ORIGINAL ARTICLE

THE QUICK AND THE DEAD? SPERM COMPETITION AND SEXUAL CONFLICT IN SEA

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Our view of sperm competition is largely shaped by game-theoretic models based on external fertilizers. External fertilization is of particular interest as it is the ancestral mode of reproduction and as such, relevant to the evolution and maintenance of anisogamy (i.e., large eggs and tiny, numerous sperm). Current game-theoretic models have been invaluable in generating predictions of male responses to sperm competition in a range of internal fertilizers but these models are less relevant to marine broadcast spawners, the most common and archetypal external fertilizers. Broadcast spawners typically have incomplete fertilization due to sperm limitation and/or polyspermy (too many sperm), but the effects of incomplete (<100% fertilization rates) fertilization on game-theoretic predictions are unclear particular with regards to polyspermy. We show that incorporating the effects of sperm concentration on fertilization success changes the predictions of a classic game-theoretic model, dramatically reversing the relationship between sperm competition and the evolutionarily stable sperm release strategy. Furthermore, our results suggest that male and female broadcast spawners are likely to be in conflict at both ends of the sperm environment continuum rather than only in conditions of excess sperm as previously thought. Across the majority of the parameter space we explored, males release either too little to too much sperm for females to achieve complete fertilization. This conflict could result in a coevolutionary race that may have led to the evolution of internal fertilization in marine organisms.

KEY WORDS: Anisogamy, evolutionary stable strategy, game theory, sperm competition.

Sperm are numerous and tiny relative to eggs because of sperm competition. For over 20 years, this has been the prevailing view of the evolution of anisogamy (Parker et al. 1972; Parker 1982, 1990). Classic game theory developed for external fertilizers predicts that because sperm compete numerically, males producing smaller, more numerous gametes have an advantage when competing for eggs (Parker 1982). Although debate surrounding the evolution of eggs has continued (Randerson and Hurst 2001), the fact that sperm competition led to the evolution of many tiny sperm is often taken as a given and indeed, this theory has produced some successful predictive models (Gage and Morrow 2003). Game-theoretic models of sperm competition predict that an increase in the risk or intensity of sperm competition will result in selection for a change in ejaculate size (Parker and Ball 2005). The basis of this theory is that sperm competition operates on a raffle principle: males that access ova with the most sperm have the highest probability of fertilization success. This prediction is supported by comparative data from a wide range of organisms—species with intense sperm competition have larger testes than species in which sperm competition is unlikely (Stockley et al. 1996; Stockley 1997; Byrne et al. 2002). Similarly within species, males facultatively adjust the amount of sperm that they release with increasing risk of local sperm competition (Hosken and Ward 2001; Gage and Morrow 2003). Overall, the predictions of sperm competition game theory are well supported across a wide range of taxa with internal fertilization, but how relevant are they to the largest group of external fertilizers, the broadcast spawners?

Broadcast spawning (the release of sperm and eggs into the surrounding medium) represents the ancestral state of reproduction and is the main mode of reproduction in the sea (Levitan 1996; McHugh and Rouse 1998). Broadcast spawning marine invertebrates such as sea urchins have become a model for examining

the evolution of anisogamy, mate choice, and species recognition, and have repeatedly been cited in sperm competition models (Ball and Parker 1996, 1997; Levitan 1998; Mesterton-Gibbons 1999; Palumbi 1999; Levitan and Ferrell 2006). Importantly, empirical observations of broadcast spawning males show that even under sperm competition, males tend to release their sperm slowly in a range of species (McEuen 1988; Selvakumaraswamy and Byrne 2000; Levitan 2002). Although many models of sperm competition tend to be based on a hypothetical external fertilizer (e.g., Ball and Parker 1996, 1997, 1998), they typically make assumptions that are less relevant for broadcast spawners. Most sperm competition models assume the complete fertilization of a clutch of eggs: a single male is capable of fertilizing an entire clutch of eggs and fertilization success plateaus at 100% (Parker 1982; Ball and Parker 1996, 1997; Williams et al. 2005). Thus, a fundamental conclusion of most previous models is that when there is low sperm competition, the evolutionarily stable strategy (ESS) for males is to release as little sperm as possible (to maximize the number of separate "mating events" he can participate in; see references above). Conversely, when sperm competition is likely, males should generally release much more of their sperm but less frequently to better compete in the fertilization raffle (Parker 1982, 1990). These assumptions are probably appropriate for internal fertilizers, but in broadcast spawners the assumptions of complete fertilization and the independence of fertilization from sperm concentration will rarely apply.

The fertilization success of broadcast spawned eggs depends on local sperm concentration: at low sperm concentrations, the chances of a sperm encountering an egg are low (Vogel et al. 1982). As sperm concentrations increase, the chances of an egg being contacted by sperm greatly increase and fertilization success increases. However, once the sperm concentration exceeds a certain point, the proportion of successfully fertilized eggs rapidly decreases (Stan 1998; Millar and Anderson 2003; Marshall 2006). This is because, in broadcast spawners, there is a lag between when an egg is fertilized by one sperm and when that egg becomes impermeable to subsequent sperm (Gould and Stephano 2003). If additional sperm enter the egg before the block is formed, that egg will die (known as "polyspermy"). Thus, the current assumptions of sperm competition models have limited applicability to broadcast spawners: first, the release of minute quantities of sperm will typically fail to result in complete fertilization because sperm dilution effects will severely limit fertilization. Thus broadcast spawning males should gain fertilizations by releasing more than the absolute minimum, even in the absence of competition from other males. Second, when sperm competition is high and sperm are in excess, fertilization success will decrease due to polyspermy. Thus releasing more sperm will decrease, rather than increase, the fertilization success of that batch of eggs overall. An earlier model (Mesterton-Gibbons 1999) considered the effects of incorporating incomplete fertilization on ESS sperm release strategies, but did not consider the other extreme of the sperm environment continuum: polyspermy. Clearly, incorporating incomplete fertilization through both sperm limitation and polyspermy into extant sperm competition models has the potential to alter their predictions. Importantly, both sperm limitation and polyspermy can limit the fertilization success of natural populations in the wild (Brawley 1992; Brawley et al. 1999; Franke et al. 2002; Marshall et al. 2002, 2004). If we hope to understand the selection pressures acting on broadcast spawners, and more generally, the evolution of anisogamy, then new models that incorporate the specific dynamics of fertilization in this ancestral group are required. We incorporated sperm concentration effects (sperm limitation and polyspermy) into a traditional model of sperm competition and found that the inclusion of these factors dramatically reversed the predictions of traditional models. We then explored the potential for sexual conflict between male and female broadcast spawners.

Modeling approach

Following models of sperm competition developed by Parker, Ball and others, we used a game-theoretic framework that assumes each male's mating strategy is constant across his lifetime (Parker 1990; Parker and Begon 1993). Males are therefore unable to adjust their sperm release in response to the level of sperm competition in any one mating, an assumption that seems likely to hold in marine invertebrate broadcast spawners but may not be appropriate in other systems (e.g., fish, Alonzo and Warner 2000). As in earlier models, the fitness of a mutant male with a per-mating sperm release strategy of s, in a population with a per-mating strategy of s^*, is denoted by $W(s, s^*)$. The fitness of this mutant is therefore a product of the number of mating events a male participates in relative to other males in the population ($n(s,s^*)$), and the expected fertilization success achieved by the mutant from each mating event ($v(s,s^*)$), so that

$$W(s, s^*) = n(s, s^*)v(s, s^*). \qquad (1)$$

SPECIFICATION OF THE NUMBER OF MATING EVENTS: $n(s,s^*)$

The number of mating events (n) that a male with a particular sperm release strategy (s) can participate in is determined by the amount of resources the males has available (R), and the cost of contributing to any spawning event (c), giving the equation: $n = R/(c+s)$. Therefore, assuming that all males in the population have access to equal resources, it follows that the number of matings gained by the mutant male with sperm release strategy s relative to the population with sperm release strategy s^* is

$$n(s, s^*) = (c + s^*)/(c + s). \qquad (2)$$

SPECIFICATION OF FERTILIZATION SUCCESS PER MATING EVENT: $v(s,s^*)$

Most models of reproductive success at each mating event assume that fertilization obeys the raffle principle: male fertilization success depends on the relative representation of his sperm in the sperm pool competing for E eggs (Ball and Parker 2000; Parker 1990). Thus the per-mating fertilization success of the mutant male is:

$$v(s, s^*) = Es/(s + (N - 1)s^*), \qquad (3)$$

where E is the mean number or eggs available for fertilization and N is the average number of competing males. This model assumes that all eggs are fertilized, regardless of the amount of sperm released into the competing pool. However for external fertilizers, the pool of eggs available for fertilization is not independent of sperm concentration. As sperm concentrations decrease to zero, a decreasing proportion of eggs will be found by sperm, and therefore fewer will be fertilized. As the density of competing sperm increases, the number of eggs that are contacted by multiple, co-incident sperm increases, so that polyspermy reduces the number of eggs available for successful fertilization (Styan 1998; Franke et al. 2002; Millar and Anderson 2003). One of the critical changes in the present model relative to earlier work is that we include the effect of different sperm concentrations on the number of eggs that achieve monospermic fertilization. Although there are fertilization kinetics models available for predicting the proportion of monospermic and polyspermic fertilizations, the predictions from these models are sensitive to specific gamete traits for any one species and can vary widely (Vogel et al. 1982; Styan 1998; Millar and Anderson 2003; Luttikhuizen et al. 2004). For analytic tractability and generality, we use an equation that matches the general form of polyspermy-mediated decreases in the pool of available eggs (Marshall 2006). We assume that the number of eggs that can be monospermically fertilized responds to the sperm pool in the following manner:

$$v(s, s^*) = (Ae/2)^2(s + (N-1)s^*)^2 \exp(-A(s + (N-1)s^*)) \quad (4)$$

where A is a "catch all" parameter that defines the relationship between the total amount of sperm that is released and the fertilization success of eggs (i.e., the shape of the curve: see Figure 1 in the Appendix). Variation in A could come from changes in characteristics of eggs (bigger eggs are larger targets for sperm but are more sensitive to polyspermy; Levitan 1996; Marshall et al. 2002), distances between spawners, or hydrodynamic conditions (Levitan 1995). The sperm release level that ensures complete fertilization (the assumption of previous models) occurs only at the point where the amount of sperm in the pool is: $N.s = 2/A$. From this point, lower concentrations leave some eggs unfertilized but higher concentrations of sperm result in egg destruction through

polyspermy (see Figure 1 in the Appendix). This result (and all of our results reported below) was robust (with regard to qualitative predictions) to the form of the sperm competition model: repeating our analyses using a continuous external fertilization model (Ball and Parker 1997) had no qualitative effect on our findings (M. Bode and D. J. Marshall, unpubl. data). For simplicity and brevity, we therefore present the results of the instantaneous fertilization model here.

MODEL ANALYSIS

As in traditional models, the evolutionary stable strategy (ESS) level of sperm release per mating event, s^*, is such that, if all males within the population employ s^*, no mutant strategy can invade (i.e., have higher fitness). For those less familiar with an ESS approach, this means that, if all the males in the population are employing the ESS, then no male, regardless of whether he releases more or less sperm than the ESS can achieve higher fitness and therefore invade the population (Maynard Smith 1982). In fact, any male that does deviate from the ESS once the entire population employs this strategy will have lower fitness (for a more general discussion of ESS's, see Maynard Smith 1982) Mathematically, the ESS is found by determining the value of s^* such that

$$\left.\frac{dW(s, s^*)}{ds}\right|_{s=s^*} = 0 \qquad (5)$$

Substituting equations (1), (2), and (4) into equation (5), and solving for s^* yields a sperm release ESS of

$$s^* = \frac{1 - ANc + \sqrt{(ANc + 1)^2 + 4AN^2c}}{2AN}. \qquad (6)$$

Results

MALE RELEASE STRATEGIES

The central finding of our model is that the relationship between the ESS for sperm release and the number of competing males in the population is negative. When males face no sperm competition, males should release most or all (depending on the value of A) of his sperm but as the number of competing males increases, he should release fewer sperm (Fig. 1). Any male that releases more or less sperm than the ESS for any single density of spawning males is predicted to have lower fitness.

EFFECT OF VARYING SPAWNING COSTS AND RELATIONSHIP BETWEEN [SPERM] AND FERTILIZATION

Changing the relationship between the fertilization of eggs and the local sperm concentrations affects the ESS for sperm release— the more sensitive eggs are to sperm (i.e., increasing A), the less sperm that should be released per mating event. However, varying A does not affect the negative relationship between the number of
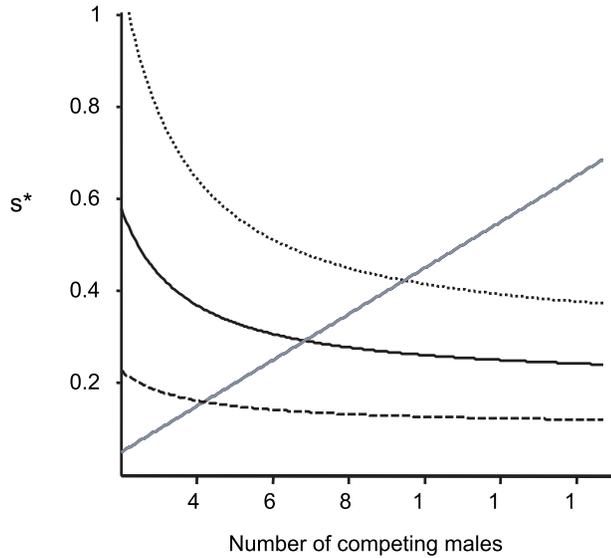
Figure 1. Effect of sperm concentration effects on predictions of the evolutionarily stable sperm release strategy (ESS) for males under different levels of sperm competition (as shown by the x-axis varying *N*, the number of competing males). The solid gray line indicates previous predictions of the ESS for males where female fertilization success is independent of sperm concentration (see text for details) and the black, solid, dashed and dotted lines represent the ESS for males where $A = 1, 3$, and 0.5, respectively.

competing males and the ESS for sperm release (Fig.1). The cost of participating in a spawning event (c) has strong effects on the sperm release strategy: as the costs of participating in a spawning event increase, males should participate in fewer events but release more sperm each time. However, varying c does not change the negative relationship between the number of competing males and the ESS for sperm release (Fig. 2a). Finally, there is no interaction between A and c: the effects of each on the ESS are independent of each other (Fig. 2b).

SEXUAL CONFLICT

Our model allows us to explore the role of sperm competition in promoting sexual conflict. Across the majority of the parameter space, males and females are in conflict: the males' ESS sperm strategy is very different from the strategy that would maximize female fitness (i.e., fertilize all of her eggs). When sperm competition is low and the sperm concentrations potentially limiting, the ESS for males is to release too few sperm, resulting in egg wastage due to sperm limitation (although this depends on the cost of mating, c: Fig. 3a). When sperm competition is high and fertilization is limited by polyspermy, the ESS for males is to each release more sperm than necessary for the complete fertilization of eggs, resulting in many eggs suffering polyspermy. Regardless of values of A and c that are used, there is only a very small region of overlap in what is "best" (i.e., an ESS) for males and
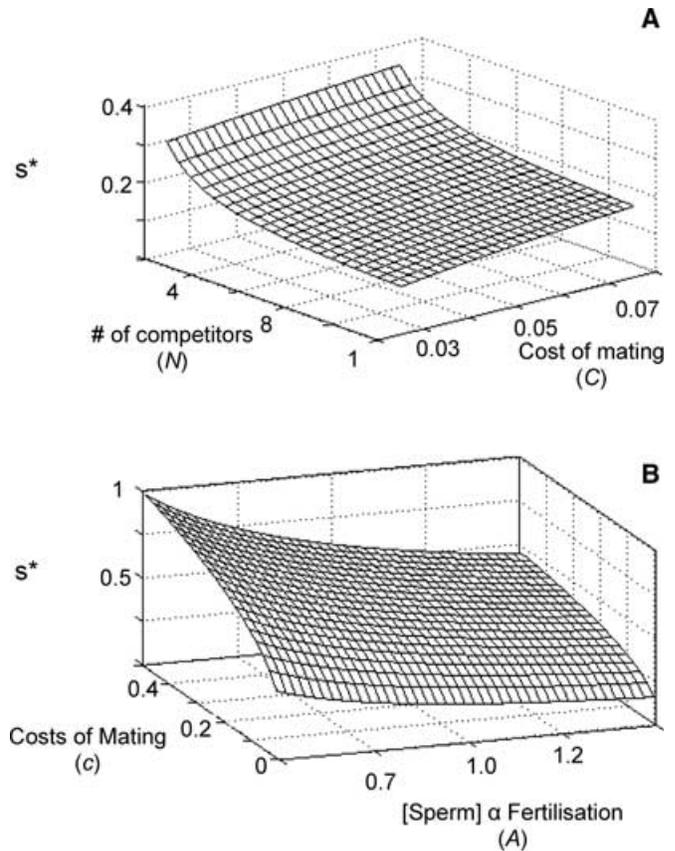

Figure 2. Effect of varying the cost of participating in a spawning event (*c*) and the relationship between fertilization success and total sperm concentration (*A*) on the evolutionarily stable sperm release strategy for males (*s**). Panel (a) shows the effect of varying *c* across different levels of sperm competition (shown on the x-axis as *N*) and Panel (b) shows the combined effects of varying *c* and *A* for a single level of sperm competition ($N = 6$). Note that the effects of *c* and *A* are independent from each other, a condition that held regardless of the level of *N*.

what is "best" (i.e., complete fertilization of eggs) for females (Fig. 3b).

Discussion

The predicted relationship between sperm competition and the ESS for sperm release in our study differs dramatically from previous considerations of this issue (Parker 1993, 1998; Williams et al. 2005). Most models predict that males (assuming they cannot assess the threat of sperm competition) should release most of their sperm quickly when sperm competition is likely (Parker et al. 1996; Williams et al. 2005). Our model predicts the converse, when sperm competition is present (and polyspermy can occur), the ESS for males is to release small quantities of sperm more often, because as the number of spawning males increases, the availability of eggs that have not become polyspermic decreases. Thus
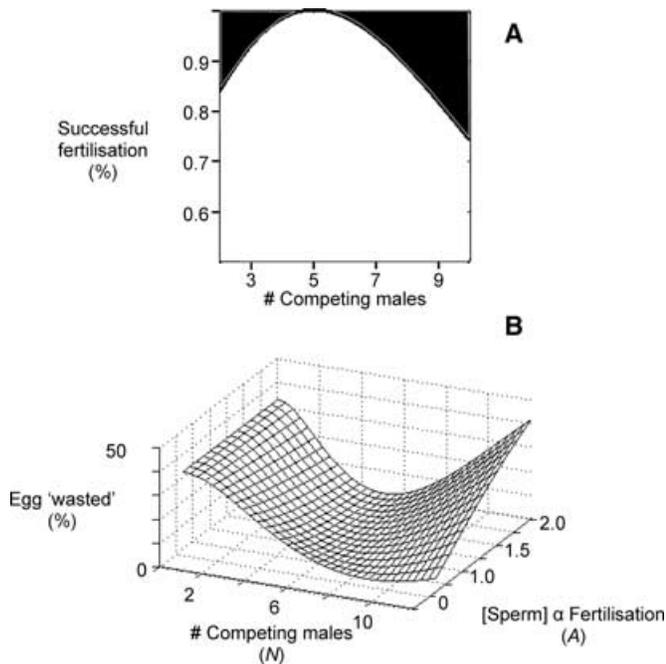
Figure 3. Sexual conflict in broadcast spawners. Panel (a) shows fertilization success across the range of sperm competition levels (where males follow the ESS for sperm release). Note that left of the peak, fertilization is incomplete due to the male population releasing too few sperm. To the right of the peak fertilization is incomplete due the male population releasing too many sperm. Thus, sexual conflict occurs across the majority of the parameter space. Panel (b) shows level of sexual conflict (shown on the z-axis as the proportion of eggs that were not successfully fertilized or "wasted") across varying levels of sperm competition (shown as *N* on the x-axis) and the relationship between the total sperm concentration and fertilization success (shown as *A* on the y-axis).

when sperm competition is present, the negative effects of increasing rates of polyspermy outweigh the benefits of a slightly better chance of securing fertilizations. Qualitatively, the prediction that releasing fewer sperm is a preferred strategy under sperm competition fits better with observations of marine broadcast spawning invertebrates in the wild: males tend to release sperm more slowly than females release eggs (reviewed in Marshall and Bolton in review).

SEXUAL CONFLICT IN THE SEA

Our results predict that the strategies that maximize reproductive success of male and female broadcast spawners will provoke conflict across most of our parameter space. At low population densities our model predicts that the male ESS is to release less sperm than would ensure the complete fertilization of a female's brood of eggs. At high densities, the ESS for males is to release more sperm than is necessary for the complete fertilization of the available egg pool and as a consequence, a high proportion of the eggs are destroyed by polyspermy. This finding is robust to

changes in the relationship between fertilization success and the total level of sperm present (*A*) and so is likely to apply to a range of species and conditions. However, we note that our findings are probably more applicable to sedentary and sessile marine invertebrates than to broadcast spawning fish that pair during spawning events and can adjust the amount of sperm they release in any one spawning (e.g., Warner et al. 1995; Alonzo and Warner 2000).

Polyspermy-mediated sexual conflict has been linked to the rapid evolution of polymorphic sperm–egg receptor proteins and ultimately, to reproductive isolation and speciation in broadcast spawners (Panhuis et al. 2006). This suggestion is supported by initial evidence that higher density populations of broadcast spawners (i.e., those more likely to suffer polyspermy) have higher rates of evolution of sperm receptor proteins (Levitan and Ferrell 2006; Panhuis et al. 2006). One issue that has rarely been addressed in these discussions is, if polyspermy reduces both male and female reproductive success, why do males release quantities of sperm that result in polyspermy? In other words, why does this sperm release strategy persist given its negative effects on fitness of males and females? Our results provide theoretical support for the ideas suggested by Levitan and colleagues (Levitan 1996, 1998; Levitan and Ferrell 2006) that males release polyspermy inducing levels of sperm due to sperm competition. Our model suggests that populations of males that release the amount of sperm that is "just right" (i.e., does not result in polyspermy but ensures complete fertilization eggs across the population) are vulnerable to invasion by mutant males that release "too much" sperm. Thus at high population densities, the only ESS is to release more sperm than is ideal for monospermic fertilization of all the eggs. However, our findings show that there is also a limit to which increases in the levels of sperm release carry a selective benefit. When the population of males employ the ESS of sperm release, males that release even more sperm will actually have lower fitness and fail to invade the population.

The strength of sexual conflict in broadcast spawners is viewed as being strongly density dependent: at low densities, both males and females are predicted to evolve traits that increase fertilization success but at high population densities, males and females will be in conflict (Levitan 1998, 2005a). In contrast, our model predicts that sexual conflict is also possible at low population densities: a major departure from the current theory that anticipates sexual conflict only when sperm are in excess (Levitan 1998, 2005b; Franke et al. 2002; Levitan and Ferrell 2006). The ESS for males at low population densities is to not release all their sperm in a single event, rather, they should release over multiple periods, even though this results in the incomplete fertilization of eggs at any one time. Thus males and females will be involved in a "chase" at both ends of the continuum. When sperm are limiting (sperm competition is low), selection will act on eggs to become more "fertilizable" (e.g., increase egg size, accessory structures

etc.). Simultaneously, selection will act to decrease the ESS for sperm release (i.e., as A increases, S decreases, Fig. 2). We suggest that this coevolutionary chase between males and females under sperm limiting conditions may contribute to the evolution of brooding offspring in marine invertebrates.

SEXUAL CONFLICT AND THE EVOLUTION OF INTERNAL FERTILIZATION

Egg size appears to affect the probability of fertilization in a range of marine invertebrates and it has been suggested that sperm limitation selects for the production of larger, more fertilizable eggs (Levitan 2002, 2004; Marshall et al. 2002). According to our model, any increase in eggs size should (represented as A in our model) select for lower levels of sperm release, further enhancing selection for more fertilizable eggs. This coevolutionary race could have lead to the evolution of the sperm concentrating structures that appear to mitigate sperm limitation in a range of marine invertebrates that brood (relatively) large offspring (Pemberton et al. 2003; Bishop and Pemberton 2006; Lasker 2006). Interestingly, in species with smaller body size (and therefore small testes that release fewer sperm), brooding appears to be more common in marine invertebrates (Strathmann and Strathmann 1982; Strathmann et al. 1984). The relationship between smaller body size and brooding is not constant with the size "threshold" for brooding differing among taxa, challenging the generality of the body size-brooding hypothesis. However, if fertilization limitation via sexual conflict has played a role in the evolution of brooding, then this may explain the variable threshold with regards to body size and brooding: different taxa live in very different sperm environments due to differences in population density and hydrodynamic conditions. Such a hypothesis remains highly speculative but it would be interesting to test whether small-bodied species that have retained external fertilization typically live at higher densities (or spawn during lower water flow conditions) than small-bodied species that brood their offspring. At the very least, sexual conflict in broadcast spawners may have led to the evolution of egg accessory structures such as jelly coats and follicle cells as these structures appear to increase fertilisability although potentially decreasing the risk of polyspermy (Podolsky 2004).

IMPLICATIONS FOR THE EVOLUTION OF ANISOGAMY

Sperm competition has long been regarded as a driving factor in the evolution of anisogamy (Parker et al. 1972). Our results suggest that when polyspermy is a threat, sperm competition is unlikely to maintain anisogamy, as releasing more sperm during sperm competition carries little benefit. High-density populations of males that release all their sperm quickly are vulnerable to invasion by mutant males that release their sperm more slowly. As such, we support Levitan's (1996, 1998) suggestion of an alternative explanation: that sperm are numerous and tiny to counter sperm limitation. This effect, at the opposite end of the sperm competition continuum, is a more likely mechanism for the maintenance of anisogamy in external fertilizers. However, this does not preclude sperm competition as a factor that facilitated the transition from isogamy to anisogamy: in the ancestral condition of isogamy, presumably polyspermy was less of an issue as "proto-sperm" do not outnumber "proto-eggs." In such conditions, the traditional, positive relationship between sperm competition and the evolutionary stable sperm release strategy may be more likely to apply.

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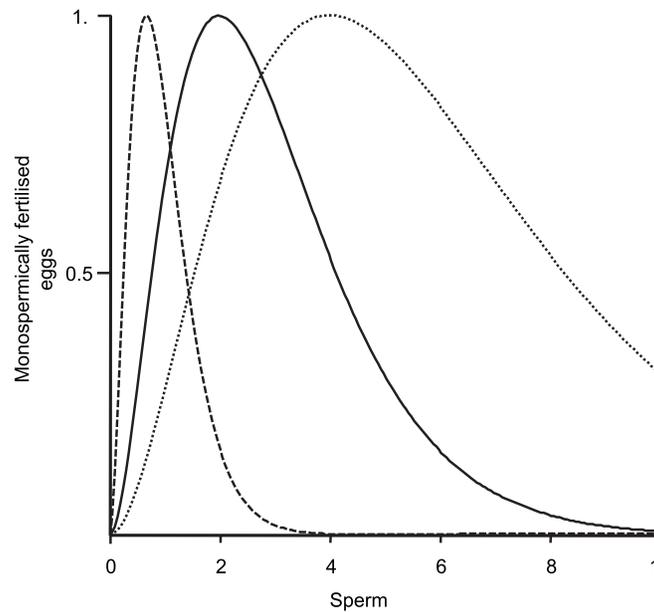
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Appendix

Figure 1. Graphical representation of the sperm concentration–fertilization success relationship used in our game-theoretic model. Different lines indicate different values of *A*, the parameter that defines the relationship between the total amount of sperm present and fertilization success. The solid line represents a situation in which "moderate" levels of sperm induce complete fertilization success (*A* = 1), the dashed line represents a situation in which "low" levels of sperm induce complete fertilization success (*A* = 3) and the dotted line represents a situation in which "high" levels of sperm are required to induce complete fertilization success (*A* = 0.5).