

and Higgins' warning – that the transient behaviour of these models may have more practical significance than the final behaviour – should be of great importance to future studies.

I agree with Paradis that a model that assumes that reproduction in one population can be inhibited by the action of a far-distant population seems biologically implausible. However, the model of Csilling *et al.* does not necessarily rest on such an assumption. To me, a more plausible alternative assumption underlying the model of Csilling *et al.* is that the timescale of dispersal is much quicker than that of reproduction, so that all rounds of dispersal are always comfortably accomplished before the next round of reproduction is triggered.

I feel that Csilling *et al.* have made an important step in adopting the assumption that reproduction and dispersal occur on different timescales. However, they (and Hastings and Higgins) follow convention in assuming that reproduction and migration occur in separate time compartments, all reproduction being completed before dispersal occurs and vice versa. While this is realistic for some species, in others reproduction and migration events will not occur in such an ordered way. There has been at least one published attempt to model the latter case⁴, although the model formulation used has since been criticized as unbiological⁵. However, future studies should shed light on how the assumption of temporal ordering affects model predictions⁶.

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Biological markets

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In biological markets, two classes of traders exchange commodities to their mutual benefit. Characteristics of markets are: competition within trader classes by contest or outbidding; preference for partners offering the highest value; and conflicts over the exchange value of commodities. Biological markets are currently studied under at least three different headings: sexual selection, intraspecific cooperation and interspecific mutualism. The time is ripe for the development of game theoretic models that describe the common core of biological markets and integrate existing knowledge from the separate fields.

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intraspecific cooperation, respectively. These fields are traditionally studied separately, in spite of some obvious analogies: (1) individuals exchange commodities to their mutual benefit; (2) the exchange value of commodities is a source of conflict; (3) behavioural mechanisms such as partner-searching, partner choice, and contest among competitors determine the composition of trading pairs or groups. We call situations with these characteristics 'biological markets' because of the analogy with human markets.

As far as we are aware, the market mechanism was not recognized as a common evolutionary mechanism of sexual selection, cooperation and mutualism until last year⁴. This does not mean that market mechanisms have not been implicitly or explicitly recognized in each discipline separately. The existence of mating markets is assumed throughout the literature on sexual selection. A 'market effect' was described for intraspecific cooperation⁵. Selection through partner choice has also been postulated⁶ and shown⁷ for obligate mutualisms between pollinators and plants.

The idea of market selection (Box 1) applies to traits, such as providing nuptial gifts, helping unrelated young, and nectar production, that would not evolve under natural selection in the absence of opportunities for the formation of mutually beneficial partnerships. Market selection is best recognized by its effect on easily quantified chosen traits, but is expected to determine the degree of choosiness as well. Trading may take place on the basis of an honest signal that is correlated with the access to a commodity, instead of being based on the commodity itself.

Box 1. Market jargon

The following terms have been inspired either by sexual selection jargon or by idiom commonly used in connection with human markets.

Market selection: selection of traits that maximize fitness in biological markets, such as the ability to compete with members of the same class, the ability to attract trading partners, the ability to sample alternative partners efficiently.

Commodity: a benefit that members of one trader class can offer to members of another trader class. Alternatives are: 'service' for an intangible commodity (e.g. an alarm call) and 'reward' for a tangible commodity (e.g. nectar).

Trader class: all traders that offer the same kind of commodity. Members of the same class may belong to different species, sexes, etc. Any entity that can 'choose' a strategy independently qualifies as a trader. Some traders have to compete with abiotic sources of commodities.

Trader-class ratio: the relative number of traders belonging to each class. In parallel with sexual selection, an operational class ratio can be defined.

Partner choice: the preference for a partner based on the value of the commodity offered. The value can be relative or absolute, depending on the sampling strategy of the choosing individual.

Outbidding competition: (used in contrast to contest competition) a trader 'outbids' another trader belonging to his own class, if he secures the favours of a member of the other class by making a better offer.

Market models

Here, we limit ourselves to two-sided markets with unrelated traders, in which the members of each class compete for the favours of the members of the other class by outbidding each other.

The best strategy for a trader depends on the behaviour of the members of both his own and the opposite class. Game theory is especially suited to model this two-layered frequency dependence. The important concepts in evolutionary game theory are the evolutionarily stable strategy (ESS) for intraspecific interactions and the coevolutionarily stable strategy

Scorpionfly females accept or reject a nuptial gift of a certain size depending on the number of males that they are likely to encounter¹. Caterpillars of lycaenid butterflies adjust the amount of nectar offered in reaction to the number of ants protecting them². Male pied kingfishers bring food to unrelated nestlings, probably to enhance their chance to mate with the mother in the future, and increase the amount in reaction to an increase in the number of helpers³.

The above examples stem from sexual selection, interspecific mutualism, and

Box 2. Cooperation: from two to many players

Two trends can be identified in the recent literature¹⁴: the addition of partner-switching to Prisoner's Dilemma-based models in which the emphasis remains on the cheating problem²⁶⁻²⁸, and the development of multi-player models with an emphasis on the consequences of partner choice^{4,6,13,29}. It is important to distinguish between partner-switching and partner choice. Partner-switching is but one strategy to exert partner choice, reminiscent of the sequential search strategy with a fixed threshold known from sexual selection theory^{17,19}. Partner-choice models, however, consider the full range of choice strategies, including choice on the basis of the relative quality of partners.

A serious problem for cooperation theory is the lack of good empirical examples. There is hardly an example of reciprocal altruism or 'tit-for-tat' behaviour that has not been seriously criticized^{10,30,31}. The fate of a theory of cooperative markets could be similar, since potential empirical examples of cooperative markets seem much harder to find than markets in sexual selection and mutualism. The truth of the matter could be that cooperation among unrelated conspecifics is a rare phenomenon indeed.

combination for the case of interspecific interactions⁸.

One would perhaps expect relevant market models to be readily available in the vast literature on economic game theory. However, in economics, the behaviour of single individuals is usually hidden in the 'demand function', which describes the behaviour of the members of a specific trader class (for example, 'consumers') in a global way. Models of human markets from the 'cooperative' branch of economic game theory are unsuited for biological models⁹. In biology, models of intraspecific cooperation have traditionally been based on game theory, but do not take the possibility of partner choice into account (Box 2). Game theory has been employed in some models of sexual selection and mutualism, but none of these encompasses all aspects of markets (Boxes 3 and 4). Therefore, specific models of biological markets have to be developed. (For an example, see Fig. 1.)

Issues common to all biological markets

At first sight, the questions asked in the various disciplines seem rather diverse. The proposal to develop common models implies that we see common issues. The following topics are of general importance, but have not received equal attention in all fields.

Free-riding cheaters

Some individuals may profit from an interaction between two classes of traders by disguising themselves as members of a

Box 3. Sexual selection: the gamete market

The market philosophy implicitly plays a role in all aspects of sexual selection theory. The market is perhaps too obvious to challenge theoreticians to make explicit models. Clutton-Brock and Parker³² extensively discuss, for example, the phenomena that influence the 'operational sex ratio' (OSR)³³, but do not discuss the mechanism that connects the OSR to the degree to which a sexually selected trait is expressed.

Which sex is choosy and which sex competes (as well as the strength of the competition) depend on the **gamete market**: the relative number of male and female gametes available at any one time in a sexually interacting population. In the case of sperm, the relevant parameter is the amount necessary to fertilize one egg ('sperm packet'). The **operational gamete ratio** can thus be calculated as follows:

$$\frac{\bar{N}_{\text{eggs per female}}}{\bar{N}_{\text{sperm packets per male}}} \times \frac{N_{\text{females available for mating}}}{N_{\text{males available for mating}}}$$

The left-hand term is also known as the ratio of 'potential reproductive rates'³⁴, the right-hand term, as the 'operational sex ratio'. These two parameters are closely related to each other³². A gamete ratio of <1 is likely to lead to choosy females and competing males; with a ratio of >1, reversed sex roles are likely.

trader class without delivering its typical commodity in an appropriate quantity. There are two aspects to be considered: the effect of 'free riding' on the members of the class that is mimicked or parasitized, and the effect of 'cheating' on the members of the class trading with such free riders.

Honest traders are unlikely to exert control over free riders in their own class, since they find themselves in an *n*-player Prisoner's Dilemma: who is willing to pay the cost of policing on behalf of the class as a whole? Therefore, the persistence of free riding depends largely on the discriminatory abilities of the trading partners.

Guarding against cheating trade partners

Guarding against cheating has been the central issue in the development of models of cooperation among unrelated conspecifics. This aspect of cooperation is elegantly described by models based on the repeated two-player Prisoner's Dilemma.

Findings from such models are not necessarily valid for market situations, however. In two-player models, the only alternative to an interaction with the partner is no interaction at all, while there are alternative partners to turn to in multi-player models. This additional option influences the cost of ending a relationship as well as the impact of the threat to do so.

There are possibilities other than monitoring the partner's actions. Trading can be limited to partners signalling their honest intentions, given that the honesty of the signal is guaranteed. One possibility is that signals take the form of morphological traits that cannot be changed overnight and limit their carriers to a certain role⁴. For example, helpers in birds with juvenile-like plumages have difficulty in taking over the breeder role.

The risk of cheating is not a characteristic of all biological markets. We use mutualisms in which ants serve as guards to illustrate some general principles:

- Certain commodities can easily be assessed and cannot be pulled back or changed, once they are put on the market. An example is a food body that a plant offers as a reward to its attending ants. Conversely, ants can hardly defend food bodies without defending the plant as a whole.
- A trader is severely limited in his possibilities to cheat, if he cannot afford the risk of losing his partner. This risk is greatest if there is an asymmetry in dependence on the mutualistic relationship, as is the case if one trader depends on one specific partner to obtain a vital commodity, while the partner has alternative sources. Numerous exclusion experiments have shown that homopterans are very vulnerable to predation and parasites as soon as they lose the protection of ants¹⁰. The degree of protection, in turn, depends on the quality of the homopterans' honeydew¹¹. Thus, wingless morphs that hatch on the territory of an ant colony have little choice but to deliver honeydew of an appropriate quality, since they are not mobile enough to search for ants that would protect them at a lower cost.
- Some alternatives to trading with cheaters may have punishment as a side-effect. Ants may kill and eat homopterans that do not deliver food¹², simply because this is a more profitable behaviour for the ants. Behaviour with punishment as its sole function should, in theory, only occur when it results in future benefits.
- Traders will not be tempted to end a profitable relationship and reap higher immediate benefits when the continuation of the relationship is under their own control. Ants could cheat by eating both the homopteran and its honeydew, but the long-term gain of a living producer is usually higher than the nutritional value of its body, provided that predators of the homopterans and other consumers of their honeydew can be excluded.

Nevertheless, it will be hard to prevent being cheated in a number of cases: when

Box 4. Mutualism: interspecific markets

A large number of interspecific mutualisms have been described, ranging from weak, facultative interactions to strong, obligate interactions and symbiosis^{10,35}. The complexity of mutualistic interactions often depends on the number of species involved, from two closely interacting species (e.g. a single fig species with a single fig wasp species) to pollination networks with many species of flowering plants interacting with many flower-visiting animals. In both cases, however, one can speak of a pollination market with two classes of traders.

A recent review³⁵ reveals some peculiarities of the discipline. First, there is a strong bias towards empirical, descriptive studies – theoretical developments are not as influential as, for example, in the study of sexual selection. Second, the emphasis is often on one of the participating species only. Third, most studies that do consider evolutionary dynamics can be classified as population ecological studies with an emphasis on density-dependent effects at the population level. Derivatives of the Lotka-Volterra equations are central to most theoretical reflections, while game theory is rarely used. There is good evidence that market dynamics play an important role in mutualistic systems^{4,6,7,11}. The market approach may prove especially useful for questions on the transitions between parasitic or predatory relationships to mutualistic relationships and from facultative to obligatory and symbiotic relationships.

strategy independently' (Box 1), which is not necessarily the same as a biological individual. The problem of counting the number of traders can again be illustrated with an ant-homopteran mutualism. Ants live in eusocial, highly related colonies, while many aggregations of homopterans are clones. The number of genotypes trading on this market is thus much lower than is apparent at first sight. A whole ant colony should be considered as a single trader, if its members do not compete among each other over the access to homopterans. Similarly, it can be assumed that the members of a clone cannot be played off against each other and therefore the entire clone acts as a single player.

Sampling costs

Early papers on sampling mechanisms, studied in connection with mate choice, ignored the cost of searching and assessment¹⁷, but later studies demonstrated the importance of these factors^{18–20}. Sampling costs are also crucial to market models, because they determine the number of potential partners⁴. Imagine a market with a mobile and a sessile class. The number of sessile traders that the average mobile trader interacts with depends on the costs of searching in relation to the variance in value of the sessile traders' commodities. Factors influencing searching costs are: the density of the sessile class, and the depletion rate due to other mobile traders.

Consequences of variation in commodity value

We discuss two types of biological market. The first can be compared to a producer-consumer market, in which a single product of uniform quality is sold. The second resembles an employment market, in which jobs with various salaries are matched with candidates of various quality.

Exchange rates in producer-consumer markets

In this type of market a commodity of fixed value is traded against a commodity of varying value. In Fig. 1, there are two possible values only. The exchange rate on such markets does not simply correlate to the trader-class ratio. This is most easily illustrated with an example. Suppose females allow a single mating for a single nuptial gift in a population with an operational sex ratio of two males per female. In such a market, males are played off against each other and there is a strong selection towards the largest possible gifts. Now imagine a population with a similar 2:1 sex ratio in which females mate several times at low cost. It pays females to mate with any male that has at least

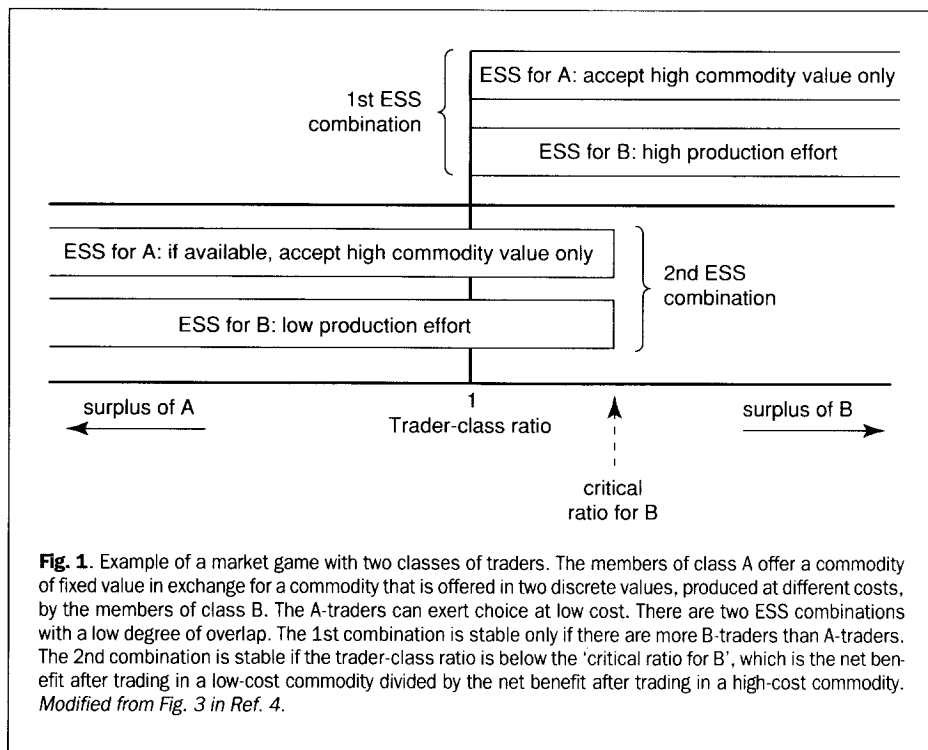


Fig. 1. Example of a market game with two classes of traders. The members of class A offer a commodity of fixed value in exchange for a commodity that is offered in two discrete values, produced at different costs, by the members of class B. The A-traders can exert choice at low cost. There are two ESS combinations with a low degree of overlap. The 1st combination is stable only if there are more B-traders than A-traders. The 2nd combination is stable if the trader-class ratio is below the 'critical ratio for B', which is the net benefit after trading in a low-cost commodity divided by the net benefit after trading in a high-cost commodity. Modified from Fig. 3 in Ref. 4.

subtle cheating is possible; when signals associated with future transfers of commodities are occasionally dishonest; or when a commodity is simultaneously delivered to a cluster of receivers containing both free riders and honest partners.

Partner switching and partner choice

Partner choice is a central theme in sexual selection, but its importance has only recently been emphasized for co-operation^{5,13} and mutualism^{6,7} (for review, see Ref. 14). As mentioned above, most co-operation models have been based on the repeated two-player Prisoner's Dilemma. The drawback of this paradigm is that it ignores the option of partner-switching and its repercussions. Recently, a number of theoretical studies of cooperation have considered the implications of partner-switching, but very few have considered partner choice (Box 2).

The possibility of swapping partners depends not only on their availability, but also on the costs of the switch. In an extreme case, the interaction is reduced to a pure, two-individual interaction. An apparent two-player interaction can, however, also result from strategies that increase the costs of partner-switching. An example is egg-trading in the black hamlet (*Hypoplectrus nigricans*), a simultaneously hermaphroditic fish. This species only spawns in the afternoon, which makes it virtually impossible to find an alternative partner before the eggs become inviable overnight¹⁵. This example shows that, even in some apparent two-player situations, the existence of a market of potential partners in the background is relevant¹⁶.

Who is a trader?

A trader in a biological market is defined as 'an entity that can choose a trading

something to offer, and selection on the size of the males' gift is weak. The crucial point is that in the former case the females' commodity is rare, while in the latter case receptive females are common in spite of the male-biased sex ratio.

Markets with variable commodities

The analysis of markets in which the values of commodities vary gradually on both sides is much more complex and remains a challenge for the future. There are several theoretical developments in different fields that may point the way forward.

- Sexual selection theory: assortative mating. Males and females often pair off nonrandomly in such a way that certain female and male attributes become correlated. Several mechanisms leading to 'assortative mating'^{21,22} have been proposed; those involving mate choice are especially interesting in the present context. Specific to mate choice is the genetic coupling between the degree of preference and preferred attribute, which can be both a cause and an effect of assortative mating. Genetic coupling is, however, not an inevitable effect of assortative mating²³, nor does assortative mating apply to heritable traits only. Therefore 'assortative mating models'¹⁸ may have general validity for other biological markets as well.

- Optimal foraging theory: adjustment of patch value. For example, ants protect the larvae of lycaenid butterflies in return for nectar produced by the larvae. The larvae can vary the amount produced in reaction to the number of ants attending them². How many ants will visit a patch of a certain value can be described by optimal foraging models. Conversely, optimal foraging models could be used to predict the amount of nectar that has to be produced per larva in order to attract a minimal number of ants.

- Cooperation theory: the pairing of animals of adjacent rank. Seyfarth²⁴ published a model that explains why grooming will be observed primarily among female mon-

keys of adjacent rank, although all lower-ranking individuals strive to have grooming relations with the highest-ranking females. The relevant factors are preference for certain social partners and contest competition over access to such partners.

- Economic game theory: the job-searching problem. In the economic literature the problem of matching individuals belonging to two classes (e.g. employers and employees) is studied under the headings 'job-searching problem', 'secretary problem' and 'marriage problem'²⁵.

Conclusion

The market approach is based on the insight that trading is an essential element of many mutually beneficial interactions. This idea is incorporated in biological market models, which help not only to explain why unrelated individuals can be engaged in mutually beneficial interactions, but also to clarify quantitative aspects of such transactions.

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