embryos $r = 0.312$, $n = 63$, $P < 0.02$; ready-to-hatch embryos $r = 0.521$; $n = 31$, $P < 0.005$) and 1984 ($r = 0.505$, $n = 28$, $P < 0.01$; $r = 0.654$, $n = 13$, $P < 0.02$, respectively). When the regressions of eyeless versus ready-to-hatch embryos were compared, the slopes did not differ in either year (1983 $F_{1,90} = 0.07$, NS; 1984 $F_{1,37} = 0.32$, NS), but ready-to-hatch embryos were heavier than eyeless embryos in 1983 (adjusted means tested: $F_{1,91} = 4.98$, $P < 0.05$) and lighter in 1984 ($F_{1,38} = 8.72$, $P < 0.01$). As the slopes did not differ, the large embryos of large males did not decrease more in weight than small embryos of small males during pregnancy. There was a positive correlation between respiration rate and the average weight of an embryo (w in mg; $r = 0.565$, $n = 14$, $P < 0.05$):

$$\mu l\ O_2/\text{embryo} \cdot h = 0.441 \cdot w - 14.32$$

Thus, large embryos respire more than small ones, and therefore consume their energy stores at a higher rate than small embryos. Consequently, larger embryos would decrease more in weight than small embryos unless males with large embryos counteract this by transferring more energy to their offspring. Hence, large males with large embryos invest more energy per embryo.

All these correlations suggest that a large individual will increase the reproductive success of its

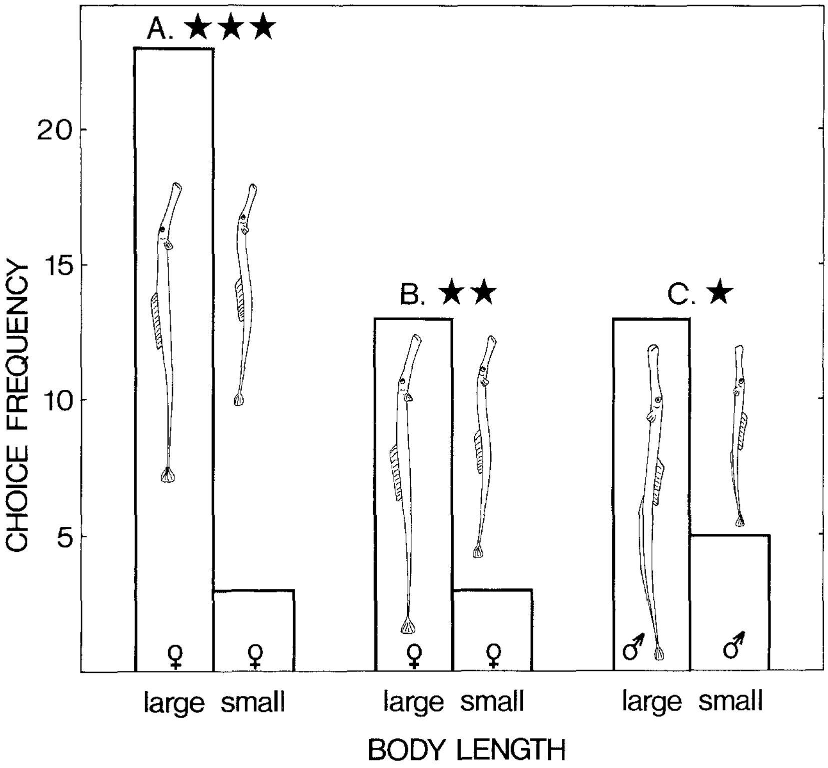

Fig. 5A–C. Mate choice experiments in *Syngnathus typhle*. In experiment **A** one male chose between two differently sized females; in **B** the two females were isolated from each other by plastic enclosures; and in **C** one female chose between two differently sized males. *P* according to one-tailed binomial tests, corrected for continuity, is indicated as *, $P<0.05$; **, $P<0.01$; and ***, $P<0.001$. There was no significant difference between treatment **A** and **B** (Fisher's exact $P=0.83$)

mate. We therefore predicted that large mates would be preferred by both males and females in mate choice experiments. The results of three mate choice experiments with *S. typhle* are shown in Fig. 5. In experiment A (one male and two differently sized females per aquarium) males chose the large female. In experiment B (as A, except that females were separated by enclosures, preventing female interactions) males also chose the large female. In experiment C (one female and two differently sized males) females transferred their eggs more often to the large male.

Discussion

Nerophis ophidion males preferred females with large areas of blue colouring. Nothing about the behaviour of the females suggested that one female was dominant in any respect or more active in courtship; rather, the male actively followed one female during courtship, and the females did not interfere with each other. In this experiment female size was held constant, but in nature the amount of blue in females is positively correlated with both body size and clutch size (Table 1). It may be difficult for a small female to "cheat" and produce large areas of blue colouring, as colour may reflect physical condition (cf. Kodric-Brown and Brown 1984). In nature, the male preference for blue colour would result in larger and more fecund females being chosen. Furthermore, it is likely that female size, independent of colour, is used by males as a cue to fecundity, as females possess appearance-enlarging skin folds along their body. Thus, we interpret increased female size and blue coloration as a result of both natural selection (a positive correlation between female size and fecundity, Table 1) and sexual selection (more blue females being preferred by males).

The number of offspring carried by *N. ophidion* males is not correlated with male size, i.e. small males may have large broods and vice versa. Thus, a male can probably accommodate all the eggs a female can produce. This was not the case in *Syngnathus typhle* males, probably because the brood pouch and the large embryo size in this species is more of a constraint on male carrying capacity than in *N. ophidion*. The latter species lacks a brood pouch and has small embryos. Furthermore, as *N. ophidion* males, compared to *S. typhle* males, invest relatively little energy in their offspring (Berglund et al. 1986), male size may be less important. If this is correct, we would not expect females to have preferences for males of any particular size. Hence, in *N. ophidion*, natural and sexual selection on male body size is relatively weak compared with selection on female size, resulting in the observed sexual dimorphism.

Conceivably, natural selection for a reduced food competition can contribute to the observed size dimorphism, if differently sized pipefish consume differently sized prey. However, *Zostera* beds are highly productive (Adams 1976), and competition for food may be weak or absent. Also, no size dimorphism exists in the sympatrically occurring *S. typhle*, indicating that niche separation between the sexes is of little or no importance in this related species. Furthermore, if niche separation with regard to prey size is important, size dimorphism in mouth characters ought to be greater than in overall body weight: if selection acts to minimize food overlap, selection would be stronger on traits directly related to foraging than on overall body size. We have chosen snout height as the mouth character because this measurement probably reflects the maximum prey size that can be handled (Muller and Osse 1984). If intersexual food competition is important, males should have smaller snouts for their body size than females. As neither slope nor intercept in snout height vs body weight regressions differed significantly between the sexes, we conclude that intersexual food niche separation is probably not responsible for the observed sexual size dimorphism in this species.

In *S. typhle* males preferred larger females in mate choice experiments. The outcome was the same whether females were physically separated from each other or not (Fig. 5), indicating that female – female interactions are less important than male choice in influencing mating patterns. Courtship behaviour appeared normal even when females were enclosed in plastic bags. The basis of the male choice may be that larger females transfer more eggs per copulation than do small females (Fig. 1) and, in addition, larger females produce larger eggs (Fig. 2). As a result of the first factor a male will need fewer, potentially dangerous copulations to obtain a full brood pouch (the pair leaves the *Zostera* vegetation and swims to the surface during the nuptial dance, thereby exposing themselves to the risk of being eaten by predators). Owing to the second factor a mate will have a higher reproductive success if larger initial offspring size results in larger adult size or in higher offspring survival.

Similarly, females preferred larger males in our experiments. It is unclear whether this result reflects female choice or male dominance. We never observed antagonistic male – male interactions during the experiments, and females inspected both males before the nuptial dance began, suggesting female choice as the mechanism behind the experimental outcome. A larger male can accommodate more eggs (Fig. 3), but as a female usually transfers fewer eggs than can be accommodated, this does not provide an adaptive explanation of female choice.

Furthermore, a large male carries heavier embryos than does a small male (Fig. 4), but this is only because larger males tend to mate with larger females and hence receive heavier eggs. We suggest that females prefer larger males because large males invest more energy (i.e. oxygen and nutrients) per offspring. As zygote respiration rate increases with zygote size, we predicted that larger zygotes would decrease more in weight relative to smaller ones during the period of brooding, unless larger males (with larger zygotes from the beginning) invest more energy per offspring. If large males do not invest more energy per offspring than small males, a steeper slope in the regression of eyeless embryo weight on male weight would result than in the regression of ready-to-hatch embryo weight on male weight, i.e. the larger embryos of larger males would have decreased more in weight than the small embryos of small males. Slopes did not differ, however, and therefore we infer that larger males did invest more energy per zygote, which explains female choice. In other words, large zygotes respire more, and hence deplete their energy stores at a higher rate, but do not decrease more in average weight during pregnancy. There are two sources of energy: the yolk, provided by the female and fixed from conception, and placental nutrients, provided by the male and variable in time. Thus, larger embryos must have received their extra energy from the variable energy source, i.e. from the male.

In a species where both sexes prefer large mates, and reproductive success increases equally with size in both sexes, a sexual size dimorphism is not expected to evolve (Ridley 1983). The lack of sexual dimorphism in *S. typhle* is consistent with this expectation.

In conclusion, we have demonstrated a nonrandom mating pattern due to male choice in both species, and that this choice has distinct reproductive consequences, affecting fecundity and/or quality of offspring in males. In *S. typhle* we also found evidence for adaptive female choice, reflecting male ability to brood offspring, which is correlated with male size. Furthermore, sexual dimorphism in *N. ophidion*, manifested in size, colour and behaviour, can be attributed to both natural and sexual selection: fecundity increases with size in females but not in males, and males prefer to mate with more colourful and thus larger females. The sexual monomorphism in *S. typhle* is a result of natural and sexual selection acting in the same direction in both sexes: fecundity increases with size in both males and females, and both sexes prefer to mate with large mates.

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Erratum

Crozier RH, Page RE (1985) On being the right size: male contributions and multiple mating in social Hymenoptera. Behav Ecol Sociobiol 18:105–115

The authors greatly regret that two manuscript errors, omission of the numeral "2" and insertion of a superfluous parenthesis, occurred in the numerator of the second term of Eq. 11 of the above paper. The simulations based on this equation, however, employed the correct version. This equation should read:

$$\begin{aligned} N_{TT} = &\{K(1-Z)^2\}/\{1+[(K-N_0)/N_0]e^{-rt}\} \\ &+\{2KZ(1-Z)\}/\{1+[(K-N_0)/N_0]e^{-rt(1-D/2)}\} \\ &+\{KZ^2\}/\{1+[(K-N_0)/N_0]e^{-rt(1-D)}\} \end{aligned} \tag{11}$$

The authors thank Blaine Cole for bringing this error to their attention.