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Direct reciprocity stabilizes simultaneous hermaphroditism at high mating rates: A model of sex allocation with egg trading

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Simultaneous hermaphroditism is predicted to be unstable at high mating rates given an associated increase in sperm competition. The existence of reciprocal egg trading, which requires both hermaphroditism and high mating rates to evolve, is consequently hard to explain. We show using mathematical models that the presence of a trading economy creates an additional fitness benefit to egg production, which selects for traders to bias their sex allocation toward the female function. This female-biased sex allocation prevents pure females from invading a trading population, thereby allowing simultaneous hermaphroditism to persist stably at much higher levels of sperm competition than would otherwise be expected. More generally, our model highlights that simultaneous hermaphroditism can persist stably when mating opportunities are abundant, as long as sperm competition remains low. It also predicts that reciprocity will select for heavier investment in the traded resource.

KEY WORDS: Cooperation, dioecy, gamete trading, gonochorism, reciprocal altruism.

Most altruistic behavior is directed toward close relatives, where it is thought to have evolved due to indirect fitness benefits according to the theory of kin selection (Hamilton 1964; West et al. 2002; Sachs et al. 2004). Apparent altruism toward nonkin is nonetheless a regular occurrence in some species (Dugatkin 1999). For example, vampire bats share blood meals with both kin and nonkin (Wilkinson 1984; Carter and Wilkinson 2013) and allogrooming in social mammals is similarly not restricted to close relatives (Hart and Hart 1992; Barrett et al. 1999). Such behavior is often most plausibly explained as direct reciprocity, whereby two individuals alternate in helping each other at an immediate cost to their own fitness (Trivers 1971; Sachs et al. 2004; Bshary 2010).

For direct reciprocity to be adaptive, the net fitness benefit of receiving help must exceed the cost of helping, so that both individuals expect to come out ahead over multiple interactions. Direct reciprocity is thus strictly speaking a kind of asynchronous cooperation; however, it is sometimes referred to as "reciprocal altruism" because each act of helping is costly to the donor when viewed in isolation from the recipient's delayed response (Trivers 1971; West et al. 2007; Krams et al. 2008; Rutte and Taborsky 2008).

Direct reciprocity between nonkin is apparently rare outside of humans and few instances have been documented rigorously (Hammerstein 2003; Clutton-Brock 2009). A likely reason for this rarity is that an individual only benefits from cooperating if its partner returns the favor. Consequently, some level of conditional cooperation must already be present before direct reciprocity can invade (the "bootstrapping problem": André 2014). This pre-existing cooperation must have arisen via a mechanism other than reciprocity, although how this happens is poorly understood (André 2015).

To explain the origins and maintenance of direct reciprocity in general, it is helpful to view these questions in the context of the few well-documented examples of reciprocity in nature. One of the most convincing cases is "egg trading" among simultaneous hermaphrodites (Petersen 2006; Crowley and Hart 2007). When egg traders mate, they do not release all of their eggs in one go. Instead, they divide their clutch into several small parcels, and partners take turns in offering each other a parcel of eggs to fertilize externally. Partners that do not reciprocate egg release may be deserted and another partner sought (Friedman and Hammerstein 1991). Egg trading has been demonstrated in several species of the seabass family (Fischer 1981; 1984a; Fischer and Petersen 1987; Petersen 1995, 2006), and may also occur in some polychaete worms and an opisthobranch sea slug (Leonard and Lukowiak 1984; Sella et al. 1997; Sella and Lorenzi 2000).

By offering eggs only to partners who reciprocate, traders increase their reproductive success in the male role, effectively using their eggs as “bargaining chips” in exchange for fertilization opportunities. Egg trading thus partially resolves the sexual conflict that arises from a general preference for the male mating role in many hermaphroditic species (Anthes et al. 2006; Hart et al. 2011; Schärer et al. 2014). This mating role preference is an expected consequence of anisogamy. Eggs are costlier than sperm to replenish, which means that the optimal mating rate is higher in the male role than in the female role. It consequently pays to be choosier when mating as a female (Clutton-Brock and Parker 1992; Schärer et al. 2012; Henshaw et al. 2014b; although note that this argument can break down if individuals mating in the male role provide direct benefits to their partners such as nuptial gifts or parental investment: Clutton-Brock and Vincent 1991; Johnstone et al. 1996; Kokko et al. 2006).

Like most cases of direct reciprocity, the origins of egg trading are yet to be fully explained. Previous theory has, however, shown that egg trading can go to fixation in a population once traders are sufficiently common, a form of positive frequency-dependent selection (Henshaw et al. 2014b). Here, we model how egg trading affects the evolution of sex allocation and the stability of hermaphroditism. We show that once egg trading has evolved, it selects for female-biased sex allocation. This protects hermaphroditism from invasion by separate sexes under the “twice-the-fitness rule” (Charnov 1982; Fischer 1988; Michiels et al. 2009; see below). Simultaneous hermaphroditism (and, by extension, egg trading) can then persist under higher levels of sperm competition than would otherwise be predicted.

SPERM COMPETITION AND THE RATE OF MATE ENCOUNTERS

Sperm competition is incorporated into our model in the form of “streaking,” in which unpaired individuals approach a spawning pair and attempt to fertilize any released eggs with their own sperm (Fischer 1984a, 1987). Streaking is observed in most (though not all) species of egg-trading serranid fish (Petersen 2006) and similar behaviors known taxon-dependently as “streaking” or “sneaking” are widespread in external fertilizers (Taborsky et al. 2008). Streakers are often physically more distant from released eggs than the mating pair and may be the target of aggression from the individual mating in the male role (Oliver 1997). As a result, streakers may not compete for paternity on an equal footing (Crowley and Hart 2007; Hart et al. 2011). We account for this by incorporating a paternity “discount” for streakers relative to the male-role mate.

We follow previous theory in assuming that when encounters with potential mates occur more often, opportunities to streak are also more frequent (arrow A in Fig. 1; Henshaw et al. 2014b). This is biologically plausible if both mating and streaking opportunities depend on underlying factors such as population density and movement patterns (c.f. Kokko and Rankin 2006). However, we also consider the effects of streaking independent of the mate encounter rate by varying the maximum number of streakers per mating pair and the window of time that streakers have to make a successful approach after a pair commences spawning (see Supporting Information). This is important because previous theory indicates that high mating rates facilitate the fixation of egg trading, whereas high streaking rates impede it (arrows B and C in Fig. 1; Henshaw et al. 2014b).

THE TWICE-THE-FITNESS RULE

Before considering how egg trading and simultaneous hermaphroditism interact in our model, it is helpful to revisit the logic underlying most models of the evolution of hermaphroditism. Every individual produced by sexual reproduction has exactly one mother and one father. The average fitness gained through male and female roles must therefore be equal when viewed across the whole population (the Fisher condition: Houston and McNamara 2005). An immediate consequence is that the average overall fitness in a population of hermaphrodites must equal twice the average fitness in either the female role or male role alone.

For a pure female to invade a hermaphroditic population, her expected fitness must equal or exceed that of an average hermaphrodite. By the above argument, this is equivalent to twice the average female-role fitness of a hermaphrodite (Charnov 1982). Assuming that female-role fitness increases roughly in proportion to egg production, this means that pure females can invade only if they produce at least twice as many eggs as hermaphrodites (Charlesworth 1999; Michiels et al. 2009). Pure males can similarly invade if they gain twice the male-role fitness of hermaphrodites. This is unlikely to result from simply doubling their sperm production, however, because fertilization success is rarely due to a pure lottery-like process that yields linear returns on sperm production (Pannell 2002; Charlesworth 2008; see below).

SPERM COMPETITION, SEX ALLOCATION, AND THE STABILITY OF HERMAPHRODITISM

The “twice-the-fitness rule” helps to explain why simultaneous hermaphroditism is predicted to be stable only when sperm competition is low (Heath 1977; Charnov 1979; Puurtinen and Kaitala

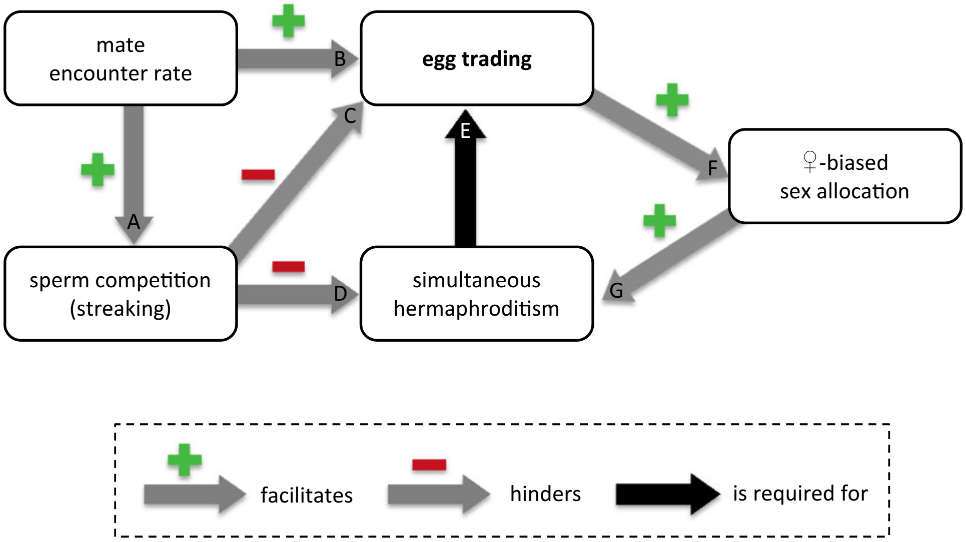

Figure 1. Processes predicted to influence the evolution and maintenance of egg trading.

2002; Eppley and Jesson 2008). Two key assumptions underlie most theoretical work on this topic. First, individuals have fixed budgets for gamete production, such that investments in sperm and eggs trade off against each other in a linear way (Charnov 1996; Schärer 2009). Second, pure males and pure females have larger gamete budgets than hermaphrodites, owing to efficiency advantages when specializing in one gamete type (Heath 1977; Charnov 1982; Van de Paer et al. 2015).

When the risk of sperm competition is low, hermaphrodites only need to make enough sperm to fertilize their mates' eggs (Michiels et al. 2009). Assuming as above that excess reproductive capacity is diverted toward egg production, this means that hermaphrodites will show strongly female-biased sex allocation. Consequently, for a pure female to double the egg production of an average hermaphrodite, her budget for eggs must be substantially larger than a hermaphrodite's overall gamete budget. For example, if hermaphrodites allocate 0.75 of their resources toward the female function, then a pure female's budget must be 1.5 times larger than a hermaphrodite's to invade. We refer to this number as the invasion threshold for pure females. When sperm competition is weak, the invasion threshold is high. Any efficiency advantage that females gain by specializing in one sex may then be insufficient to exceed the threshold. In this case, simultaneous hermaphroditism is stable against invasion by pure females.

Pure males also fare poorly when sperm competition is weak, because this leads to strongly diminishing male-role fitness returns as sperm production increases (i.e., share of paternity is not linearly related to sperm production: Schärer 2009). The fitness of pure males is consequently only slightly higher than the male-role fitness of hermaphrodites, falling short of the double fitness needed to invade. As a whole, therefore, simultaneous hermaphroditism is predicted to be stable under low sperm competition, because neither pure females nor pure males invade easily under these conditions.

Conversely, strong sperm competition can destabilize simultaneous hermaphroditism (arrow D in Fig. 1). When an individual faces many sperm competitors, any increase in its sperm production will result in nearly linear fitness returns. Hermaphrodites are consequently selected to split their reproductive resources roughly equally between sperm and egg production (Charnov 1982; Fischer 1984b). Pure females then require only a small efficiency advantage to double the egg production of hermaphrodites and exceed the invasion threshold (Heath 1977). Similarly, the almost linear fitness returns on sperm production mean that pure males can outcompete hermaphrodites by producing slightly more than twice as many sperm.

HOW DOES EGG TRADING PROTECT SIMULTANEOUS HERMAPHRODITISM FROM INVASION?

Egg trading is predicted to evolve most easily when the risk of sperm competition (i.e., streaking) is low, but to be stable once it is fixed in a population (Henshaw et al. 2014b). We show here that not only is egg trading stable itself, it also helps protect simultaneous hermaphroditism from invasion by separate sexes. This allows hermaphroditism to persist stably at higher levels of sperm competition than would be predicted in the absence of egg trading.

Egg trading selects against both pure males and pure females, although for different reasons. Since pure males produce no eggs of their own, they cannot gain fitness by swapping eggs with traders. Instead, their only pathway to reproductive success in a trading population is via streaking on mating pairs. This puts them at a disadvantage to hermaphrodites, which gain fitness through both trading with mates and streaking.

For pure females, egg trading is disadvantageous because it selects for female-biased sex allocation. The existence of a trading economy creates an additional source of values for eggs: they can be used as "bargaining chips" in exchange for fertilization opportunities. Higher egg production thus increases fitness in both the male and female roles. Of course, the trade-off between egg and sperm production still applies, and so traders that increase their egg production will achieve lower paternity under sperm competition. The increased value of eggs in a trading population nonetheless selects for more female-biased sex allocation than is predicted among non-traders. By the same "twice-the-fitness" argument as above, this makes it more difficult for pure females to invade and thereby stabilizes simultaneous hermaphroditism (arrows F and G in Fig. 1).

Model

Our model considers large, well-mixed populations of simultaneous hermaphrodites in which generations overlap and sexual reproduction is obligate. We assume that all reproduction occurs via outcrossing, because although many egg-trading species are self-compatible, self-fertilization has never been observed under natural conditions (Fischer and Petersen 1987; Sella et al. 1997; Petersen 2006). We model trading behavior 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 will offer up its own eggs for fertilization only if its mate is also carrying eggs. In contrast, non-traders always offer up their eggs, regardless of whether their mate can reciprocate. This simple model of trading yielded similar results to more sophisticated simulations of "egg-for-egg" trading in a previous study (Henshaw et al. 2014b).

We first calculate evolutionarily stable sex allocation for populations of traders and non-traders to show that egg trading leads to relatively female-biased sex allocation. We then determine the conditions under which pure males and pure females can invade a hermaphroditic population. As is standard in invasion analyses, we assume that unisexual individuals are initially rare, so that all of their mating interactions are with hermaphrodites. Our invasion criteria are based on the assumption of nuclear inheritance of genes for sex allocation (see Discussion).

SEX ALLOCATION FROM A FIXED BUDGET

We assume that all hermaphrodites have the same fixed resource budget of one unit for gamete production (Parker 2011). A proportion r of this budget is allocated to male reproduction, while $1 - r$ goes to female reproduction (Charnov 1996). We allow that pure males and pure females have a larger budget of $A > 1$ due to efficiency advantages of specialising in one type of gamete (Heath 1977; Henshaw et al. 2014a; Van de Paer et al. 2015).

Hermaphrodites that are not already carrying eggs produce a new batch at a rate of $1 - r$. This means that individuals with more female-biased sex allocation replenish their eggs more quickly after they are fertilized. On the other hand, individuals that allocate greater resources to male function gain higher paternity under sperm competition (see below).

MATING AND PATERNITY

All individuals, regardless of whether or not they carry eggs, encounter potential mates at a rate of m per unit time. A mating commences if both individuals are traders carrying eggs, or if at least one individual is a nontrader carrying eggs. A mating pair may also be joined by unpaired streakers that release sperm but not eggs. Streakers are chosen at random from the general population (i.e., they are not a distinct class of individual). We derive our main results assuming that there is at most one streaker per mating pair, but we relax this assumption in the Supporting Information online.

After a mating commences, there is a fixed window of time τ during which a streaker can join the mating pair. If we assume that streakers encounter mating pairs at the same rate as unpaired individuals encounter one another, then the probability that a streaker arrives during this window is given by (Otto and Day 2007)

$$s = 1 - \exp(-m\tau). \tag{1}$$

Larger windows of time τ correspond to a higher chance that a streaker is present, and thus to stronger sperm competition.

If there are no streakers, then all released eggs are fertilized by the mating partner. When streakers are present, however, paternity is decided by a skewed raffle, where each individual's share of paternity increases according to its investment r in sperm production (Parker 1990). To account for possible disadvantage to streakers in competition for fertilizations, we discount their expected paternity by a factor of $0 < d \leq 1$ relative to the male-role individual in the mating pair. At the upper limit of $d = 1$, streakers are at no disadvantage relative to the male-role mate, whereas smaller values of d correspond to increasing streaker disadvantage.

Consider now a mutant individual with sex allocation r' in a population where every other individual has sex allocation r. When the mutant mates with another individual, there is a probability s that the pair is joined by a streaker. In this case, the mutant's average share of paternity is $\frac{r'}{r'+dr}$. If no streaker attends the mating, which occurs with probability $1 - s$, then the mutant gains full paternity. The mutant's average share of paternity is thus

$$p'_{\mathrm{M}} = s\left(\frac{r'}{r' + dr}\right) + 1 - s. \tag{2}$$

By a similar argument, when the mutant individual acts as a streaker, its average share of paternity is given by

$$p'_{\mathrm{S}} = \frac{dr'}{r + dr'}. \tag{3}$$

SEX ALLOCATION OF NON-TRADERS

We now show that populations of egg traders have female-biased sex allocation relative to nontrading populations. We begin by calculating the evolutionarily stable sex allocation r^*_{N} for non-traders.

Consider a nontrading population with sex allocation r that is invaded by a mutant with sex allocation r'. The mutant can gain reproductive success from three possible sources: fertilization of its own eggs by a mate or streaker; fertilizing the eggs of a mating partner; and streaking. We consider each of these sources in turn.

First, the mutant produces new batches of eggs at a rate of $1 - r'$ and gets them fertilized at a rate of m (this includes fertilization by both the male-role mate and streakers). The average proportion of time that it spends carrying eggs is thus $q'_{\mathrm{N}} = \frac{1-r'}{m+1-r'}$. Since the mutant encounters mates at a rate of m, this leads to its own eggs being fertilized at a rate of mq'_{N} batches per unit time.

Second, since a proportion $q_{\mathrm{N}} = \frac{1-r}{m+1-r}$ of the population is carrying eggs at any one time, the mutant encounters egg-carrying mates at a rate of mq_{N}. The mutant's average share of paternity from such encounters is p'_{M}, yielding male-role reproductive success of $p'_{\mathrm{M}}q_{\mathrm{N}}$.

Lastly, each mating pair is attended by a streaker with probability s, and so the mutant encounters streaking opportunities at a rate of $\frac{1}{2}sm$ (the factor of one half arises because each mating pair consists of two individuals). Each individual in the mating pair is carrying eggs with probability q_{N}, so the expected total number of egg batches released by both individuals is $2q_{\mathrm{N}}$. The mutant fertilizes an average proportion p'_{S} of these eggs, leading to male-role reproductive success of $p'_{\mathrm{S}}\ smq_{\mathrm{N}}$ due to streaking.

Combining these three sources gives us the mutant's total reproductive success:

$$w'_{\mathrm{N}} = mq'_{\mathrm{N}} + p'_{\mathrm{M}}mq_{\mathrm{N}} + p'_{\mathrm{S}}mq_{\mathrm{N}}. \tag{4}$$

The evolutionarily stable sex allocation r^*_{N} is then given by solving the equation

$$\left.\frac{\partial w'_{\mathrm{N}}}{\partial r'}\right|_{r'=r} = 0, \tag{5}$$

subject to the second-derivative test (Christiansen 1991). This yields

$$r^*_{\mathrm{N}} = 1 + \frac{\beta - \sqrt{\beta^2 + 8d(1+d)^2 sm}}{4ds}, \tag{6}$$

where

$$\beta = \left(2ds + (1+d)^2\right)m.$$

SEX ALLOCATION OF TRADERS

We now calculate the evolutionarily stable sex allocation r^*_{T} in a population of traders. We write q_{T} for the proportion of time a typical trader spends carrying eggs. As before, such individuals produce new batches of eggs at a rate of $1 - r$. However, they offer eggs only to mates that can reciprocate, which they encounter at a rate of mq_{T}. The value of q_{T} is thus found by solving the equation $q_{\mathrm{T}} = \frac{1-r}{mq_{\mathrm{T}}+1-r}$. Similarly, for a mutant with sex allocation r' the proportion of time spent carrying eggs is given by $q'_{\mathrm{T}} = \frac{1-r'}{mq_{\mathrm{T}}+1-r'}$. For the same sex allocation, traders spend a greater proportion of their time carrying eggs than non-traders, because they are choosier about releasing eggs.

By analogous reasoning to the non-trader case, a mutant trader's total reproductive success is given by

$$w'_{\mathrm{T}} = mq_{\mathrm{T}}q'_{\mathrm{T}} + p'_{\mathrm{M}}mq_{\mathrm{T}}q'_{\mathrm{T}} + p'_{\mathrm{S}}smq^2_{\mathrm{T}}. \tag{7}$$

We can then calculate the equilibrium sex allocation r^*_{T} for traders numerically using the analogue of equation (5).

EGG TRADING LEADS TO FEMALE-BIASED SEX ALLOCATION

By comparing the results of the previous two sections, we see that egg-trading populations have consistently more female-biased sex allocation than non-traders (Fig. 2A) regardless of the mating rate m and the risk of streakers being present (as determined by the window of time for streakers τ). This is because of the additional value eggs gain by their role in the trading economy. In both trading and nontrading populations, sex allocation moderates a trade off between male and female fitness. Any increase in egg production reduces the resources available for sperm, which diminishes an individual's success in sperm competition. For traders, however, higher egg production also means having more eggs to trade, which generates additional mating opportunities in the male role. Increases in female allocation are thus less detrimental to male fitness in traders than they are in non-traders, and this results in relatively female-biased sex allocation in trading populations.

If multiple streakers can attend a mating pair, our prediction of female-biased sex allocation among egg traders continues to hold, at least for biologically reasonable choices of the parameter values (Fig. 2A; see Supporting Information online for details). For example, the prediction holds whenever the maximum number of streakers attending any given mating pair $s_{\max} \leq 10$, the mating rate $m \leq 100$, and the window of time for streakers $\tau \leq 0.2$. To justify these values, we note that if $m > 100$ then individuals would encounter more than one hundred potential mates in the time that it takes to produce a batch of eggs, while $\tau > 0.2$ would

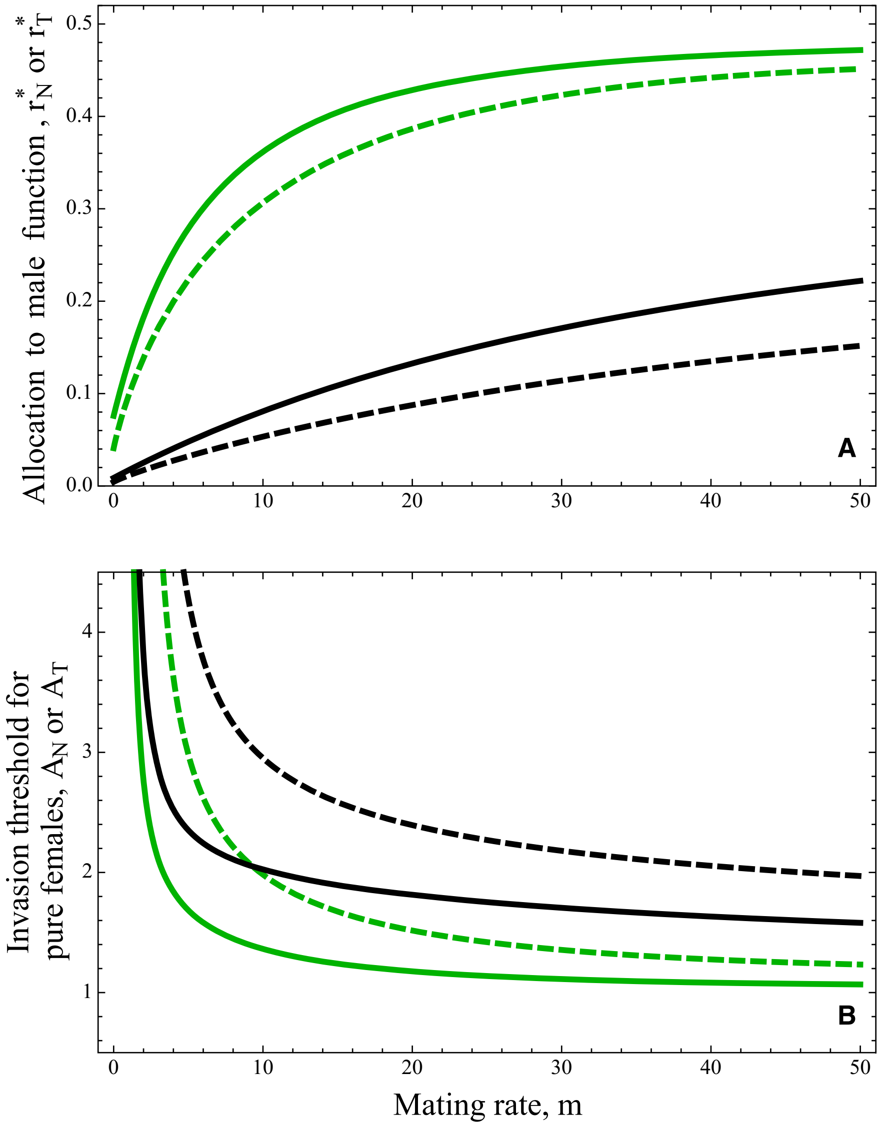

Figure 2. **(A) Egg trading selects for relatively female-biased sex allocation, with allocation to male function lower in traders (dashed lines, r_T^*) than in non-traders (solid lines, r_N^*). (B) Egg trading stabilizes simultaneous hermaphroditism against invasion, as shown by a higher invasion threshold for pure females in trading populations (dashed lines, A_T) than in nontrading populations (solid lines, A_N). Both panels are shown with sperm competition high (green lines: window of time for streakers $\tau = 0.2$ and maximum number of streakers $s_{max} = 10$) and low (black lines: window of time for streakers $\tau = 0.02$ and maximum number of streakers $s_{max} = 1$) relative to the rate of mate encounters *m*. Paternity of streakers is discounted by $d = 0.5$.**

mean that spawning takes more than one tenth as much time as egg production (assuming sex allocation of $r < 0.5$, as our model predicts).

WHEN CAN SEPARATE SEXES INVADE? THE NONTRADER CASE

We now show that female-biased sex allocation protects egg-trading populations from invasion by separate sexes. We assume that both pure males and pure females have a resource budget of $A > 1$ for gamete production. Hermaphroditic populations use their equilibrium sex allocations r_N^* or r_T^* (derived above). We also assume that mutations affecting sex allocation and trading behavior occur at separate loci, so that unisexual mutants follow the trading strategy of the population they invade (e.g., pure female mutants in a trading population are also traders). The existence of pleiotropic mutations affecting both sex allocation and trading behavior would change our conclusions (see Supporting Information).

Consider first a population of nontrading hermaphrodites. Typical individuals in the population are carrying eggs a proportion $q_N^* = \frac{1-r_N^*}{m+1-r_N^*}$ of the time and get them fertilized at a rate of m. This results in average reproductive success of mq_N^* in the female role. Since average reproductive success in the male and female roles must be equal (due to the Fisher condition), the average total reproductive success of a hermaphrodite is simply

$$w_{\mathrm{N}} = 2mq_{\mathrm{N}}^{*}. \tag{8}$$

Consider now a pure male mutant in a population of nontrading hermaphrodites. The male can gain reproductive success both as a mate and via streaking. Since the male's sperm production is proportional to A, his average paternity as the male-role mate in a pair is

$$p_{\mathrm{M}}^{\mathrm{m}} = \mathrm{s}\left(\frac{A}{A+dr}\right) + 1 - s. \tag{9}$$

His average paternity when streaking is similarly

$$p_{\mathrm{S}}^{\mathrm{m}} = \frac{dA}{r+dA}. \tag{10}$$

The mutant male's total reproductive success is then given by the sum of his reproductive success as a mate and as a streaker:

$$w_{\mathrm{N}}^{\mathrm{m}} = p_{\mathrm{M}}^{\mathrm{m}} mq_{\mathrm{N}}^{*} + p_{\mathrm{S}}^{\mathrm{m}} smq_{\mathrm{N}}^{*}. \tag{11}$$

Similarly, a pure female mutant produces new batches of eggs at a rate of A and gets them fertilized at a rate of m. She therefore spends $\frac{A}{m+A}$ of her time carrying eggs and her average reproductive success is

$$w_{\mathrm{N}}^{\mathrm{f}} = m\left(\frac{A}{m+A}\right). \tag{12}$$

Under which conditions can a unisexual individual invade a population of non-traders? For pure males, it is impossible that $w_{\mathrm{N}}^{\mathrm{m}} > w_{\mathrm{N}}$, because each of s, $p_{\mathrm{M}}^{\mathrm{m}}$ and $p_{\mathrm{S}}^{\mathrm{m}}$ is less than one. This means that pure males cannot invade when we make the assumption, used in this section, that there is at most one streaker per mating pair. On the other hand, a pure female can invade if $w_{\mathrm{N}}^{\mathrm{f}} > w_{\mathrm{N}}$. By substituting in equations (8) and (12) and simplifying, this inequality holds if and only if both of the following conditions are met:

$$\begin{gathered} A > A_{\mathrm{N}} = \frac{2m\left(1-r_{\mathrm{N}}^{*}\right)}{m-\left(1-r_{\mathrm{N}}^{*}\right)}. \\ m > 1 - r_{\mathrm{N}}^{*} \end{gathered} \tag{13}$$

In other words, a pure female can invade when potential mates are encountered at least as often as eggs batches are produced, and when the efficiency advantage of producing only one type of gamete exceeds the invasion threshold A_{N}. This threshold thus represents the minimum efficiency advantage that pure females would need to invade. For example, if $A_{\mathrm{N}} = 1.2$, then a pure female can only invade if her expenditure on egg production is at least 20% greater than the overall gamete budget of a hermaphrodite. Note that the invasion threshold is always greater than one, so at least some efficiency advantage is required for a pure female to invade (see Discussion).

WHEN CAN SEPARATE SEXES INVADE? THE TRADER CASE

For populations of traders, the calculations are similar. Hermaphrodites spend q_{T}^{*} of their time carrying eggs, where q_{T}^{*} is found by solving the equation $q_{\mathrm{T}}^{*} = \frac{1-r_{\mathrm{T}}^{*}}{mq_{\mathrm{T}}^{*}+1-r_{\mathrm{T}}^{*}}$. They encounter egg-carrying mates at a rate of mq_{T}^{*}. This leads to reproductive success of $m(q_{\mathrm{T}}^{*})^2$ in the female role and to total reproductive success of

$$w_{\mathrm{T}} = 2m\left(q_{\mathrm{T}}^{*}\right)^{2}. \tag{14}$$

For a pure male mutant, the only possible source of reproductive success is streaking, since no one will trade eggs with an individual that does not reciprocate. The total reproductive success of a pure male is thus

$$w_{\mathrm{T}}^{\mathrm{m}} = p_{\mathrm{S}}^{\mathrm{m}} sm\left(q_{\mathrm{T}}^{*}\right)^{2}. \tag{15}$$

A pure female mutant produces new batches of eggs at a rate of A and gets them fertilized at a rate of mq_{T}^{*}. This means that she spends a proportion $\frac{A}{mq_{\mathrm{T}}^{*}+A}$ of her time carrying eggs and her reproductive success is

$$w_{\mathrm{T}}^{\mathrm{f}} = mq_{\mathrm{T}}^{*}\left(\frac{A}{mq_{\mathrm{T}}^{*}+A}\right). \tag{16}$$

As in the nontrader case, it is impossible for a pure male to invade a population of egg-trading hermaphrodites. Pure females can invade if $w_{\mathrm{T}}^{f} > w_{\mathrm{T}}$, which holds if both:

$$\begin{gathered} A > A_{\mathrm{T}} = \frac{2mq_{\mathrm{T}}^{*}\left(1-r_{\mathrm{T}}^{*}\right)}{mq_{\mathrm{T}}^{*}-\left(1-r_{\mathrm{T}}^{*}\right)}. \\ q_{\mathrm{T}}^{*}m > 1 - r_{\mathrm{T}}^{*} \end{gathered} \tag{17}$$

This means that a pure female can invade if egg-carrying mates are encountered at least as often as it takes to produce a batch of eggs and if the efficiency advantage of specialising in one type of gamete exceeds the invasion threshold A_{T}.

EGG TRADING PROTECTS HERMAPHRODITISM FROM INVASION

We can now determine how egg trading affects the stability of simultaneous hermaphroditism. Since egg traders have relatively female-biased sex allocation, we must have $r_{\mathrm{T}}^{*} < r_{N}^{*}$, and we also know that $q_{\mathrm{T}}^{*} < 1$. Consequently, the invasion threshold for traders A_{T} defined in equation (17) is higher than the threshold for nontraders A_{N} in equation (13). This means that unisexual individuals need a larger gamete budget (i.e., a greater efficiency advantage) to invade an egg-trading population than to invade a nontrading population. Egg trading therefore makes it more difficult for separate sexes to invade a hermaphroditic population (Fig. 2B).

This prediction continues to hold if we allow multiple streakers to attend a mating pair, assuming biologically reasonable parameter values as above (Fig. 2B). In this more general scenario, it is sometimes possible for pure males, and not only pure females, to invade a population of hermaphrodites. This is because when multiple streakers can attend a mating pair, the resultant increase in sperm competition and opportunities for streaking make sperm production a more profitable path to fitness. The conditions for pure male invasion are, however, more stringent than those for pure females, so we should still expect females to invade more easily than males.

THE EFFECTS OF STREAKING AND THE RATE OF MATE ENCOUNTERS

For both traders and non-traders, our model predicts that higher rates of streaking should lead to more equal (i.e., less female-biased) sex allocation (Fig. 2A). As a result, pure females can invade a hermaphroditic population more easily when streaking is common (Fig. 2B). This also means that hermaphroditism is less stable when potential mates are encountered frequently, since we assume a positive relationship between streaking and mate encounter rates. If streaking is completely absent, our model predicts highly female-biased sex allocation and stable hermaphroditism.

If streakers are highly disadvantaged in sperm competition (small d), then sex allocation is more female-biased and it is more difficult for unisexual individuals to invade (Fig. S2 in the Supporting Information online). This is because a strong bias against streakers reduces the effective level of sperm competition.

Discussion

Like most cases of direct reciprocity, the initial evolution of egg trading is puzzling (André 2015): how can trading invade a population, given that its success relies on an established market for eggs (Fischer 1984a; Noë 2001)? Our model shows that, when viewed in the context of hermaphroditic mating systems, the abstract conditions for the evolution of reciprocity have fascinating consequences. Fertilized eggs are the final pathway to fitness in the female role and so egg trading interacts with both individual sex allocation and the population stability of simultaneous hermaphroditism. This raises an interesting dilemma. Previous theory has indicated that egg trading will go to fixation only if encounters with potential mates occur frequently, because this increases the chances that a rare egg trader will find a reciprocating partner (Henshaw et al. 2014b). However, hermaphroditism itself is predicted to be unstable at high mating rates if there is an associated increase in sperm competition due to streakers more often encountering mating pairs (Heath 1977; Charnov 1979; Puurtinen and Kaitala 2002; Eppley and Jesson 2008).

To resolve this dilemma, it is helpful to distinguish between conditions favoring the fixation of egg trading and those that ensure its maintenance. Once egg trading is established in a population, our model predicts that it will "protect" simultaneous hermaphroditism from invasion by unisexual individuals (Fischer 1988; Michiels et al. 2009). Egg trading and hermaphroditism can then persist stably under a broad range of mating parameters, including under conditions of strong sperm competition where hermaphroditism would normally be predicted to be unstable (Fig. 2B and Fig. S2).

Egg trading protects against invasion of both pure females and pure males, but for different reasons. The existence of a trading economy increases the fitness value of eggs, as they can be traded for fertilization opportunities in the male role. Traders consequently bias their sex allocation toward the female function (cf. Greeff and Michiels 1999, where reciprocal sperm exchange is associated with increased male allocation). This female-biased sex allocation makes it harder for pure females to double the egg production of hermaphrodites, as they must do to invade (the "twice-the fitness" rule: see Introduction). Pure males are also disadvantaged by egg trading, but in a more straightforward way: it excludes them entirely from the trading economy (i.e., pair mating), so that their only path to fitness is via streaking.

Our model explains how simultaneous hermaphroditism is maintained once egg trading is fixed in a population. However, we are left to understand how hermaphroditism can persist without egg trading at the high mating rates needed for trading to initially become established (Henshaw et al. 2014b). One possibility is that trading evolves in species where high rates of mate encounter do not elevate the strength of sperm competition. In some egg-trading species, sperm competition is indeed low or even nonexistent, although in others streaking is frequent (Fischer 1984b; Petersen 2006). It is thus possible that ancestral egg-trading species combined low sperm competition with abundant mating opportunities. Our model predicts that simultaneous hermaphroditism will be stable under these conditions (cf. Charnov 1979).

One potential cause for low sperm competition is if streakers are highly disadvantaged in competition with the male-role mate of a spawning pair. This is possible if male-role individuals can easily monopolize their mates, or if female-role individuals prefer to mate monandrously (Taborsky 1998). Our model predicts more strongly female-biased sex allocation in such cases, which makes it more difficult for pure females to invade. Analogous reductions in sperm production are predicted in many situations where paternity is skewed heavily toward some males over others, such as when there is strong first- or last-male sperm precedence

(Parker 1990; Greeff et al. 2001; Williams et al. 2005; Fromhage et al. 2008).

It is important to note that hermaphroditism may persist even under high sperm competition due to phylogenetic constraints on the evolution of separate sexes (Williams 1975; Michiels et al. 2009). Current theory is inadequate to explain when and how such constraints operate (Schärer 2009; Leonard 2013). Although phylogenetic inertia undoubtedly plays a role, fine-grained theoretical studies such as ours have the potential to reveal general "rules" that explain far more of the distribution of hermaphroditism than is currently possible (Erisman et al. 2013). For instance, our results suggest that understanding the relationship between mate availability and the level of sperm competition is crucial to explaining the distribution of hermaphroditism.

Our model predicts that unisexual individuals can only invade a hermaphroditic population if they gain an efficiency advantage from specializing in one type of gamete (i.e., the predicted invasion thresholds A_{N} and A_{T} always exceed one). This result depends on our assumption that egg traders do not self-fertilize, which is consistent with the empirical evidence (Fischer and Petersen 1987; Sella et al. 1997; Petersen 2006). By contrast, in hermaphroditic species that self-fertilize to some extent, inbreeding depression may reduce the average fitness of offspring. Pure females may then invade more easily, potentially even without any resource advantage, if they produce offspring of higher quality than self-fertilizing hermaphrodites (Charlesworth and Charlesworth 1978; Charlesworth 1999). The evolution of cytoplasmic "male sterility" factors may also allow the invasion of pure females without an increase in overall resources for gamete production. Such mutations are selected for if they produce any increase in female-role fitness, even if this means a reduction in overall fitness, but they may be opposed by counter-selection for nuclear modifiers that reduce or nullify their effects (Charlesworth 1999).

While much theoretical work seeks to explain the evolutionary origins of direct reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Nowak 2006; André 2015), fewer studies have explored its consequences for the evolution of other traits. Our model predicts that once reciprocity has evolved, individuals will tend to invest more heavily in producing the traded resource (in our case, eggs). This may occur in other systems where the currency of reciprocity must be produced or collected. For instance, individuals in food-sharing species may gather more food than they would need in the absence of a trading economy, due to the expected future benefits of donating excess food (Rutte and Taborsky 2008; Carter and Wilkinson 2013).

Our model reveals general patterns but it has a few important limitations. First, it assumes that all individuals are alike in their gamete production, their desirability as mates, and their streaking potential. Evidence in several egg-trading species suggests, however, that both fecundity and the number of female partners increase with an individual's body size, and in some species streaking rates are higher for smaller individuals (Petersen and Fischer 1996; Oliver 1997; Petersen 2006). There may consequently be interrelationships between sex allocation and mating behavior for which our model fails to account. Second, our model assumes that the only resource trade-off an individual faces is between sperm and egg production, whereas reproductive success may also depend heavily on investment in attracting or competing for mates (Parker et al. 2013). Indeed, many egg-traders engage in vigorous courtship displays prior to spawning, which presumably divert resources away from gamete production (Sella 1985; Fischer and Petersen 1987; Friedman and Hammerstein 1991; Lorenzi et al. 2006). Third, our model does not consider cheating in any other form than opportunistic streaking; traders are always assumed to reciprocate egg release perfectly (note that other theoretical studies have considered this issue in detail: Friedman and Hammerstein 1991; Crowley and Hart 2007). Fourth, our model only considers the initial invasion of unisexual individuals into a hermaphroditic population. It does not predict whether a successful invasion will eventually lead to separate males and females (dioecy) or to females coexisting with hermaphrodites (gynodioecy). Thus, despite being rare as a mating system, egg trading appears to offer ample opportunities for further study of the dynamics of cooperative exchanges.

Finally, why is egg trading so rare, despite its protective effect on simultaneous hermaphroditism? Although egg trading stabilizes hermaphroditism once fixed, it cannot facilitate the invasion of hermaphrodites into a dioecious population. Egg trading can only evolve if hermaphroditism is already established. More importantly, egg trading is itself under positive frequency-dependent selection, which creates a barrier to its initial invasion regardless of the level of sperm competition or mating rates (Henshaw et al. 2014b). This bootstrapping problem is common to all forms of direct reciprocity and is perhaps the primary reason why such behavior is rare in nature (André 2015). Many aspects of mating systems are similarly subject to complex evolutionary feedbacks, including different conditions for the origin and maintenance of traits, and formal models are needed to disentangle the stage-dependent changes in selection in these systems (Lehtonen and Kokko 2012).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1: Stability of hermaphroditism when nontrading pure females can evolve via a single mutation.

Figure S2: Effect of streaker disadvantage on the stability of hermaphroditism.