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Solving the Complementarity Dilemma: Evolving Strategies for Simultaneous Hermaphroditism

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We introduce the *complementarity dilemma*, a two-player, binary response game in which the payoffs are highest when the two players respond differently. Using the classifier system EvA, we determine the evolutionary dynamics and structure of strategies that evolve to play an iterated version of this game, and we relate the results to the evolution of major types of sexual reproduction, particularly simultaneous hermaphroditism. We find that complementarity strategies consistently evolve under a broad range of conditions, but that those most consistent with simultaneous hermaphroditism can predominate only when a substantial cost of repeatedly adopting the female role is imposed. The cost is analogous to the fecundity reduction to be expected when a single partner must repeatedly produce the eggs in sexual reproduction.

Introduction

Cooperation in nature and its evolution have stimulated much recent work in evolutionary ecology (e.g. see Dugatkin, 1997 and references therein). Because cooperation is inherently contingent and expresses the nature of interactions among individuals, the conceptual underpinnings of this vibrant field were firmly established with the application of mathematical game theory (Rappoport & Chammah, 1965; Trivers, 1971; Axelrod & Hamilton, 1981). Pairwise, binary-response interactions—in which individual selfishness (defection) is rewarded, but mutual cooperation is more beneficial than mutual defection—are thought to be well represented in nature. To address them, theorists have relied heavily on the Prisoner's Dilemma game (PD; see Axelrod & Hamilton, 1981; Axelrod & Dion, 1988). These and other studies show that individuals engaged in an iterated series of PD games (i.e. an IPD) should achieve mutual cooperation at high frequency, as long as the series is sufficiently long and of indeterminate length (e.g. see Axelrod & Hamilton, 1981). But recent doubts about the broad applicability of the standard IPD representation to nature have underscored the need to consider other conceptual tools for analysing cooperative interactions (Noe, 1990; Dugatkin *et al.*, 1992; Clements & Stephens, 1995; Heinsohn & Packer, 1995).

Here we introduce a new approach—the *complementarity dilemma* (CD, or ICD in its

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iterated form). Situations arise in nature in which a pair of repeatedly interacting individuals, each capable at any particular time of playing any one functional role from a finite set of such roles, must consistently adopt different and *complementary* roles to maximize their fitness. When both adopt the same role, the result is less rewarding or even disastrous. For example, in some species with altricial offspring, one parent must forage while the other tends the young. When both parents forage simultaneously, the offspring are left unprotected, and when both parents simultaneously tend the offspring, no food is obtained. Thus, at any particular time, the parents must sort out who forages and who stays at home.

It is especially important to understand how this kind of complementarity can arise even between individuals unable or unwilling to signal their intentions, such as early in the evolution of this phenomenon within a species, or whenever the two roles are differentially advantageous. Suppose for simplicity (as in the PD) that each of two interacting individuals must adopt one of two possible roles (A or B) in each interaction without signaling intentions, and that these roles are adopted simultaneously, as for the parents in the parental-care example. Let the reward or fitness gain for the focal individual in a single interaction be $f(ij)$, where the focal plays i (i.e. adopts role i) and the other plays j, and where i and j may or may not be the same. Then the CD is defined as $f(\mathrm{BA}) > f(\mathrm{AA})$ and $f(\mathrm{AB}) > f(\mathrm{BB})$. In the special case of the symmetrical complementarity dilemma (SCD), $f(\mathrm{AB}) = f(\mathrm{BA})$; all other cases of the complementarity dilemma are considered asymmetrical (ACD). Payoff matrices for a simple SCD and for two ACDs are illustrated in Fig. 1.

(a)

		Focal	
		C (Female)	**D** (Male)
Other	**C** (Female)	0	1
	D (Male)	1	0

(b)

		Focal	
		C (Female)	**D** (Male)
Other	**C** (Female)	0	1.2
	D (Male)	0.8	0

(c)

		Focal	
		C (Female)	**D** (Male)
Other	**C** (Female)	0	1.5
	D (Male)	0.5	0

FIG. 1. Example payoff matrices for the complementarity dilemma game (CD). (a) A symmetrical complementarity dilemma (SCD) payoff matrix, (b), (c) payoff matrices for two asymmetrical cases (ACD).

There are of course other games in the biological and game-theory literature related to the Prisoner's Dilemma but sharing the non-PD property that the payoff for cooperation against defection exceeds the payoff for mutual defection. The best known of these are Chicken (e.g. Rapoport & Chammah, 1965; also note their Matrix 25), the Cruel Bind (Trivers, 1972), and the Battle of the Sexes (e.g. Colman, 1995). See Mesterton-Gibbons & Dugatkin (1992) for a categorization of two-player games that fits this situation into theoretical context.

As for the Prisoner's Dilemma, one Complementarity Dilemma game between two individuals assumed to be unable to communicate with each other is not very interesting, but sequences of games open some new possibilities. In a single SCD game, an individual within a randomly constituted pair may be equally likely to make either alternative play, resulting in complementarity with probability 0.5. But in a sequence of such games (an ISCD), certain strategies based on the previous plays of one or both players can quickly yield consistent complementarity, as we will demonstrate.

Mating systems provide prime examples of complementarity, and for individuals capable of functioning either as a male or as a female (i.e. as simultaneous hermaphrodites), mating seems to present a CD. Well-studied examples of simultaneous hermaphroditism include egg trading in the fishes *Hypoplectrus nigricans* (Fischer, 1980, 1981, 1987), *Serranus tortugarum* (Fischer, 1984; Fischer & Hardison, 1987), *Serranus tabacarius* (Petersen, 1995), the sea-basses as a group (Fischer & Petersen, 1987), and *Lythrypnus zebra* (St. Mary, 1996); egg trading in polychaete worms *Ophryotrocha diadema* (Akesson, 1976; Sella, 1988, 1991; Premoli & Sella, 1995a), *O. socialis* (Ockelmann & Akesson, 1990), and *O. gracilis* (Sella *et al.*, 1997); and sperm trading in the sea slug *Navanax inermis* (Paine, 1965; Leonard & Lukowiak, 1985; Leonard, 1990, 1991). Progress has been made in developing a theoretical framework for understanding the evolution of this reproductive mode (Tomlinson, 1966; Fischer, 1988; Leonard, 1990; Connor, 1992). Fischer (1988) described egg trading in sea basses as a special case of the Tit-for-Tat (TFT) strategy—in this context, TFT would be to cooperate by providing eggs to your partner unless your partner fails to provide eggs to you in the previous exchange. Fischer noted, however, that egg trading differs from TFT, because eggs are not offered by both partners at the same time.

In the present study, we view simultaneous hermaphroditism as complementarity. We use the classifier-system model EvA (Crowley, 1996) to study the evolution of strategies for playing the ICD with the payoff matrices of Fig. 1. We find that the strategy most consistent with egg trading in simultaneous hermaphrodites does consistently evolve but tends to be relatively uncommon unless constraints analogous to physiological costs of rapidly repeated egg production are imposed. We then consider the implications of these results for the evolution of mating systems and cite some other examples of complementarity in nature that deserve attention in future work.

Methods

We focus initially in the present analysis on interactions that resemble those resulting in egg-trading in small populations with high pairing fidelity, as seen in laboratory studies of the polychaete *Ophryotrocha diadema* (Akesson, 1976; Sella, 1985, 1988, 1991). In *O. diadema*, young juveniles are protandrous males but with increasing length are soon also capable of producing eggs, reaching full maturity at a length of about 5 mm. Hermaphrodites prefer to mate with other hermaphrodites (Sella, 1985). Spawning is synchronized by close contact during a courtship lasting for several hours and is followed by mating that features regular alternation of sex roles between partners (Sella, 1985). The reproductive success of reciprocating individuals is twice as high as for non-reciprocators (Sella, 1988). Brood care, which increases offspring survival (Sella, 1988), is provided by both parents. Though apparently nothing is known about reproductive behavior of this species in nature (G. Sella, pers. commun.), slow adult dispersal and low population densities suggest that an individual's entire reproductive output may result from a single pairing (see Premoli & Sella, 1996b). We therefore emphasize monogamous pairings in the present study.

To simulate the evolution of strategies appropriate for addressing this sort of complementarity scenario, we used EvA, a classifier system capable of exploring a wide range of pairwise, binary-response interactions within small populations [Crowley, 1996; classifier systems and some close conceptual relatives were developed by John Holland and colleagues—see Holland (1992) and Goldberg (1989) for theory and applications of this powerful family of techniques]. In EvA, individuals are algorithms composed of rules that specify how the focal individual should respond in the current game, given a particular pattern of most recent responses by one or both players in earlier games of the sequence. Rule syntax can be summarized as:

$$f_i f_{i-1} \ldots f_1 / o_j o_{j-1} \ldots o_1 : f_0,$$

where the f_i-to-f_1 sequence indicates the focal's responses in the last i games ($i \geqslant 0$), the o_j-to-o_1 sequence indicates the other player's responses in the last j games ($j \geqslant 0$), and f_0 is how the focal should respond in the present game. The *order* of a rule is defined as $i + j$. In applying EvA to the

ICD, we retain the PD convention of representing the two possible responses as C and D, where C (cooperate) represents the female role as egg supplier and D (defect) the male role as provider of the much less energetically expensive sperm. For example, the third-order rule C/DD:C says that if the focal individual cooperated in the last game and the other individual defected in the last two games, then the focal should cooperate in the present game.

In EvA, the rules that constitute an algorithm (= individual = strategy) operate under the following three "laws":

1. *Higher-order rules supercede lower-order rules when both apply*. For example, the three-rule algorithm (/:C, /C:C, D/C:D) will respond with D to a preceding game in which the focal played D and the other played C, because the more specific third rule overrides the more general first and second rules—though all three fit the relevant history.
2. *When same-order rules apply*, *the rule invoked is chosen randomly*. For example, the four-rule algorithm (/:C, /:D, C/:C, /C:D) is equally likely to respond with C or D to either mutual defection (first two rules both apply) or mutual cooperation (last two rules both apply).
3. *Every algorithm must contain at least one zero-order rule* (i.e. /:C or /:D). This ensures that the algorithm provides a response to every possible history.

EvA begins with a population of algorithms composed of random rules, and randomly allocates the algorithms to "trait-group" subsets that play a round-robin ICD tournament against each other (see Spohn, 1995). (In most of the runs described in this article, each pair of mating individuals constitutes a trait group.) Once these fitness-evaluation tournaments are complete, the total points accumulated by all players in the population are compared to calculate each individual's expected proportional contribution of offspring to the next generation. (In the present study, this is simply an individual's total fitness points, divided by the population's total fitness points.) In the reproductive phase of each generation, a new population is generated, one offspring at a time, through fitness-weighted bi-parental reproduction. Each offspring inherits its algorithm from one parent—except that one or more rules may be replaced by rules from the other parent (crossover), loci within rules may mutate between C and D, and rules may randomly change length (see Crowley, 1996 for details). But overall, the new generation strongly resembles the most successful ICD players in the previous generation. This process of fitness determination followed by reproduction then repeats for some substantial number of generations, during which certain evolutionary trends and dominant strategies generally appear.

The definitions and default magnitudes of the main parameters of the classifier-system simulation are listed on the left side of Table 1. Each of the 50 replicate runs extended for 400 generations, with fitness averaged over only the last 200 to eliminate any initial transient behavior. To keep the run-duration and analysis manageable but permit sufficient evolutionary experimentation, we set the default population size at 20 individuals. Previous work demonstrating that memory of only about one previous game was retained, even when memory-retention carried negligible cost in a similar iterated-game scenario (Crowley *et al*., 1996; Spohn & Crowley, 1997), convinced us to include only responses from the immediately preceding game in rules of the default run.

Algorithms consisted of 10 rules, a number consistent with relatively high levels of mutual cooperation in the IPD (Crowley, 1996), yet permitting relatively easy interpretation by visual inspection. As previously explained, individuals were randomly and permanently paired. Each pair played a total of 171 consecutive CD games per generation. This number allowed us in later comparisons to expand the trait (mating) groups to 10 or 20 individuals each, while playing equal numbers of games with each other individual in the group (i.e. 19 or 9 games with each other individual, respectively) to accumulate the 171 games per individual.

The default payoff matrix [Fig. 1(a)] was chosen to reflect monogamy; though eggs may be more physiologically costly to produce, lifetime reproductive success within pairs of strictly monogamous males and females must be the same. To impose a fitness cost on both members of a pair when one of them attempts to provide

TABLE 1

Parameter definitions, default and alternative magnitudes, and results for each alternative[a]

Definition	Default Magnitude	Alternative Magnitude 1	Fitness/CAD frac.	Alternative Magnitude 2	Fitness/CAD frac.
Total number of generations per run	400	200	0.873 ± 0.021/0.150	800	0.968 ± 0.009/0.196
Number of generations used to generate data per un	200	100	0.934 ± 0.020/0.268	400	0.922 ± 0.016/0.205
Number of individuals in the population	20	10	0.801 ± 0.031/0.452	40	0.981 ± 0.003/0.140
Number of previous games remembered	1	3	0.946 ± 0.010/0.262	—	—
Number of rules per algorithm	10	5	0.885 ± 0.025/0.200	20	0.958 ± 0.012/0.261
Total number of games per individual per generation	171	60	0.920 ± 0.015/0.156	500	0.959 ± 0.016/0.156
Trait-group (= mating group) size	2	10	0.867 ± 0.011/0.304	20	0.740 ± 0.014/0.233
Payoffs for playing D against C and C against D	1, 1	1.2, 0.8	0.962 ± 0.012/0.292	1.5, 0.5	0.957 ± 0.014/0.142
Fitness multiplier for consecutive identical responses	1	< 1	See Fig. 4	See Fig. 4	See Fig. 4
Probability of crossover at a given rule locus	0.21	0.1	0.958 ± 0.012/0.277	0.4	0.964 ± 0.010/0.310
Probability of rule-length mutation per algorithm	0.0002	0.00002	0.948 ± 0.017/0.244	0.002	0.966 ± 0.001/0.217
Probability of rule-data mutation per data locus	0.0002	0.00002	0.956 ± 0.014/0.196	0.002	0.954 ± 0.003/0.207

[a] Results presented are fitness means ± standard error over the 50 replicates and CAD fraction—the number of replicate runs in which CAD becomes fixed in the population, divided by the number of replicate runs in which either CAD or DorC becomes fixed. Default results are 0.954 ± 0.012 (fitness mean ± standard error) and 0.255 (CAD fraction).

eggs twice in a row, we introduced a fitness multiplier parameter (abbreviated *repco*, for repeat coefficient) into EvA; in the default runs, however, this is set to 1.0 and therefore has no effect. The crossover frequency per rule locus was set at 0.21, to maintain the same degree of genetic linkage as for single-break crossover of linear segments (see Crowley, 1996). Mutation rates were chosen to permit consistent eventual fixation or near-fixation of a single algorithm, while retaining substantial variation over at least the initial part of the evolutionary sequence (see Table 1).

Our analysis proceeded as follows. We conducted the default runs to determine whether algorithms capable of achieving a high frequency of complementarity would consistently evolve. The frequency of complementarity for the relevant payoff matrix [Fig. 1(a)] was expressed directly by mean fitness. We calculated the standard error over the 50 replicate fitness means in each run set and used non-overlap of error bars as a rule of thumb for statistically distinguishing overall means between such run sets. We also carefully examined the strategies that emerged from the 400th generation of the 50 replicate default runs, with particular interest in the frequency of algorithms capable of achieving and maintaining alternating complementarity (i.e. the CAD strategy—Cooperation Alternating with Defection). Because another group of algorithms capable of achieving and maintaining complementarity without alternation (i.e. the DorC strategy—Defection or Cooperation) predominated, we calculated the CAD fraction as the number of the 50 replicate runs in which CAD became fixed in the population, divided by the number in which either CAD or DorC became fixed.

To gain some sense of how strongly our default results depended on the parameter magnitudes used, we then conducted a sensitivity

CAD			DorC			Long Transient	
/:C	/:C	/:C	/:C	/:C	/:C	/:C	/:D
/:D	/:D	/:D	/:D	/:D	/:D	/:D	D/:D
C/D:D	C/:D	D/:C	C/D:C	C/:C	D/:D	D/:C	/D:C
D/C:C	/C:C	/D:D	D/C:D	/C:D	/D:C	/D/:D	
						D/D:C	

Facultative		Random		Fixed		Alternator	
/:C	/:C	/:C	/:C	/:D	/:C	/:C	/:D
/:D	/:D	/:D	/:D	D/:D	/:D	/:D	/C:C
D/:C	D/:D	D/:D	D/:D	C/C:D	D/:D	C/:D	C/D:D
/D:D	/D:C	/D:C	/D:C	C/D:D	C/:C	D/:C	
C/C:C	C/C:D	/D:D	C/:D				
	D/D:C		/C:C				

FIG. 2. Some strategies that evolve in the ICD game. The dominant strategies over a very wide range of parameter magnitudes are CAD (Cooperate Alternating with Defect) and DorC (Defect or Cooperate), and the Long Transient variations. These strategies settle into complementary response sequences with a genetically identical or otherwise compatible partner, either with both players adopting constant and complementary roles (DorC), or with the players alternating responses out of phase with each other (CAD). Some CAD and DorC strategies feature deterministic rather than probabilistic responses to a previous attempt by both players to adopt the same strategy; this can sometimes increase the number of games required to achieve sustainable complementarity (note the potential effects of the D/D:C rule and the single zero-order rule in the Long Transient examples). Other strategies may resemble CAD or DorC and be capable of complementarity but also capable of displaying non-complementarity (e.g. the Facultative strategies containing the C/C:C rule or the C/C:D & D/D:C rule pair). Some may be incapable of settling into a repeated pattern (Random), while others inevitably lock onto a fixed response regardless of the other individual's behavior (Fixed). Some strategies other than DorC or CAD are capable of achieving complementarity in games against DorC (Fixed) or CAD (Alternator), but are unable or less likely to do so in games against another identical algorithm.

analysis. In this exercise, the magnitude of only one parameter at a time was changed (usually by a factor of two where appropriate) from its default value, and the response was assessed by comparing the resulting mean fitness and CAD fraction to corresponding values from the default run. To account for the low CAD fractions in most of the default and sensitivity runs, we calculated expected fitnesses for interactions of importance early in these evolutionary sequences. We then documented two relevant sequences graphically, and identified the rules and rule combinations likely to facilitate the evolutionary success of DorC and CAD. Finally, we imposed fitness costs of consecutive-game oviposition by the same individual to determine whether this might shift the balance between the DorC and CAD strategies.

Results

In the default run set, over 95% of CD games in the last 200 generations of the replicate runs yielded complementary behavior (fitness mean ± standard error = 0.954 ± 0.012). In most of these replicates, algorithms consistent with complementarity became dominant well within the first 100 of the 400 generations per run.

At the end of 400 generations, the evolved population usually consisted exclusively of identical algorithms, though with considerable variability among runs in structural details. Nevertheless, closely related classes of algorithms resulting in very similar behavior were easily recognizable. In the default output, 35 of the 50 fixed or predominant algorithms were of the DorC (i.e. D or C) type, which has the following key behavioral features in games against others of its type: (1) usually a brief initial non-complementary transient, followed by (2) a consistent, single repeated behavior to the end of the sequence that is (3) complementary to that of its opponent and (4) equally likely to repeat D or C. Structurally, this requires one or more rules that help determine the transient, and at least one pair of matched first- or second-order rules that allow DorC to settle into playing either D or C (see Fig. 2; note that the 3-rule long-transient algorithm is also a DorC example).

Twelve of the other 15 runs in the default set produced algorithms of type CAD (C Alternating with D). In games against itself, CAD has the first three of the four features listed above for DorC. But instead of settling into an equiprobable repeat of D or of C, CAD locks onto an alternation of C and D out of phase with the other player. In structure, CAD is very similar to DorC, except that the matched pair of first- or second-order rules specify responses opposite to those in the equivalent DorC rules (Fig. 2; note that the 5-rule long-transient algorithm is of type CAD). It is these matched rules that shuttle behavior back and forth between C and D. CAD is the strategy most consistent with egg trading and other alternating forms of reciprocity, but it represented only about one-quarter of these two dominant types of complementarity that evolved in the default runs (i.e. a CAD fraction of 0.255).

Using geometric-series approximations, expected duration of the non-complementary transient when a DorC or CAD strategy plays another of its type can be shown to be minimized at one game by equiprobable C and D following mutual defection or mutual cooperation. The examples under the DorC and CAD headings of Fig. 2 are minimal-transient cases. In contrast, the 3-rule DorC algorithm has an expected transient duration of three games against another of its type. In short ICD sequences, longer transients can substantially reduce fitness.

In the default and other runs of EvA using the payoff matrices of Fig. 1, a few other categories of algorithms appeared, most of which represented variations of the DorC and CAD types (Fig. 2). Some of these expressed constant behavior independent of the other player's behavior (Fixed); some could achieve alternating complementary behavior against CAD but only inconsistently or not at all against another player of their type (Alternator); some were incapable of attaining a consistent behavior pattern at all (Random); and others could express more than one of the other types, depending on chance during the initial generations (Facultative). All of these types illustrated in the lower part of Fig. 2 were rare after 100 generations of an ICD sequence, but they figured prominently in the early generations of each run.

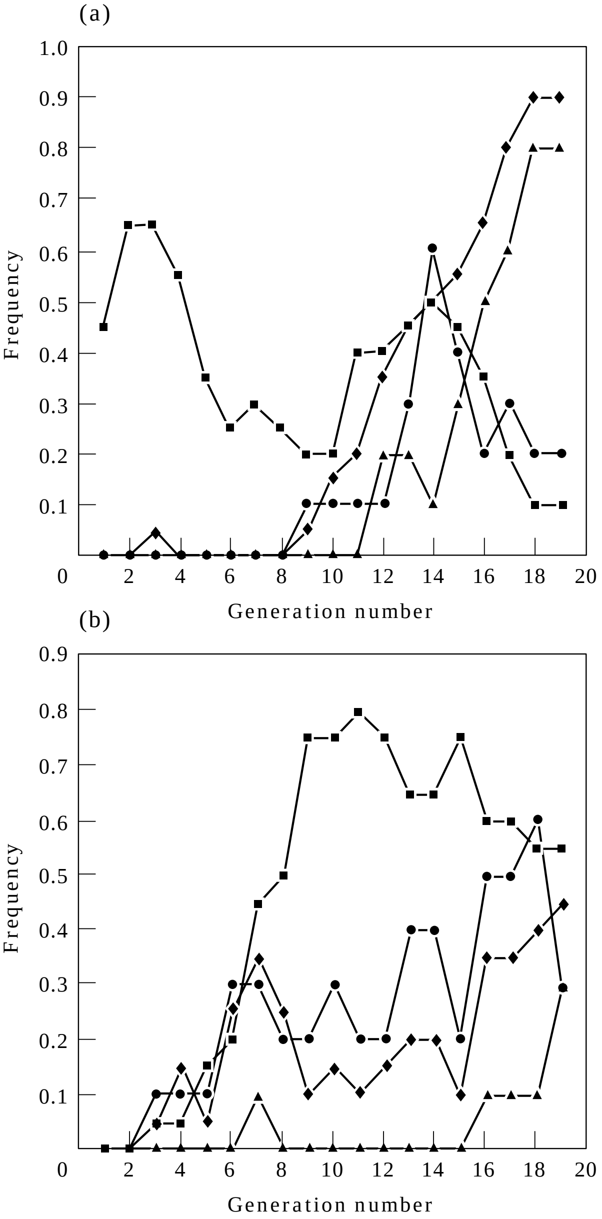

FIG. 3. Frequencies of certain strategies and interactions in the first few generations of two sequences, each leading to fixation of one of the two dominant strategies. (a) Fixed strategies are relatively abundant early in this sequence, interacting effectively with the first few DorCs that appear. Thereafter, DorCs quickly increase in frequency and outcompete fixed strategies and others; (b) a CAD and an Alternator (a non-CAD nevertheless capable of achieving an alternating pattern complementary to CAD) appear simultaneously and interact to mutual advantage, leading to an abundance of Alternators that eventually allow CADs to take over. (a) (◆) DorC; (■) fixed; (▲) DorC/DorC; (●) DorC/fixed; (b) (◆) CAD; (■) alt; (▲) CAD/CAD; (●) CAD/alt.

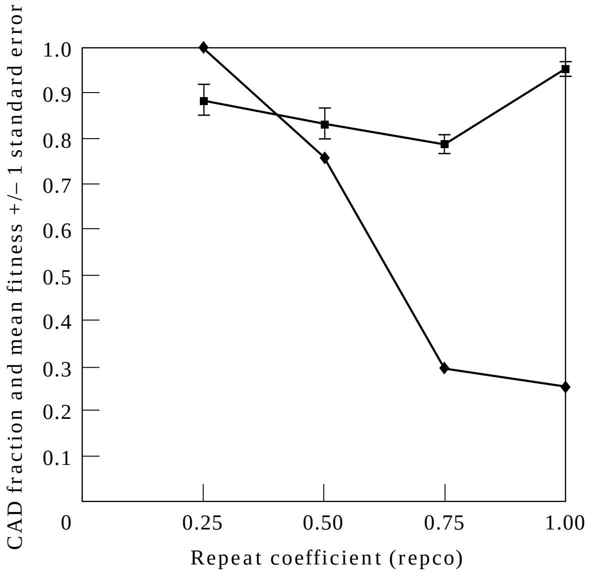

FIG. 4. The fraction of complementarity strategies (CAD plus DorC) evolving to fixation that are CAD (i.e. the CAD fraction), and the mean and standard error of fitness, for different magnitudes of the repeat coefficient (repco). As the fitness cost of having either player cooperate twice in a row goes up (i.e. as repco, the fitness multiplier, goes *down*), the CAD fraction rises in a sigmoid pattern to 1.0, while fitness declines somewhat and then partially recovers. (◆) CAD fraction; (■) mean fitness.

Results of the sensitivity analysis are presented in Table 1. There were strong and consistent responses to doubling or halving the population size. Populations of size 40 achieve higher fitness with even greater dominance of DorC over CAD than in the default, whereas populations of size 10 only achieved about 80% complementarity in which CAD was almost as frequent as DorC. Enlarging the trait or mating group size also sharply reduced the amount of complementarity, though with little effect on the CAD fraction. Results related to the number of generations run or used to obtain data were consistent with the interpretation that most non-complementary behavior disappears within the first 100 generations of the evolutionary sequences. Surprisingly, making the two complementary payoffs different from each other had no clear effect, nor did the number of previous games remembered or the crossover or mutation rates. Reducing the number of rules per algorithm or the sequence length reduced fitness and the CAD fraction somewhat, though increasing these parameters had little effect. Responses to changes in the fitness multiplier (repco) are described below. Overall, the sensitivity analysis indicated that results did not depend strongly on any of the more arbitrary parameter values, though trends associated with population size will be addressed further in the Discussion.

To account for the dominance of DorC over CAD in these simulations, we examined the initial few generations of some evolutionary sequences. Examples are presented in Fig. 3. Fixed strategies were relatively common early on in most of these sequences [e.g. Fig. 3(a)], providing an important advantage for DorC strategies that happened to appear (see Appendix A). Once DorC became common by adopting roles complementary to those of Fixed strategies, DorC could outcompete Fixed strategies by virtue of its role flexibility. CAD strategies were similarly dependent on the presence of Alternators to become abundant and eventually win out, but Alternators appeared less frequently than did Fixed strategies by mutation and recombination. This is true because, though structurally similar to Fixed strategies, Alternators must contain a pair of the first- or second-order rules consistent with switching behaviors back and forth (e.g. see Fig. 2), whereas Fixed strategies need only follow a single rule to keep doing the same thing.

When a fitness cost of repeating the egg-provided role in sequential games was introduced, however, CAD became more common, and DorC completely disappeared when this cost was sufficiently high (Fig. 4). When the second of two consecutive clutches provided only about 75% as many eggs as the first (i.e. repco $= 0.75$), mean fitness declined to about 0.8, perhaps in response to a relatively high diversity of algorithms. But with the cost at 50% or more reduction of the second clutch (i.e. repco $\leqslant 0.5$), fitness recovered to higher levels, and CAD predominated.

Discussion

This analysis has demonstrated that strategies able to achieve and maintain complementarity of binary behavior without signaling intentions can evolve consistently in a classifier system model of iterated pairwise interactions. The strategies require memory of responses in only the immediately preceding interaction and can consist of as few as three very simple rules. Interaction sequence lengths of about 10 or more are required for these complementarity strategies to predominate among the evolutionary end-products.

The CAD strategy, which features alternation of C and D out of phase with its partner, encodes the role-swapping logic characteristic of simultaneous hermaphroditism. We have shown that CAD predominates when there is a substantial fitness cost of a player's repeating C in consecutive games; with little or no cost of such repetition, DorC predominates. The DorC strategy, in which an individual repeats the response complementary to the one being repeated by its partner, produces opportunistic gender-role playing as in many sequential hermaphrodites and other species capable of facultative gender change.

Note that the scenario in the runs presented here, in which each individual's fitness is determined by its mating success with one or more *randomly* chosen partners, resembles the situation faced by non-selfing individuals in populations at very low densities. The prospect of having very few mating opportunities can create the sort of strong selective advantage for hermaphroditism (e.g. see Tomlinson, 1966) that produced DorC and CAD strategies in our simulations. Even allowing for significant fitness advantages of permanent gender specialization in gonochores (corresponding to our invariant types AllC and AllD), hermaphroditic mutants should invade and replace the gonochores when mating opportunities are sufficiently rare (see Appendix B). The evolution of simultaneous from sequential (or facultative) hermaphroditism, or vice versa, appears much less likely than the evolution of hermaphrodites from gonochores, according to the analysis presented here (cf. Premoli & Sella, 1995b, p. 34).

Benthic polychaete worms encompass a broad range of biparental reproductive types, including 31 species of simultaneous hermaphrodites (e.g. *Ophryotrocha diadema* emphasized above), 36 sequential hermaphrodites, and an unknown but probably larger number of gonochoristic species (Premoli & Sella, 1995b). Certain fishes, particularly the seabasses of the family Serranidae, also exhibit these types (e.g. Fischer & Petersen, 1987). In all of the well-studied cases of hermaphroditism in these groups, partners signal to each other via courtship displays and often physical contact before mating, facilitating physiological compatibility and reducing the possibility of wasting gametes during mating itself. Though apparently expensive in both time and energy (e.g. see Fischer, 1980, 1984; Sella, 1985), courtship presumably increases the overall energetic and reproductive efficiency of the mating process. The initial transient phase of the strategies evolved by EvA, by the end of which complementarity has been attained, correponds in some sense to this expensive yet important pre-reproductive phase in natural systems. But our analysis demonstrates that signaling is not a prerequisite for the evolution of behavioral strategies ensuring the sort of complementarity essential for phenomena like hermaphroditism.

Similarly, we have made no attempt explicitly to incorporate the advantages of egg (or sperm) trading into the simulations, though these are undoubtedly important to a full understanding of simultaneous hermaphroditism in many taxa. Our focus has instead been on the logical structure and the evolutionary dynamics that generate simultaneous hermaphroditism under minimal assumptions. Such phenomena as egg parceling by seabass (Fischer & Petersen, 1987) and maturation of fewer eggs but more frequently within the polychaetes (Premoli & Sella, 1995b) may, like signaling, represent evolutionary polish on an already established, simultaneously hermaphroditic reproductive mode.

We believe that the concept of complementarity will prove useful in clarifying a considerable number of pairwise interactions in nature. Our focus here has been on sexual reproduction and some of its main variations. We have also alluded to a parental-care example in the Introduction. Food provisioning (e.g. Wilkinson, 1984, 1990) may sometimes fit the pattern, though extensive sequences of provisioning between two unrelated individuals have rarely been documented. In contrast, grooming behavior, particularly in mammals (Seyfarth & Cheney, 1984; Hart & Hart 1992), is well studied and often yields long sequences of reciprocity. All of these types of interactions have been addressed mainly using theory derived from the Prisoner's Dilemma, in which mutual cooperation is assumed to be simultaneous, rather than the kind of asynchronous complementarity characteristic of these examples. Among other things, the complementarity framework may be less dependent on the restrictive PD assumption of simultaneous decision-making (see Dugatkin *et al*., 1992; and see below), since in at least some cases one behavior (e.g. egg release) may immediately trigger complementary behavior (e.g. sperm release) by the other player.

Dominance (and submissiveness) may also represent another important type of complementarity, in which the risk of injury may lead even to the relatively arbitrary settling of differences in social rank by convention. "Dear enemy" relationships among neighboring territorial males map such conventional rank differences onto space (Ydenberg *et al*., 1988; Qualls & Jaeger, 1991; Fox & Baird, 1992; Godard, 1993). These and other examples of complementarity should be identified and considered carefully from this non-PD viewpoint.

A number of possible modifications of the classifier system model might improve and extend the present analysis.

1. The sensitivity analysis indicated that larger populations increase both mean fitness and the dominance of DorC strategies. Though ad hoc run sets have demonstrated that reducing the fitness multiplier (repco) still allows CAD to dominate at larger population sizes, a more thorough exploration of larger populations is clearly needed.
2. Asymmetrical payoff matrices need more extensive analysis. For example, the dynamics may be different if a third possible response (i.e. $Q = \text{quit}$) is added to the behavioral array, enabling a player to opt out of an ICD with another who fails to cycle through both the higher- and lower-payoff roles.
3. Additional simulations need to be conducted that allow more extensive memory to be used. It is already clear that new and otherwise

impossible strategies can appear in this case (e.g. one that alternated two consecutive cooperations with two consecutive defections). It seems likely that rules invoking a "quit" response would often need to rely on additional memory to be effective. Perhaps much longer sequences of generations will also be needed to produce the potentially more complex strategies based on additional memory.

4. Recent work on the alternating Prisoner's Dilemma (Nowak & Sigmund, 1994; Frean, 1994; Leimar, 1997) suggests another way of analysing a subset of situations in which complementarity might be expected. In cases like egg-trading in fishes or grooming in mammals, where cooperation offered by one partner can be assumed to be automatically accepted by the other, then complementarity may be represented simply as a sequence of cooperative behaviors alternating between individuals. This way of conceptualizing these behavioral sequences does not require a simultaneous defection to match each cooperation; instead, "defection" means failure to provide the cooperative act by an individual during its turn to respond. It would be instructive systematically to compare results obtained under this scenario with those generated by our approach.

We hope that the analysis presented here will stimulate empirical work, including both additional documentation of complementarity and experimental studies capable of identifying the behavioral rules underlying the strategies of importance in nature.

We close with some words once sung about reciprocity, very much in the context of reproductive behavior:

> And in the end,
> The love you take
> Is equal to the love you make.
> (The Beatles, *Abbey Road*)*

* Lyrics taken from "The End" by John Lennon and Paul McCartney, by kind permission of Sony/ATV Music Publishing Ltd.

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APPENDIX A

Expected Fitnesses of CAD and DorC in an ICD against an Invariant Response

We focus here on the functionally identical, minimal-transient forms of DorC and of CAD illustrated in the upper portion of Fig. 2. For any of these forms of DorC or CAD, whether this focal individual and any opponent responded identically or differently from each other in the previous game completely determines the probability that the focal repeats its previous play or switches behavior in the next game. This is true independently of the specific responses (i.e. C or D) by the two players and of entries in the payoff matrix. In this sense, the expected sequences of responses are equivalent, whether the behaviorally invariant individual is AllC (i.e. functionally identical to the one-rule algorithm /:C) or AllD (i.e. /:D). Moreover, the expected payoffs against the two behaviorally invariant opponents are the same when the ICD is symmetrical. To keep things simple here, we therefore use the payoff matrix in Fig. 1(a) and consider only AllC as the behaviorally invariant opponent.

When DorC plays AllC, the number of games required to achieve complementarity is uncertain. The probability that the first game must be played to achieve complementarity is of course 1.0; the chance that at least one additional game must then be played to reach complementarity is 0.5; the chance that yet another game is required is 0.25; and so forth—generating a geometric series for the expected number of games that sums to 2. This means that for an ICD sequence long enough for non-negligible values in the tail of this series to be counted, DorC and AllC average one non-complementary game, followed by complementarity. Once DorC has attained complementarity with an opponent, it locks in that behavior through the entire sequence. For a "long" sequence of length n, this and the payoff matrix of Fig. 1(a) ensure that the expected payoff per game is based on the average case of no fitness points in the first game and one point in each subsequent game, or $(n-1)/n$. As the sequence length n is increased, this expected payoff per game approaches 1.0 asymptotically. Thus DorC is expected to average slightly less than 1 fitness unit per game in long ICD sequences against a behaviorally invariant opponent.

Determining the expected payoff per game for CAD against a behaviorally invariant opponent is only slightly more complex. Let (C,D) represent a response that is equally likely to be C or D. In a game against AllC, (C,D) has an expected payoff of 0.5, since DC pays 1 but CC pays 0, and these outcomes are equally likely. Suppose that we visualize such a sequence as a series of cycles, each beginning with (C,D) plays by CAD until complementarity is achieved, after which CAD immediately plays C in a futile and unrewarded attempt to initiate alternation. This cycle then repeats for the entire ICD sequence. By the same argument as for the probabilistic initiation of the DorC-vs.-AllC sequence described above, the expected number of (C,D) plays per cycle is two, twice as many as the number of zero-payoff C plays, resulting in an overall expectation of one-third of a fitness point per game. Simply following the probability tree of CAD plays across games indicates rapid convergence on the expected two plays of (C,D) for each play of C.

For completeness, consider the expected payoff for CAD and DorC playing each other. Again breaking the game into cycles, we find that the expected number of games to achieve complementarity is still two, because having both players rather than a single player choosing responses at random has no effect on the probability of achieving complementary behavior. Once complementarity is reached, DorC repeats its previous behavior, and CAD switches, generating a zero-payoff, non-complementary combination, followed by the beginning of a new cycle. This is the same pattern as for CAD vs. AllC, thus yielding the same expected payoff per game.

To summarize, DorC achieves high fitness against a behaviorally invariant opponent in an ICD of more than a few games, whereas CAD fares poorly. Moreover, CAD vs. DorC generates the same low fitness expectation as for CAD against the behaviorally invariant opponent.

These results can be obtained more elegantly and rigorously by expressing the transitions between response combinations as a first-order Markov process (Nowak *et al*., 1995), under the assumption that rare response errors occur. Let strategy $\mathbf{p} = (p_1, p_2, p_3, p_4)$ and strategy $\mathbf{q} = (q_1, q_2, q_3, q_4)$, where p_i and q_i are probabilities of playing C in the next round, given the response combination i in the present round, and the $i = 1 \ldots 4$ correspond to the focal-other response combinations CC, CD, DC, and DD, respectively. In this notation, the minimal-transient versions of strategies considered in this appendix are: DorC, (0.5, 1, 0, 0.5); CAD, (0.5, 0, 1, 0.5); AllC, (1, 1, 1, 1); and AllD, (0, 0, 0, 0). For an ICD sequence, a 4 × 4 transition matrix can be constructed, for which each entry is a probability derived from appropriate elements of the ordered quadruples representing the two strategies. For example, the probability that the response combination CC will be followed by DD is $(1 - p_1)(1 - q_1)$; in an ICD between CAD and DorC, this is $(1 - 0.5)(1 - 0.5) = 0.25$. For infinitely long ICD sequences, the proportion of games resulting in each response combination is then the left eigenvector of the transition matrix for the eigenvalue 1. The payoff for a particular strategy is the sum of payoffs for each response combination, weighted by its frequency according to this stationary distribution. See Nowak *et al*. (1995) for details.

APPENDIX B

Conditions for Invasion of a large Population of AllC & AllD by DorC and CAD

As in the simulations, assume that mating partners are drawn at random from the population and that fitnesses are determined in long ICD sequences according to the payoff matrix of Fig. 1(a). Then frequency-dependent selection will maintain the ratio of AllC to AllD very close to 1:1, since if either type becomes less abundant, it is more likely to pair with the *other* type and thus achieve higher fitness. Because the 1:1 ratio implies that each invariant responder is equally likely to draw a partner of the same or opposite type, the expected payoff for such partnerships is 0.5. Allowing for the possibility that repeated cooperation by the same individual in successive games multiplies the resulting fitness by the repeat coefficient r, this expected payoff becomes $r/2$.

A DorC mutant can always successfully invade this population of invariant strategies by virtue of having a higher expected payoff (r) in a long sequence with an invariant strategy than invariants have with each other ($r/2$). Similarly, a CAD mutant can invade the population of invariants whenever the expected payoff in a long sequence with an invariant exceeds $r/2$. When $r < 1$, CAD expects to gain higher payoffs with AllD (i.e. 1/3, as shown in Appendix A) than with AllC (i.e. $r/3$, decrementing for repeated cooperation). Thus, the expected payoff for CAD with a random invariant strategy is the average of the AllD and AllC payoffs, or $(r + 1)/6$, which exceeds $r/2$ and permits invasion whenever $r < 0.5$.

Note that a DorC population is extremely unlikely to be invaded by a mutant CAD, and vice versa. With $r < 1$, the expected payoff in a long CAD-DorC ICD sequence is $(r + 1)/6$, just as for CAD with an invariant equally likely to be AllC or AllD (cf. Appendix A). This precludes successful invasion of a CAD population by DorC, because CAD strategies have an expected payoff of almost 1.0 when interacting with each other. A successful invasion of a DorC population by CAD also seems implausible, because $(r + 1)/6$ exceeds the DorC-DorC payoff of r only when $r < 1/5$.

These results show that when pairings are random, populations of invariant strategies are readily invasible by DorC mutants—and by CAD mutants when repeated cooperation by a single individual reduces the expected payoff sufficiently. Populations of DorC or CAD strategies are very unlikely to be successfully invaded by a mutant of the other strategy type.