



Mate choice in a hermaphrodite: you won't score with a spermatophore

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Sexual selection has played a major role in shaping the wide variety of mating patterns found in species with separate sexes, but little is known about its effects on simultaneous hermaphrodites. However, many hermaphrodites possess complex reproductive systems and mating behaviour is often elaborate, suggesting that some form of mate assessment takes place. We found that the marine slug *Aeolidiella glauca*, a simultaneous hermaphrodite with reciprocal external sperm transfer via spermatophores, shows a unique mate choice behaviour by avoiding mating with conspecifics already carrying a spermatophore received during the previous mating. Current mating status did not seem to affect this behaviour, because both slugs that had mated 2–3 days before our mate choice trials and slugs that had been isolated for 4–6 weeks avoided spermatophore-carrying partners. There are two obvious reasons why slugs should avoid recently mated partners. First, they may reduce the risk of getting a partner depleted in self-sperm. Second, the risk of sperm competition may be decreased. Histological investigations of sperm reserves suggest that sperm depletion did not influence our mate choice experiments. Most slugs had sufficient sperm stored for spermatophore production. Therefore, the most likely explanation for *A. glauca*'s peculiar mate choice is that, by avoiding a recently mated partner, a sperm donor may reduce its risk of being subjected to sperm competition.

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Much progress has been made in understanding the crucial role of sexual selection in shaping the wide variety of mating patterns found in species with separate sexes (Andersson 1994). There are also several examples of sexual conflicts in simultaneous hermaphrodites (e.g. Leonard & Lukowiak 1984; Fischer 1987; Petersen 1995; Sella et al. 1997; Michiels & Newman 1998; Michiels & Streng 1998), but we still know little about mate choice and mate competition in such animals (e.g. Vreys & Michiels 1997; Michiels & Streng 1998; Michiels & Bakovski 2000). However, hermaphrodites may also compete to fertilize a given number of ova (Bateman 1948; Charnov 1979, 1996; Morgan 1994; Michiels 1998), and any characters that enable individuals to fertilize a larger portion of these eggs than the average hermaphrodite might therefore be considered sexually selected traits. However, selection on the male function is not independent of that acting on the female function. Consequently, it may be more difficult to

identify such traits in hermaphrodites (Bateman 1948; Queller 1983), and certain effects of sexual selection are restricted in hermaphrodites (Morgan 1994). For instance, selection on traits related to mate acquisition is expected to be intrinsically weaker in hermaphrodites than in gonochorists (Greeff & Michiels 1999a). In hermaphrodites, sexual selection may instead act more subtly through sperm competition or cryptic female choice (Eberhard 1996; Baur 1998).

Hermaphrodite reproductive structures often show amazing complexity, and mating behaviour can be elaborate (Hyman 1951; Lind 1976; Vreys & Michiels 1997; Michiels 1998 and references therein). Prolonged courtship gives ample opportunity for partner assessment, which may set the stage for mate choice in hermaphrodites. It is not obvious, however, which traits might be of importance in hermaphrodite mating decisions, and studies revealing precopulatory mate choice in simultaneous hermaphrodites are recent and still rare (Tomiyama 1996; Yusa 1996; Vreys & Michiels 1997; Michiels & Bakovski 2000; Michiels et al. 2001; Lüscher & Wedekind 2002).

Bateman's principle, originally designed to explain differences in mating interests between males and females, states that multiple matings primarily serve the

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male interest of an individual (Bateman 1948). This principle is also valid for hermaphroditic animals (Charnov 1979), and hermaphrodites are thus expected to mate readily, that is, donate sperm, whenever there are opportunities to do so. However, this prediction is true only provided that the male function remains cheap. When population densities are high, and multiple matings common, animals must invest more in sperm to outnumber that of their rivals. As a consequence, allocation to sperm may become as expensive as allocation to eggs (Greeff & Michiels 1999b), and sperm donors may become choosy about to whom they donate sperm.

The origin of hermaphroditism has been linked to low population density (Ghiselin 1969), suggesting little importance of sperm competition. However, hermaphrodites frequently live under high-density conditions. Furthermore, multiple matings are common in many species (e.g. Kutschera & Wirtz 1986; Baur 1988; Peters & Michiels 1996; Peters et al. 1996; Vreys et al. 1997), indicating that sperm competition may be as important in hermaphrodites as in any other animal species. Many hermaphrodites have also evolved sperm storage organs or specialized means of digesting excess sperm (Giese & Pearse 1977; Tompa et al. 1984; Sluys 1989; Michiels & Streng 1998). These specializations may select for sperm quantity or quality, as suggested in the land snail *Arianta arbustorum*, where the recipient may be able selectively to store and digest sperm from different partners (Haase & Baur 1995).

We have investigated mate choice in the simultaneously hermaphroditic nudibranch *Aeolidiella glauca*, which has a unique mating behaviour with reciprocal sperm transfer via external spermatophores (Haase & Karlsson 2000; Karlsson & Haase 2002). We conducted two experiments. The first, performed in 1998, showed that slugs choosing mates avoided conspecifics that already carry spermatophores. In 2000, we investigated whether this mate choice behaviour is affected by current mating status. Work on a planarian flatworm *Schmidtea (Dugesia) polychroa* (Michiels & Streng 1998; Michiels & Bakovski 2000), has shown that animals isolated before mating are more eager to mate, that is, donate sperm, presumably because they have more sperm than nonisolated worms. Furthermore, nonisolated animals traded sperm, unlike the isolated ones. A similar pattern of sperm allocation was found in another marine slug, *Navanax inermis* (Michiels et al. 2003). It seems plausible that mating status might also be crucial in matings of *A. glauca*. Slugs with high mating rates, which have already spent lots of resources on producing sperm, should thus be more choosy about to whom to donate sperm than isolated animals, which have had more time to replenish their self-sperm stores.

METHODS

Study Species

Aeolidiella glauca is a common nudibranch in intertidal eelgrass, *Zostera marina*, beds along the coasts of northern Europe. The species is annual, and the reproductive season

lasts from mid-June to late August. *Aeolidiella glauca* transfers sperm externally via spermatophores (Haase & Karlsson 2000; Karlsson & Haase 2002), unlike most other nudibranchs where reciprocal copulation is the rule (Hyman 1967; Hadfield & Switzer-Dunlap 1984). Usually, mating is preceded by a courtship phase where the slugs move in circles before resting in a head-to-head position, reciprocally touching each other with their tentacles and mouths. Then the slugs assume a position where the everted genital atria come into contact, and the penes are simultaneously erected shortly after. Both animals stroke the back of their partner with their penis, while depositing a spermatophore. It usually takes more than 2 h until the sperm contained in the spermatophore are set free and start to travel towards the female gonopore. Courtship can be abbreviated and often the slugs mate without displaying any preceding courtship behaviour, suggesting that chemical cues are important. Most premating interactions do not lead to matings, but when they do, sperm transfer is virtually always reciprocal and simultaneous (>88%; Karlsson & Haase 2002). Mating always involves only two animals. *Aeolidiella glauca* typically mates repeatedly throughout the reproductive season, and viable sperm can be stored for several weeks. There is no self-fertilization in *A. glauca* (A. Karlsson, unpublished data).

Collection and Maintenance

Animals were collected by scuba diving in Gullmarsfjorden on the west coast of Sweden (58°15'N, 11°28'E), in June 1998 and 2000, and transported to Klubban Biological Station. There animals were kept individually in small (250 ml) plastic jars, each with its own supply of running sea water. All slugs were fed sea anemones, *Sagartiogeton viduatus*, ad libitum. The plastic jars were cleaned and excess food removed every second day. Slugs were kept in the laboratory until mate choice trials took place 4–6 weeks later.

Experiment 1: Avoidance

Mate choice trials ($N = 34$) involving three individuals were set up in small aquaria (20×12 cm and 15 cm high) in July 1998. In each trial, two of the slugs had been mated, although not to each other, earlier the same day. Both had transferred spermatophores to their partners, but only one carried a spermatophore. The other one had either not received a spermatophore in the previous mating or had lost its spermatophore immediately after mating, that is, before sperm could be set free and reach the gonopore. The third slug had been kept isolated since capture to increase its eagerness to mate. In all trials, the previously mated slugs were of equal weight, but the unmated one was alternately smaller or larger (size difference $\geq 25\%$). Size has no direct effect on mate choice in *A. glauca* (Karlsson 2001). Therefore, we could use this set-up to recognize slugs individually. We observed slugs continuously for 12 h or until mating between any two took place. Furthermore, we monitored courtship behaviour of all slugs, primarily to ensure that

the spermatophore-carrying animals were not behaving differently, that is, were less apt to solicit matings than the other animals. When possible, we also noted which slug initiated and which terminated mating.

Experiment 2: Mating Status

Mate choice trials ($N = 110$) involving three slugs were also run in July 2000. In each trial, two of the slugs had been previously mated, but not to each other, 8–9 h before mate choice trials. Both had transferred spermatophores to their partners. One slug was allowed to keep the spermatophore, and the other slug's spermatophore was removed with a plastic pipette and forceps. The third slug, the focal animal, had either been isolated since capture (i.e. for 4–6 weeks) or had been allowed to mate, the last time 2–3 days before the mate choice trial. As in 1998, the previously mated slugs were of approximately equal size, and the unmated slug was alternately smaller or larger (size difference $\geq 25\%$). Mate choice trials involving nonisolated focals ($N = 57$) were conducted between 7 and 14 July, and those with isolated focals ($N = 53$) between 16 and 23 July. Focal animals that were inactive, that is, that did not display courtship behaviour, were excluded and replaced by others. Mate choice trials took place in small (250 ml) plastic jars and were conducted in the morning. We observed slugs continuously for 5 h or until mating between any two took place. For both previously mated slugs, we calculated a courtship index by scoring one point each for trail following and tentacle contact, and two points for oral contact and penis protrusion.

In all successful trials (i.e. where mating took place) involving nonisolated slugs, the two previously mated animals were fixed in 70% ethanol. In histological sections their auto- and allosperm reserves were checked. In both cases, we distinguished between two states. Autosperm reserves (with experimental mating trial taken into account) were divided into 'enough sperm for transferring a spermatophore' or 'not enough sperm', and allosperm reserves into 'many sperm in seminal receptacle' or 'receptacle densely packed with sperm'. In no case did we encounter a receptacle that was empty or contained only few sperm.

In both 1998 and 2000, new animals were used in each trial. We used clean aquaria/plastic jars in all trials so that possible chemical cues were not carried from one trial to the next.

RESULTS

Experiment 1: Avoidance

Mating took place within the designated observation period in 19 of the 34 trials. In the majority of cases (16 of 19), mating occurred significantly more often than expected by chance between the previously isolated animal and the previously mated individual lacking a spermatophore ($\chi^2_2 = 22.22$, $P < 0.001$). The spermatophore-carrying slugs accounted for, on average, the

expected one-third of all soliciting attempts (28%), and those without spermatophores accounted for the remaining two-thirds (72%; range of total solicitations within trios 2–25).

Because of the extreme synchronization of sperm transfer in *A. glauca*, we were able to tell which slug initiated or terminated mating in only seven of the 19 successful trials. In five of these, one slug both initiated and terminated mating. In the remaining two trials, different slugs initiated and terminated mating. In both of these instances, the slug already carrying a spermatophore took the initiative to mate, and the other slug was the first to withdraw.

Experiment 2: Mating Status

Nonisolated focals

In 17 of the 57 trials, mating took place within the designated observation period. Significantly more (13 of 17 cases) matings occurred between the focal animal and the previously mated individual lacking a spermatophore ($\chi^2_2 = 14.59$, $P < 0.001$) than expected by chance. There were three matings between the focal animal and the animal carrying a spermatophore. Only one mating involved both nonfocal animals.

Courtship activity was low, but there was no difference between previously mated slugs with and without a spermatophore (median courtship index/interquartile range/range, slugs with spermatophores: 0/0–2/0–4; slugs deprived of spermatophores: 1/0–2/0–4, $N = 17$ in both groups; Wilcoxon signed-ranks test: $Z = 0.120$, $P = 0.905$). Previously mated slugs did not differ in their sperm reserves (autosperm, $N = 32$, two ampullae lost during preparation: $\chi^2_1 = 0.52$, $P = 0.47$; allosperm, $N = 31$, three receptacles lost: $\chi^2_1 = 0.09$, $P = 0.77$). In each group, only three animals were depleted in autosperm.

Isolated focals

Mating took place in 17 of the 53 trials. In 14 cases, mating occurred between the focal animal and the animal lacking a spermatophore ($\chi^2_2 = 18.47$, $P < 0.001$). The focal animal mated with the spermatophore-carrying individual in two trials, and in one case mating took place between the two previously mated slugs.

Slugs carrying spermatophores did not differ in courtship activity from those lacking spermatophores (median courtship index/interquartile range/range, slugs with spermatophores: 0/0–0.25/0–2; slugs deprived of spermatophores: 0/0–1.25/0–3, $N = 17$ in both groups; Wilcoxon signed-ranks test: $Z = 1.633$, $P = 0.102$).

DISCUSSION

This study shows that the simultaneous hermaphrodite *A. glauca* has a unique precopulatory behaviour, where the presence of external spermatophores is used to assess partners. Slugs carrying a sign of previous mating activity, that is, a spermatophore, were discriminated against in a situation where partner choice was possible. This result

does not seem to have resulted from lack of interest on behalf of the spermatophore-equipped animals, because these animals were as active as the others in trying to solicit matings. In several trials, spermatophore carriers were involved in prolonged courtship before finally being avoided, and it seems likely that the slugs must be close to each other before they are able to detect a spermatophore.

Mating status, however, did not seem to influence spermatophore avoidance behaviour. Both slugs that had been isolated and slugs that had not been isolated refused to mate with spermatophore-carrying conspecifics. This finding was somewhat surprising, because the cost-benefit ratio of producing an ejaculate is likely to vary depending on current mating status. An animal that has been isolated has presumably been able to build up more resources than an animal involved in previous mating activities. Consequently, we would expect the isolated animal to be more eager to mate and less choosy about to whom it donates sperm. As Michiels & Bakovski (2000) found, isolated flatworms were more eager to mate than nonisolated ones and donated more sperm unconditionally. However, these flatworms donate free sperm, so it is possible that sperm production is less costly than in *A. glauca*. In our study, isolated slugs remained choosy, indicating that sperm also remained costly.

Choosiness in general may vary over the reproductive season. Early in the season, most slugs have presumably received and stored less sperm than later in the season. The risk of being subjected to sperm competition is thus likely to increase with time. The isolated focal animals were tested between 16 and 23 July, when many animals in the field would have mated. All individuals sectioned had more or less full allosperm stores. It is thus possible that all animals, regardless of mating status, show a high degree of choosiness. On the other hand, the advanced season might also result in reduced choosiness. In *A. glauca*, mortality increases as the season progresses, to be complete by the end of August. Hence, costs of mate search and choice should increase as the number of available partners and time left for mate search decrease (Real 1990; Johnstone 1997). However, this scenario does not seem to apply to our study species. Sperm is apparently too costly an investment even in a situation where mating becomes less likely.

Mating frequencies appeared to be low in our experiments. We have to be cautious with such a statement, though, because there are no data providing an expected frequency. We suggest two possible, not mutually exclusive, explanations for why the observed frequencies might have been low. In *A. glauca*, many premating interactions never lead to copulation, but when they do, sperm transfer is almost always reciprocal (>88%; Karlsson & Haase 2002). It is possible that slugs can assess the likelihood of sperm exchange before copulation, and that the mating rates in our experiments reflect some kind of discrimination behaviour against partners that may not reciprocate, or that are undesirable in some other respect. It could also be that some of the previously mated slugs had run out of as yet unknown resources for spermatophore production other than sperm. Similarly, the low courtship activity of the previously mated slugs, although

it did not prevent mating, may have resulted from depletion of resources or energy.

Why, then, were animals with spermatophores avoided as partners? One obvious advantage of such a behaviour would be to decrease the risk of sperm competition. Sperm competition in *A. glauca* is inferred from high mating frequencies observed in the field (A. Karlsson, unpublished data) and sperm storage (Haase & Karlsson 2000). Another interpretation is that, by avoiding partners with spermatophores, slugs decrease the risk of getting a partner depleted in self-sperm. If the primary aim of mating is to receive sperm, it would be highly advantageous for slugs to evolve mechanisms by which partners depleted in self-sperm can be recognized and subsequently avoided.

In this study, both previously mated slugs were, on average, equal with respect to sperm depletion. A few of the investigated slugs had low amounts of self-sperm, but most animals had more than enough sperm in store for spermatophore production. We therefore consider it unlikely that spermatophore avoidance is a mechanism to avoid partners depleted in sperm. More probably, it functions as a safeguard against sperm competition. Consequently, a spermatophore would signal that successful sperm transfer has occurred, and subsequent partners would thus do better, that is, increase their probability of fertilizing eggs, by avoiding slugs already carrying spermatophores and instead mate with someone else. This behaviour further serves the best interest of the sperm donor. By transferring a spermatophore that discourages future potential partners, the sperm donor may exercise a form of remote mate guarding, decreasing the risk of being subjected to sperm competition and increasing its own reproductive success via the male function.

Although the external spermatophores of *A. glauca* initially may have evolved for any of several different reasons, of which the simplest and most straightforward is probably packaging of sperm, they now appear to have gained a secondary function. This study shows that spermatophores function as warning flags to subsequent partners, and thus may have considerable impact on mate choice in *A. glauca*.

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