Multiple paternity and mate competition in non-selfing, monogamous, egg-trading hermaphrodites

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Multiple paternity and mate competition in non-selfing, monogamous, egg-trading hermaphrodites

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Abstract

In animals in which the two sexes invest relatively similar amounts of resources in their young, the number of mates is expected to affect male and female reproductive success similarly and gender conflicts on the number of mates may not arise. Correspondingly, in non-selfing, simultaneous hermaphrodites with long-term monogamy, the two partners are expected to alternate repeatedly their sexual roles and invest similarly in their offspring. Therefore, the gender conflict on the number of mating partners should not arise. However, when >2 conspecifics are present, hermaphrodites are known to plastically adjust their behavior and sex allocation and compete for mating repeatedly in the male role. We tested whether this leads to multiple paternities of single egg clutches in experimental replicates of small and large groups of non-selfing, egg-trading, behaviorally monogamous polychaete worms (*Ophryotrocha diadema*) by using neutral genetic markers to estimate paternity. Multiply fertilized egg cocoons were common in these worms; two or more individuals succeeded in fertilizing the same egg cocoon and mate competition increased with group size. Multiply fertilized egg cocoons had a higher proportion of eggs developing into mature worms than singly fertilized egg cocoons. Possibly singly fertilized cocoons had a lower fertilization rate owing to low sperm counts and aflagellate sperm.

Keywords

Multiple mating Egg cocoons External fertilization Polychaete worms *Ophryotrocha diadema*

Introduction

Since the publication of the seminal paper by Bateman ([1948](#)), the number of mates that males and females get has been considered crucial for the understanding of sexual behavior and the mechanisms of sexual selection. Indeed, Bateman's principle states that males and females may have conflicting interests on the number of mating partners, as a result of the asymmetry in parental investment. In this view, male fitness generally increases with the number of matings, whereas female fitness does not, as it is usually limited by the resources available to produce eggs. Besides the evidence brought by Bateman ([1948](#)) on *Drosophila melanogaster*, support for this principle comes from many observational and experimental works, which confirm that the reproductive success of males such as, for example, elephant seals and red deer, increases rapidly with matings, whereas that of females is often ensured by just one mating (Le Boeuf and Reuter [1988](#); Clutton-Brock et al. [1982](#)). These diverging interests create gender conflicts. However, multiple mating is

also advantageous for females when they obtain resources (e.g., males help in brood rearing, or donate nuptial gifts or resource-rich spermatophores) or genetic benefits (Arnqvist and Rowe 2005).

There are several exceptions from Bateman's principle such as species with monogamous mating systems. There, the two sexes invest relatively similar amounts of resources in their young. As a consequence, the number of mates is expected to affect males and females similarly and gender conflicts on the number of mates may vanish (e.g., *Rissa tridactyla*, Clutton-Brock 1983).

The distribution of paternity between and within broods is also of great interest to understand how sexual selection operates on the mating systems of hermaphroditic organisms (Leonard 2005, 2006; Lorenzi and Sella 2008; Anthes et al. 2010; Pélissié et al. 2012). In simultaneous hermaphrodites, in which the two sexual functions are tied in the same organism, the gender conflict resides within the same individual, as different gains may be obtained by mating via the male vs the female functions. For example, land snails can digest allosperm and exhibit a preference for mating in the female role, but the female role exposes snails to partner seminal fluids that reduce egg output (Koene 2006; Koene et al. 2010). Sea slugs mate traumatically, as the slugs that copulate as males pierce the integument of their partners and may inflict damages to their partner's female function (Lange et al. 2012). Other hermaphrodites have long-term monogamous mating systems (e.g., Petersen, 2006). Here, two partners are expected to faithfully mate with each other and repeatedly alternate sexual roles in successive mating events, thus playing once the male and once the female role. The regular alternation of sexual roles results in equal investments in the offspring by the two partners, and therefore the reproductive success via male and female functions should be equally affected by the number of mates—as it occurs in separate sex species with monogamous mating systems. Therefore, the gender conflict on the number of mating partners should not arise in hermaphrodites with monogamous mating systems.

Among the internally fertilizing hermaphrodites, examples of serial monogamy are offered by the sea slugs *Navanax inermis* and *Chelidonura hirundinina* (Leonard and Lukowiak 1984; Anthes et al. 2005). Among the externally fertilizing hermaphrodites, the best known examples of such mating systems are the coral reef fishes *Hypoplectrus nigricans* (Fischer 1980, 1981) and *Serranus tortugarum* (Petersen 1995, 2006), and the polychaete worm *Ophryotrocha diadema* (Sella 1985). All these hermaphrodites trade gametes (Leonard 2005). Sea slugs trade sperm, whereas in serranid fish and polychaete worms, partners trade eggs and share the costs of producing them, i.e., they "provide eggs (or access to eggs) to a partner in return for access to the partner's eggs for fertilization" (Leonard 2005, p. 857). Indeed, egg trading inhibits the success of interference competition (Leonard 2006) and may therefore have evolved just as a response to solve gender conflicts within pairs of hermaphrodites (Fischer and Petersen 1987).

In the hermaphroditic marine polychaete worm *O. diadema*, long-term monogamous pairs are expected to persist in low-density populations, in which there is no competition for mating and the cost of deserting partners may be high. Otherwise, worms aggressively compete with each other for mating in the male role (Lorenzi et al. 2006). This occurs because these hermaphrodites tend to increase their reproductive success by forfeiting their turn to spawn eggs, deserting their partners, rapidly shifting to a polygamous mating system and competing for mating in the male role (Sella and Lorenzi 2000; Lorenzi et al. 2008). Indirect evidence suggests that multiple matings do occur in these egg-trading hermaphrodites, i.e., that >1 hermaphrodites can simultaneously release their sperm on their partner's eggs. First, adult hermaphrodites compete not only with each other but also with adolescent males (protandrous phase) for the male role (Sella and Lorenzi 2003). Second, mature hermaphrodites increase the proportion of reproductive resources allocated to the male function relative to those allocated to the female function when mating opportunities increase. The enhanced male function results in aggressive interactions between conspecifics (Lorenzi et al.

2006). These observations suggest that mating repeatedly in the male role may increase the reproductive success of worms via the male function, but it is unclear whether it would also be beneficial for their female function.

Here, we tested whether multiple paternities occurred in the simultaneous hermaphrodite *O. diadema* as a result of "male–male" competition using group size as a cue for the intensity of competition. We also tested whether multiple paternity, as quantified by a genetic marker, was beneficial for offspring survival. As we knew that these monogamous hermaphrodites may prefer to mate in the male role (Di Bona et al. 2010), we expected that multiple "males" fertilize the same egg cocoon and that the intensity of mate competition increased with group size. Additionally, because these worms produce few and immotile sperm, we expected that multiple fertilization resulted in a higher fertilization rate, and might thus be beneficial for the female function as well.

Material and methods

The model species

O. diadema is a model species for studying the evolution of mating systems in hermaphrodites with external fertilization (Sella 1985, 1988, 1990, 1991). Natural populations of these polychaete worms live in organic sediments, e.g., in mussel beds in harbors. These worms are iteroparous and exhibit either the male or the female role in a single mating event; at each event, a worm plays the male role and the other the female role and partners release their gametes nearly synchronously (pseudocopulation, Westheide 1984). In pairs, worms alternate their sexual roles with a regular schedule across several successive mating events (Sella 1985). The worm taking on the male role ("male") releases its sperm inside the jelly egg cocoon that the "female" worm has just produced and that surrounds "her" body. The "female" completes egg laying and then leaves its cocoon. In general, cocoons contain 20–25 eggs, which develop into free-living larvae within 8 days and into mature hermaphrodites within approximately 45 days (Åkesson 1976). In mature worms, eggs can easily be detected through the transparent body wall as either yellow or whitish eggs. In these worms, a dominant Y allele determines a yellow egg color, while the recessive y allele determines a white egg color (Sella and Marzona 1983). In our laboratory, we rear YY and yy worms in separate cultures. By means of this genetic marker, we can identify focal worms in a group and ascribe their progeny. Following Åkesson (1976), this marker is neutral, since there is no difference in worm mortality rates before sexual maturity. However, we checked whether hatching success and survival rate differed between cocoons which produced either all-white or all-yellow or both white and yellow brood.

All specimens were obtained from our mass laboratory cultures contained in 100-ml bowls inside thermostatic chambers which were maintained at 20 °C (marine water, 1.024 g/m^3) and fed spinach. During the experiment, worms were kept in 10-ml bowls, reared at 20 °C and fed spinach ad libitum.

Experimental procedure

We set up two kinds of replicated groups of newly matured, same age and size, virgin hermaphrodites, obtained from pairs of parents bred in separate bowls. In each group there was one yellow-phenotype worm (YY genotype, thereafter focal individuals) and different numbers of white-phenotype worms (yy genotype). Small groups were composed of triplets: the focal worm and two white-phenotype worms ($n = 20$ replicates); large groups were composed of 12 worms: the focal worm and 11 white-phenotype worms ($n = 95$ replicates). We checked these groups every

second day for white-egg cocoons containing more than ten eggs. In total, we collected 250 cocoons during a period of 12 days. Each time we found a cocoon, we gently moved it into a separate 10-ml bowl and grew larvae until they developed into mature hermaphrodites. When these worms matured and had eggs in their coeloms, they expressed their yellow or white phenotypes and we assessed their paternity (i.e., about 45 days after egg laying). Maternity was known as we only reared white eggs, laid by white-phenotype worms. Paternity was assigned using the genetic marker for egg color. Because the yellow phenotype is a dominant trait, these worms had either the yellow or white phenotype, depending on whether they were sired by yellow- or white-phenotype worms (Fig. 1).
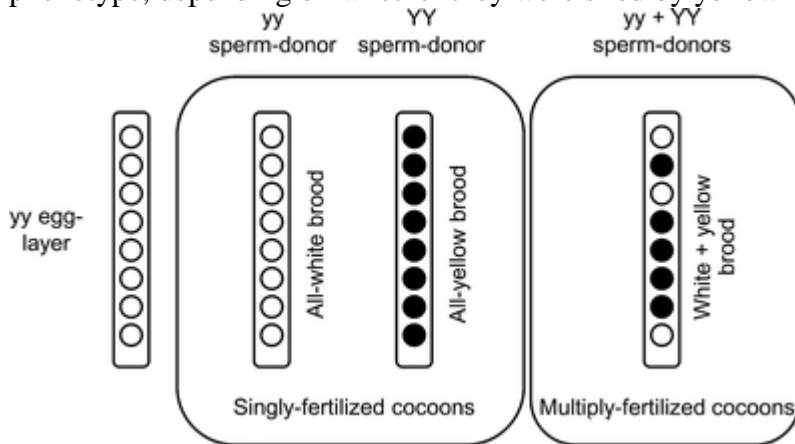

Fig. 1

Schematic view of the experiment and paternity assignements based on the genetic marker

Because we used a genetic marker which results in two alternative phenotypes, we assigned ≤2 paternities, potentially underestimating the number of potential fathers in large groups. A cocoon was multiply fertilized when the brood had partly the white phenotype and partly the yellow phenotype. From the large groups, 151 cocoons (with entirely white egg phenotype) were excluded from the analyses because it was impossible to check whether they were singly or multiply fertilized (there were ten potential white fathers in the bowls), reducing our sample size to 99 cocoons.

Brood survival rate was measured as the proportion of eggs that developed into mature worms (in about 45 days) in singly and multiply fertilized cocoons.

Statistical analyses

In the data set from small groups, we investigated whether female investment was affected by the number of sperm donors by testing whether the number of eggs differed between singly and doubly fertilized cocoons. To this aim, we used a general linear model (thereafter, GLM) on ln-transformed number of eggs (categorical predictor variable: number of sires). We also tested whether sire number and phenotype (white-phenotype sire vs yellow-phenotype sire vs both yellow- and white-phenotype sires) affected brood survival rate using a generalized linear model (thereafter, GZLM) for binomially distributed data (logit link). We fitted the number of eggs which developed into mature worms and the total number of eggs as dependent variables, and the type of brood developed from each cocoon (all-white brood, all-yellow brood, and white + yellow brood) as the categorical predictor variable.

Finally, we investigated whether cocoons were fertilized by on average more than two sperm donors using data from both small and large groups. To this aim, we used a reduced data set of 29 cocoons which were surely multiply fertilized (i.e., the brood was partly yellow and partly white)

and where >50 % of the brood developed into adult hermaphrodites. We fitted a generalized linear mixed model (GLMM) for binomially distributed data, with logit link and replicate (i.e., cocoons from the same replicate) as a random effect and tested whether the proportion of brood sired by focal worms depended on group size (i.e., the number of competitors over the male function, either one or ten). Therefore, we fitted the number of brood sired by focal worms (i.e., brood with yellow phenotypes) and the total number of brood as dependent variables, and group size as the categorical predictor variable (IBM SPSS statistics version 20). Mean values ± SE are reported.

Results

Small groups - evidence for multiple paternity

Of 19 cocoons, nine (47 %) were fertilized by the two "males", and ten by only one (four by the focal worms only and six by their rivals; Fig. 2). The size of singly and doubly sired cocoons did not differ significantly, as they had approximately the same number of eggs (singly sired cocoons, 28.30 ± 2.704 eggs; doubly sired cocoons, 24.33 ± 1.118; GLM, $F_{1,17} = 1.482$, $P = 0.240$).
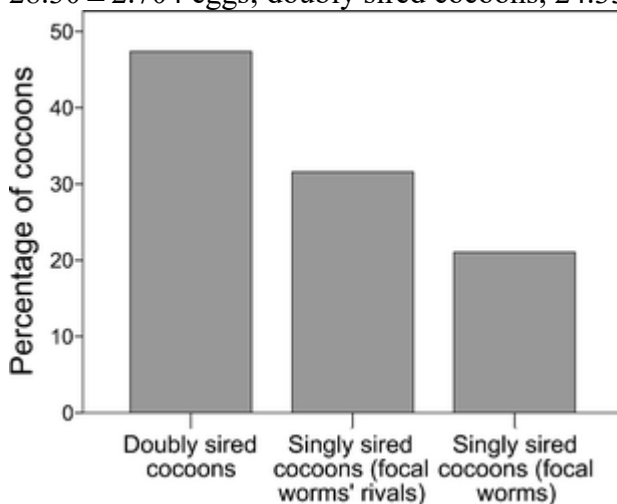

Fig. 2

The percentage of cocoons fertilized by either one or two worms in small populations

Small groups - brood survival rates and the number of sires

The proportion of eggs which developed into mature hermaphrodites differed between cocoons depending on whether the brood was doubly or singly fertilized (likelihood ratio $\chi^2 = 40.778$, df = 2, $P < 0.0001$; Fig. 3). Indeed, brood survival rate was significantly higher in doubly sired cocoons than in singly sired cocoons (either all-yellow or all-white brood; doubly sired vs all-yellow brood: Wald $\chi^2 = 21.435$, df = 1, $P < 0.0001$; doubly sired vs all-white brood: Wald $\chi^2 = 32.167$, df = 1, $P < 0.0001$). Instead, there was no significant difference in brood survival rate between cocoons which produced either all-white or all-yellow brood (all-white vs all-yellow brood: Wald $\chi^2 = 0.031$, df = 1, $P = 0.860$). We can therefore reject the hypothesis that the difference in survival rate was associated to the type of brood (e.g., a lowered survival rate of yy brood) in favor of the hypothesis that the proportion of eggs which developed into mature hermaphrodites was significantly affected by the number of sires.
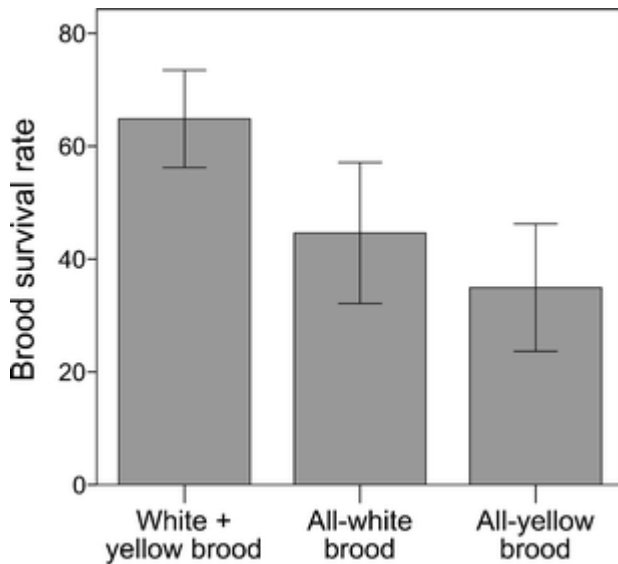
Fig. 3

Brood survival rates in doubly fertlized cocoons (which produced both white and yellow broods) and singly fertilized cocoons (which produced either all-white or all-yellow broods)

Small vs large groups - group size and paternity share

In multiply fertilized cocoons, the proportion of brood sired by focal worms was significantly different between small and large groups ($F_{1,27} = 41.876$, $P < 0.0001$; random effect: $Z = 0.575$, $P = 0.565$). In small groups, focal worms sired on average 87.5 % (± 3.7) of the brood; in large groups, focal worms sired on average 47.8 % (± 6.5) of the brood (Fig. 4). This difference suggests that the number of mates increases with group size and that >2 worms fertilized multiply fertilized cocoons in large groups. The unequal paternity share in small groups needs specific tests and suggests that yellow-phenotype worms might be better competitors over the male role than their white-phenotype rivals.
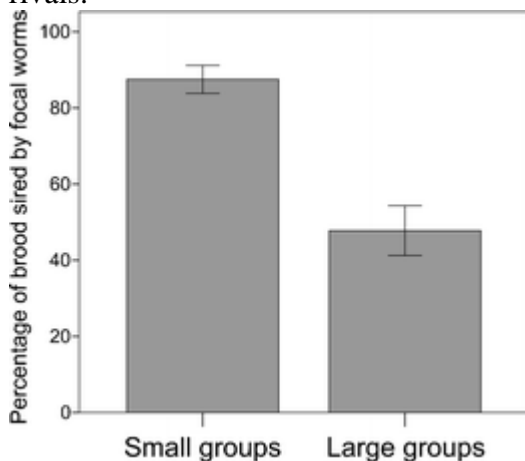

Fig. 4

The percentage of brood sired by the focal worms in small and large groups

Discussion

These results show that the number of mates in the simultaneous hermaphroditic polychaete worm *O. diadema* can be larger than one and can increase as group size increases.

These worms are often used as an example of a species with potentially truly monandrous mating systems (Sella 1985), but our data contradict this. Indeed, multiply fertilized egg cocoons, and therefore multiple paternity, were common in both small and large groups of *O. diadema* and this indicates that competition for mating may be strong in these non-selfing simultaneous hermaphrodites with externally fertilized egg cocoons. Until now, multiple mating was assumed in these worms (Lorenzi et al. 2005, 2006; Lorenzi and Sella, 2008), rather than proven using a genetic marker, and we document here that it does occur. Additionally, we showed that by manipulating group size we effectively manipulated mate competition; as group size increased, mate competition increased as well.

Our results contrast with the statement that hermaphroditism is associated with conditions where density is low and partners rarely meet each other (Charnov 1982; Puurtinen and Kaitala, 2002), as observed by Janicke and Schärer (2009a) when discussing their findings that mating group size can be relatively high in a simultaneously hermaphroditic flatworm. We showed here that hermaphrodites competed with rivals for mating, suggesting that they have evolved under pressures involving mate competition. Indeed, mating with multiple partners has long been known in hermaphrodites, especially in sessile hermaphrodites or in hermaphrodites with sperm storing capabilities (Leonard 1991; Pemberton et al. 2003; Anthes et al. 2006; Janicke and Schärer, 2009a), but also in redworms (Porto et al. 2012). The finding that multiple mating occurs in hermaphrodites and that hermaphrodites can adjust their sex allocation to mating opportunities (Lorenzi et al. 2005; Janicke and Schärer, 2009b) confute the hypothesis that mating group size is usually very small in hermaphrodites' populations.

Our results showed that focal individuals succeeded in siring different proportions of brood depending on whether they had only one rival over the male role or multiple rivals. Consequently, it was likely that more than two hermaphrodites fertilized the same egg cocoons in large groups. The number of sires in each cocoon was probably larger than two, but not much larger, as these worms mate via pseudocopulation (Westheide 1984), which might pose an upper limit to the number of sperm donors. Pseudocopulation is a special kind of external fertilization, possibly linked to sperm which are aflagellate and therefore do not move (Berruti et al. 1978). Pseudocopulation requires that the 'male' stays in contact with its partner and deposits its immotile sperm inside the jelly egg cocoon approximately at the same time when the "female" lays its eggs. It is difficult to imagine how this can involve multiple males which contemporarily (or almost contemporarily) enter the cocoon, release their sperm, and leave without damaging the delicate jelly envelope (which seals definitely soon after pseudocopulation). However, these paternity data document that multiple fertilization occurs.

Our data show that social monogamy is vulnerable to extra-pair fertilizations and support the hypothesis that in *O. diadema* cooperation and reciprocity in egg trading persists as long as there are only two worms and other potential mates are lacking (Sella and Lorenzi 2000). When mating opportunities increase, we have shown in previous work (Lorenzi et al. 2005, 2006, 2008) that these worms are able to plastically adjust their sex allocation depending on mating opportunities. They trade eggs under conditional reciprocity when mating opportunities are limited, but soon shift to a completely different mating system as mating opportunities increase (where they decrease their female allocation in favor of a male-biased behavior, Lorenzi et al. 2005, 2006). Although mating as males is costly for adolescent worms (Sella and Lorenzi 2003), it may be less costly than producing eggs for mature hermaphroditic worms. Indeed by diminishing egg production and playing the male role more often, worms live longer: functionally male-only hermaphrodites live (and fertilize eggs) almost twice as long as functional hermaphrodites (Di Bona et al. 2010).

Finally, that worms can easily shift from a monogamous egg-trading system to a polygynous system, suggests that, in the wild, mating opportunities vary often during the lifespan of these worms and that they have been selected to shift strategically between mating systems. We need more work to fully understand the extraordinary mating system of these worms and this paper is only a small step forward.

Multiple findings suggest that *O. diadema* worms prefer to mate in the male role: they prefer mature hermaphrodites to adolescent males as mating partners (Sella 1988); they abandon their reciprocating partners for worms with ripe eggs (Sella and Lorenzi 2000); they mate repeatedly in the male role (Di Bona et al. 2010) and diminish investment into their female function when mating opportunities increase (Lorenzi et al. 2005, 2006). However, current empirical evidence does not allow to exclude completely the alternative hypothesis that these worms have no sex role preference or that they even trade sperm. Indeed, the benefits of multiple mating for the female role is actually a condition that is predicted to lead to sperm trading in simultaneous hermaphrodites.

Costs and benefits of multiple matings are little known for hermaphroditic marine invertebrates (Sprenger et al. 2008). Whether multiple fertilizations are beneficial to the female function awaits experimental support in internally fertilizing hermaphrodites (Anthes 2010). In the flatworm *Macrostomum lignano* the number of mating partners had no effect on female fecundity (Janicke et al. 2011). In contrast, in *Chelidonura sandrana*, slugs that received sperm from multiple partners produced larger egg capsules and had higher brood survival rates than those that repeatedly received sperm from the same partner (Sprenger et al. 2010). In redworms, those cocoons which were fertilized by at least two sperm donors had a greater hatching success than those fertilized by just one (Porto et al. 2012). In sea slugs, intermediate mating rates increased the fitness via the female function (Lange et al. 2012). However, all these species have internal fertilization and may have cryptic female choice and/or postcopulatory manipulative effects by their partners (e.g., Koene et al. 2009). Instead, hermaphrodites with external fertilization signal their preference for a sexual role to their partner before mating (Fischer 1980; Sella 1988). In *O. diadema,* multiply fertilized cocoons resulted in higher proportion of brood developing into mature worms than singly fertilized cocoons did. Multiple mating is a fertilization insurance in some species, particularly when sperm depletion may occur (Birkhead and Parker 1997; Birne and Whiting 2008; Briefer et al. 2013). Fertilization insurance may perhaps explain the increased proportion of brood developed in these worms, if they are sperm limited. Indeed, they have very low sperm counts (estimated as 50 sperm per egg) (Sella 1990) and must deposit their sperm close to eggs because their sperm are immobile (Morrow 2004). In these conditions, multiple fertilization might increase fertilization rates and be beneficial for 'females', although it set the stage for sperm competition between immotile sperm, a condition which will require focused studies.

Acknowledgments

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