



# Sperm trading in a hermaphroditic flatworm: reluctant fathers and sexy mothers

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When matings are frequent and received sperm are digested, hermaphrodites should trade sperm when mating. We investigated sperm trading in the flatworm *Schmidtea (Dugesia) polychroa* and manipulated mating interests to investigate its possible causes. In 106 mating pairs consisting of nonisolated individuals, no sperm donation in either direction (35%) and reciprocal exchange (38%) were more common than expected by chance, whereas unilateral transfer (27%) was less frequent, confirming sperm trading. The amount of sperm donated depended on the availability of self-sperm, not on the amount received. Animals with more allosperm from previous matings had more self-sperm and consequently donated more. This suggests that sperm digestion boosts sperm production. In a second experiment, 'mixed-interest' pairs consisting of a nonisolated (N) and an isolated individual (I), N × I, were compared with I × I and N × N pairs. Whereas I × I pairs were eager and N × N reluctant to mate, N × I pairs showed an intermediate likelihood of mating. Whereas N × N pairs traded sperm, the other two groups did not. The change in behaviour in N individuals in the N × I treatment suggests precopulatory assessment and mating in relation to phenotypic mate quality. Isolated individuals are attractive, presumably because they donate large sperm clumps unconditionally and contain fewer allosperm, implying reduced sperm competition. The reduced reluctance in N individuals to mate with, and to inseminate, previously isolated partners suggests that female quality is an important factor in male sperm donation decisions. Hence, *S. polychroa* may be choosier than previously assumed.

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Studies on simultaneous hermaphrodites with internal fertilization have highlighted sexual conflicts that are unique to this mode of gender expression (Charnov 1979; Michiels 1998). The variety in mating behaviour and mechanisms is so bewildering that, despite attempts by Leonard (1991), a general rule to predict what the mating interests of two copulating hermaphroditic partners are does not appear to be straightforward (Michiels 1998).

Charnov (1979) argued that Bateman's principle, originally used to explain differences in mating interests between males and females (see review by Arnold 1994), could be applied to hermaphrodite mating systems as well. It implies that in hermaphrodites matings primarily serve the male interest of an individual, as each mating offers the opportunity to obtain more paternity (eggs fertilized in a partner), but does not necessarily lead to higher maternity (more self-produced fertilized eggs). When matings are rare or cheap, hermaphrodites should not be choosy about whom they inseminate. Absence of choosiness with regard to body size and relatedness has

indeed been found in the land snail *Arianta arbustorum* (Baur 1992; Baur & Baur 1997) and the planarian flatworm *Schmidtea (Dugesia) polychroa* (Peters & Michiels 1996a, b; Peters et al. 1996).

Greeff & Michiels (1999) showed, however, that multiple mating and allosperm digestion in the partner can increase male investment so substantially that resources available for sperm production, not the number of available mates, may determine male fertilization success. In response, two different evolutionary pathways can be envisioned. First, insemination may become more effective by changing from regular copulation to hypodermic impregnation (Michiels & Newman 1998). Alternatively, animals may insist on reciprocal insemination as compensation for the cost of their own investment in sperm (Greeff & Michiels 1999). A mating rate that is high enough to result in sperm competition is known from many hermaphrodite species and many have evolved specialized means of digesting sperm (Baur 1998; Michiels 1998).

Conditional reciprocity, or sperm trading, was described for the first time in the sea slug *Navanax inermis* by Leonard & Lukowiak (1984). Quantitative data on the

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actual availability and exchange of sperm, however, have not been presented. In the planarian *Dugesia gonocephala* the male function donates sperm packed in a spermatophore, presumably to protect it against sperm digestion (Vreys et al. 1997) and to reduce sperm competition in the bursa copulatrix. Spermatophores can be produced only once every 2–4 days, suggesting that they are costly. Not surprisingly, individuals are choosy about with whom they mate (Vreys & Michiels 1997), and when they do, sperm are exchanged in comparable volumes, even when the availability of self-sperm differs between partners (Vreys & Michiels 1998). Baur et al. (1998) showed no trading by quantity in mating pairs of the land snail *A. arbustorum* and concluded that there is no sperm trading in this species.

*Schmidtea polychroa* Ball (formerly *Dugesia polychroa* Schmidt) is a promiscuous, frequently mating, simultaneously hermaphroditic flatworm (Peters & Michiels 1996a, b; Peters et al. 1996). By comparing sexual with parthenogenetic individuals, we know that investment in sperm is high in sexual individuals (Weinzierl et al. 1998), at the expense of cocoon production (Weinzierl et al. 1999). Ejaculates contain free sperm, which are all transferred together, ca. 30–40 min after the start of the copulation. Total copulation lasts 1–2 h (Peters et al. 1996). Michiels & Streng (1998) investigated the effect of isolation duration, body size, date and the sperm donation behaviour of the partner on the occurrence and amount of sperm donation. They showed effects by all factors investigated and concluded that matings take place primarily because of an eagerness (and ability) to donate sperm rather than to replenish allosperm stores. Michiels & Streng (1998) also found that individuals seemed to insist on reciprocity. Since planarian flatworms digest most of the allosperm they receive (Sluys 1989; Vreys et al. 1997; A. Streng, personal communication), the most likely explanation is that they insist on receiving a 'nutritional compensation' for the donation of self-sperm as predicted by Greeff & Michiels (1999). Unfortunately, Michiels & Streng (1998) used individuals that had been isolated from 1 to 66 days (median 30). Out of 21 pairs isolated for 1 day, only three mated within the 6-h observation period. Hence, their study did not allow extrapolation to natural conditions, where animals live under high densities, and can mate ad libitum. The low amount of self-sperm present in nonisolated individuals suggests that matings are indeed common in the field (Michiels & Streng 1998). This has been confirmed by data on freshly received allosperm in field-collected animals (A. Streng, personal communication).

Our study was designed specifically to demonstrate sperm trading in nonisolated individuals, and to elucidate the conflict of interests that is presumed to lie at the basis of this behaviour.

In experiment 1, all animals were paired immediately after collection in the field and, owing to their greater reluctance to mate, observed continuously for 62 h. Nonisolated individuals should be more reluctant to donate sperm because they have fewer, and so we expected sperm trading to be more pronounced than in Michiels & Streng's (1998) study. We used estimates of the amounts

of self- and allosperm already present in each individual to explain some of the variation in sperm donation and for comparison with the earlier results from isolated individuals.

In experiment 2, we manipulated mating interests by isolating some individuals and keeping others in groups. Isolation increases self-sperm reserves and the willingness to inseminate (Michiels & Streng 1998). By comparing the outcome of mixed pairs (isolated × nonisolated individuals) with those of isolated × isolated and nonisolated × nonisolated pairs, we tried to elucidate the underlying causes of trading. If individuals trade because they insist on receiving sperm (Greeff & Michiels 1999), they should give up trading when the partner has been isolated, since such partners donate sperm eagerly. We found it difficult to predict a priori what nonisolated individuals would do in mixed-interest crossings. But in principle, they would benefit more from mating with an isolated partner than with a nonisolated partner because (1) the former will not insist on trading, but give sperm readily (making them attractive as a male partner) and (2) they have fewer allosperm in store which implies less sperm competition, making them also more attractive as a female partner.

## METHODS

### Experiment 1: Sperm Exchange in Nonisolated Individuals

We collected 320 individuals from the east shore of Lago di Caldonazzo near Trento, northern Italy, in May 1996 (Beukeboom et al. 1996; Michiels & Streng 1998). All individuals were isolated in 20-ml vials to avoid copulatory activity during transport. The next day they were randomly paired and transferred to 250-ml plastic containers with openings 2.5 cm in diameter on opposite sides covered with mesh. These vials were put in larger containers through which filtered water was circulated (detailed description of this set-up in Weinzierl et al. 1998). The pairs were observed continuously for 62 h, starting in the evening. Copulatory activity was checked every 15 min, which is sufficient to register all but the shortest, ineffective copulations (Peters et al. 1996; Michiels & Streng 1998). Pairs that finished copulating were killed in a drop of 5 N HCl, and fixed in 3:1 ethanol:acetic acid. All unmated pairs were also fixed at the end of the observation period. To determine amounts of sperm in different parts of the genital system we used techniques described and discussed in detail by Michiels & Streng (1998). In brief, fixed individuals were stained with Schiff's reagent and cleared. Drawings of the two sperm-filled sperm ducts were made under a binocular microscope using a camera lucida. If an individual donated (free) sperm, the resultant 'sperm clump' in the bursa of its partner was drawn as well. Using a light microscope, we also made drawings of the circumference of the sperm in the small storage organs or tubae at the anterior end of the two oviducts, near the head. The area of each drawing was measured using an image analysis system. To compare the amount of available self-sperm

between all animals, we summed the surface of the two vasa and that of the donated sperm clump (if any) in each individual. We used this as a measure of the total amount of self-sperm available before copulation. Body sizes ( $\bar{X} \pm \text{SD} = 26.9 \pm 8.4 \text{ mm}^2$ ,  $N=294$ ) were measured after the experiment and used only to check for inadvertent effects of size despite randomization. Pairs were not assembled assortatively with regard to size. We also confirmed that individuals are not more likely to mate when their partner is larger, as already shown by Peters & Michiels (1996a, b). For the effects of body size on self-sperm, we refer to Michiels & Streng (1998). These effects do not influence the analyses presented here. One pair from which one partner was lost during histological preparation was removed from the data, resulting in a final sample of 147 pairs.

### Experiment 2: Sperm Exchange When Interests Differ

We collected 300 individuals from the same locality described above in October 1996. Previous experience had shown that these flatworms are reproductively less active at that time of year, but become more sexually active when kept at ca. 18°C and fed (unpublished data). They were maintained in groups of four in 250-ml vials in the water-flow system to allow for normal mating activity and fed once weekly with minced beef liver (McConnell 1967). After 5 weeks, half of them were isolated; the other half remained in groups. After another 5 weeks, they were randomly paired in three possible ways. Group  $N \times N$  consisted of nonisolated (N) individuals only. It served as a control and was expected to show similar results to those obtained in the first experiment. Group  $I \times I$  consisted of isolated (I) individuals only. Pairs in group  $N \times I$  consisted of one nonisolated and one isolated individual. The observations were done in the same way as described above. Mating activity in group  $N \times N$  was so low (see below) that continuous observations of all groups were prolonged up to 96 h, again starting in the evening. Mating and nonmating pairs were processed as described for the first experiment.

### Statistical Analysis

For statistical analyses we used SPSS version 8.0 and StatXact-3 version 3.0.2 (Cyrus & Patel 1996). The mating experiments yielded frequency data on the three possible outcomes of a mating: no, unilateral or reciprocal sperm exchange. To test whether the observed data are indicative of sperm trading, we calculated expected frequencies in the following way. The null hypothesis is that an individual's decision to donate sperm ( $Y$ ) or not ( $N$ ) is independent of sperm donation by the partner. If this is true, the three possible outcomes of matings ( $NN$ ,  $NY$  and  $YY$ ) should be binomially distributed for a given probability of  $N$  and  $Y$ . The latter two values are the overall number of individuals that did ( $Y$ ) or did not ( $N$ ) donate sperm in a given experiment. The expected relative frequencies are then given by  $p(N)^2$ ,  $2p(N)q(Y)$  and  $q(Y)^2$

and can be used to calculate the expected number of pairs of each type when sperm donation is independent of the partner, and depends solely on an individual's own characteristics.

We used Pearson correlations where data were approximately normally distributed, and Spearman correlations where data were curvilinear, skewed, or had outliers. Traits of two partners in a pair cannot be correlated in hermaphrodites. As an alternative, we used a one-way ANOVA and calculated the intraclass correlation coefficient  $r_1$  (Sokal & Rohlf 1996; Vreys & Michiels 1997). Means are given  $\pm \text{SD}$ .  $P$  values are two tailed throughout.

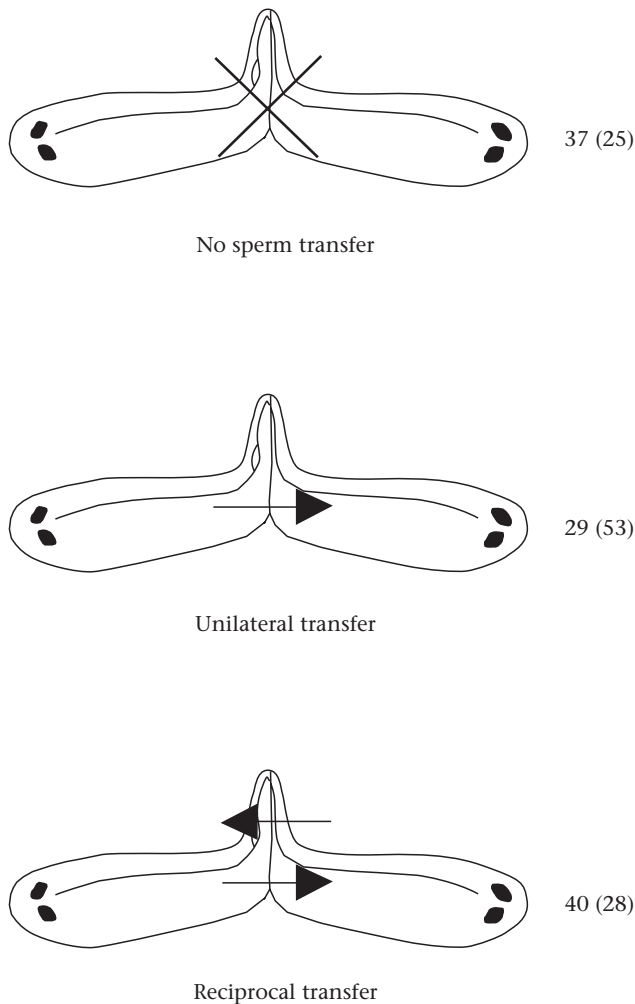
## RESULTS

### Experiment 1: Sperm Exchange in Nonisolated Individuals

Of 147 pairs, 41 failed to mate. Of the 106 that mated, 35% did not transfer any sperm (Fig. 1). Unilateral transfer (27%) and reciprocal transfer (38%) also appeared common, but the highly significant difference with the expected frequencies shows that a symmetrical outcome of matings (no or reciprocal exchange) were much more common than expected by chance, whereas unilateral transfer was rare relative to its expected frequency (50%).

Individuals differed strongly in the amount of sperm available before copulation (Fig. 2). Surprisingly, non-mating individuals had slightly more self-sperm than mating individuals. Individuals that only received sperm had the lowest self-sperm reserves. The amount of donated sperm depended strongly on the self-sperm available before copulation (Pearson correlation:  $r_{107}=0.731$ ,  $P<0.001$ ). Sperm clumps comprised a mean of  $23 \pm 12\%$  of the self-sperm available before the copulation ( $N=109$ ). Did individuals that exchanged sperm reciprocally exchange similar amounts? In a GLIM model of sperm clump size with self-sperm as a covariate, we found no difference between pairs in the amount of sperm exchanged (ANCOVA:  $F_{39,39}=1.42$ ,  $P=0.137$ ). This indicates that the amount of sperm given is independent of the amount received (intraclass correlation:  $r_1=0.17$ , see Methods).

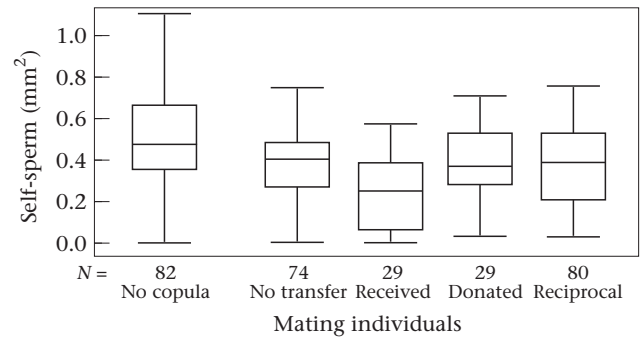
Flatworms that copulated did not have fewer allosperm stored in the sperm storage organs than those that did not copulate ( $t$  test:  $t_{292}=0.399$ ,  $P=0.69$ ). In fact, none of the five groups shown in Fig. 2 differed significantly from the others in the amount of allosperm stored (ANOVA:  $F_{4,289}=0.57$ ,  $P=0.68$ ). Considering all individuals, those that had more allosperm in store also had more self-sperm (Spearman correlation:  $r_s=0.303$ ,  $N=294$ ,  $P<0.001$ ). This effect was also significant within each group separately. As a result, individuals that had more allosperm in store also donated more self-sperm to their partner (Fig. 3). Since full allosperm stores are indicative of recent mating, this suggests that individuals produce and donate more sperm if they received more in the recent past.



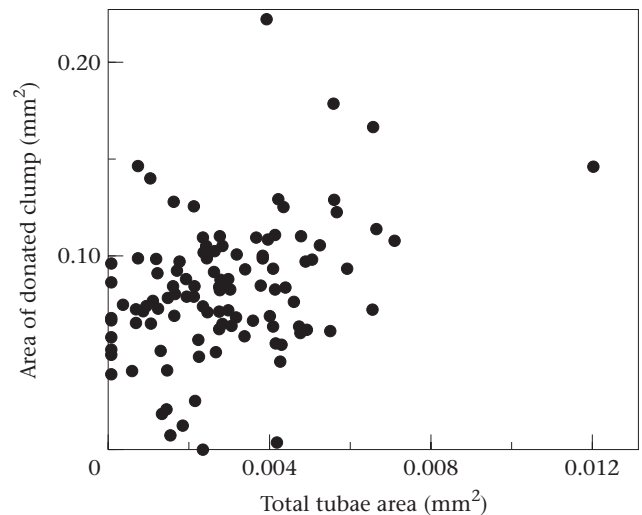
**Figure 1.** Experiment 1: the observed frequencies of no sperm transfer and sperm transfer in 147 pairs of *Schmidtea polychroa*. The expected values (in parentheses) were calculated from a binomial distribution as described in the Methods. In our sample the proportions  $p$  and  $q$  are given by the total numbers of mating individuals that did ( $Y$ ) or did not ( $N$ ) donate sperm:  $N:Y=103:109=0.486:0.514$ . Observed versus expected frequencies: chi-square test:  $\chi^2_1=21.8$ ,  $P<0.001$ . Note that the degrees of freedom have been reduced by one because  $p$  and  $q$  were calculated from the observed data.

### Experiment 2: Sperm Exchange When Interests Differ

Despite prolonged observation (96 h) only 16 out of 30 nonisolated  $\times$  nonisolated ( $N \times N$ ) pairs mated, whereas 27 out of 29 isolated  $\times$  isolated ( $I \times I$ ) and 25 out of 29 nonisolated  $\times$  isolated ( $N \times I$ ) pairs did (Table 1). This difference was highly significant (chi-square test:  $\chi^2_2=15.3$ , exact  $P<0.001$ ). Most  $I \times I$  pairs mated very soon after the start of the experiment, whereas  $N \times I$  pairs showed a delay, despite the clear initial increase (Fig. 4). The slow, linear increase in  $N \times N$  pairs shows that in this group matings took place at a low, constant rate. Although data for  $N \times I$  pairs could not be allocated to either the  $N$  or  $I$  individual, it is obvious that  $N$  individuals not only mated more readily with their  $I$  partner



**Figure 2.** Experiment 1: box plot of self-sperm (before copulation) in flatworms that (1) did not copulate, (2) copulated but neither received nor donated sperm, (3) received sperm without donating any, (4) donated sperm without receiving any, and (5) donated and received sperm. The box plot represents the median  $\pm 1$  quartile (box) and the range (lines). Difference between all five groups: ANOVA:  $F_{4,289}=8.9$ ,  $P<0.001$ . The difference is caused mainly by the nonmating and the 'received only' individuals (Scheffé's post hoc test).



**Figure 3.** Experiment 1: amount of self-sperm donated during a mating in relation to the amount of allosperm already present in the sperm storage organs (tubae) from previous mating(s). Spearman rank correlation:  $r_s=0.312$ ,  $N=109$ ,  $P=0.001$ .

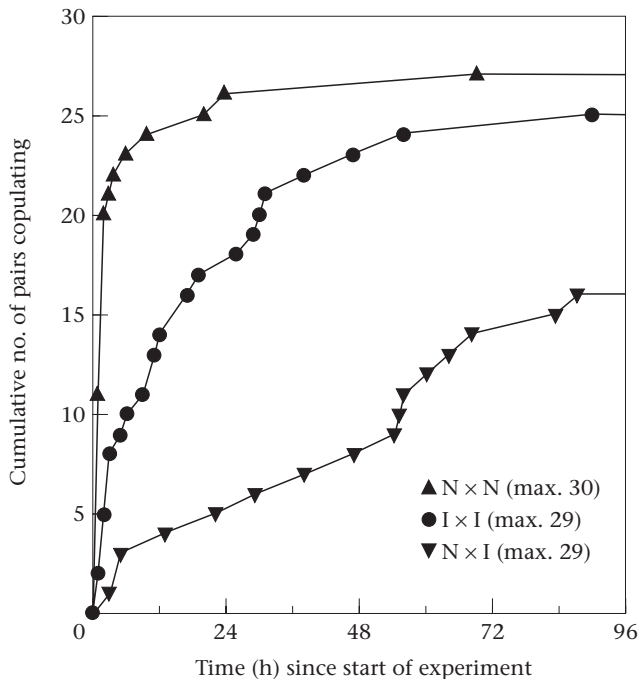
(Fig. 4), but also donated sperm more often (reciprocal transfers in Table 1) than  $N$  individuals in the  $N \times N$  results. Since the occurrence of a mating is determined by the willingness of the most reluctant individual, these data show that  $N$  individuals changed their behaviour depending on who was available.

There were also differences in the outcome of the matings. In  $N \times N$  pairs, symmetrical outcomes with either no or reciprocal transfer were more common than expected (Table 1), whereas unilateral transfer was less common than expected. This coincides with the results from experiment 1. In the other two groups, however, conditional sperm exchange disappeared and animals appeared to donate independently of sperm donation by their partner.

**Table 1.** Observed frequencies of sperm transfer in three groups in experiment 2

	N×N	I×I	N×I
No sperm transfer	6 (3.5)	7 (4.9)	2 (2)
Unilateral transfer	3 (8)	9 (13.2)	10 (10)
Reciprocal transfer	7 (4.5)	11 (8.9)	13 (13)

N×N: Nonisolated×nonisolated; I×I: isolated×isolated; N×I: nonisolated×isolated. The expected frequencies (in parentheses) were calculated as for Fig. 1. Observed and expected frequencies were significantly different only for N×N (chi-square test:  $P < 0.05$ ).



**Figure 4.** Experiment 2: cumulative number of pairs that copulated since the beginning of observations in the three experimental groups: nonisolated×nonisolated (N×N), isolated×isolated (I×I) and nonisolated×isolated (N×I). All groups were observed for 96 h. Kolmogorov–Smirnov: N×I versus N×N pairs:  $Z = 1.45$ ,  $P = 0.029$ ; N×I versus I×I:  $Z = 1.95$ ,  $P = 0.001$ .

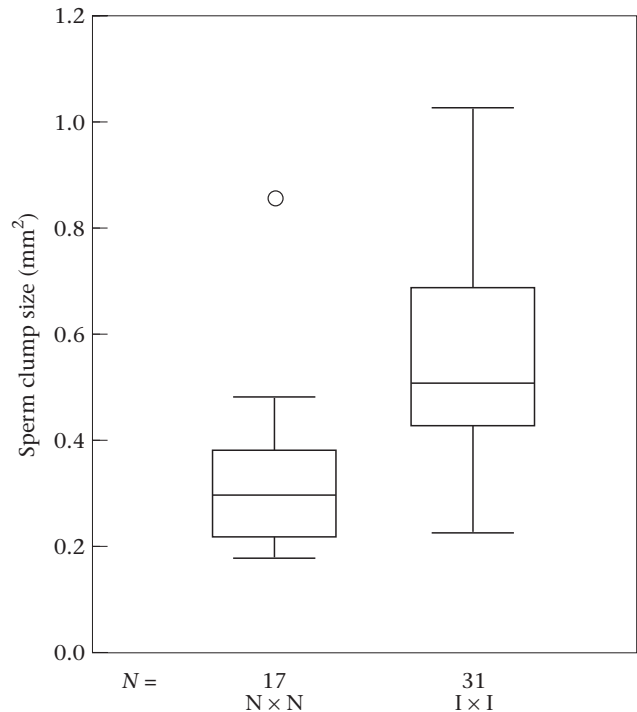
The sperm clumps in N×N pairs were smaller than those in I×I pairs (Fig. 5). Owing to the experimental design, we could not differentiate between N and I individuals in N×I pairs. This group is therefore not shown.

There was less allosperm in the tubae of mating individuals in isolated pairs (I×I:  $\bar{X} \pm SD = 4.5 \pm 5.2 \mu\text{m}^2$ ,  $N = 54$ ) than in non-isolated pairs (N×N:  $8.9 \pm 9.9 \mu\text{m}^2$ ,  $N = 32$ ; Mann–Whitney  $U$  test:  $Z = -2.66$ ,  $P < 0.01$ ).

## DISCUSSION

### Mating When Interests Are Similar

In nonisolated *S. polychroa* individuals, matings ended without sperm exchange in 35% of cases. Combined with the high incidence of reciprocal exchange (38%), this is a clear indication that sperm donation often depends on



**Figure 5.** Experiment 2: box plot of sperm clump size in nonisolated×nonisolated (N×N) and isolated×isolated (I×I) pairs. The box plot represents the median±1 quartile (box) and the range (line); O: outlier. Student's  $t$  test (unequal variances):  $t_{42} = 4.49$ ,  $P < 0.001$ .

sperm receipt in *S. polychroa*. Hence, they trade ejaculates, even if this is not obligatory, as shown by the 27% unilateral inseminations. Individuals did not trade sperm by volume, as in *D. gonocephala* (Vreys & Michiels 1998). Although the availability of self-sperm influenced sperm donation (as in Michiels & Streng 1998), it is insufficient to explain the observed pattern, as it would result in a partner-independent mating pattern. Our results confirm the prediction that sperm trading should be more explicit in nonisolated individuals. Michiels & Streng (1998) found 17% no sperm transfer and 63% reciprocal exchange. The shift towards the latter must be attributed to the fact that they worked predominantly with isolated individuals.

In other hermaphrodites, in which unilateral insemination is absent or rare, mates may assess the likelihood of sperm exchange before rather than during copulation. In the land snail *A. arbustorum*, for example, most premating interactions do not lead to copulation, but when they do, sperm transfer is virtually always reciprocal. Although Baur et al. (1998) did not consider this trading, it remains to be shown whether an individual that is capable of donating sperm refuses to do so when the partner signals that it is not willing to reciprocate.

Full allosperm stores are characteristic for individuals that have received sperm recently (Michiels & Streng 1998; this study). Since mating also involves the donation of a large ejaculate, one could expect recently mated individuals to have fewer self-sperm. Surprisingly, the opposite was true: individuals with more allosperm in

store had more self-sperm available, irrespective of what they did during the experiment (mating or not, sperm donation or not). Those that did mate also donated more if they had received more in the recent past (as indicated by large allosperm stores). It suggests that digestion of ejaculates enhances self-sperm production. Hence, by donating an ejaculate, planarians may enhance the male function of their partner, rather than providing a nuptial gift to the female function. This is an exciting possibility, but we should consider two alternatives.

First, some individuals may be more 'male', others more 'female' biased. The resultant higher investment in sperm and frequent matings in the former, and vice versa in the latter, would result in the same effect. Data from Peters et al. (1996), however, suggest only limited variation in sex allocation in *S. polychroa*. Rather than finding a trade-off between mating and cocoon production, they showed that individuals that produced many cocoons also mated more often and vice versa. In addition, potential sperm donors would be under strong selection not to inseminate male-biased individuals, making this alternative less likely.

Second, individuals in good condition may produce more sperm, mate more and therefore receive more. Although this is very plausible, we would have expected to see differences when comparing mating and nonmating individuals in our experiment. The relationship between allosperm and self-sperm existed in all groups, and allosperm stores were equally full in all of these.

### Mating When Interests Are Dissimilar

Our second experiment showed that isolated individuals mated immediately after the trial started and abandoned conditional reciprocity. It suggests that when matings are rare and self-sperm plentiful, the cost-benefit balance of sperm donation favours indiscriminate donation. This coincides with the prediction of male-biased mating when matings are not common (Greeff & Michiels 1999).

The  $N \times I$  pairs were intermediate in terms of reluctance to mate, whereas the likelihood of insemination was similar to that in  $I \times I$  pairs. Assuming that in  $N \times I$  pairs the most reluctant individual (presumably  $N$ ) determines whether a mating takes place, our results indicate that individuals use precopula information to make mating decisions. Hence, although body size (Peters & Michiels 1996b) and relatedness (Peters & Michiels 1996a) do not play a role in mate choice in *S. polychroa*, the reproductive condition of a partner does.

There are at least two reasons why nonisolated individuals may readily accept a previously isolated partner. First, the data show that the latter is more eager to donate, it will do so unconditionally, and it will give a large ejaculate. Hence, isolated individuals represent a nutritional resource for nonisolated conspecifics: they pay more for sex. Second, an isolated individual is also attractive as a female. It is likely to have less allosperm stored in its tubae (Michiels & Streng 1998; this study), and therefore represents a lower risk of sperm competition and a higher chance that its eggs can be fathered.

Although we did not differentiate between  $N$  and  $I$  individuals in the  $N \times I$  treatment, the relatively high number of reciprocal matings suggests that nonisolated individuals did not simply accept a free meal, but were also seduced by the 'sexy mother' effect.

In conclusion, our data confirm that *S. polychroa* trades sperm. They also suggest that when mating takes place ad libitum, it is not simply the cost of sperm donation and the benefit of sperm receipt but also the female quality of the partner that appears to determine whether an individual will insist on sperm trading. Our results suggest that sperm are donated more eagerly when the partner is more attractive as a female. Since in a natural population the reproductive value of an individual is likely to vary over time, female quality may offer an explanation for why 27% of the pairs in the first experiment donated sperm unilaterally. Hence, although the primary function of matings in hermaphrodites may still be to inseminate rather than to become inseminated, sperm donors will have to be bribed with sperm when mating opportunities are plenty and mate quality (measured in fertilization chances) accordingly poor. A very interesting suggestion that emerged from this study is that individuals may actually digest sperm to produce more self-sperm, but this needs to be confirmed in an experiment that is specifically designed for this question. The picture that emerges is subtler than the conclusion of Peters et al. (1996) and Peters & Michiels (1996a, b), that mate choice is of minor importance in this species.

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