

The Economics of Egg Trading: Mating Rate, Sperm Competition and Positive Frequency-Dependence

Jonathan M. Henshaw · Michael D. Jennions ·
Hanna Kokko

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Abstract Egg trading—the alternating exchange of egg parcels during mating by simultaneous hermaphrodites—is one of the best-documented examples of reciprocity between non-relatives. By offering eggs only to partners who reciprocate, traders increase their reproductive success in the male role, but at a potential cost of delaying or reducing fertilisation of their own eggs. Although several authors have considered the evolutionary stability of egg trading once it has evolved, little attention has been paid to how egg trading can invade a population in the first place. We begin to tackle this problem by formally showing that egg trading is under positive frequency-dependent selection: once the proportion of traders in a population exceeds a certain threshold, egg trading will go to fixation. We show that if mate encounters occur frequently, then the cost of withholding eggs from unreciprocating partners is reduced, making it easier for egg trading to evolve. In contrast, the presence of opportunistic ‘streaking’, where unpaired individuals join mating pairs but contribute only sperm, makes it more difficult for egg trading to invade. This is because streakers weaken the link between the number of eggs an individual can offer and its male-role reproductive success.

Keywords Altruism · Cooperation · Direct reciprocity · Mate choice · Assortative mating

1 Introduction

An organism behaves altruistically when it acts to increase another organism’s fitness at a cost to its own. The existence of altruism is a puzzle for evolutionary theory, because any gene that imposes net fitness costs on its bearer should reduce its transmission via that bearer

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J. M. Henshaw (✉) · M. D. Jennions · H. Kokko
Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia
e-mail: jonathan.henshaw@anu.edu.au

and, all else being equal, be eliminated from the population [29]. The most widely accepted solution is the theory of kin selection: altruistic behaviour that is directed towards genetic relatives can increase the total transmission of the underlying genes, because there is a higher than average probability that a relative will carry the same genes [16,33,40].

Altruism towards non-kin is more contentious and has been documented rigorously in very few species [7,36,37]. One mechanism by which acts that *appear* altruistic could evolve between individuals with no common ancestry is known as ‘direct reciprocity’ [5,33,38]. It is a form of asynchronous cooperation whereby individuals that interact repeatedly take turns in helping each other at a cost to themselves. For direct reciprocity to evolve, the net fitness benefits of receiving help must exceed the costs of giving it, so that both individuals end up ahead over the course of multiple interactions.

‘Egg trading’ in simultaneous hermaphrodites is one of the best-supported examples of direct reciprocity in non-human animals [9,31]. During mating, egg traders do not offer all their eggs to their partner in one go. Instead, individuals divide their clutches into several small parcels and take turns in offering a parcel of eggs to their partner for fertilisation. A partner that does not reciprocate may be abandoned and another partner sought [15].

Egg trading appears to be rare. It has been studied in detail in several species of seabass [11,12,14,30,31] and may also occur in some polychaete worms and in an opisthobranch sea slug [26,34,35]. The term ‘egg trading’ is generally reserved for species that release their eggs to be fertilised outside the body. A similar behaviour known as ‘sperm trading’ occurs in some internal fertilisers in which mating individuals match the volume or duration of their sperm transfer to that of their partner [2,3,39].

1.1 Why Trade Eggs?

When two hermaphrodites mate, a decision must be reached over which role (male or female) each individual will take at any given moment. In many species, there is a general preference for mating in the male role, because sperm are cheaper to replenish than eggs [3]. If both individuals in a mating pair would prefer to mate only as males, then a conflict arises: for the mating to go ahead, at least one individual must (also) mate in the non-preferred female role [1,17].

One possible resolution of mating role conflicts is for each individual to mate in both roles. However, without a mechanism to ensure reciprocity, this resolution is open to ‘cheating’ [38]. Whichever mating roles are taken first, the individual in the preferred role has an incentive to desert its partner afterwards, rather than reciprocating in the non-preferred role.

Egg traders appear to resolve this problem by alternating roles repeatedly within a single mating event and releasing only a small proportion of their eggs each time. This reduces the benefits of desertion after mating in the preferred role, because deserting individuals cannot fertilise their partner’s remaining eggs. Egg trading thus ensures that reciprocity is advantageous to both individuals in a mating pair [33].

1.2 Egg Trading Economics

Previous studies have sometimes treated the offering of eggs as costly [8,13], but the nature of this cost has not always been made clear [7,9]. Eggs are nutritionally more expensive to produce than sperm, but their production and fertilisation must result in a net fitness benefit on average, even after predation and other factors are taken into account. If this were not so, then we would expect individuals to reduce their allocation of resources towards egg production.

Even if offering eggs is not costly per se, however, it can still pay to be selective about who fertilises them. For instance, some partners may be genetically superior or more compatible than others, leading to offspring of higher fitness [21,27]. Alternatively, there may be direct material benefits associated with offering eggs to more than one partner, or some partners may provide greater material benefits than others [22].

In egg-trading species, there is an additional benefit to being choosy about who fertilises your eggs. When an individual offers eggs to a partner that cannot reciprocate, it loses those eggs as ‘bargaining chips’ in future matings with other individuals. There is, thus, an opportunity cost to mating indiscriminately in the female role, because it reduces male-role reproductive success in future matings.

Choosiness comes with its own potential costs, however. First, an individual that holds on to its eggs rather than offering them to the first available partner risks its eggs becoming non-viable, before they can be fertilised. Second, carrying unfertilised eggs for longer than necessary may delay the production of new eggs if body space is limited. Third, an individual may die before it finds another mate. These are the hidden costs of egg trading. Since they are highest when mate encounters are infrequent, we should expect egg trading to evolve more easily when mating rates are high.

1.3 Our Models

Although several studies have considered the evolutionary stability of egg trading once it has evolved [8,9,13,15], little theoretical attention has been paid to how trading can invade a population in the first place. Here we begin to tackle this problem by showing that egg trading can go to fixation once traders exceed a threshold proportion of the population. We show that this threshold is small when mating rates are high, allowing traders to take over more easily.

We also consider the effects of opportunistic ‘streaking’, in which unpaired individuals join mating pairs but contribute only sperm [12,14]. Streaking often results in shared paternity of egg clutches, because the sperm of streakers competes with that of the male-role individual in the mating pair. Because streakers are often physically more distant from eggs than the mating pair, they may not compete for paternity on an equal footing [9,17]. We account for this by incorporating a paternity ‘discount’ for streakers relative to the male-role mate of the mating pair. We predict that streaking makes it more difficult for egg trading to evolve, because it weakens the link between the number of eggs an individual can offer and its male-role reproductive success.

We first construct a simple analytic model to demonstrate that egg trading will take over a population once traders are sufficiently common. We then support the predictions of this model with an individual-based simulation under biologically more realistic assumptions, including the presence of streakers. Neither model is intended to closely reflect the life history of any one egg-trading species (e.g. neither sea bass nor polychaete worm, which have rather different life histories). Rather, we consider only the minimal set of features that is necessary to explain how egg trading evolves. This seems sensible given that egg trading may well occur in a wider range of taxa than those currently known.

2 Analytic Model

Our models assume a population of simultaneous hermaphrodites in which sexual reproduction is obligate, generations overlap, and there is no self-fertilisation (for the last assumption,

see [14,35]). The population consists of two types of individuals: ‘traders’ and ‘non-traders’. For simplicity we assume a haploid genetic system with a single locus coding for trading or non-trading. This means that each individual’s trading behaviour is determined by a single gene, and that each offspring inherits the gene of its mother or father with equal probability.

For the purposes of the analytic model we consider trading behaviour of a very simple type. At any point in time, each individual in the population either is or is not carrying a batch of eggs. When a trader encounters a potential mate, it offers up its own eggs for fertilisation only if its mate is also carrying eggs. In contrast, when a non-trader encounters a mate, it always offers up its eggs for fertilisation, regardless of whether the mate can reciprocate. We model a more sophisticated type of trading in the simulation below. In the analytic model we assume that all matings occur between two individuals with no sperm competition, but we relax this assumption in the simulation, where we consider the effect of streakers.

We assume that it takes one unit of time on average for an individual without eggs to produce a new batch. All individuals, regardless of whether they are carrying eggs, encounter potential mates at a rate of m per unit time. This means that the average time that an individual must wait to encounter a mate is $1/m$. Note that, unlike in traditional time-step models, m may exceed one if more than one mate is encountered per unit time on average.

2.1 Calculating the Proportion of Individuals of Each Type

We write T_e for the proportion of the population made up by traders carrying eggs, T_o for traders with no eggs, N_e for non-traders carrying eggs, and N_o for non-traders with no eggs. Since these are proportions, they must add to one:

$$T_e + T_o + N_e + N_o = 1 \tag{1}$$

We assume that recruitment and mortality occur at low rates relative to mating and egg production. This has two consequences. First, the proportion of traders and non-traders in the population changes relatively slowly over time. Second, the rate at which new eggs are produced is approximately equal to the rate at which they are fertilised, because relatively few eggs are lost due to the death of their parents.

Let us write P for the size of the population. Non-traders produce new eggs at a total rate of $N_o P$ batches per unit time. Since non-traders give up their eggs at every mating opportunity, this must equal the rate $mN_e P$ at which egg-carrying non-traders encounter mates. Thus, we have

$$N_o = mN_e \tag{2}$$

Traders similarly produce new eggs at a total rate of $T_o P$. Egg-carrying traders encounter potential mates at a total rate of $mT_e P$ but give up their eggs only when their mate can reciprocate, which occurs in a proportion $T_e + N_e$ of encounters. Consequently, traders’ eggs are fertilised at a rate of $m(T_e + N_e)T_e P$ batches per unit time, and so we have

$$T_o = m(T_e + N_e)T_e \tag{3}$$

By solving Eqs. (1)–(3) simultaneously, we can write the proportion of individuals of each type in terms of T_e , the number of egg-carrying traders:

$$\begin{aligned} T_o &= \frac{mT_e(1 + mT_e)}{1 + m + mT_e} & N_e &= \frac{1 - T_e - mT_e^2}{1 + m + mT_e} \\ N_o &= \frac{m(1 - T_e - mT_e^2)}{1 + m + mT_e} \end{aligned} \tag{4}$$

2.2 When will Traders Take Over?

We now show that if the proportion of traders in the population exceeds a certain threshold, then traders will take over the population, but that otherwise they will be eliminated. In other words, trading is under positive frequency-dependent selection [24]. Traders will increase in frequency over time if their reproductive success is greater than that of non-traders. Reproductive success comes from two sources: fertilisation of an individual’s own eggs by a mate (female function), and fertilising a mate’s eggs (male function).

Non-traders spend a proportion $\frac{1}{1+m}$ of their time carrying eggs. During this time, they encounter mates at a rate of m per unit time, and any such encounter results in the fertilisation of the non-trader’s eggs. Non-traders thus gain reproductive success through female function at a rate of

$$w_N^F = \frac{m}{1+m}, \tag{5}$$

measured in batches of fertilised eggs per unit time. To gain reproductive success through male function, a non-trader must encounter a mate that is carrying eggs. Encounters with egg-carrying non-traders occur at a rate of mN_e and, since non-traders offer their eggs to any available mate, male reproductive success is guaranteed in these cases. Similarly, encounters with egg-carrying traders occur at a rate of mT_e . However, traders only offer up their eggs when the non-trader can reciprocate, which occurs in a fraction $\frac{1}{1+m}$ of encounters. The male reproductive success of non-traders is thus given by

$$w_N^M = mN_e + \frac{mT_e}{1+m} \tag{6}$$

Similarly, traders spend $\frac{1}{1+m(T_e+N_e)}$ of their time carrying eggs. They offer their eggs for fertilisation only when they find a mate that can reciprocate, which occurs at a rate of $m(T_e + N_e)$ per unit time. Consequently, the female reproductive success of traders is given by

$$w_T^F = \frac{m(T_e + N_e)}{1+m(T_e + N_e)} \tag{7}$$

Lastly, traders encounter egg-carrying non-traders at a rate of mN_e and fertilise their eggs each time. They also encounter egg-carrying traders at a rate of mT_e but fertilise their eggs only in the proportion $\frac{1}{1+m(T_e+N_e)}$ of encounters in which they are themselves carrying eggs. Traders’ male reproductive success is thus

$$w_T^M = mN_e + \frac{mT_e}{1+m(T_e + N_e)} \tag{8}$$

By comparing Eqs. (5) through (8), we see that traders outperform non-traders as males ($w_T^M > w_N^M$) but are less successful as females ($w_T^F < w_N^F$). Traders outcompete non-traders overall when

$$w_T^F + w_T^M > w_N^F + w_N^M \tag{9}$$

This occurs if and only if $T_e > \frac{1}{m}$. Writing $T = T_e + T_o$ for the total proportion of traders in the population, this condition is equivalent to

$$T > \frac{3m + 2}{m(m + 2)} = T^* \tag{10}$$

If the initial proportion of traders exceeds this threshold, then traders will increase in number until they take over the population. Conversely, if the initial proportion of traders falls below the threshold, then non-traders will take over and drive traders to extinction.

Note that the threshold T^* decreases as the mating rate m increases (Fig. 1). This means that when mate encounters are frequent, it is easier for traders to take over. This is an intuitive result: if it is easy to find mates, then egg-carrying individuals can afford to be picky and wait for a mate that can reciprocate. If mates are scarce, however, individuals should offer up their eggs for fertilisation at every opportunity, because they may need to wait a long time for the next one. When mate encounters are very frequent, the threshold for traders to take over approaches zero, meaning that an arbitrarily small initial proportion of traders is sufficient for a successful invasion.

When the mating rate is very low, conversely, traders cannot persist at any frequency. Equations (4) and (9) together imply that $\frac{1}{m} < T_e < \frac{2}{1+\sqrt{1+4m}}$ and hence that $m > 2$. This means that if individuals encounter fewer than two mates on average in the time it takes to produce a batch of eggs (i.e. if $m < 2$), then traders will be eliminated no matter what proportion of the population they make up.

3 Simulation

We now develop an individual-based simulation that supports the predictions of the analytic model under more realistic assumptions.¹ As before, each individual in the population is either a trader or a non-trader, and trading behaviour is determined by two alleles at a single haploid locus.

The simulation differs from the analytic model in four ways. First, rather than simply dividing individuals into those with eggs and those without, we allow each individual to produce and accumulate eggs continually during its lifetime. Second, we consider a more sophisticated form of trading, where individuals in a mating pair alternate in offering eggs for their partner to fertilise. Third, we allow sperm competition in the form of ‘streaking’, where unpaired individuals join mating pairs but contribute only sperm. Fourth, we explicitly model the death of individuals.

3.1 Events: Sex and Death

Our model consists of a series of ‘events’, where each event is either a death or a mate encounter. We write d_k for the total rate of mortality in the population after the k th event. Similarly, m_k is the total rate of mate encounters. We assume that both rates increase with the square of population density (Sect. 3.4).

We decide whether the next event will be a death or a mating by generating two exponential random variables $D_k \sim \text{Exp}(d_k)$ and $M_k \sim \text{Exp}(m_k)$. If $D_k < M_k$, we remove an individual at random from the population. If $M_k < D_k$, then we choose two individuals at random to encounter each other and potentially mate. The mating pair is also joined by random number S_k of streakers, chosen according to a Poisson distribution. We assume that the average number of streakers per mating pair increases linearly with population density (Sect. 3.4). Streakers are chosen at random from the general population (i.e. they are not a distinct class of individual).

¹ Computer code for the simulation is provided in the supplementary material online.

3.2 Eggs are Produced Continually

Regardless of whether mating or death occurs, a time of $t_k = \min(M_k, D_k)$ elapses between the k th and $(k + 1)$ st events. The number of eggs each individual is carrying will accordingly increase in proportion to t_k . We model the increase in the i th individual's number of eggs as a Poisson random variable $E_{ik} \sim \text{Poisson}(t_k)$. This gives an average rate of increase of one egg per individual per unit time. For simplicity, we refer to the accumulation and trading of individual eggs, but our model applies with minor alterations when the unit of trade is a fixed-size parcel of eggs (for the evolution of the size and number of egg parcels, see [9]). Unlike eggs, we assume that sperm are replenished quickly after mating, so that individuals are never sperm-depleted.

3.3 Mating, Paternity and Offspring Genetics

When a mate encounter occurs, we choose an individual at random to go first. The two mating individuals then take turns either to offer an egg to their partner or to delay and wait for their partner's next turn. The mate encounter ends when two turns have passed with neither individual offering an egg.

We assume that individuals can recognise whether a potential mate is carrying eggs, but not how many eggs it is carrying [15]. If a trader goes first, it offers an egg only if its partner is also carrying eggs. On subsequent turns, traders only offer an egg if their partner did so on the previous turn. A non-trader offers an egg every turn, regardless of its partner's behaviour. To check the robustness of our results, we also constructed a similar model (not shown) in which individuals could not distinguish egg-carrying mates from those without eggs. The results were qualitatively similar to those presented below.

Streakers contribute only sperm to a mating and not eggs. If there are no streakers, then each member of the mating pair fertilises the other's eggs. When streakers are present, paternity is determined by a skewed raffle, with a streaker's average share of paternity discounted by a factor of $0 < d \leq 1$ relative to the male-role individual in the mating pair. This means that each streaker has an average share of paternity of $\frac{d}{1+dS_k}$, while the male-role mate has average share $\frac{1}{1+dS_k}$.

Each offspring inherits an allele for trading behaviour from its mother or father with equal probability. For simplicity, we assume that offspring are immediately recruited into the population as adults with no eggs. We do not consider a juvenile stage with developmental delay and stage-specific mortality. We do not expect that this assumption will alter our main conclusions.

3.4 Rates of Mortality, Mate Encounters and Sperm Competition

We allow the rates of mortality and mate encounters to depend on population size (density). Let us write P_k for the size of the population after the k th event. We assume that an individual's instantaneous rate of mortality increases linearly with population size as $\frac{P_k}{K}$, where K is a fixed constant that determines the approximate carrying capacity of the population. This gives a total mortality rate of $d_k = P_k^2/K$ across the population. Similarly, the rate at which each individual encounters potential mates increases as mP_k/K , where m is a fixed constant [19]. The total rate of mate encounters in the population is then $m_k = \frac{mP_k^2}{2K}$.

We assume that there is a fixed window of time τ after a mating commences during which streakers can join the mating pair. If streakers arrive independently, then the number

of streakers for a given mating pair is given by a random variable $S_k \sim \text{Poisson}(\tau m P_k / K)$. This means that the average number of streakers per mating pair increases linearly with the mating rate m . Longer windows of time τ correspond to higher levels of streaking for a given mating rate.

3.5 Initialisation and Parameters

We initialised all simulations with a population of size $P_0 = 500$ and approximate carrying capacity $K = 500$. We ran the simulations until either trading or non-trading went to fixation, eliminating the other strategy. The median number of events until fixation was approximately 125 000 across all simulation runs, corresponding to a median time of about 34 units (i.e. fewer than 34 generations).

We investigated how the rate of mate encounters affects the threshold proportion of traders needed to take over by running one simulation for each combination of the mating rates $m = 2, 4, \dots, 40$ with the initial proportions of traders $T_{\text{init}} = 0.1, 0.2, \dots, 0.9$. We checked the robustness of the results to the length of the window of time for sneakers by repeating all simulations four times with $\tau = 0, 0.05, 0.1, 0.2$. The paternity discount for streakers was held fixed at $d = 0.5$.

We also explored the effects of streaking in more detail by running one simulation for each combination of the window of time for sneakers $\tau = 0, 0.025, 0.05, \dots, 0.5$ with the initial proportion of traders $T_{\text{init}} = 0.1, 0.2, \dots, 0.9$. We held the mating rate fixed at $m = 20$ and the paternity discount for streakers at $d = 0.5$.

3.6 Simulation Results

The simulation results confirm that egg trading is under positive frequency-dependent selection, as predicted by the analytic model. This is despite the fact that the models differ in the type of trading behaviour, the type of cost that traders incur by delaying fertilisation (slower egg production versus dying with eggs), and the presence of streaking. Trading took over the population only when both the initial proportion of traders T_{init} and the mating rate m were sufficiently high (Fig. 1). Streaking made it more difficult for trading to evolve: as the window of time for streakers increased, traders took over less often (Fig. 2).

4 Discussion

Our models predict that once egg trading is sufficiently common in a population, it can go to fixation, driving non-traders to extinction. This positive frequency-dependent selection arises because the value of eggs as ‘bargaining chips’ depends on the proportion of potential mates that recognise the trading convention [28]. When traders are rare, there is little point in withholding eggs from an unreciprocating partner, because there are few opportunities to trade these eggs with future mates. The benefits of trading are consequently outweighed by the costs of delaying fertilisation. Conversely, when traders are common, the trading value of eggs is high, and so egg trading is under positive selection.

The cost of withholding eggs arises in slightly different ways in the two models. In the analytic model, traders only produce new eggs once their current batch of eggs has been fertilised. Withholding eggs consequently leads to slower egg production overall and hence to reduced lifetime reproductive success in the female role. In the simulation, on the other hand, eggs are produced at the same rate regardless of mating behaviour. However, individuals

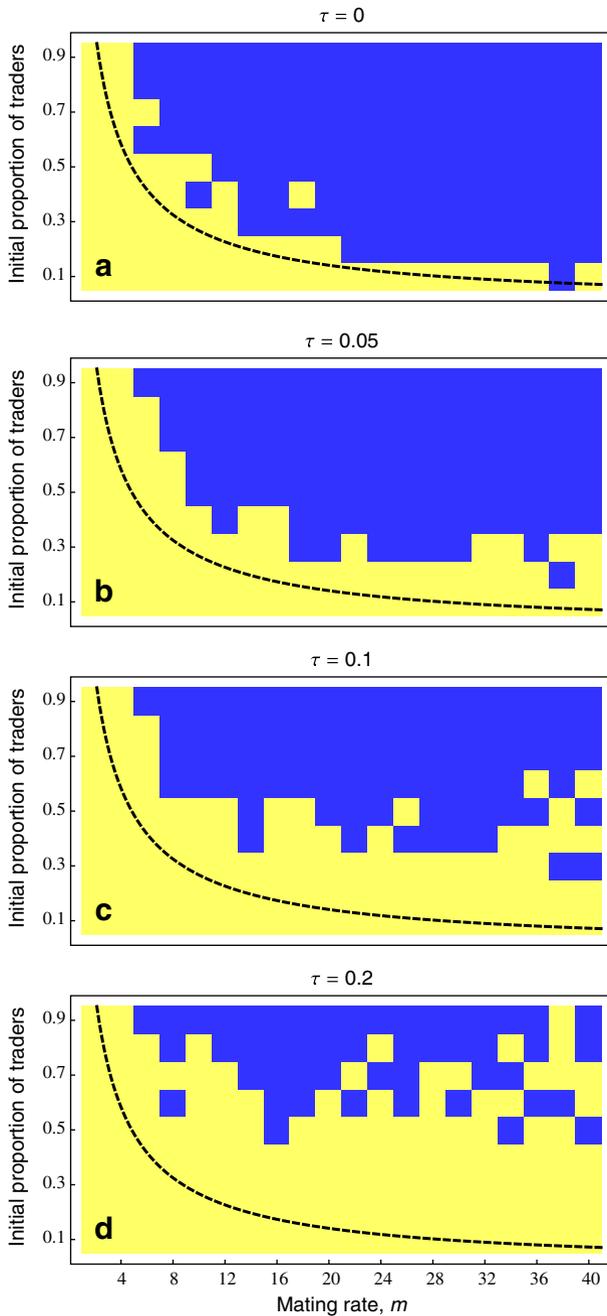


Fig. 1 Fixation of trading (blue) and non-trading (yellow) in simulation runs as the mating rate m and the initial proportion of traders varied. The window of time τ for streakers to join a mating pair varies between panels (a)–(d) as shown. The black dotted line reproduced in each panel shows the analytic model’s predicted relationship between mating rate m and the threshold proportion of traders T^* needed to take over the population. When $m < 2$, the analytic model predicts that trading can never take over. Note that the analytic model assumes there is no streaking (corresponding to $\tau = 0$) (Color figure online)

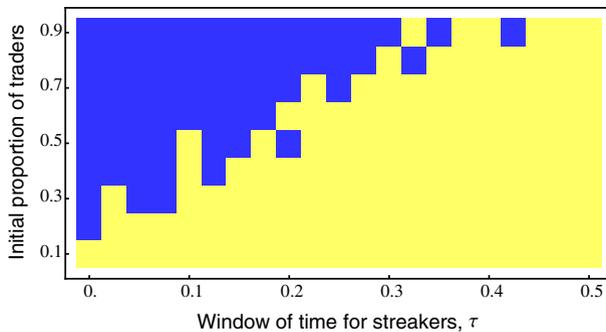


Fig. 2 Fixation of trading (*blue*) and non-trading (*yellow*) in simulation runs as the window of time τ for streakers to join a mating pair and the initial proportion of traders varied. Shown with mating rate $m = 20$ (Color figure online)

that delay fertilisation of their eggs are more likely to die before they are fertilised. A third potential cost is incorporated into neither model but is probably biologically important: if mating is delayed, then eggs might senesce and become non-viable.

Both our models predict that the costs of withholding eggs are higher when mates are scarce. Consequently, trading should evolve more easily when the rate of mate encounters is high. This prediction raises an interesting dilemma, because the evolution of simultaneous hermaphroditism is thought to be associated with low rates of mate encounters [6, 10, 18, 32] but simultaneous hermaphroditism would seem to be a prerequisite for egg trading to evolve. Fischer suggested that egg trading might ‘protect’ hermaphroditism against invasion by separate sexes if mating rates increase but this idea has never been formally modelled [13, 25]. The relationship between egg trading and mating rate may be further complicated if intermediate mate availability allows dominant individuals to monopolise mates and specialise as males, an idea for which there is some support [14, 31].

For fixed mating rates, our model predicts that sperm competition in the form of streaking makes the evolution of egg trading less likely. This is because streakers circumvent the trading economy by gaining fertilisation success as males without offering eggs in return. High rates of streaking thus weaken the link between the number of eggs an individual can offer and its mating success as a male.

Our models predict an initial barrier to the invasion of trading due to positive frequency-dependent selection. This can perhaps explain why egg trading is so rare, even though simultaneous hermaphroditism is fairly common [20]. Nonetheless, we are left to explain how egg trading can initially evolve at all. Fischer [13] suggested that trading might have originated as a form of synchronised egg release, but his argument assumes rudimentary conditionality of the very kind that we want to explain. Initial clustering of traders due to relatedness is also unlikely, because the fertilisation behaviour of egg-trading species leads to high dispersal [4, 13]. Another possibility is that trading originated from a general preference for mating with fecund individuals, due to the genetic benefits of fecundity being passed on to offspring [23]. This could lead to assortative mating by fecundity, with more fecund (attractive) individuals withholding eggs from less fecund individuals [14, 17]. It far from clear how egg trading and assortative mating would coevolve, however, and formal models are needed to make sense of these interactions.

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