

The Evolution of Egg Trading in Simultaneous Hermaphrodites

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ABSTRACT: Egg trading—whereby simultaneous hermaphrodites exchange each other's eggs for fertilization—constitutes one of the few rigorously documented and most widely cited examples of direct reciprocity among unrelated individuals. Yet how egg trading may initially invade a population of nontrading simultaneous hermaphrodites is still unresolved. Here, we address this question with an analytical model that considers mate encounter rates and costs of egg production in a population that may include traders (who provide eggs for fertilization only if their partners also have eggs to reciprocate), providers (who provide eggs regardless of whether their partners have eggs to reciprocate), and withholders (cheaters who mate only in the male role and just use their eggs to elicit egg release from traders). Our results indicate that a combination of intermediate mate encounter rates, sufficiently high costs of egg production, and a sufficiently high probability that traders detect withholders (in which case eggs are not provided) is conducive to the evolution of egg trading. Under these conditions, traders can invade—and resist invasion from—providers and withholders alike. The prediction that egg trading evolves only under these specific conditions is consistent with the rare occurrence of this mating system among simultaneous hermaphrodites.

Keywords: egg trading, simultaneous hermaphroditism, cooperation, direct reciprocity.

Introduction

Sexual conflict arises when there is a conflict of interest between the two members of a mating pair over sexual reproduction (Hammerstein and Parker 1987; Kokko and Jennions 2014). In simultaneous hermaphrodites, such a conflict arises with respect to the male and female functions and often manifests as a preference for mating in the male role (Charnov 1979). Such preference has been interpreted as a direct consequence of anisogamy: since

eggs are more energetically costly to produce than sperm, reproductive success is expected to be limited by access to eggs specifically (Bateman 1948; for a more recent perspective, see also Parker and Birkhead 2013). Mating in the male role should therefore be preferred, which creates a conflict of interest between mating partners: both would prefer to mate in the male role, but for the mating to be successful, one partner needs to mate in the less preferred female role (Leonard 1993).

Egg trading is a specific mating system whereby simultaneous hermaphrodites trade each other's eggs for fertilization, which contributes to resolve this type of conflict. Egg trading evolved independently in fishes (Fischer 1980, 1984; Pressley 1981; Petersen 1995; Oliver 1997) and polychaetes (Sella 1985; Sella et al. 1997; Sella and Ramella 1999; Sella and Lorenzi 2000; Picchi et al. 2018). When mating, a pair of egg traders take turns in fertilizing each other's eggs. By linking male reproductive success to female reproductive success, egg trading disincentivizes spawning in the male role predominantly or exclusively, as opportunities to fertilize a partner's eggs depend on providing eggs to that partner (Fischer 1980). More broadly, egg trading constitutes one of the few rigorously documented and most widely cited examples of direct reciprocity among unrelated individuals in animals (Axelrod and Hamilton 1981). Direct reciprocity (also known as reciprocal altruism; Trivers 1971) operates when an individual acts at an immediate fitness cost to benefit another individual, who in turn reciprocates that benefit back. It provides a mechanism for the evolution of cooperation among genetically unrelated individuals (Sachs et al. 2004; Lehmann and Keller 2006; Nowak 2006; Van Cleve and Akçay 2014).

To date, most theoretical work on egg trading has sought to explain (1) its evolutionary stability against invasion by cheaters (hereafter referred to as withholders) who fertilize their partners' eggs but do not reciprocate by releasing eggs (Leonard 1990; Friedman and Hammerstein 1991; Crowley and Hart 2007) and (2) its role in making simultaneous hermaphroditism evolutionarily stable relative to gonochorism (Fischer 1980; Henshaw et al. 2015). While

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these studies addressed the stability and evolutionary consequences of egg trading once it is already established, how egg trading may evolve in the first place turned out to be a problematic question. Axelrod and Hamilton (1981) speculated that egg trading might have evolved through a low-density phase that would have favored self-fertilization and inbreeding, which would have in turn allowed kin selection to operate. However, this hypothesis has been challenged on the grounds that many egg traders do not (and might not have the physiological ability to) self-fertilize (Fischer 1981, 1988).

More recently, Henshaw et al. (2014) provided a combination of analytical and simulation models that constitutes the first thorough attempt to explicitly address the evolution of egg trading. Their analytical model considers mate encounters in a population that includes nontraders (individuals who provide eggs at every mating opportunity, hereafter referred to as providers) and traders (individuals who provide eggs only if their partner have eggs to reciprocate). Their results show that, as with other instances of direct reciprocity (André 2014), egg trading is under positive frequency-dependent selection and counterselected unless the proportion of traders in the population reaches a critical threshold. Egg trading can therefore reach fixation in this model only when the strategy is already represented by a certain proportion of the population, leaving it open how rare egg-trading mutants may initially persist and spread. Henshaw et al. (2014) showed that the egg-trading invasion barrier is easier to overcome when encounters between mates are frequent, as such high encounter rates increase the chances that a rare egg trader will find a partner with eggs to reciprocate. This relationship between encounter rates and the evolution of egg trading raises an interesting dilemma since high encounter rates have also been found to destabilize egg trading by allowing withholders to invade a population of egg traders (Crowley and Hart 2007). Consequently, it is not clear how egg trading can initially spread or to what extent it can resist invasion by withholders under the high encounter rates that are thought to facilitate its establishment.

Here we build on the analytical model of Henshaw et al. (2014) and extend it by adding four fundamental features. First, we allow for the possible occurrence of withholders, who never provide eggs and only mate in the male role, in addition to traders and providers. Second, we relax the implicit assumption of Henshaw et al. (2014) that egg production has no costs in terms of availability for mating. This assumption does not generally hold in nature since the time and energy devoted to the acquisition of resources for egg production often trade off with the time and energy available for mate search (Puurtilinen and Kaitala 2002). A direct implication of this trade-off is that individuals who are in the process of producing new eggs are expected to be less

available for matings (in the male role since they have no eggs) than individuals carrying eggs. Third, we assume that traders can detect withholders with some positive probability and punish them by not providing eggs. Fourth, we incorporate the biologically important feature, discussed by Henshaw et al. (2014) but not incorporated in their model, that eggs might senesce and become unviable before a partner is found. We show that the first three additions generate complex evolutionary dynamics that allow traders to invade (and resist invasion from) both providers and withholders when encounter rates are intermediate and further both the costs of egg production and the probability that withholders can be detected are sufficiently high. The fourth addition (egg senescence) shapes the trade-offs that affect the evolution of egg trading.

Model

We posit a large, well-mixed population of simultaneous hermaphrodites in which generations overlap and there is no self-fertilization. At any given time, each individual in the population is either carrying a batch of eggs or not. Eggless individuals produce a new batch of eggs at a normalized rate of 1. Egg-carrying individuals encounter potential mates at the positive encounter rate m , while eggless individuals (who are producing new eggs) encounter potential mates at a discounted rate λm , where $0 < \lambda \leq 1$. The parameter λ measures the degree to which individuals who are in the process of producing eggs are available for mating. Being unavailable for mating constitutes a cost of egg production in terms of missed opportunities for reproduction in the male role. Thus, low values of mating availability λ imply high costs of egg production, with the extreme case $\lambda = 0$ implying maximal cost (mating in the male role is impossible while producing eggs). Conversely, high mating availability λ implies a low cost of egg production, with $\lambda = 1$ implying minimal cost (individuals who are in the process of producing new eggs can always mate in the male role). We also incorporate egg senescence, with eggs becoming nonviable at a rate $\rho \geq 0$.

We consider three different mating strategies: trading (T), withholding (H), and providing (P). All three strategies mate in the male role (i.e., fertilize eggs) whenever possible but differ on the conditions under which they provide eggs to partners for fertilization. Traders are choosy: they provide eggs only if mates have eggs to reciprocate. Withholders are stingy: they never provide eggs and reproduce only through their male function. Indeed, the only function of their eggs is to elicit egg release from traders; that is, withholders cheat on their partners by failing to reciprocate eggs. Providers are generous: they provide eggs to any partner, regardless of whether the mate has eggs to reciprocate. We further assume that traders can

detect withholders with a positive probability q , in which case eggs are not provided. In the absence of withholders (there are only providers and traders in the population) and after setting $\lambda = 1$ (egg production is costless in terms of availability for mating) and $\rho = 0$ (eggs do not senesce), our model recovers the analytical model of Henshaw et al. (2014), after identifying our providers with their nontraders.

In line with game-theoretic approaches (Maynard Smith 1982), we assume a one-locus haploid genetic system, so that each individual's mating strategy is determined by a single gene inherited from the mother or the father with equal probability. Moreover, we assume a separation of time-scales such that the demographic variables (the proportions of individuals carrying and not carrying eggs within each strategy) equilibrate much faster than the evolutionary variables (the proportions of individuals following each strategy). With these assumptions, we can write the evolutionary dynamics of our model as a system of replicator equations (Weibull 1995; Hofbauer and Sigmund 1998) for the three strategies T, H, and P, with frequencies given by x , y , and z , respectively. That is, we write the evolutionary dynamics of our model as

$$\dot{x} = x(w_T - \bar{w}), \quad (1a)$$

$$\dot{y} = y(w_H - \bar{w}), \quad (1b)$$

$$\dot{z} = z(w_P - \bar{w}), \quad (1c)$$

where dots denote time derivatives; w_T , w_H , and w_P are the fitnesses to each strategy; and $\bar{w} = xw_T + yw_H + zw_P$ is the average fitness in the population. Fitnesses are given by the rate of offspring production in both the male and the female roles and are nontrivial functions of the parameters of the model and of the proportions of the different strategies when carrying and not carrying eggs at the demographic equilibrium. The state space Δ is the simplex of all (x, y, z) with $x, y, z \geq 0$ and $x + y + z = 1$.

In the following we present a summary of our results. Our formal model and the analytical derivation of all results are given in appendixes A and B (apps. A–C are available online).

Results

The replicator dynamics has three monomorphic equilibria: a homogeneous population of traders (T), a homogeneous population of withholders (H), and a homogeneous population of providers (P). Among these equilibria, H is always unstable: for any parameter combination, a homogeneous population of withholders can be invaded by traders, providers, or a mixture of both strategies. In addition to these three monomorphic equilibria, and depending

on parameter values, the replicator dynamics can have up to two out of three polymorphic equilibria on the boundary of the simplex Δ (fig. 1): (1) an equilibrium R along the TP edge, where traders and providers coexist but withholders are absent (fig. 1B, 1C); (2) an equilibrium Q along the TH edge, where traders and withholders coexist but there are no providers (fig. 1C, 1D); and (3) an equilibrium S along the HP edge, where withholders and providers coexist but there are no traders (fig. 1D, 1E). When these polymorphic equilibria exist, R is a saddle (repelling for points along the TP edge and attracting for neighboring points in the interior of Δ), Q is stable (attracting from neighboring points in Δ), and S is a saddle (attracting for points along the HP edge and repelling for neighboring points in the interior of Δ). These equilibria are rather complicated functions of the model parameters, so we report their expressions in appendix B. The replicator dynamics has no equilibria in the interior of Δ ; that is, no population composition with all three strategies coexisting is an equilibrium.

We find that both the stability of the monomorphic equilibria T and P and the existence of the polymorphic equilibria Q, R, and S depend on how the mating availability λ compares with the critical value

$$\lambda_* = \frac{m - (1 + \rho)}{\rho(1 + \rho) + m(2 + \rho)}, \quad (2)$$

and on how the encounter rate m compares with the critical values

$$m_* = (1 + \rho)[1 + \lambda(1 + 2\rho)], \quad (3)$$

$$m^* = \frac{(1 + \rho)(1 + q)[1 - q + \lambda(1 + q + 2\rho)]}{(1 - q)^2}. \quad (4)$$

First, the stability of the monomorphic equilibrium P depends on how the mating availability λ compares with the critical value λ_* . A homogeneous population of providers is stable against invasions by the other two strategies if and only if mating availability is high ($\lambda > \lambda_*$). As λ decreases and crosses the threshold λ_* , P becomes unstable against both traders and withholders, and the saddle S is created along the HP edge.

Second, the stability of the monomorphic equilibrium T depends on how the encounter rate m compares with the critical values m_* and m^* . A homogeneous population of traders is (1) unstable against invasion by providers but stable against invasion by withholders if the encounter rate is low ($m < m_*$), (2) stable against both withholders and providers if the encounter rate is intermediate ($m_* < m < m^*$), and (3) stable against invasion by providers but unstable against invasion by withholders if the encounter rate

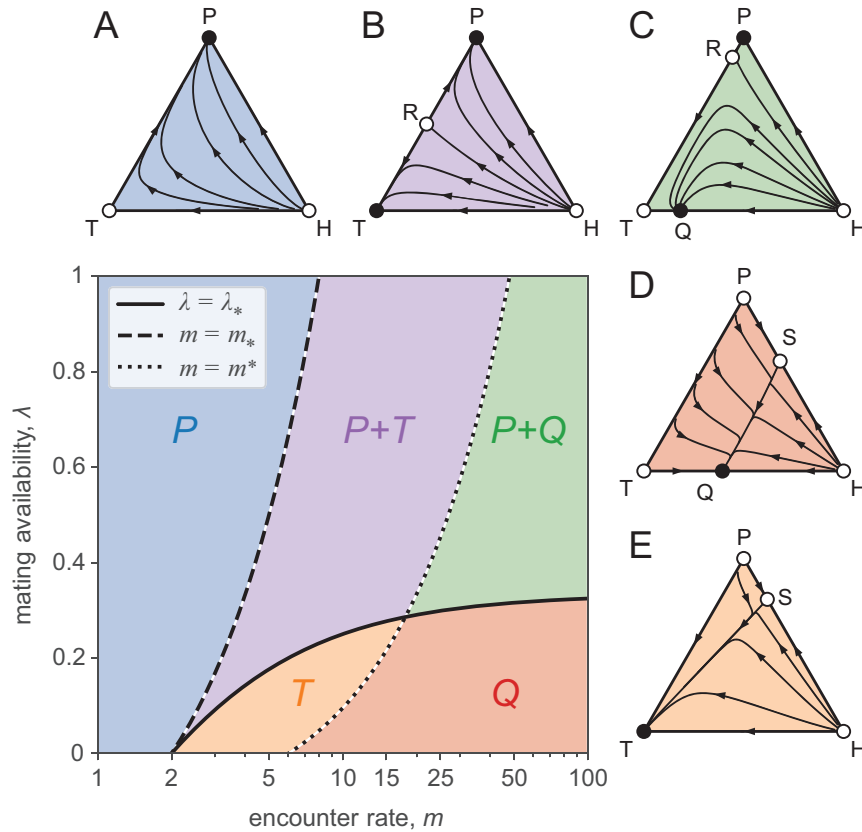


Figure 1: Effects of mating availability and encounter rates on the evolutionary dynamics of egg trading. The parameter space can be divided into five disjoint regions (P , $P + T$, $P + Q$, Q , and T) depending on how availability λ compares with the critical availability λ^* (eq. [2]) and on how the encounter rate m compares with the critical encounter rates m_* (eq. [3]) and m^* (eq. [4]). Triangles represent the state space $\Delta = \{(x, y, z) \geq 0, x + y + z = 1\}$, where x , y , and z are the frequencies of traders, withholders, and providers, respectively. The three vertices T , H , and P correspond to homogeneous states where the population is entirely comprised of traders ($x = 1$), withholders ($y = 1$), or providers ($z = 1$). Solid circles represent stable equilibria (sinks); open circles represent unstable equilibria (sources or saddle points). *A*, In region P , trajectories in Δ converge to P . *B*, In region $P + T$, trajectories converge to either P or T , depending on initial conditions. The equilibrium R on the TP edge is a saddle point dividing the basins of attraction of P and T . *C*, In region $P + Q$, trajectories converge to either P or the equilibrium Q along the TH edge, depending on initial conditions. *D*, In region Q , trajectories converge to Q . The equilibrium S along the HP edge is a saddle. *E*, In region T , trajectories converge to T . Parameters: $\rho = 1$; $q = 0.5$; $m = 2$ (*A*), 12 (*B*), 50 (*C*, *D*), 8 (*E*); $\lambda = 0.7$ (*A*–*C*), 0.1 (*D*, *E*).

is high ($m > m^*$). As m increases and crosses the threshold m_* , T becomes stable while spawning the unstable equilibrium R along the TP edge; as m increases further and crosses the threshold m^* , T becomes unstable and the stable equilibrium Q (where traders and withholders coexist) is created along the TH edge.

All in all, the parameter space can be partitioned into five dynamical regions (fig. 1), each having qualitatively different evolutionary dynamics. Among these, only regions Q and T (for which availability is low; i.e., $\lambda < \lambda^*$ holds) allow traders to invade a resident population of providers, and only region T allows traders to both invade providers and resist invasion by withholders. A key requirement for this last scenario is that encounter rates are neither too high nor too low ($m_* < m < m^*$).

The encounter rate m is a key parameter in our model. For low encounter rates ($m < m_*$; region P), P is the only stable equilibrium and the outcome of the evolutionary dynamics. This makes intuitive sense: if potential mates are difficult to find, individuals should provide eggs at every mating opportunity; being picky in this context is risky because another partner might be difficult to find before eggs become unviable. For higher encounter rates ($m > m_*$; regions $P + T$, T , $P + Q$, and Q), finding mates becomes easier, and it pays to reject eggless partners in the hope of finding partners carrying eggs. Very large encounter rates ($m > m^*$; regions $P + Q$ and Q) even allow withholders (who never release their eggs and mate only in the male role) to be successful in the long run and coexist with traders at the equilibrium Q . The proportion of traders at

such an equilibrium decreases as the mate encounter rate increases, down to 50% in the limit of high encounter rates.

The benefits of being choosy are particularly salient when the costs of egg production are high (i.e., when the mating availability λ is low). Indeed, a lower mating availability λ has two related and reinforcing consequences. First, low availability means fewer opportunities to mate in the male role when not carrying eggs and hence higher opportunity costs to mate indiscriminately in the female role. Second, low availability also implies that the probability of finding another potential mate without eggs after having rejected previous potential partners is lower, thus decreasing the risk of being choosy. In line with these arguments, we find that for sufficiently high costs of egg production ($\lambda < \lambda_*$; regions *Q* and *T*), *P* can be invaded by strategies that do not mate indiscriminately in the female role (traders and withholders). For high encounter rates ($m > m^*$; region *Q*) traders invade but are not able to displace withholders, and the population composition at equilibrium is a mixture of traders and withholders. Otherwise, for moderate encounter rates ($m_* < m < m^*$; region *T*) traders invade and take over the whole population while resisting invasion by withholders.

The probability that traders detect withholders, q , plays an essential role in stabilizing the trading equilibrium *T* in our model (fig. 2). Indeed, some amount of withholder detection (as encapsulated by the parameter q) is necessary for trading to be evolutionarily stable in the presence of withholders. This is so because the critical encounter rate m^* tends to m_* (which does not depend on q) as q tends to zero. Thus, in this limit, regions *P* + *T* and *T* cease to exist and the trading equilibrium *T* is unstable for all encounter rates. In addition, the critical encounter rate m^* is an increasing function of q (fig. 2). Because $m \leq m^*$ is a necessary and sufficient condition for a monomorphic population of traders to resist invasion by withholders, larger values of q imply that more stringent conditions (i.e., higher encounter rates) are required to destabilize *T*.

Finally, we note that the critical mating availability λ_* and the critical encounter rates m_* and m^* are all functions of the rate of egg senescence ρ . The critical availability λ_* is decreasing in ρ (fig. 2). The evolutionary consequence of this effect is that the higher the rate of egg senescence ρ , the lower the critical availability λ_* below which traders (and withholders) can invade a monomorphic population of providers. This makes intuitive sense because providers give up their eggs more freely and are thus less likely to suffer the consequences of a higher egg senescence than traders and withholders. Additionally, both critical encounter rates m_* and m^* are increasing in ρ (fig. 2). Therefore, the higher the ρ , the higher the minimal encounter rate m_* (maximal encounter rate m^*) required for a mono-

morphic population of traders to resist invasion by providers (withholders).

Discussion

A general prediction of our model is that there are only three possible evolutionarily stable equilibria: a homogeneous population of providers, a homogeneous population of egg traders, or a polymorphic population that includes both egg traders and withholders. The first stable equilibrium would correspond to simultaneous hermaphrodites that do not trade eggs. This equilibrium is attained in a large area of the parameter space, which is consistent with the fact that the majority of simultaneous hermaphrodites do not trade eggs. The second stable equilibrium would correspond to egg traders and can be attained under the specific conditions that we discuss below. The closest situation to the third stable equilibrium in nature would correspond to egg-trading species in which mating also occurs in the male role only through streaking, that is, the furtive release of sperm in competition with the male of an egg trading pair (Pressley 1981; Fischer 1984; Petersen 1995; Oliver 1997). Streaking was not explicitly incorporated in our model, but we note that, as our withholders, such streakers are not pure males but simultaneous hermaphrodites that mate in the male role. We are not aware of simultaneously hermaphroditic species in which egg trading is facultative, which is consistent with the fact that there is no stable equilibrium in our model involving both traders and providers.

When mating availability (λ) is equal to 1 and egg senescence (ρ) is equal to 0, the only difference between our model and the one by Henshaw et al. (2014) is that we incorporate withholders. Doing so does not affect the conclusion from Henshaw et al. (2014) that there is an initial barrier that traders need to overcome in order to invade a population of providers. Further, as predicted by Henshaw et al. (2014), higher encounter rates make this invasion barrier smaller. In this sense, high encounter rates thus promote the evolution of egg trading. However, very high encounter rates ($m > m^*$) will also inevitably allow withholders to invade the trading equilibrium and thereby lead to the emergence of a stable polymorphic population of traders and withholders. In particular, in the limit of very high encounter rates (so that the invasion barrier becomes arbitrarily small), the evolutionary outcome is not the invasion and fixation of trading predicted by Henshaw et al. (2014) but (as we show in app. B) a stable polymorphic population consisting of 50% traders and 50% withholders. Such a polymorphic population is stable because with very high encounter rates, withholders prosper in a population where there are ample opportunities to reproduce in the male role (as will be the case if traders, who are willing to provide their eggs with probability $1 - q$, are frequent), while they fare

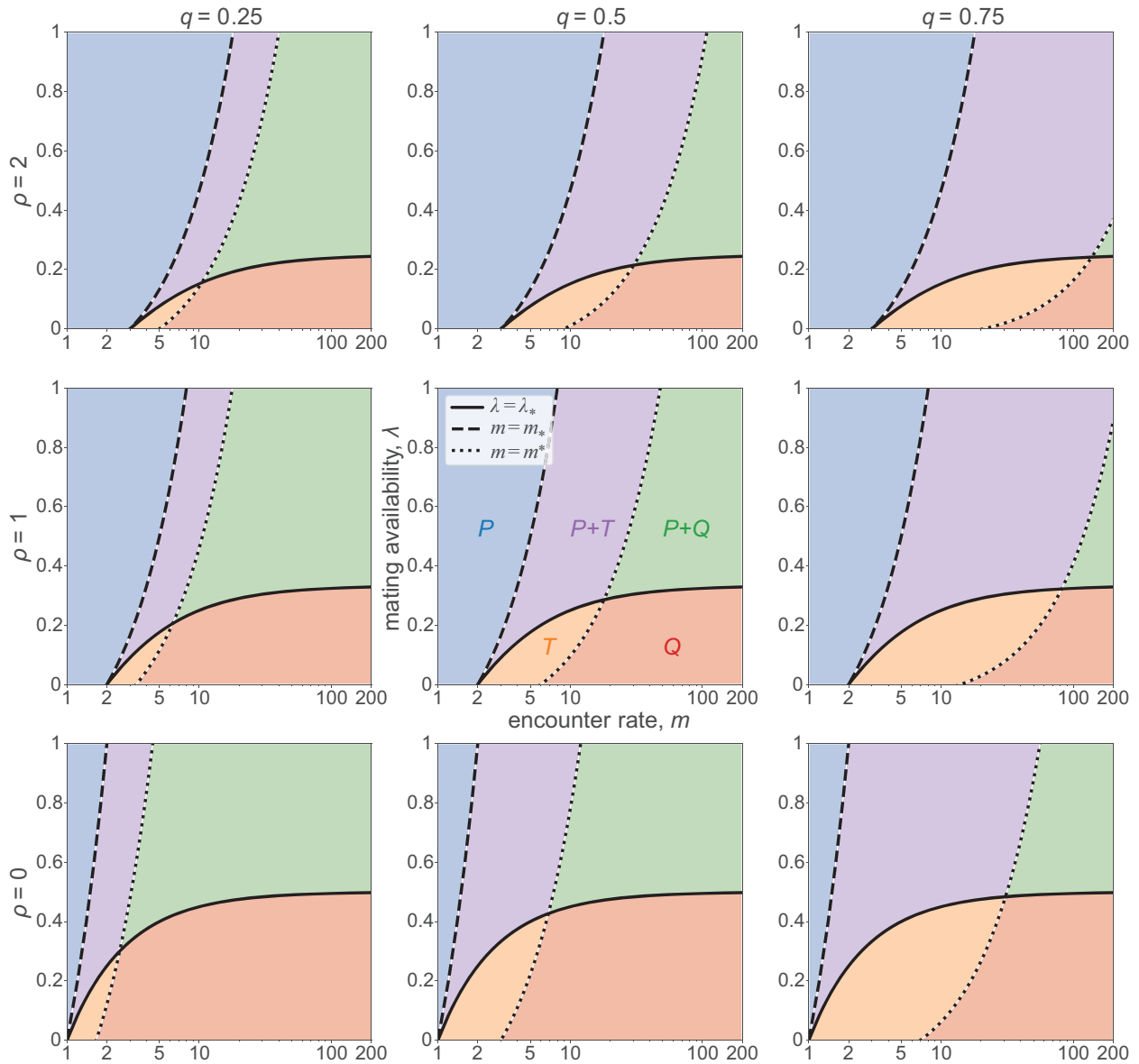


Figure 2: Effects of egg senescence and probability of withholder detection on the evolutionary dynamics of egg trading. Panels represent, for different combinations of egg senescence ρ and probability of withholder detection q , the critical mating availability λ_* (eq. [2]) and the critical encounter rates m_* (eq. [3]) and m^* (eq. [4]) that define the boundaries of the five dynamical regions (P , $P + T$, $P + Q$, Q , and T) into which the parameter space can be divided. For fixed ρ and λ , increasing q increases the values of the encounter rate m at which $m = m^*$ holds, thus increasing the areas of regions $P + T$ and T (where the trading equilibrium T is evolutionarily stable) and shrinking the areas of regions $P + Q$ and Q (where withholders invade T). For fixed q and m , increasing ρ decreases the values of the mating availability λ at which $\lambda = \lambda_*$ holds, thus decreasing the combined area of regions Q and T , where traders can invade the providing equilibrium P . The center panel corresponds to the parameter values ($\rho = 1$, $q = 0.5$) used in figure 1.

poorly in a population with few opportunities to reproduce in the male role (as will be the case in a population consisting predominantly of withholders who never provide their eggs).

Recognizing the possibility of costly egg production by allowing mating availability to be <1 is another important

way in which our model differs from Henshaw et al. (2014). Indeed, our analysis reveals that the cost of egg production plays a crucial role in the evolution of egg trading. In particular, for encounter rates that are neither too high nor too low, traders can both invade providers and be stable against invasion by withholders. This result implies that

neither a combination of self-fertilization and kin selection (Axelrod and Hamilton 1981) nor high encounter rates (Henshaw et al. 2014) that would promote the invasion by withholders are necessary for the evolution of egg trading, and it thereby resolves the dilemma on the relationship between encounter rate and the evolution of egg trading.

The trade-off between the time and energy allocated to acquire resources for egg production versus mate search that is captured by our parameter λ has been documented in egg traders. For example, in hamlets (*Hypoplectrus* spp.), one of the fish groups in which egg trading is best described, individuals meet on a daily basis in a specific area of the reef for spawning at dusk (Fischer 1980). This can imply swimming over hundreds of meters of reef (Puebla et al. 2012). Not all individuals show up in the spawning area on each evening, but most individuals that are present are observed spawning in both the female and the male role (implying that they carry eggs). The majority of individuals who do not spawn are not present in the spawning area and are therefore not available for mating, even in the male role only, which is exactly what the parameter λ captures. This said, our model is not meant to represent any group of egg traders in particular but to capture the minimal set of parameters that are relevant for the evolution of egg trading. Mate encounter rate had been identified as such a parameter by Henshaw et al. (2014); we added here the opportunity costs of egg production. Our results indicate that the evolution of egg trading from an ancestral state where the population consists of only providers requires at the very least a minimum of egg production costs.

Once egg trading is able to invade a population of providers, two different evolutionary scenarios are possible. First, trading can reach fixation and be established at an evolutionarily stable equilibrium. Second, trading can be sustained at a polymorphic equilibrium featuring egg traders and withholders. Which of these two scenarios is reached depends to a large extent on the ability of egg traders to detect withholders (q). A necessary condition for the first scenario to be reached is that q is positive, that is, that there is at least some withholder detection. Moreover, the higher q (i.e., the better the abilities of traders to detect withholders), the larger the set of values for the other parameters under which trading is evolutionarily stable against withholding and the first scenario prevails.

There are at least two ways in which egg traders may be able to detect withholders in nature. The first one is through reputation and learning in small populations where mating encounters occur repeatedly among the same set of individuals (Puebla et al. 2012). In this situation, individuals who fail to reciprocate eggs might be identified as withholders and avoided in subsequent mating encounters.

The second one is through parcelling of the egg clutch, which occurs in several egg-trading species (Fischer 1980; Fischer and Hardison 1987; Petersen 1995; Oliver 1997). In this case, eggs are divided into parcels that the two partners take turns in providing and fertilizing. This constitutes an efficient mechanism to detect partners that fail to reciprocate and also provides the opportunity to terminate the interaction before all eggs are released if the partner does not reciprocate.

By and large, the conditions that are required for the invasion and fixation of egg trading (intermediate encounter rates, sufficiently high costs of egg production, and possibility to detect withholders) are rather restrictive. In addition, egg trading requires that individuals interact directly to trade eggs, which implies that they are mobile. It is therefore not surprising that egg trading is a rare mating system, documented in only Serraninae fishes (Fischer 1980, 1984; Pressley 1981; Petersen 1995; Oliver 1997) and dorvilleid polychaetes in the genus *Ophryotrocha* (Sella 1985; Sella et al. 1997; Sella and Ramella 1999; Sella and Lorenzi 2000). Hermaphroditism, on the other hand, occurs in 24 out of 34 animal phyla and is common to dominant in 14 phyla, including sponges, corals, jellyfishes, flatworms, mollusks, ascidians, and annelids (Jarne and Auld 2006). The rare occurrence of egg trading among simultaneous hermaphrodites suggests that simultaneous hermaphroditism can readily evolve and be maintained in the absence of egg trading. This is what motivated our choice to focus on the evolution of egg trading among simultaneous hermaphrodites as opposed to the joint evolution of egg trading and simultaneous hermaphroditism. In our model, this is illustrated by the fact that although withholders mate in the male role exclusively, they are nonetheless not pure males but hermaphrodites that keep producing eggs to elicit egg release by traders. In principle, the rarity of egg trading might also be due to the possibility that egg trading ultimately leads to a loss of hermaphroditism and consequently of egg trading itself. However, this scenario goes against the results of Henshaw et al. (2015), who show that egg trading can help stabilizing hermaphroditism by selecting for a female-biased sex allocation in traders, which in turn prevents pure females from invading a population of traders.

We assumed a very simple genetic architecture of the trait under consideration, namely, a one-locus haploid genetic system. Since most simultaneously hermaphroditic species are diploid, and since egg trading is likely to be a complex trait under the control of many genes, this is clearly a simplifying assumption that trades biological reality for model tractability, that is, an example of the phenotypic gambit often endorsed in evolutionary models (Grafen 1984; Gardner et al. 2011). In our case, this simplifying assumption is justified both by the fact that the specific genetic architecture of egg trading is so far unknown for any species

and by our goal of comparing our model and results with the existing literature, which has also explicitly or implicitly endorsed the phenotypic gambit. That being said, egg trading and other traits affecting mating strategies are particular because they influence who mates with whom and can thus potentially lead to assortment of alleles at the zygotic level. Additional work is needed to investigate the effect of the genetic system (e.g., number of loci, dominance) on the evolutionary dynamics of egg trading.

A key dynamic that is characteristic of systems subject to sexual conflict over mating, such as the one investigated here, is the coevolution of male coercion and female resistance (Clutton-Brock and Parker 1995). While male coercion has been considered in the context of egg trading (Fischer and Hardison 1987), there is little evidence of this phenomenon among egg traders. Nevertheless, the streaking behavior displayed by some egg-trading species (Pressley 1981; Fischer 1984; Petersen 1995; Oliver 1997) may be interpreted as a form of male coercion. Henshaw et al. (2014) included streaking in their simulation model and found that it makes the evolution of egg trading less likely (for the effects of streaking on the role played by egg trading in stabilizing hermaphroditism, see also Henshaw et al. 2015). This is because streakers (as our withholders) bypass the trading convention and gain reproductive success as males without offering eggs in return. This form of male coercion could be counteracted by strategies of female resistance that increase the costs of coercion, such as the parcelling of the egg clutch observed in some egg traders (Fischer 1980; Fischer and Hardison 1987; Petersen 1995; Oliver 1997). This calls for the incorporation of both streaking and egg parcelling in future analytical models to better understand the evolution of egg trading.

We modeled social interactions as a game with three distinct strategies (traders, providers, and withholders) and analyzed the resulting evolutionary process using the replicator dynamics. A caveat of this approach is that withholding is an evolutionary dead end, as a population of withholders would completely fail to reproduce. This may cast some doubt on the suitability of modeling withholding as a pure strategy and on the results we obtained. To dispel this potential criticism and to test the robustness of our results, appendix C presents a model where traders compete against nontraders playing a mixed strategy that provides eggs with probability s and withholds them with probability $1 - s$. We use adaptive dynamics (Geritz et al. 1998; Doebeli 2011) to determine the evolutionary end point of the quantitative trait s in a population of nontraders and then investigate the conditions under which traders are able to invade such a population. The results of this analysis demonstrate the robustness of our conclusion that traders can invade nontrading populations if the encounter rate is intermediate and mating availability is suf-

ficiently low. A more ambitious analysis could fully embrace a continuous representation of the phenotype space and use multidimensional versions of adaptive dynamics (e.g., Leimar 2009; Débarre et al. 2014; Mullon et al. 2016) to investigate the coevolution of rates of providing, withholding, and trading eggs in a relatively economic way.

Our model of egg trading is related to game-theoretic models of food sharing and social foraging, where individuals either produce by searching for food or scrounge by not searching and instead exploiting others' food discoveries (Vickery et al. 1991; Giraldeau and Caraco 2000). In these producer-scrounger games, it is assumed (1) that information about the location of food clumps discovered by producers is immediately acquired by scroungers and (2) that single individuals are able to process the food clumps they discover. Our model of egg trading can be thought of as a variant of a producer-scrounger game in which information about the location of resources is instead private, where two individuals are needed to access or handle a resource (e.g., large prey) and where mating corresponds to entering a partnership to successfully exploit the resource. From this perspective, the providers of our model are equivalent to producers that search for food and share information with all individuals, withholders are equivalent to scroungers that either do not search or always withhold information, and traders are equivalent to individuals that search but share information on discovered food items only with partners that have acquired new information.

Our model of egg trading also shares features with more general models for the evolution of cooperation, in particular with models of partner choice (Bull and Rice 1991; Noë and Hammerstein 1994) and indirect reciprocity (Nowak and Sigmund 2005). First, our model is related to models of partner choice where potential partners are encountered at a certain rate and where strategies or individuals can vary both in their choosiness and in their cooperativeness (e.g., McNamara et al. 2008; André and Baumard 2011). Importantly, however, in our model individuals discriminate partners not directly on the basis of their perceived cooperativeness but rather on their state or physiological condition (i.e., on whether the partner is carrying eggs), which serves as an indirect measure of partner quality. Second, the transitions a given focal individual makes between different states or physiological conditions are mediated by social actions; for example, an egg carrier becomes eggless when it decides to offer its eggs to a partner. This resembles the way models of indirect reciprocity work, where an individual's reputation changes depending on both its decision to cooperate and the particular social norms to assign reputations enforced in the population (e.g., Nowak and Sigmund 1998; Leimar and Hammerstein 2001; Panchanathan and Boyd 2003; Ohtsuki and Iwasa 2006; Santos et al. 2018).

Our model predicts that egg trading should occur in simultaneously hermaphroditic species for which (1) encounter rates are intermediate, (2) egg production entails a cost in terms of mating availability, and (3) withholders can be detected to some extent. Testing this prediction calls for an empirical estimation of these factors (as well as rates of egg senescence) in egg-trading and closely related non-egg-trading species. The incorporation of egg parcelling and sperm competition through streaking into our model would also allow us to refine our predictions.

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Data and Code Availability

The code used for creating the figures in this article builds on Inom Mirzaev and Drew F. K. Williamson's Python package `egtplo` (<https://github.com/mirzaevinom/egtplo>). Our source code in Python is publicly available on GitHub (<https://github.com/jorgeapenas/eggtrading>) and the Dryad Digital Repository (<https://doi.org/10.5061/dryad.9tb689h>; Peña et al. 2020).

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