Egg-trading in simultaneous hermaphrodites: an alternative to Tit-for-Tat

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Introduction

Reciprocal Altruism or reciprocity occurs when an individual performs a costly act for the benefit of another individual in anticipation of receiving beneficence via a costly act in return (Trivers 1971, Connor 1986, Rothstein and Pierotti 1988). Thus the key defining feature of reciprocity is that in any given exchange an individual would do better by, in the absence of punishment, not reciprocating.

Connor (1986) introduced the term 'pseudo-reciprocity' for a widespread phenomenon that had often been interpreted as reciprocity. Organisms often engage in activities which benefit themselves but which also incidentally benefit conspecifics or members of different species. In the pseudo-reciprocity paradigm, and individual A performs a beneficent act for an individual B in order to increase the probability of receiving incidental benefits from B. Because the return benefits to A derive from behaviors B performs to benefit B, there is no cheating in pseudo-reciprocity.

Here I will describe a mechanism in which two individuals may exchange benefits by parcelling those benefits to manipulate each other's optimal strategy. The resulting exchange of beneficence is similar to reciprocity in that an individual A performs a costly act for another individual B in anticipation of B performing a costly act for A in return. However, in reciprocity, an individual would realize short-term benefits by cheating on any given interaction. This is not the case in the model presented here.

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The model

Assume that two unrelated individuals, A and B each have a divisible resource the other requires and that they do not engage in reciprocity or 'Tit-for-Tat'. Assume also that each could obtain the needed resource elsewhere, but at some cost. If A gives B all of the resource that B needs in one move B needs nothing more from A and thus gives A nothing in return. However, the picture changes if A divides the resource into n parcels, and gives B one parcel and offers another contingent upon B giving A an equivalent parcel of the resource A needs. B then has to make a cost-benefit decision. B can leave and attempt to obtain the resource elsewhere at some cost or B can remain and pay A $1/n$ of the resource that A needs in anticipation of receiving another parcel from A. B will stay and pay if the benefits of staying (Bs) less than the costs of staying (Cs) outweigh the benefits of leaving (Bl) less the cost of leaving (Cl): Bs-Cs > Bl-Cl. If the left side of the inequality is larger then 'cheating' is not a viable option. Thus by parcelling, each individual is manipulating the cost/benefit equation of the other. On the next move, A has to make a similar decision, and the result can be an alternation of giving benefits which closely resembles reciprocity. However, provided that there is no uncertainty over who has the last parcel, once A and B reach the point where they need only one more parcel they will be in a stalemate. If A, for example, gives B the last parcel B needs, A has nothing left to extract the last parcel from B that A needs. By dividing the resource into increasingly smaller parcels, A and B can continue to exchange benefits and each may approach the amount they need as a limit. Such a mathematical solution is, however, highly unrealistic as numerous constraints on time, ability to divide the resource etc., come into play. Parcelling may, however, work in a context in which each individual derives some benefit by giving up the last parcel. Such may be the case in the phenomena called "egg-trading" found among simultaneous hermaphrodites (Fischer 1980, 1981, 1987, Fischer and Peterson 1987, Fischer and Hardison 1987, Leonard and Lukowiak 1984, Sella 1985).

Mating systems in seabases (serranidae)

Simultaneous hermaphroditism is common among the shallow water seabasses of the family Serranidae. Fischer and Petersen (1987) describe three mating systems among simultaneously hermaphroditic seabasses: harem polygyny, 'permanent' monogamy, and serial monogamy. The Pacific serranine *Serranus fasciatus* exhibits harem polygny. A male *S. fasciatus* patrols a territory containing the territories of one to several hermaphrodites with whom he mates once each daily. One permanently monogamous species is known (Pressley 1981). Pairs of the harlequin bass, *Serranus tigrinus*, share a territory that is used for feeding, spawning and "sleeping". Each member of the pair produces a non-parceled clutch of eggs for the other member to fertilize. 'Serially monogamous' species are solitary most of the day but pair up for mating in the late afternoon. An individual may mate with more than

one partner in succession on a given day, but individuals tend to pair up the same partner on successive days. Egg trading is found only among serially monogamous species and has been studied in detail by Fischer (1980, 1984) in the black hamlet *Hypoplectrus nigricans* and the chalk bass, *Serranus tortugarum*. Egg-trading is an interaction between two individuals that consists of three components (Fischer 1980, 1984): 1) each individual divides its clutch of eggs into parcels, 2) individuals alternate in offering parcels of eggs for fertilization, and 3) the offering of eggs is "advertized" via courtship displays.

Egg-trading in the black hamlet and chalk bass

Black Hamlets are strictly diurnal. Hamlets are solitary during the day, defending individual feeding territories. Mating occurs year round on spawning sites which are defended. Eggs must be spawned on the same day they are produced or they will become inviable. All reproductive activity takes place in the 2 hours before sunset when individuals move from their feeding territories to a spawning area where they pair up with another individual for mating. During a spawning period, hamlets typically mate with only one other individual but sometimes spawn with two and occasionally three others. There is no parental care; eggs are planktonic and float away from the spawning sites. Hamlets are self-compatible but self-fertilization does not occur because eggs and sperm are shed at different times. Individuals often alternate courtship displays, with the last individual to display being the first to release eggs. Each individual's clutch is released in parcels, typically 4–5 during a spawning bout, and individuals generally alternate in releasing eggs.

Chalk Bass are found in larger aggregations than Hamlets. Fischer (1984) observed groups ranging from 10–300 individuals. Individuals forage in loose aggregations during the day and do not defend individual feeding territories. Chalk Bass do, however, defend spawning sites and sleeping holes. Egg trading in Chalk Bass is generally similar to that found in hamlets. Spawning cues are more subtle and individuals do not alternate displays in Chalk Bass. The subtlety of spawning cues is thought to be associated with the prevalence of 'streakers' which attempt to fertilize the eggs released during a spawn.

Egg-trading as Tit-for-Tat

Trivers (1971) suggested that reciprocity could be modeled as a two-person Prisoner's Dilemma game. There are four possible payoffs to individuals in a Prisoner's Dilemma game, where the two options are to cooperate or defect (cheat): T is the payoff to a cheater, R is the payoff to each player if both cooperate, P is the payoff to each if both defect, and S is the payoff to a cooperating individual when his opponent defects. A game is a Prisoner's Dilemma if $T > R > P > S$ and $R > (T + S)/2$. Axelrod and Hamilton (1981) found that the Tit-for-Tat strategy

(cooperate on the first move and mimic your opponents previous move on subsequent moves) is effective against other strategies in an iterated Prisoner's Dilemma provided that the probability of an additional interaction between opponents (w) was sufficiently high.

Given that individuals alternate in releasing eggs and that eggs are more costly to produce than sperm (Fischer 1987, Fischer and Hardison 1987), trading eggs can be viewed as trading acts of beneficence and should be vulnerable to cheating (Fischer 1980). Upon receiving a clutch of eggs to fertilize, a "cheater" could simply offer fewer or no eggs in return and leave to seek out another sucker. To understand how such a system could be stable, Fischer (1988) analyzed egg-trading in the context of Axelrod and Hamilton's (1981) Tit-for-Tat (TfT) model of reciprocity and concluded that egg-traders may be playing a variant of TfT.

Individual black hamlets and the chalk bass exhibited a longer interval between successive spawning if their partners failed to reciprocate. This does not fit Tit-for-Tat, in which a player defects if its partner defects, but would fit a 'nicer' strategy which forgave occasional defection (Fischer 1988). Fischer (1988) hypothesized that the evolutionary history of egg trading may have proceeded as follows: during initial conditions favoring hermaphroditism, such as a low density of conspecifics, individuals traded non-parceled clutches of eggs. Then, as changing ecological conditions provided a greater abundance of mates, parcelling appeared as a strategy to increase mating success as males. A parcelling individual in a population of non-parcellers would have an advantage if they could obtain eggs from additional individuals. Once common, egg trading met the assumptions of the Prisoner's Dilemma and TfT could become a stable strategy.

Parcelling to keep T < R

Fischer (1988) casts the costs and benefits of cooperating and defecting into a matrix which fits the assumptions of the Prisoner's Dilemma: $T > R > P > S$. However the costs and benefits of the standard Tit-for-Tat model only take into account the interaction between the two players; the option of desertion was not considered by Fischer (1988) because desertion would end the game. The alternative model incorporates two aspects of egg-trading which violate assumptions of the Tit-for-Tat model: 1) the option to desert an opponent to seek out a new opponent and 2) the fact that decisions are made sequentially, not simultaneously.

Consider an individual that has received a parcel of eggs from its opponent and that the individuals are not playing Tit-for-Tat. After fertilizing the eggs, it has to make a decision. It can remain to offer eggs in return in anticipation of receiving another batch to fertilize, or it can leave and search for another mate. It if finds another mate if may be able to again fertilize a batch of eggs without offering any in return. There are, however, costs to leaving. The individual has simply to evaluate the costs and benefits of staying versus leaving. The costs of staying are eggs the individual must pay to receive more eggs and the benefits are eggs the

individual will receive in the next interaction. The benefit of receiving more eggs is devalued by the probability that the partner will stay to offer them (and not defect). The costs of leaving are searching and courtship costs, and perhaps a higher risk of predation (Fischer 1980). The benefit of leaving is the probability of acquiring more eggs from other individuals. Thus, I suggest that individuals may be parcelling eggs to manipulate the cost/benefit equations of its opponent so that cheating is not the favored option by the opponent (ie., Bs-Cs > Bl-Cl). Stated another way, by parcelling its eggs an individual is maintaining $T < R$ for its opponent and thus keeping it out of a Prisoner's dilemma. Because each individual is attempting to manipulate the cost/benefit equation for the other, the result is an alternation of roles that looks superficially like Tit-for-Tat.

As Fischer (1986) states, the optimal number of parcels should depend on the availability of alternative mates and the costs of spawning repeatedly. The right side of the inequality Bs-Cs > Bl-Cl is presumably larger for aggregating species than for solitary ones. In accord with this reasoning, individuals of the aggregating species *S. tortugarum* produce nearly twice as many parcels as members of the solitary species, *H. nigricans* (Fischer 1986). Individuals of aggregating species facing a larger Bl-Cl in their opponent may compensate by offering a smaller proportion of the clutch and thus maintaining a larger Bs-Cs.

It is significant that the mating is restricted to the 2 hr period prior to sunset (Fischer 1980). Thus, as an individual's clutch shrinks during a spawning bout (and thus the benefit to its opponent for staying) the costs of leaving (not finding an available mate) will be increasing at the same time. The permanently monogamous species *S. tigrinus* has an even narrower window for reproduction; all spawning occurs in the interval 22 minutes before to 10 minutes after sunset (Pressley 1981). Individuals of *S. tigrinus* do not parcel their clutches, but offer the entire clutch to the other member of the pair. Pressley (1981) offered a similar explanation to that given here for egg-trading species: "by delaying spawning until just prior to taking nighttime shelter, each pair member increases its probability of receiving eggs by limiting its partner's ability to search out other mates". That is, *S. tigrinus* individuals are keeping $T < R$ for their partners by synchrony alone, rather than synchrony plus parcelling as in chalk bass and hamlets.

The model for egg-trading presented here closely resembles reciprocity (and Tit-for-Tat). As Fischer (1988) states, egg trading " in appearance alone could pass for an archetypal example of reciprocity." As in reciprocity, unrelated individuals exchange acts of beneficence, but cheating is precluded by each individual parcelling the benefits it offers to the other. Further, consider a game with a known number of interactions. The only stable strategy in the Tit-for-Tat model is to defect (Axelrod and Hamilton 1981), but in the $T < R$ model an individual should decide to stay and pay eggs until the last move when it has only one parcel left. Of course, in this particular case each individual may decide to pay its last parcel of eggs even when the opponent has no more because it benefits by having its eggs fertilized.

Unlike pseudo-reciprocity, parcelling to maintain $T < R$ may be rare in nature. The egg-trading case may apply because each individual benefits in having their

eggs fertilized. In most kinds of interactions, individuals can employ other non-co-operative strategies such as aggression to obtain what they need.

Acknowledgements

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