Simultaneous Hermaphroditism, Tit-for-Tat, and the Evolutionary Stability of Social Systems

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Egg trading is a kind of mating behavior occurring in simultaneously hermaphroditic coral-reef fishes in the family Serranidae. It is a form of delayed reciprocity in which individuals give up eggs to be fertilized in exchange for the opportunity to fertilize the eggs of a partner. The behavior is consistent with the Tit-for-Tat model of cooperation. Egg trading possesses three unusual but potentially important features. First, it almost certainly originated through interactions among unrelated individuals, unlike other examples of delayed reciprocity. Second, it probably originated not as cooperation but as a form of defection or cheating. Third, egg trading and related behavior can account at least in part for the maintenance of the monogamous mating systems of several serranines under ecological conditions in which such systems would not be expected to originate or persist. The reason is that the effects of such behavior patterns are positively frequency-dependent. Much social behavior probably has frequency-dependent effects, and internally generated stability may therefore be involved in the evolution of many animal social systems. However, the extent of its influence is not yet known.

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A simultaneous hermaphrodite produces both male and female gametes. This sexual pattern seems to fly in the face of what one would expect given anisogamy, the production of small male and large female gametes. It is logical to suppose that anisogamy, itself a product of disruptive selection (Parker et al. 1972; Cox and Sethien 1985), would lead to disruptive selection for specialization in one or the other sexual functions in individuals. In fact, simultaneous hermaphroditism is uncommon in animals with a high potential for specialization in competition by

males (Ghiselin 1974; Maynard Smith 1978). Among the vertebrates, it occurs only in the fishes, and almost all of the hermaphroditic species live in the deep sea (Smith 1975). They presumably occur at low densities, where this sexual pattern is advantageous (Tomlinson 1966; Maynard Smith 1978).

The Serranidae is the only shallow water family in which simultaneous hermaphroditism is common. The sexual pattern occurs in several common Caribbean and Mediterranean species in the subfamily Serraninae, the seabasses (Fischer 1986; Robins and Starck 1961; Smith 1965). Serranids in the other two subfamilies, the Epinephelinae and the Anthiinae, are protogynous, starting life as females and later changing to males (Thresher 1984). Many seabasses are far too common for their hermaphroditism to be accounted for by low density, and they do not self-fertilize (Fischer 1981, 1984a). However, several species advertise female investment in courtship and apparently use it as a means of obtaining mating success as a male.

The two best known species exhibit an unusual form of mating behavior known as egg trading (Fischer 1980, 1984a). Individuals form pairs in the late afternoon. Before spawning, two mates alternate courtship displays, and the last fish to display releases eggs, while its partner releases sperm (fertilization is external and eggs are planktonic). Each fish releases only part of its clutch during a given spawning act, and partners regularly alternate release of eggs.

Egg trading appears to be a classic example of delayed reciprocity. As in any case of this form of cooperative behavior, defection is a potential problem (Trivers 1971; Axelrod and Hamilton 1981). How can an individual maximize the chance that it will receive a parcel of eggs to fertilize after giving one up? Because sperm are so much cheaper to make than eggs, there should be strong selection pressure to fertilize eggs without giving any up. What is to prevent a partner from fertilizing eggs without permitting its own eggs (if indeed it has any) to be fertilized?

One possibility is that egg trading is a manifestation of the Tit-for-Tat strategy of cooperation (Axelrod and Hamilton 1981). The central purpose of this paper is to examine that possibility and its consequences. Three main points will be made: 1) egg trading is best explained as a kind of Tit-for-Tat; 2) it probably originated through interaction among unrelated individuals, and the most likely origin of the behavior was not as a form of reciprocity but rather as a kind of "cheating" in giving up eggs for fertilization; and 3) the frequency-dependent fitness effects of egg trading and related behavior patterns generate a kind of internal stability that can make simultaneous hermaphroditism evolutionarily stable in circumstances in which it could not have originated. These results suggested that behavior patterns with frequency-dependent effects, arising from interactions even among unrelated individuals, may substantially enhance the evolutionary stability of social systems in response to ecological change.

THE PUZZLE OF SIMULTANEOUS HERMAPHRODITISM IN SERRANINES

Of the five best studied serranines, four are found in the Carribbean and one in the Eastern Pacific (Barlow 1975; Clark 1959; Fischer 1980, 1981, 1984a, 1986; Fischer and Petersen 1987; Hastings and Petersen 1986; Petersen and Fischer 1986). All but one of these are in the genus *Serranus*. They all spawn in the late afternoon, and the Caribbean forms mate daily or nearly daily year-round. All have external fertilization and planktonic eggs (no parental care), and all are known or thought to be obligate outcrossers. Planktonic eggs float away from the reef where they are spawned and disperse widely. Such a dispersal pattern almost certainly prevents kin selection from being a significant force in the evolution of social behavior in serranids, as has been demonstrated in one anthiine (Avise and Shapiro 1986).

Sex allocation theory predicts that simultaneous hermaphroditism is more likely in circumstances where the potential for mate competition is comparatively low (Charnov 1979, 1982; Fischer 1981, 1986; Fischer and Petersen 1987). Where the potential is high, a pattern such as protogyny (female-to-male sex change) is expected (Warner 1984). Many serranids are in fact protogynous (Thresher 1984). Mating system theory predicts that monogamous mating systems should generally be associated with comparatively low mate competition and polygyny with high mate competition (Emlen and Oring 1977; Vehrencamp and Bradbury 1984). Consequently, one generally expects simultaneous hermaphrodites to be monogamous and protogynous species to be polygynous. An understanding of the forces shaping the mating systems should therefore lead to an understanding of the evolution of the sexual patterns.

The predicted association between mating system and sexual pattern holds well among reef fishes (Warner 1984; Fischer 1986). However, the ecological conditions in which some simultaneously hermaphroditic serranines occur should be associated with polygynous mating systems and protogyny, given our current understanding of sexual selection, and it is difficult to imagine how monogamy could have originated under such conditions (Fischer 1986; Fischer and Petersen 1987). The mating systems cannot generally be accounted for by low density, parental care, or joint resource defense, as has been suggested for some other monogamous fishes (Barlow 1984).

An extreme example of this puzzle is exhibited by the chalk bass, *Serranus tortugarum*. This aggregating planktivore occurs in localized groups at high densities, with as many as 500 fish in a single aggregation. Individuals pair up and spawn daily in the late afternoon. Despite the high potential for mate competition, the mating system is essentially monogamous (Fischer 1984a, 1986). In contrast, serranids in the subfamily Anthiinae have similar

feeding and reproductive ecology but are polygynous and protogynous (Shapiro 1979; Yogo 1985).

The puzzle is compounded by the diversity of mating systems and sexual patterns within the serranines. Although most seabasses are simultaneous hermaphrodites, two species have a mixed sex allocation pattern, with small hermaphrodites and large males. These species have harem polygynous mating systems (Hastings and Petersen 1986; Petersen and Fischer 1986), thereby demonstrating that simultaneous hermaphroditism itself does not prevent polygyny.

This striking departure from the typical serranine pattern is not accompanied by any known differences in feeding, density, size, or predation (Fischer 1986). However, the harem species are more site-attached than all but one of the monogamous serranines (Fischer 1986; Fischer and Petersen 1987).

Site attachment has two potential effects on the potential for polygyny and mate competition. On the one hand, the potential for monopolizing access to a mate increases with the degree of site attachment. Strong site attachment could lead to the destabilization of monogamy and hermaphroditism, since a hermaphrodite could not easily desert a male. On the other hand, the potential number of available mates in a local population, and therefore the potential for competition and polygyny, varies inversely with the degree of site attachment. Consequently, lack of site attachment does not itself provide a mechanism for maintaining monogamy. In addition, the degree of site attachment can only explain the distribution of mating systems to the extent that it is independent of them. The mating systems themselves may influence selection on site attachment.

Of course, it is possible that some as yet unknown environmental factor may be found to account for the persistence of monogamy in most serranines. However, it seems reasonable at this point to look elsewhere for the causes of this pattern. One possibility is egg trading, which in appearance alone could pass for an archetypal example of reciprocity.

MATING BEHAVIOR AND DELAYED RECIPROCITY IN SERRANINES

Delayed reciprocity refers to any situation in which two individuals alternately perform actions that cost the performer and benefit the recipient, and the opportunity for cheating (failing to return the action) exists (Trivers 1971). In the egg-trading serranines, partners alternate courtship displays before spawning, and the last fish to display releases eggs, while its partner releases sperm. Courtship is therefore associated with the offering of eggs rather than being a direct offer to fertilize those of the mate. A clutch is divided into parcels released alternately by partners (about 80% of the time,

on average). Part or all of this suite of behavior patterns is known to occur in six serranines altogether (Fischer 1984a, 1986).

By trading eggs, a serranine gets to fertilize on average about as many eggs as it produces (Fischer 1980). Since each individual also invests more heavily in female than in male functions (Fischer 1981, 1984b), the reproductive success of an egg trader is substantially higher than would be that of a female. For example, the gonad of a chalk bass consists of 75% ovary and 25% testis, a ratio that is less female-biased than other serranines, presumably because of the high levels of sperm competition in chalk bass (Fischer 1984b). If we assume that a fairly linear relationship exists between ovary size and fecundity, an egg-trading chalk bass will have about 1.5 times the mating success of a pure female. Also, a pure male would have to fertilize all the eggs of at least two hermaphrodites in order to do better than an egg trader.

However, what is to prevent a partner from defecting on any given interaction—i.e., fertilizing eggs without giving any up to be fertilized? Eggs are expensive to make, and access to sperm does not limit success as a female in serranines (Fischer 1987). Since individuals appear to offer their eggs readily to be fertilized, the temptation to defect is potentially high. Yet defecting does not appear to be a successful strategy in egg traders (Fischer 1980, unpublished). Why not?

EGG TRADING AND TIT-FOR-TAT

Defection is a potential problem in any case of delayed reciprocity (Trivers 1971). An effective response was discovered by modelling cooperation as an iterated two-person Prisoner's Dilemma game (Axelrod 1984; Axelrod and Hamilton 1981). The response is Tit-for-Tat (TfT), which consists of cooperating on the first move, and thereafter doing whatever the opponent did on its previous move. Let R = the payoff to each player if both cooperate, P = that if both defect or cheat, S = that for cooperating when the opponent defects, and T = that for defecting if the opponent cooperates. A game is a Prisoner's Dilemma if

$$T > R > P > S \tag{1a}$$

and

$$R > (T + S)/2. \tag{1b}$$

TfT is evolutionarily stable in the iterated version of this game provided that

$$w \geq (T - R)/(T - P) \tag{2a}$$

and

$$w \geq (T - R)/(R - S), \tag{2b}$$

where w = the probability of an additional interaction between two participants.

To determine if egg trading is an evolutionarily stable form of TfT requires four steps. First, mating behavior in the serranines must satisfy the conditions for the iterated Prisoner's Dilemma. Second, the animals must exhibit some form of TfT. Third, the probability of an additional interaction in a given game must be large enough to make this form of TfT evolutionarily stable. Fourth, the TfT behavior cannot be accounted for by alternative mechanisms.

The first criterion can be investigated by examining the appropriate payoff matrix. For simplicity, a game between two partners is defined as the sequence of mating interactions between them during a spawning period. A round or iteration consists of the release of a parcel of eggs by a fish and the response of its mate—either release of a parcel or failure to release. It is also assumed that a response within an iteration is not affected by the mate's response during that iteration (a property of the Prisoner's Dilemma), and that the partner that goes first is determined at random.

Defection consists of failing to give up a parcel of eggs to a partner. It is therefore not a specific behavioral act but the absence of an act. Tit-for-Tat consists of initially giving up a parcel of eggs, then continuing to release parcels if the partner does, and failing to give up more if the partner does not reciprocate. Desertion in response to nonreciprocation is not part of TfT, since leaving the mate would end the game. TfT assumes that the length of the game (determined by w) is independent of the behavioral strategies employed by the participants.

Let B = the net fitness gain from fertilizing a parcel of eggs, and C = the cost per spawn of releasing eggs (both energy and risk of predation). This cost is probably small, but it certainly exists. It is assumed that eggs are fertilized whether or not they are parcelled. The model therefore treats female reproductive success as a constant. Note also that this is not a sex allocation model, since relative investment in male and female functions is not a variable.

Let p = the probability that a defector will give up a parcel ($0 \le p \le 1$) during a given iteration. Since a cooperator always gives up a parcel, its cost is C and its partner always gains B in a given round. A defector suffers an average cost pC and its mate obtains pB. Note that if the clutch is divided into a large number of parcels, B is small, but C, the cost of spawning, does not change with the way that the clutch is divided up. Combining these features yields the following payoff matrix.

	C	D	
C	$R = B - C$	$S = pB - C$	(3)
D	$T = B - pC$	$P = pB - pC$	

By substituting the given payoffs into equations (1) and (2), it can be

shown that this matrix meets the assumptions of the Prisoner's Dilemma if $p < 1$ and $B > C > 0$; and that TfT is an ESS in this iterated game, provided that $w \geq C/B$. Although C cannot currently be estimated, this result makes good theoretical sense. The larger the cost–benefit ratio, the more interaction is needed between partners for TfT to be an ESS. Since the probability of an additional interaction cannot exceed 1, TfT should never be an ESS if $C > B$. Note also that by broadening the definitions of B, C, and p, the result obtained here can be seen to apply generally to energetic models of TfT. For example, it can be derived from the energetic version of the Prisoner's Dilemma analyzed by Brown, Sanderson, and Michod (1982). The version of the conditions for stability given here is more intuitively obvious and is potentially more explicitly testable than those given by Axelrod and Hamilton (1981).

TfT predicts that an egg trader should be reluctant to release an additional parcel if its mate fails to reciprocate. Evidence from the black hamlet, *Hypoplectrus nigricans*, and the chalk bass, *Serranus tortugarum*, support this prediction. If a partner failed to reciprocate, its mate waited significantly longer to release a batch of eggs than it did if the partner did reciprocate (Fischer 1980, unpublished).

Another, more subtle form of cheating would consist of giving up fewer eggs per spawning than the partner. The implications of this possibility for the evolution of parcelling are discussed later. However, evidence from the black hamlet failed to support its current importance in that species. Fish that released a small number of eggs in a spawning usually took the female role in the next spawning, but alternation usually occurred if the fish released a full parcel (Fischer 1980). Differences in the mating behavior of chalk bass and hamlets have so far prevented a determination of whether a similar phenomenon occurs in the former species.

The release of more than one parcel in the absence of reciprocation is common enough to suggest that egg traders do not play a pure form of TfT. In his tournament analysis, Axelrod (1984) found that the strategies that did best combined the following three properties: niceness (they began by cooperating), provokability (they defected quickly in response to defection), and forgiveness (they resumed cooperating when their opponent did). It could be that egg trading is nicer or more forgiving than simple TfT. One possible reason is that a simple TfT can get locked into defection when playing against a similar strategy that defects just once (Axelrod 1984). TfT leaves no room for mistakes. A strategy that occasionally offers an olive branch would avoid this problem.

At least two kinds of mistakes may occur between egg traders. First, an individual may simply forget who released eggs last, especially if an outside disturbance interrupts a spawning sequence. Second, two individuals may vary in the rate at which they ready eggs for spawning (Fischer and Hardison 1987). Thus, one may be ready to release two or more parcels before its partner is.

Axelrod (1984) argued that the advantage of a nicer strategy than TfT depends on the balance between the risk of extended defections and the benefits for exploiting niceness. In a game such as egg trading, the time constraints on spawning (Fischer 1980; Fischer and Peterson 1987) may make the costs of extended defection greater than the benefit of obtaining an extra parcel or two. Egg trading may also be forgiving because of the difficulty of detecting defection, which consists of the absence of a behavioral response. In such a game of incomplete information, a nicer variant of TfT may permit a more definitive determination of whether defection has indeed occurred.

VIOLATION OF ASSUMPTIONS

One possible problem with applying TfT to egg trading is that a given interchange in the Prisoner's Dilemma is always simultaneous, whereas in egg trading and other forms of delayed reciprocity, each interchange is sequential, with one participant making its offering before the other. Consequently, the individual making the second move obtains information about the strategy of its partner before responding. In the Prisoner's Dilemma, the two participants have no information about the current move of the opponent.

This difference is less serious than it might seem (Maynard Smith 1983; Trivers 1971). To see why, suppose that an interchange consists of two sequential moves, one by each participant, and that the probability that a given player will make the first move is $\frac{1}{2}$. Further suppose that a cooperating hermaphrodite gives up a parcel of eggs whether it moves first or second, but a defector gives one up only if it makes the first move. The result of these assumptions is that $p = \frac{1}{2}$, and the conditions for the evolutionary stability of TfT are the same as in Equation 3.

Another way in which egg trading may differ from simple TfT is that it is potentially a nested game, i.e., interactions are repeated between as well as within spawning periods. In a between-spawning-period game, a fish playing TfT should decrease the number of parcels given up to its mate in response to a decrease by the same mate on the previous day. Available evidence does not support this prediction (Fischer unpublished), but the test was not particularly powerful, because of the overall variability in the number of parcels released in a spawning period.

TfT assumes that the interactions of individuals are totally independent of the influence of coercion, sequestering, or preference. Aggressive male courtship, as in the harem polygynous serranines (Fischer and Petersen 1987; Petersen and Fischer 1986; Petersen 1987) could allow defection, but available evidence indicates that it is not a significant factor in egg traders. Sequestering and preference do appear to occur, but they seem to reinforce reciprocity. Individuals tend to spawn reciprocally with the same partner

on successive nights, and pairs react aggressively to intruders (Fischer 1980, 1984a, unpublished).

In general, TfT should lead to selection favoring preferential interaction with other cooperators. Thus, simple TfT should be rare in natural systems, because the evolution of such preferences violates the assumption that w is independent of the strategy employed. However, it is obvious that preferential interactions can enhance the stability of TfT-like behavior.

The above considerations indicate that egg trading can be reasonably viewed as a variant of TfT. The next question is whether the observed patterns are explained better by an alternative hypothesis, suggested by another way that egg trading violates the assumptions of simple TfT. A donation can be freely given or freely withheld in TfT. The players do not exhaust the supply of offerings. In the serranines, by contrast, eggs are produced in the late afternoon and must be spawned on the day that they are produced, or they will become inviable. Egg traders begin spawning 2–3 hours before sunset and end shortly after sunset. There is considerable overlap in the timing of individual bouts of parcel release (Fischer 1986; Fischer and Petersen 1987).

This pattern suggests that selection may have favored some overall synchronization of spawning, an effect that has been predicted and observed in a variety of situations involving competition for mates (Knowlton 1979; Thornhill and Alcock 1983). If so, interpreting the observed high rates of alternation as TfT could be an example of the "church clock fallacy" (Cullen 1972). Rather than being a result of active synchronization between two individuals, they may result from independent synchronization with a common external referent, such as time of day. Preliminary analysis of spawning sequences indicates that a clock mechanism alone is insufficient to account for observed rates of alternation in the release of parcels by pairs. Details will be reported elsewhere.

ORIGINS OF EGG TRADING

In a population of defectors, simple TfT cannot increase (under the assumptions of Axelrod and Hamilton [1981]) unless cooperators somehow interact preferentially. This restriction led Axelrod and Hamilton (1981) to propose that egg trading might have originated under ancestral conditions involving kin selection. As stated earlier, the extended and obligate larval dispersal stage in serranids makes kin selection extremely unlikely (Avise and Shapiro 1986). It is also unnecessary, because egg trading probably originated as a form of cheating ("subtle" cheating in the sense of Trivers [1971]), which then evolved into a kind of delayed reciprocity.

To see why, imagine a population of nonparcelling hermaphrodites in which some extrinsic ecological factor such as low density causes the opportunities for polygamous matings to be low. If the influence of this factor

is relaxed, the potential for multiple matings will increase. A rare individual that divided its clutch into two parcels and offered them to different mates would fertilize more eggs than the common type. This result can be seen by examining a general payoff matrix where P and P_1 are strategies that divide a clutch of eggs into N and $N + 1$ parcels, respectively. Let E = the payoff obtained from a single clutch of eggs (produced or fertilized); L = the cost of a single male or female spawning act; and M = the cost of finding a mate, including the first mate. For simplicity, assume that M is independent of the total number of mates. Also assume that a fish that has more parcels than its partner will desert and look for a second mate after fertilizing the eggs of its partner. As earlier, assume that all the eggs that a fish produces are fertilized.

A fish releasing N parcels in a population consisting of other P individuals releases all of its eggs to a single partner and fertilizes all of the eggs of that fish. Each therefore gets a benefit of $2E$ and suffers a mate-finding cost of M and a spawning cost of $2NL$. The payoff is the same for a P_1 individual in a population of P_1's, less the additional spawning cost for producing $N + 1$ rather than N parcels. A P individual in a population of P_1's gets E from the eggs it produces and $EN/(N + 1)$ from those it fertilizes. Its total spawning cost is $2NL$, and its mating cost is M, because it has only one partner.

A P_1 in a population of P gets E from the eggs it produces. Because it is rare, we can assume that it always gets to pair with a second mate that has eggs. (Relaxation of this assumption would not qualitatively change the results of the model, as long as the probability of getting a second mate with eggs was positive.) Therefore, it gets a total of $E(N + 1)/N$ from the eggs that it fertilizes. Since it spawns $2(N + 1)$ times altogether, its spawning cost is $2(N + 1)L$. It must also find two mates, for a mating cost of $2M$. The resulting payoff matrix is given below. Note that payoffs listed are totals for the whole spawning period, not just for a single round of an iterated game as in the earlier model.

	P	P_1
P	$2E - 2NL - M$	$\dfrac{E(2N + 1)}{N + 1} - 2NL - M$
P_1	$\dfrac{E(2N + 1)}{N} - 2(N + 1)L - 2M$	$2E - 2(N + 1)L - M$

P_1 will increase when rare if $E > 2NL + NM$, and it is evolutionarily stable if $E > 2L(N + 1)$. Note that a polygamous mating advantage exists only when P_1 is the rare strategy.

The number of parcels into which the clutch is divided at equilibrium will depend on the cost of spawning and on the opportunities for multiple matings. The model predicts that in situations where more opportunities exist for polygamy, M should be lower and the amount of parcelling higher. Avail-

able data are consistent with this prediction. The average number of parcels released by chalk bass, an aggregating planktivore that lives in high densities, is nearly twice that found in the black hamlet, a solitary, gleaning carnivore (Fischer 1986). However, possible alternative influences, such as differences in egg predation and sperm competition, have not yet been ruled out.

The above model can account for the evolution of parcelling, given that reciprocal spawning already occurs. It is easy to see that in the absence of perfect reciprocation, parcelling will be favored if offering eggs decreases the latency for a mate to release eggs. This assumption is reasonable for the proposed ancestral situation in which environmental constraints such as low density resulted in a low potential for polygamy. Under such conditions, short latencies might be expected as a result of selection for coordination of mating. In the one known serranine that reciprocates without parcelling, the harlequin bass, *Serranus tigrinus*, mates release their parcels within a few minutes of each other (Pressley 1981). The same is true for the rare cases of reciprocation observed in the haremic *S. fasciatus* (C. W. Petersen, personal communication).

The above considerations suggest the following hypothesis for the evolutionary history of egg trading. Egg offering and alternation of egg release preceded parcelling and occurred originally in conditions, such as low density, in which the assumptions of the Prisoner's Dilemma were not satisfied. As ecological conditions changed and the potential availability of mates increased, parcelling evolved initially because it increased male mating success. Once it was common, the combination of egg offering, parcelling and waiting for the mate to reciprocate satisfied the conditions for TfT.

Peck and Feldman (1986) have suggested that alternative routes such as that proposed here may be fairly common paths to the establishment of TfT. Testing ideas about the origin of a behavior pattern is difficult, but the hypothesis offered does make the prediction that polygamy in nonparcelling reciprocators should be restricted by factors, such as joint territory defense, that do not occur in egg traders. Unfortunately, the determinants of the mating system of the one currently known species (Pressley 1981) are still poorly understood.

EGG TRADING AND THE EVOLUTIONARY STABILITY OF HERMAPHRODITISM

I have shown that egg trading in serranines satisfies the conditions for the Prisoner's Dilemma and TfT, and that its origins can be explained without resorting to special assumptions, such as kin selection, leading to preferential interaction among initially rare cooperators. Egg traders do not appear to play simple TfT, but a variant that is more forgiving and incorporates preferential interaction with previous cooperators. The next question is, how do egg trading and related phenomena such as spawning synchronization influ-

ence the evolutionary stability of the mating systems and sex allocation patterns in the serranines?

The models presented above are not sex allocation models. They deal with the evolution of reciprocity, not simultaneous hermaphroditism per se. The ways that mate competition affects the evolution of this sexual pattern have been dealt with elsewhere (e.g., Charnov 1979, 1982; Fischer 1981, 1984). That work demonstrates that a low potential for male mating success is a prerequisite for the evolutionary stability of simultaneous hermaphroditism.

A major effect of egg trading is that it decreases this potential by lowering the advantage of polygynous mating. In a population of egg traders, an individual will do as well reproductively by exchanging eggs with only one partner during a spawning period as it can by having several mates. The reason is that the number of eggs that an individual fertilizes is limited by the number that it produces, and eggs are expensive to manufacture. The close overlap in the pattern of egg production and the timing of spawnings by individuals in local populations of egg traders also decreases the advantages of polygamy (Fischer 1980, 1986; Fischer and Hardison 1987; Fischer and Petersen 1987). These behavior patterns enhance the evolutionary stability of reciprocal spawning and, consequently, the simultaneously hermaphroditic sex allocation pattern exhibited by egg traders. Note that the crucial factor is reciprocity, not monogamy per se, but selection for one will also favor the other.

The environmental determinants of mating systems can be divided into spatial and temporal factors (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). Egg trading and synchronization of spawning are temporal in nature. These factors are frequency-dependent. The strength of their effect increases with the frequencies of the traits in a given population. When the traits are common, these effects are at least partly independent of spatial components such as patterns of space use and food resource defendability. Therefore, such traits can increase the stability of the mating systems in response to changes in spatial and other extrinsic factors. In other words, although the mating behavior may have evolved under extrinsic ecological conditions that were conducive to the maintenance of simultaneous hermaphroditism, egg trading and related phenomena can permit the sex allocation pattern to persist in changed ecological conditions that would themselves no longer select for the pattern. The frequency-dependence therefore leads to a kind of internally generated enhancement of evolutionary stability.

The range of ecological conditions under which stability persists will depend on the strength of the frequency-dependence. Although specific models have not yet been devised for the complex of systems exhibited by the serranines, a simple heuristic model will illustrate this point. Let A and B be two alleles coding for different behavior patterns. As in most ESS models, assume haploid or asexual inheritance. Let x = an extrinsic environmental variable, $0 \leq x \leq 1$, and t = a threshold value of x such that

$W_A = (1 - x)t$ and $W_B = x(1 - t)$, where W_A and W_B are fitness values of A and B. Strategy A will then be favored if $x < t$, and B will be favored if $x > t$. Zones of stability of strategies A and B over the range of x are depicted in the example below:
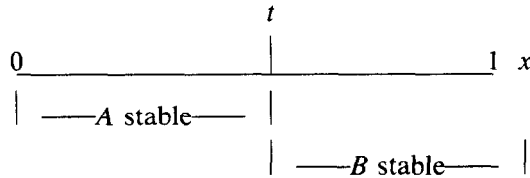
Now add a positive frequency-dependent effect, such that A's get $1 + a$ in interactions with other A's, where the fitness effects from all other interactions equal one. Strategy A is now stable over a greater range of x, because in a population of A's, $W_A = (1 - x)t(1 + a)$ (assuming multiplicative fitness effects) and all other fitnesses are unchanged. To get the upper stable point for A, we solve for x when $W_A = W_B$ and obtain $S_A = (a + 1)/(a + 1/t)$. The range of stability therefore increases with the strength of the frequency-dependence. Note that the situation depicted here leads to alternative stable states (Maynard Smith 1982). There is a range of x over which A and B are each evolutionarily stable—a population will consist of all A or all B, but the model cannot predict which. This situation is illustrated below.
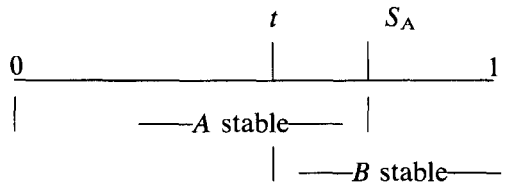
If the fitness of B is also positively frequency-dependent, then the range of x over which A and B are alternative stable states is even larger. In extreme cases, the extrinsic factor may have almost no predictive power.

The persistance of simultaneous hermaphroditism in serranines that are aggregating and planktivorous, as well as some that are territorial and predatory, suggests that the system has high internally generated stability. However, the existence of the two harem polygynous species implies that the limits of stability have been passed at least once (Petersen and Fischer 1986; Fischer and Petersen 1987). It also raises the question of whether such harem systems have their own internally generated stability. The possibility that they do is reasonable, since All-Defect is an evolutionarily stable response to the iterated Prisoner's Dilemma (Axelrod and Hamilton 1981).

Frequency-dependent effects may well be operating in the harem species. Hermaphrodites in these species do not divide the clutch into parcels. It is nonetheless puzzling that they rarely spawn reciprocally, when each individual could apparentliy double its reproductive success by trading eggs

with another hermaphrodite. One possibility is that they are simply prevented from reciprocating by the male harem masters. Since harems are usually contiguous, hermaphrodites cannot escape males simply by leaving the harem. If this hypothesis of social control is correct, then the monogamous and polygynous mating systems may well have overlapping zones of stability, which could account in part for the lack of association between density and mating systems in the Serraninae (Fischer 1986). However, other factors such as patterns of site attachment may also play an important role (Petersen and Fischer 1986).

The kind of delayed reciprocity exhibited by egg traders may also occur in some other hermaphrodites. Two invertebrate simultaneous hermaphrodites are known to mate reciprocally, with repeated alternation of sex roles (Leonard and Lukowiak 1984; Sella 1985). In these cases, observed rates of alternation were close to those of the serranines. However, it is not known whether alternation provides a similar advantage in these invertebrates, or what its effects might be on the mating systems.

Other known examples of reciprocity in fishes are unlikely to have important effects on the internally generated stability of social or mating systems. The classic cleaner wrasse example that Trivers (1971) cited in his original paper on reciprocal altruism is not relevant because the purported reciprocity is interspecific. The applicability of Milinski's recent attempt (1987) to test TfT in responses to predators by sticklebacks is unclear, since his experimental conditions were highly artificial.

IMPLICATIONS FOR SOCIOECOLOGY

Historically, attempts to understand the evolution of social systems have tended to concentrate on the importance of extrinsic ecological factors such as resource distribution and predation pressure (e.g., Alexander 1974; Crook 1965, 1970; Terborgh 1983). It has become increasingly clear in recent years that these considerations are inadequate and that frequency-dependent effects may be important (Jarman 1982; Vehrencamp and Bradbury 1984; Wrangham and Rubenstein 1986).

Most research has concentrated on negative frequency-dependence, which favors intermediate frequencies of alternative traits at equilibrium. Examples are mixed ESS's (Maynard Smith 1982; Maynard Smith and Price 1973) and heterozygote advantage (Crow and Kimura 1970). The concept has been fruitful in helping to understand the evolution of the sex ratio (Charnov 1982) and alternative mating strategies (Gross 1984).

The possible importance of positive frequency-dependence in the evolution of social systems seems to have been less well appreciated. Although the concept of alternative stable states in ESS theory (Maynard Smith 1982) is based on positive frequency-dependent selection, it is usually invoked to explain the occurrence of alternative ways of dealing with similar extrinsic

selection pressures. For example, Maynard Smith (1977) showed that male only or female only parental care may be evolutionarily stable in conditions in which only one parent is needed to guard the young. Which pattern will be found cannot be predicted from the payoff matrix alone.

The idea of internal stability emphasizes a more hidden aspect of the concept of alternative stable states by showing that positive frequency-dependence can broaden the range of extrinsic ecological conditions under which a mating or social system is evolutionarily stable, including even conditions under which the system would not be expected to originate. It therefore can lead to a historical decoupling of factors involved in the origin and maintenance of such a system.

Socioecologists often contend that the spatial distribution of females is determined largely by the distribution of resources and other nonsocial factors, and the distribution of males is in large part a response to female grouping (Wrangham 1982; Wrangham and Rubenstein 1986). Does this mean that the internal stability proposed for serranine social systems is a special case, limited to species in which males and females are not separate individuals? Such a limitation is unlikely, simply because frequency-dependent effects can operate on animals with separate sexes as well as hermaphrodites.

ESS theory suggests that many social behavior patterns will have frequency-dependent effects on fitness. If these effects are positive, it is hard to escape the conclusion that they will enhance the evolutionary stability of the social systems that the behavior patterns help to generate. In some cases, such as the serranines, internal stability may be a major factor in the persistence of a particular social system that a given species or taxonomic group exhibits in a variety of environments. It may also be involved in the persistence of different social systems in different species living in similar environments.

For example, in animals with biparental care, including many fishes (Gross and Shine 1981), the availability of additional mates may be much lower than in those with uniparental care. Furthermore, selection may lead to synchrony of reproduction as a result of competition among females (Knowlton 1979) and further reduce the potential benefits of desertion. Since biparental care may involve repeated interactions among partners, it also lends itself readily to the development of reciprocity. These effects would be at least partly independent of the distribution of resources and could enhance the stability of biparental care in the face of changing ecological conditions.

If internally generated stability is so potentially important, why has it not been more widely examined? One problem is that it is an onerous concept, easy to invoke but difficult to test. Another is that most socioecologists study birds and mammals, whose more complex systems may tend to obscure the phenomenon. These systems may be particularly difficult to compare, because grossly similar ones often differ in so many ways that it may be difficult to say whether they should in fact be classified together (Dunbar

1986; Wrangham and Rubenstein 1986). However, social systems that are influenced by behavior patterns, such as reciprocity, having high positive frequency-dependent effects on fitness, should exhibit greater internally generated stability. The effect may be found more widely once it is looked for carefully.

REFERENCES

Alexander, R.D. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5: 325–383, 1974.
Avise, J.C., and Shapiro, D.Y. Evaluating kinship of newly settled juveniles within social groups of the coral reef fish *Anthias squamipinnis. Evolution* 40: 1051–1059, 1986.
Axelrod, R. *The Evolution of Cooperation.* New York: Basic Books, 1984.
——, and Hamilton, W.D. The evolution of cooperation. *Science* 211: 1390–1396, 1981.
Barlow, G.W. On the sociobiology of some hermaphroditic serranid fishes, the hamlets, in Puerto Rico. *Marine Biology NY* 33: 295–300, 1975.
——. Patterns of monogamy among teleost fishes. *Archive fuer Fischereiwissenschaft* 35: 75–123, 1984.
Bradbury, J.W., and Vehrencamp, S.L. Social organization and foraging in emballonurid bats. III. Mating systems. *Behavioral Ecology and Sociobiology* 2: 1–17, 1977.
Brown, J.S., Sanderson, M.J., and Michod, R.E. Evolution of social behavior by reciprocation. *Journal of Theoretical Biology* 99: 319–339, 1982.
Charnov, E.L. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* 76: 2480–2484, 1979.
——. *The Theory of Sex Allocation.* Princeton, N.J.: Princeton Univ. Press, 1982.
Clark, E. Functional hermaphroditism and self-fertilization in a serranid fish. *Science* 29: 215–216, 1959.
Cox, P.A., and Sethian, J.A. Gamete motion, search, and the evolution of anisogamy, oogamy, and chemotaxis. *American Naturalist* 125: 74–101, 1985.
Crook, J.H. The adaptive significance of avian social organizations. *Symposia of the Zoological Society of London* 14: 181–218, 1965.
——. The socio-ecology of primates. In *Social Behaviour of Birds and Mammals,* J. H. Crook (Ed.). London: Academic Press, 1970, pp. 103–166.
Crow, J.F., and Kimura, M. *An Introduction to Population Genetics Theory.* New York: Harper and Row, 1970.
Cullen, J.M. Some principles of animal communication. In *Non-Verbal Communication,* R. A. Hinde (Ed.). Cambridge, England: Cambridge University Press, 1972, pp. 101–121.
Dunbar, R.I.M. The social ecology of gelada baboons. In *Ecological Aspects of Social Evolution,* D. I. Rubenstein, and R. W. Wrangham (Eds.), Princeton, N.J.: Princeton University Press, 1986, pp. 332–351.
Emlen, S.T., and Oring, L.W. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–233, 1977.

Fischer, E.A. The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans* (Serranidae). *Animal Behaviour* 28: 620–633, 1980.

——. Sexual allocation in a simultaneously hermaphroditic coral reef fish. *American Naturalist* 117: 64–82, 1981.

——. Egg trading in the chalk bass, *Serranus tortugarum*, a simultaneous hermaphrodite. *Zeitschrift fuer Tierpsychologie* 66: 143–151, 1984a.

——. Local mate competition and sex allocation in simultaneous hermaphrodites. *American Naturalist* 124: 590–596, 1984b.

——. Mating systems of simultaneously hermaphroditic serranid fishes. In *Indo-Pacific Fish Biology: Proceedings of the Second Conference on Indo-Pacific Fishes*, T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (Eds.), Tokyo: Ichthyological Society of Japan, 1986, pp. 776–784.

——. Mating behavior in the black hamlet—gamete trading or egg trading? *Environmental Biology of Fishes* 18: 143–148, 1987.

——, and Hardison, P.D. The pattern of ovulation as a constraint on mating success in a hermaphroditic fish. *Environmental Biology of Fishes* in press, 1987.

——, and Petersen, C.W. The evolution of sexual patterns in the seabasses. *Bioscience* 37: 482–489, 1987.

Ghiselin, M.T. *The Economy of Nature and the Evolution of Sex*. Berkeley: Univ. of California Press, 1974.

Gross, M.R. Sunfish, salmon, and the evolution of alternative reproductive strategies. In *Fish Reproduction: strategies and tactics*, G. W. Potts, and R. J. Wootton (Eds.). London: Academic Press, 1984, pp. 55–75.

——, and Shine, R. Parental care and mode of fertilization in ectothermic vertebrates. *Evolution* 35: 775–793, 1981.

Hastings, P.A., and Petersen, C.W. A novel sexual reproductive pattern in serranid fishes: simultaneous hermaphrodites and secondary males in *Serranus fasciatus*. *Environmental of Biology of Fishes* 15: 59–68, 1986.

Jarman, P.J. Prospects for interspecific comparison in sociobiology. In *Current Problems in Sociobiology*, King's College Sociobiology Group (Eds.). Cambridge, England: Cambridge Univ. Press, 1982, pp. 323–342.

Knowlton, N. Reproductive synchrony, parental investment, and the evolutionary dynamics of sexual selection. *Animal Behaviour* 27: 1022–1033, 1979.

Leonard, J.L., and Lukowiak, K. Male-female conflict in a simultaneous hermaphrodite resolved by sperm trading. *American Naturalist* 124: 282–286, 1984.

Maynard Smith, J. Parental investment: A prospective analysis. *Animal Behaviour* 25: 1–9, 1977.

——. *The Evolution of Sex*. Cambridge, England: Cambridge Univ. Press, 1978.

——. *Evolution and the Theory of Games*. Cambridge, England: Cambridge Univ. Press, 1982.

——. Game theory and the evolution of cooperation. In *Evolution from Molecules to Man*, D. S. Bendall (Ed.). Cambridge, England: Cambridge University Press, 1983, pp. 445–456.

——, and Price, G.R. The logic of animal conflict. *Nature* 246: 15–18, 1973.

Milinski, M. Tit for tat in sticklebacks and the evolution of cooperation. *Nature* 325: 433–435, 1987.

Parker, G.A., Baker, R.R., and Smith, V.G.F. The origin and evolution of gamete dimorphism and the male-female phenomenon. *Journal of Theoretical Biology* 36: 529–553, 1972.

Peck, J.R., and Feldman, M.W. The ievolution of helping behavior in large, randomly mixed populations. *American Naturalist* 127: 209–221, 1986.

Petersen, C.W. Mating tactics and gender allocation in *Serranus fasciatus*. *Animal Behaviour*, in press, 1988.

——, and Fischer, E.A. Mating system of the hermaphroditic coral-reef fish, *Serranus baldwini*. *Behavioral Ecology and Sociobiology* 19: 171–178, 1986.

Pressley, P.H. Pair formation and joint territoriality in a simultaneous hermaphrodite—the coral-reef fish *Serranus tigrinus*. *Zeitschrift fuer Tierpsychologie* 56: 33–45, 1981.

Robins, C.R., and Starck II, W.A. Materials for a revision of *Serranus* and related fish genera. *Proceedings of the National Academy of Sciences*, Phila. 113: 259–314, 1961.

Sella, G. Reciprocal egg trading and brood care in a hermaphroditic polychaete worm. *Animal Behaviour* 33: 938–944, 1985.

Shapiro, D.Y. Social behavior, group structure, and the control of sex reversal in hermaphroditic fish. *Advances in the Study of Behavior* 10: 43–102, 1979.

Smith, C.L. The patterns of sexuality and the classification of serranid fishes. *American Museum Novitates* 2207: 1–20, 1965.

Smith, C.L. The evolution of hermaphroditism in fishes. In *Intersexuality in the Animal Kingdom*, R. Reinboth (Ed.). New York: Springer-Verlag, 1975, pp. 295–310.

Terborgh, J. *Five New World Primates*. Princeton, N.J.: Princeton University Press, 1983.

Thornhill, R., and Alcock, J. *The Evolution of Insect Mating Systems*. Cambridge, Mass.: Harvard Univ. Press, 1983.

Thresher, R.E. *Reproduction in Reef Fishes*. Neptune City, N.J.: TFH Publications, 1984.

Tomlinson, J. The advantage of hermaphroditism and parthenogenesis. *Journal of Theoretical Biology* 11: 54–58, 1966.

Trivers, T.L. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35–57, 1971.

Vehrencamp, S.L., and Bradbury, J.W. Mating systems and ecology. In *Behavioural Ecology*, J. R. Krebs, and N. B. Davies (Eds.). Sunderland, Mass.: Sinauer, 1984, pp. 251–278.

Warner, R.R. Mating behavior and hermaphroditism in coral reef fishes. *American Scientist* 72: 128–136, 1984.

Wrangham, R.W. Mutualism, kinship and social evolution. In *Current Problems in Sociobiology*, King's College Sociobiology Group (Eds.). Cambridge, England: Cambridge Univ. Press, 1982, pp. 269–290.

——, and Rubenstein, D.I. Social evolution in birds and mammals. In *Ecological Aspects of Social Evolution*, D. I. Rubenstein, and R. W. Wrangham (Eds.). Princeton, N.J.: Princeton Univ. Press, 1986, pp. 429–451.

Yogo, Y. Studies on the sexual maturation and reproductive ecology in three protogynous fishes. *Report of Fisheries Research Laboratory Kyushu University* 7: 37–83, 1985.