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Biological Markets: Supply and Demand Determine the Effect of Partner Choice in Cooperation, Mutualism and Mating

Author(s): Ronald Noë and Peter Hammerstein

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Ronald Noë · Peter Hammerstein

## Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating

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**Abstract** The formation of collaborating pairs by individuals belonging to two different classes occurs in the contexts of reproduction and intra-specific cooperation as well as of inter-specific mutualism. There is potential for partner choice and for competition for access to preferred partners in all three contexts. These selective forces have long been recognised as important in sexual selection, but their impact is not yet appreciated in cooperative and mutualistic systems. The formation of partnerships between members of different classes has much in common with the conclusion of trade agreements in human markets with two classes of traders, like producers and consumers, or employers and employees. Similar game-theoretical models can be used to predict the behaviour of rational traders in human markets and the evolutionarily stable strategies used in biological markets. We present a formal model in which the influence of the market mechanism on selection is made explicit. We restrict ourselves to biological markets in which: (1) Individuals do not compete over access to partners in an agonistic manner, but rather by outcompeting each other in those aspects that are preferred by the choosing party. (2) The commodity the partner has to offer cannot be obtained by the use of force, but requires the consent of the partner. These two restrictions ensure a dominant role for partner choice in the formation of partnerships. In a biological market model the decision to cooperate is based on the comparison between the offers of several potential partners, rather than on the behaviour of a single potential partner, as is implicitly assumed in currently accepted models of cooperation. In our example the members of one class A offer a commodity of fixed value in exchange for a commodity of variable value supplied by the other class, B. We show that when the B-class outnumbers the A-class sufficiently and the cost for the A-class to sample the offers of the B-class are low, the choosiness of the A-

class will lead to selection for the supply of high value commodities by the B-class (Fig. 3a). Under the same market conditions, but with a high sampling cost this may still be the evolutionarily stable outcome, but another pair of strategies proves to be stable too: relaxed choosiness of class A coupled with low value commodities supplied by class B (Fig. 3b). We give a number of examples of mating, cooperative and mutualistic markets that resemble the low sampling cost situation depicted in Fig. 3a.

**Key words** Market games · ESS · Cooperation  
Mutualism · Sexual selection

### Introduction

The importance of partner choice as a selective force has long been recognised in the context of sexual selection, but its importance has not yet been generally acknowledged in the case of intra-specific cooperation and inter-specific mutualism. The formation of cooperative and mutualistic partnerships has so much in common with the formation of reproductive partnerships that the formulation of a single basic model seems warranted. In all forms of reproductive and mutualistic pair formation, and in many cases of intra-specific cooperation, the partners belong to two distinct classes, e.g. males and females, figs and fig wasps, or breeders and helpers. Members of different classes can offer each other commodities, e.g. gametes, food or shelter, that are either under the exclusive control of one class, or can only be obtained from alternative sources at high costs.

The exchange of commodities between individuals belonging to two different classes can be compared to the exchange of goods between two classes of traders in human markets. Market mechanisms cannot function if it is possible to appropriate desired commodities without the consent of the owner, or to eliminate by force members of the same class competing for the same partner. Assuming that the use of force is excluded, competi-

tion for preferred partners can only take place in the form of outbidding each other in the value of the commodity offered. This form of competition can only play a role, however, when the members of the complementary class are indeed able to exert partner choice on the basis of the value offered.

As in human markets, the exchange rate of commodities on biological markets is determined by the law of supply and demand. In many cases a commodity in high demand will be exchanged for one in low demand. In such a case one can distinguish between a 'choosing' class, the members of which can find a partner in any case, and a 'chosen' class, the members of which have to outbid their class members in order to gain access to partners. Skewed markets can occur when one class outnumbered another, e.g. in a monogamous species with a male-biased sex ratio, or when one class offers many more units of its commodity than the other, e.g. in a polygynous species in which males may copulate many times, but females mate only once. In both examples the females belong to the 'choosing' class.

Noë et al. (1991), elaborating on an earlier paper by Noë (1990), explored the effect of market mechanisms on the division of labour in intra-specific cooperation, e.g. the relationship between the workload of helpers at the nest and the number of helpers relative to breeder pairs in a population. Such changes in the contribution to cooperative relationships are behavioural adjustments to local market situations, and do not necessarily imply adaptations in an evolutionary sense. In the present paper we concentrate on the influence of market mechanisms on the selective force of partner choice in general. The potential of mate choice as a selective force has been recognised since Darwin (1871) and market effects have implicitly been acknowledged throughout the literature on sexual selection. The potential importance of partner choice as a selective agent in mutualistic systems has been pointed out before by Bull and Rice (1991).

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### **Market models compared with other models of cooperation**

Several authors (Bull and Rice 1991; Dugatkin et al. 1992; Noë 1992) have pointed out a dichotomy between the market paradigm and a longer-established model based on the iterated two-player Prisoner's Dilemma game (Axelrod and Hamilton 1981). Several multi-player derivations of the original two-player model have been proposed too (Eshel and Cavalli-Sforza 1982; Dugatkin and Wilson 1991; Friedman and Hammerstein 1991; Enquist and Leimar 1993). Below we explain in what respect these models differ from the market approach.

### **Models based on the Prisoner's Dilemma and related paradigms**

The central theme of the majority of publications dedicated to the Prisoner's Dilemma approach to biological cooperation is partner verification (see e.g. reviews by Axelrod and Dion 1988; Boyd 1992; Dugatkin et al. 1992). The question is asked: how can an individual prevent cheating by its partner? The emphasis on the cheating problem in Prisoner Dilemma-based models is reflected in the two-player form of the game used. The decision to cooperate with the partner is assumed to be taken on the grounds of expected fitness gains relative to the alternative of no cooperation at all. The decision is taken on the basis of some form of bookkeeping of the partner's behaviour in the past.

Two-player models assume that the pairs are formed by some external mechanism, or are paired off randomly. This is a reasonable assumption in some cases. Whitehead (1987), for example, suggested plausibly that owners of neighbouring territories are caught in a Prisoner's Dilemma. Territory owners cannot usually choose their neighbours. It is a matter of taste, however, whether one considers this to be cooperation rather than conflict resolution. The assumption that individuals have no choice among different partners is obviously not a valid assumption in many cases. Therefore a number of models, which also focus on the cheating problem, allow for the possibility that individuals may switch partners (Eshel and Cavalli-Sforza 1982; Dugatkin and Wilson 1991; Friedman and Hammerstein 1991; Enquist and Leimar 1993). These models show that the possibility of switching partners can have two opposite consequences: on the one hand cheating by the partner can be punished by exchanging the cheater for another partner, but on the other hand cheating can be easier if one can switch to an interaction with a new partner before the old one can retaliate effectively. The latter form of cheating can be controlled by preventing the partner from switching to alternative partners. Examples are the guarding of reproductive partners (Sakaluk 1991) and the 'last minute' egg-trading in simultaneous hermaphrodites (Fischer 1980, 1988).

### **Market models**

Switching partners is also an essential feature of the market model we present here, but cheating is not. We left cheating as a strategic option out of consideration, since we wanted to concentrate on the market effect itself: the extent to which members of one class can 'force' members of another class to evolve traits that would have a negative effect on fitness in the absence of the cooperative interaction. To our minds the cheating option can safely be ignored in the large number of cases in which either the commodity cannot be withdrawn or changed in quality or quantity once it is offered on the market, or when cheating is effectively controlled. 'Food

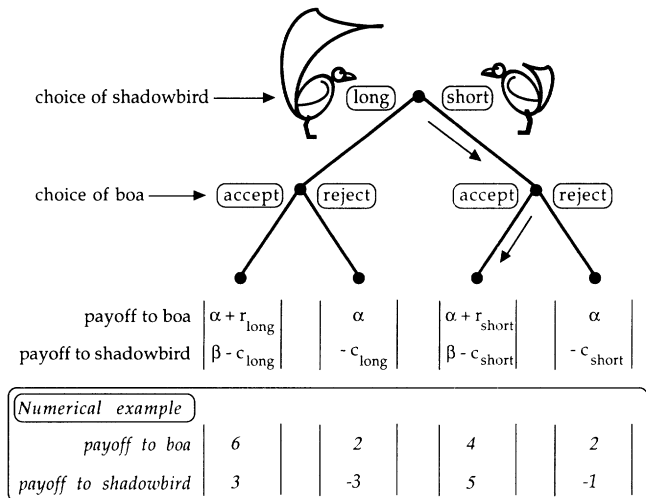
bodies' of myrmecophilous plants are examples of such irretrievable offers. Some plants grow 'food bodies' in order to attract ants, which defend the plant against herbivores and parasites. Once the plant has 'decided' to provide a quantity  $x$  of food bodies these remain available to the ants. The ants will provide protection to the plant as long as they defend the plant's food bodies in their own interest.

According to the market approach the expected future gain from cooperation with a partner is compared to the expected gain from cooperation with other potential partners, as well as to the expected fitness in the absence of cooperation. An essential feature of market models is that the expected future gains are actively influenced by playing off potential partners against each other (Noë 1990, 1992; Noë et al. 1991). Market models are thus based on games with at least three players, but typically have many players divided into two or more classes. The bookkeeping of the relationship with a single partner is replaced by the sampling of several partners simultaneously. In its simplest form a member of the choosing class samples several offers simultaneously or successively (for classifications of sampling tactics see Janetos 1980; Wittenberger 1983), but a decision may also be based on bookkeeping, if the choosing individual interacts with several partners over a longer period (see Noë 1990 for an example). The cost of sampling alternative partners, which plays an important role in models of sexual selection (see reviews by Harvey and Bradbury 1991; Maynard Smith 1991), is therefore an important parameter in market models of cooperation too.

In conclusion, the central theme of market models, the effect of supply and demand, is fundamentally different from the central theme of current models of cooperation, partner verification. The models therefore do not compete with each other, but rather apply to different biological problems. How one judges the biological relevance is a matter of taste. We think that cooperative systems (including reproductive cooperation and interspecific mutualism) in which cheating plays an insignificant role are more common than systems in which partner verification is a major problem for the individuals involved. This may be so, however, because the potential for cheating leads to the break down of most forms of cooperation that could potentially exist. Nonetheless it may be important to treat cheating and market mechanisms simultaneously in future models. One can imagine partner verification models in which decisions to cooperate are not only taken with the expected fitness without cooperation as a reference point, but also on the basis of a comparison with benefits to be expected from cooperation with alternative partners.

### From two to three players: the tale of the 'boa constructor' and the 'shadowbirds'

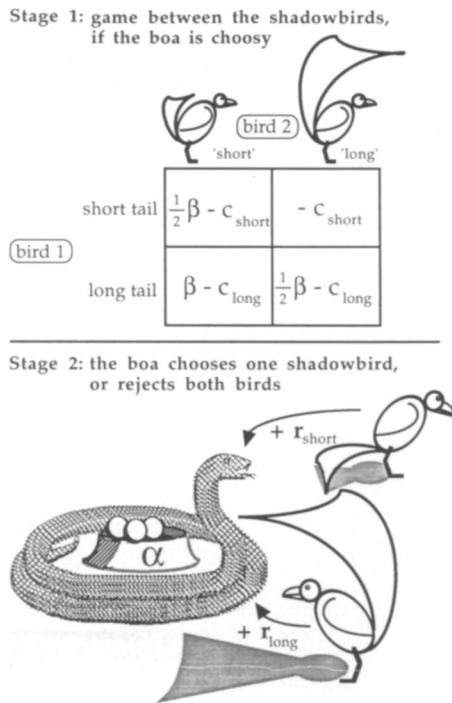
In order to show the importance of the crucial step from two-player to three-player models, we discuss a case in



**Fig. 1** Partner acceptance game in extensive form. The players are a 'boa constructor', who owns a nest-mound, and a 'shadowbird', who applies for a vacant position in the boa's nest. Before applying, the shadowbird moults and has the choice between growing either a short or a long tail. The boa can either accept or reject the applicant. After rejection, the snake will have no other applicant. The shade provided by the bird's tail benefits the boa's eggs. The boa's basic payoff without assistance is  $\alpha$ ; the reward for accepting the shadowbird is an increase in fitness of  $r_{\text{short}}$ ,  $r_{\text{long}}$  units respectively. The basic payoff for the shadowbird is zero, when not able to breed, and  $\beta$ , when able to breed. Depending on its length, the tail incurs a cost of  $c_{\text{short}}$ ,  $c_{\text{long}}$  respectively. All parameters are positive numbers. The shadowbird has a lower cost with a short tail ( $c_{\text{short}} < c_{\text{long}}$ ); the boa gains more if the bird has a long tail ( $r_{\text{short}} < r_{\text{long}}$ ). The evolutionarily stable strategy (ESS) of this game can be found by backward induction. In both choice situations the boa is better off if she accepts the bird. This weakens the boa's position: the bird's ESS is to wear a short tail

which the two models generate opposite predictions. We use an imaginary inter-specific mutualism: The 'boa constructor' female constructs a simple nest-mound in an open desert environment on which she lays her eggs. The snake guards her nest against all egg predators. In order to keep the eggs from overheating during the day the snake needs the cooperation of a 'shadowbird'. The shadowbird female lays her eggs in the boa's nest too and incubates them, providing shade for herself and both her own and the boa's eggs with her fan-like tail. The bird's eggs cannot survive without the protection of a boa; the boa's fitness is correlated with the amount of shade on her eggs. The larger the bird's tail the higher the boa's fitness. The bird's fitness is negatively correlated with tail length when it is not breeding and when it is breeding in the absence of egg-predators. In our example the birds can have a tail that is either 'short' or 'long'.

Game 1 is a two-player game with one boa and one shadowbird (Fig. 1). The bird is the only applicant for the free nest space. The bird's choice of tail length precedes the snake's choice and is irreversible for the breeding season. A numerical example may illustrate the payoffs shown in Fig. 1. Imagine that without the cooperation of a shadowbird on average two of the snake's eggs survive, with a short-tailed bird four, and with a long-



**Fig. 2** Partner choice game with one boa and two shadowbirds. Payoffs as in Fig. 1. The conflict is modelled as a two-stage game. At stage 1 the birds choose their tail length independently. At stage 2 the snake can find herself in three different situations: both applicants have a short tail, both have a long tail, or they differ in tail length. The boa can either accept one of the shadowbirds, or reject both of them. If the boa decides to accept one of two identical looking candidates, they have an equal chance of being selected. The owner's ESS at stage 2 is to show preference for a long-tailed shadowbird. This induces a Prisoner's Dilemma game between the birds at stage 1 [assuming  $\beta > 2(c_{\text{long}} - c_{\text{short}})$ ]. Thus, in this three-player game the owner's option to choose acts to her advantage: the ESS-solution for the shadowbirds is to defect in the Prisoner's Dilemma, i.e. to choose the less profitable long tail

tailed bird six, i.e.  $\alpha = 2$ ,  $\alpha + r_{\text{short}} = 4$  and  $\alpha + r_{\text{long}} = 6$ . Without the cost of growing a shade-providing tail, a shadowbird would be able to lay six eggs, i.e.  $\beta = 6$ . The cost of growing a relatively short tail, sufficient to protect only the bird and her eggs, costs the equivalent of one egg, the long tail needed to give shade to the snake's clutch as well, costs the equivalent of three eggs, i.e.  $c_{\text{short}} = 1$  and  $c_{\text{long}} = 3$ . The boa has to accept the shadowbird regardless of tail-length. Therefore the bird plays the 'short-tailed' strategy at evolutionarily stable equilibrium, in spite of the boa's preference for a long-tailed subtenant.

Game 2 has one nest-owning boa and two shadowbirds, and thus represents the smallest possible market (Fig. 2). The birds choose their tail length independently. The snake selects one of them, or accepts neither. With a payoff configuration as in game 1, the snake will always prefer to have a bird on its nest. So far the game resembles the previous one. However, with two applicants the boa has the opportunity to exert choice. This means that if the birds differ in tail-length, the one with the longest tail will be chosen. Since the birds compete

for a single position, they are forced to outbid each other. They find themselves in a single-round Prisoner's Dilemma, and will therefore both opt for a long tail.

## Market models

Simple three-player models fall short in describing the two-layered frequency-dependent selection typical of biological markets. A typical market game has many players. Pursuing the market paradigm, we draw a parallel with trading between two classes of traders, who exchange two class-specific commodities. A deal is concluded when two traders agree on the exchange value of the two commodities. The exchange value is governed by the law of supply and demand, and may vary in time, between generations, and between populations. In many cases the exchange value will depend directly on the relative number of members of each class, but a class can be heterogeneous with several species offering the same commodity, and even abiotic sources may play a role. We restrict ourselves to relatively clear-cut cases with two homogenous classes, such as males and females, or figs and fig wasps.

The dynamics of a market depend among other things on the number of options the traders have. At one extreme of the spectrum one finds traders that possess a single unit of a commodity with a fixed value. Such players have only two options: trading in their merchandise, or holding it back. Their strategic decision is between trading in for a high value only, or eventually accepting a low value too. On the other extreme there are traders that can gradually adjust the value of their offer, e.g. a plant offering various quantities of nectar to its pollinators. The majority of biological markets we examined are of the fixed-variable type. Typical features of such markets can be shown in models in which the variable commodity can have two discrete values only. Biological markets can be differentiated further on the grounds of the sampling costs of the class with the fixed commodity.

## Market games with two classes of traders

We show two examples of market games with two classes of traders in which one class, A, offers an indivisible commodity of fixed value,  $x$ , to B-traders. The members of class B can offer their commodity, which differs from the commodity produced by A, in two discrete values. B-traders have the strategic decision to produce their commodity with low effort at a low cost  $c_l$ , or with high effort at a high cost  $c_h$ . Low production effort yields a commodity of low value,  $r_l$ , with probability  $1-\varepsilon$ , and of high value,  $r_h$ , with probability  $\varepsilon$ , where  $\varepsilon$  is small. Conversely, high production effort yields high and low value with probabilities  $1-\varepsilon$ ,  $\varepsilon$ , respectively. There is thus some variation in the value of B-produced commodities, even if they are all produced at the same cost. This vari-

ation guarantees the possibility of choosiness even in strategically monomorphic populations. In our first example the members of class A have low sampling costs, while choosing among members of B. This is the case, for example, when multiple members of the class with the variable commodity present themselves simultaneously to members of the fixed value class. In the second example the sampling costs are high, as is the case if a choosy individual has to search the members of the opposite class one by one.

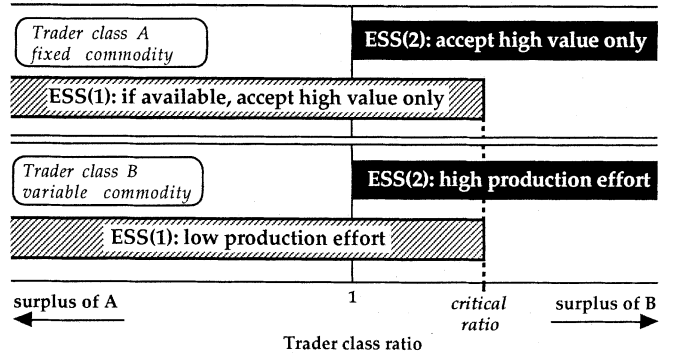
### Low sampling costs

The market mechanism is defined as follows. Single traders of class A are randomly drawn from the population and paired at random with small, randomly drawn groups of B-traders until one of the trader classes is exhausted. In each trade group the A-trader decides whether or not and with whom to exchange commodities. All individuals that do not conclude a deal reach the next round at a low cost. In each round the same procedure is repeated with the remaining subset of traders. In this model traders of class A can choose between high and low values without paying a price for comparing a few offers. There are two different evolutionarily stable strategy (ESS) combinations with some range of overlap. In the first combination, ESS(1), B-traders produce with low effort and A-traders accept the highest value available in their trade group. The approximate upper bound for ESS(1) is given by the critical ratio:  $(x-c_l)/(x-c_h)$ . In the second strategy combination, ESS(2), B-traders produce with high effort and A-traders accept high value only. Outside the range of overlap between ESS combinations the market's supply and demand structure fully determines the nature of an evolutionarily stable deal. Within this range the two ESS combinations represent alternative solutions.

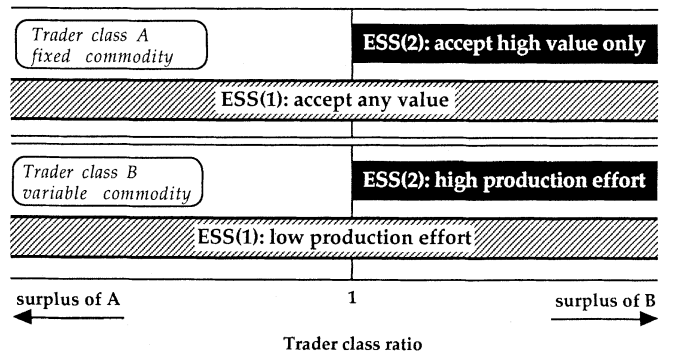
### High sampling costs

The market mechanism differs from the game presented above in two aspects. (1) During one round of the game an A-trader meets only a single B-trader. (2) If the A-trader rejects the possible deal, he has to pay a substantial price, the search or sample cost  $s$ , in order to participate in the next round of the remaining game. The ESS(1) combination 'accept any quality – low production effort' is very robust with regard to variation in the trade class ratio. In this sense, the principle of supply and demand fails to operate as an effective evolutionary market force. However, there is an alternative ESS combination, equivalent to combination (2) described above, which has a lower bound at the trader class ratio 1, under the assumption that  $s < r_h - r_l$ .

### a. Low cost of sampling by class A



### b. High cost of sampling by class A



**Fig. 3a,b** Market games 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 by the members of class B. Two models with different market mechanisms are considered (see text for explanation). In model *a* the A-traders have low sampling costs, in model *b* these sampling costs are high. In both models there are two evolutionarily stable strategy combinations with partial overlap. In each graph ESS combination (1) is depicted by *hatched bars*, ESS combination (2) by *black bars*. **a** The low degree of overlap between ESS(1) and ESS(2) shows that the outcome of the evolutionary game is largely determined by the law of supply and demand. ESS(1) is stable beyond trader class ratio 1 for the following reason. Consider a population playing this strategy. With a slight surplus of B the chances per B individual to be accepted are close to one. A mutant producing with high effort can only increase this probability to one. This slight increase in the chance of being accepted is not worth the high production effort as long as the surplus of B does not exceed the critical ratio. **b** Due to the high cost of sampling ESS(1) is very robust. This means, however, that the law of supply and demand determines the outcome of the evolutionary game to a much lesser extent than in the model above. The lower limit of ESS(2) is the only indication of the existence of market forces. Further explanations in the text

## Empirical examples of biological markets

Below we discuss three types of markets, on the basis of two examples each. We looked for examples of systems with a clear dichotomy between a 'choosing' and a 'chosen' class, for which it can be assumed that the choosing class has low sampling costs (corresponding to Fig. 3a). According to our model, adaptations in the chosen class that would be costly in the absence of cooperation can

be expected in those cases. We did not expect to find enough information to check the model in detail. However, the validity of the following assumptions could be verified for the examples: (1) It is plausible that pairs are formed according to the preference of at least one party, although the specific mechanism of partner choice has only been studied in the mating markets. (2) Partners cannot, as a rule, be forced to hand over their commodity without their consent. (3) Competitors cannot be excluded by force from contacts with the opposite class, leaving outbidding each other as the most likely form of competition. (4) Cheating, that is changing the value of the commodity offered after the pair has been formed, is not possible.

#### Mating markets: females trading with conspecific males

##### *Scorpionflies*

Male scorpionflies (*Hylobittacus apicalis*) offer insect prey of various sizes as a nuptial gift to receptive females (Thornhill 1984). Catching larger prey involves greater costs, especially due to the higher risk of flying into spider webs. It has been shown in another scorpionfly (*Panorpa vulgaris*) that the inclination to provide large prey is inherited (Thornhill and Sauer 1992). Males advertise the availability of a gift by releasing pheromones. Females thus have limited search costs and probably gain additional information on the number of males in the market as well. Females can exert choice either by refusing matings, or by interrupting matings before any sperm is transferred. Cheating by males is virtually impossible, since females can assess the gift immediately (Thornhill 1976). The amount of sperm transferred correlates with the gift size (Thornhill 1976), so females either do not or cannot cheat. The data show a clear market effect: females reject males with small prey when many males offering prey are available, but accept any prey when there are few offers on the market.

##### *Bushcrickets*

In a number of species of bushcrickets (*Tettigoniidae*) males provide females with a nuptial gift of substantial value in the form of a nutritional part of a large spermatophore (Gwynne 1984, 1986, 1990, 1991; Heller and von Helversen 1991). The question is whether the usually male-biased operational sex ratio (OSR; Emlen and Oring 1977) in bushcrickets permitted the females to selectively admit fertilisation by males with large nuptial gifts only, which would result in selection for large spermatophores. An alternative explanation is that large spermatophores were selected because they represent paternal investment, and males with larger spermatophores would have higher fitness, even in the absence of female choice (Gwynne 1986, 1988, 1991). The pater-

nal investment hypothesis has been criticised, however (Wickler 1985), and is at least highly improbable in the case of some bushcricket species (Heller and von Helversen 1991). In any case, we refer to the ancestral function of the nuptial gift, which is likely to be an increase in the chance of mating with choosy females (Simmons and Parker 1989). Whatever its primary function, a large nuptial gift is to the advantage of the receiving female, and we hypothesise therefore that variance in the value of the nuptial gift and a male-biased OSR will lead to a selection for spermatophores of larger size. Market forces will automatically brake the evolution towards ever larger nuptial gifts: the larger the spermatophore, the longer it takes to produce it, and the less male-biased the OSR becomes (Heller and von Helversen 1991). However, in some species selection on the male may result in the evolution of larger spermatophores than expected on the basis of female choice under market conditions (Gwynne 1990).

A simple relationship between the degree of skew in the OSR and the size of the spermatophore should not be expected, since the OSR may fluctuate strongly. Moreover, species-specific sampling costs of females and the extent to which males guard females play an important role too. In the Mormon cricket (*Anabrus simplex*), the operational sex ratio may even reverse from time to time in some populations, and males instead of females can exert choice (Gwynne 1984). At low densities many males have spermatophores available and sing, and females exert mate choice. At high densities few males are able to produce a sufficiently large spermatophore, and these males can afford to choose from the large number of females attracted by their song.

#### Cooperation markets: males trading with conspecific males

In the following examples the barriers between the different classes are not absolute. The class division arises because animals, following a single conditional strategy, choose different options. Some males are forced to take the subordinate role of helpers on the grounds of age or size, while the dominants act as owners of crucial resources, e.g. breeding territories. In this case a form of cheating may arise that differs from withdrawing the commodity that was offered, or reducing its value: the subordinates may attempt to usurp the owners' position, or act as sneak-copulators. Therefore, we expect the 'choosing' class, i.e. the dominants, to prefer partners with an 'honest signal' of inferiority: an easily perceptible character that cannot change overnight, and that constrains its bearer to keep to its role. Such characters may fall into four classes: (1) observable physical weakness; (2) badges of subordination (Barnard and Sibly 1981; Rohwer and Ewald 1981); (3) absence of characters preferred by the opposite sex; and (4) signs of reduced fertility. A helper with a badge of subordination would not be tempted to challenge an owner of a crucial



resource, even if he physically could, since he would be an obvious target for attacks by outsiders and risk losing access to the commodity altogether. Sexually handicapped assistants (cases 3 and 4), although perhaps able to appropriate the resource, could not use it to attract females. Again, helpers wearing such signals have little to gain in the short run from the acquisition of the resource. This 'inferior competitor hypothesis' thus asserts that partner choice can counterbalance natural and sexual selection. The hypothesis is a general form of the 'status signalling hypothesis', formulated by Lyon and Montgomerie (1986) as an explanation for delayed plumage maturation in birds. The ruff and purple martin cases have much in common: the dominant males control a crucial resource and choose between several candidates simultaneously present. In both species accepted assistants wear a visible 'badge of inferiority'. In both examples the badge is an honest signal: light-coloured ruffs are significantly smaller (van Rhijn 1983; Höglund and Lundberg 1989), while yearlings, recognisable as such in purple martins due to delayed plumage maturation, are weaker than older males in many birds.

### Ruffs

Mating in the ruff, a shorebird (*Philomachus pugnax*), takes place on leks (van Rhijn 1973, 1983, 1991). Males have one of three roles: 'territorials' defend a territory on the lek; 'satellites' are tolerated on territories, but are subordinate to the owners; 'marginals' have no access to territories and virtually never copulate. Satellites benefit owners by strongly enhancing the attractiveness of the territory. The satellites, in turn, obtain opportunities to mate on the territory (Hill 1991). The satellites are not 'sneakers' that deceive the territorial males, but rather they obtain surplus females according to a simple 'priority of access' model (Altmann 1962). The mating tactics of males are strongly correlated with the colours of the ruff and head-tuft: the lightest birds are invariably satellites, the darkest usually territory owners. The role played by intermediate birds depends on the composition of the local population: territorials accept them as satellites only in populations in which light coloured males are scarce (van Rhijn 1991: p. 103). The colour of the ruff and head-tuft does not change between years, and these colours, as well as the correlated behavioural patterns, are probably under the control of the same genes (van Rhijn 1973; 1991).

### Purple martins

A comparable form of male-male cooperation is found in the purple martin (*Progne subis*) (Morton 1987; Morton and Derrickson 1990; Morton et al. 1990). Territory owners monopolise multiple nest-holes, but cannot use them to install multiple females, because of the obligate bi-parental care in this species. The solution is to exploit

another male to raise surplus offspring. Owners advertise the availability of a nest-hole by means of a dawn song and accept a subordinate pair as subtenants. Both the dominant and the subordinate male sire the female's offspring, which is then raised by the subordinate pair. Cheating by the assisting male is not possible, because he cannot distinguish between his own and the dominant male's offspring. The subordinate male nevertheless gains by this arrangement, since he would otherwise not be able to reproduce at all. Territory owners preferentially accept yearlings, easily recognised as such by their distinct juvenile-looking plumage.

### Mutualistic markets: ants trading with nectar producers

There are a large number of examples of mutualistic markets in which ants provide protection against enemies in exchange for food or shelter (reviews: Beattie 1985; Hölldobler and Wilson 1990; Bristow 1991; Cushman and Addicott 1991; Cushman and Beattie 1991; DeVries 1991; Pierce et al. 1991). We discuss the interaction between ants and species that reward ants with food. Many species of homopterans (especially aphids and membracids), the larvae of a large number of lycaenid and riodinid butterflies, as well as plants with extra-floral nectaries offer ants a sugar-rich solution, hereafter called 'nectar'. From a market point of view, all nectar-producing individuals belong to the same trade class and are indeed observed to compete intra-specifically (Pierce et al. 1987; Cushman and Whitham 1991) as well as inter-specifically (Buckley 1983; Cushman and Addicott 1989) for the protection provided by the ants. In inter-specific competition this may lead to a specialisation in providing food sources that other species cannot provide.

### Ants and lycaenid butterflies

The dorsal nectar organ, which produces a nutritious fluid, has probably evolved once in the lycaenids (Fiedler 1991), and once more in the riodinids (DeVries 1991). The sole function of this 'nectar', which is produced at a substantial metabolic cost, is to serve as a reward for ants (Pierce et al. 1987; Robbins 1991). The first step in the evolution has probably been in the form of appeasement or manipulation of the ants by the caterpillars with the help of allomones, which are secreted by all species. Larvae in close contact with ants were probably forced to replace their dishonest signals with a real reward.

The market model can be used to explain the evolution of the dorsal nectar organ itself, and differences in secretion rates between populations and species. Fine-tuned adjustments to temporal changes in the supply-demand ratio can also be observed at the level of individual larvae, as recently shown by Leimar and Axén



(1993). Caterpillars kept singly produced more nectar when the number of attending ants was increased from one to two, but when many ants were present the amount was reduced again.

Lycaenid species can be classified as obligate, facultative, or non-mutualistic. As a rule, the larvae of obligate mutualistic species occur in larger clusters, those of facultative species in smaller clusters or alone, and the non-mutualistic species alone (Kitching 1981). In several obligate mutualists the females use the ants as a cue for egg-laying (Pierce 1987). The ants have on average low sampling costs with species whose eggs are laid in clusters at their doorstep, but high sampling costs with those that occur alone and at greater distances. The fact that the former species produce much more nectar than the latter is in agreement with our model.

The formation of aggregations of producers opens the door for cheating. Food competition prevents the obligate mutualistic lycaenid larvae from forming tight clusters, however (Pierce et al. 1987), in contrast to the homopterans discussed below. As a result the attention of the ants is directed to individuals rather than clusters. Non-producing larvae may either get little protection, or are killed by the ants, depending on the efficiency of the appeasement signals of the larvae. Another form of cheating by the lycaenids is beyond the scope of this paper: in some species the larvae act as nest parasites and prey on the brood of the ants (Pierce 1987; Hölldobler and Wilson 1990).

The ants could cheat by eating the caterpillars after reaping their nectar. It seems plausible, however, that an individual that is continuously producing nectar has more nutritional value to the ant colony than its dead body, since a single individual can produce a considerable amount of nectar (Pierce et al. 1987; Fiedler and Maschwitz 1988). The 'nutritional value' is, however, dependent on alternative sources of food, and thus strongly dependent on the market situation for nectar. This calculation changes instantly at the moment the non-producing butterflies emerge from the nectar-producing pupae: the imagos of some species are vulnerable to predation by their mutualistic partners (Fiedler and Maschwitz 1989a).

#### *Ants and homopterans*

Analogously to the ant-lycaenid mutualism discussed above, the ants protect the homopterans against predation, and sometimes competition. The protection by ants is essential for the survival of the homopterans in many cases (e.g. Cushman and Addicott 1989; Cushman and Whitham 1991; Seibert 1992). Apart from protection the ants may benefit homopterans by taking over tasks that the homopterans otherwise would have to do themselves, such as cleaning their bodies, and locomotion to food plants and hiding places (Buckley 1987; Bristow 1991).

In contrast to the lycaenids, the homopterans reward the ants with a waste product, 'honeydew', produced at

no extra cost. A major leap, comparable to the evolution of the lycaenids' dorsal nectary organ, has probably not been made in the evolution of the homopterans. Nevertheless the myrmecophilous homopterans show a number of morphological adaptations to attract the ants and to improve the transfer of honeydew, like 'filter chambers', 'trophobiotic organs' and inter-specific signals to advertise the availability of a droplet of honeydew (Kunkel and Kloft 1977; Buckley 1987; Hölldobler and Wilson 1990; Bristow 1991). Moreover, some species may synthesise the sugar melezitose specially because it is highly preferred by ants (Kiss 1981), while others may seek out food plants that provide nutrients that benefit the ants rather than themselves (Bristow 1991). It seems plausible that selection for these adaptations, in so far as they would reduce fitness in the absence of ants, has been driven by partner choice. Intra-specific competition for protection by ants has been shown by several authors (Cushman and Addicott 1989; Cushman and Whitham 1991; Seibert 1992; Breton and Addicott 1992). Seibert (1992) suggests that the ants weed out abnormally behaving aphids, which makes it likely that badly producing individuals are removed.

The costs for the ants of sampling the offers of various clusters of homopterans are likely to be low. A number of ant species permanently control their 'cattle' and transport them between their nests and the host plants. In several of these systems alate morphs are lacking and the formation of wings, and thus dispersal, may even be suppressed by the ants (Hölldobler and Wilson 1990; Seibert 1992). By preventing dispersal the ants can increase the size of clusters and skew the market in their advantage. In several species with dispersing morphs the females lay eggs only where ants are present (Cushman and Whitham 1991; Seibert 1992). Sampling costs are not completely negligible, however. Generally speaking the further clusters of homopterans are away from the ants' nests, the less they are visited (Seibert 1992). Note that competition over ants takes place between clusters rather than within clusters (Cushman and Whitham 1989). Many of those clusters are formed by parthenogenetically reproducing clones, which means that selection takes place at the level of the egg-laying females.

Cheating by the homopterans, in the sense of no, or reduced, offering of honeydew, is highly improbable. Once the ants take over the task of cleaning away the honeydew, it is in the interest of the homopterans to signal that it is available. Within clones cheating is unlikely. Between clusters the ants' selectivity can prevent cheating, as we argued above for single lycaenid larvae.

The ants, however, can cheat by eating the homopterans instead of tending them. As discussed above, this decision is dependent on the nutritional value of the living homopterans, which in turn depends on the market situation. Way (1954) showed, for example that he could switch the behaviour of ants from tending to predation simply by offering them a better alternative source of sugars.

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## Discussion

### Partner choice in cooperation theory

In our opinion partner choice has been underrated as a selective force in the context of intra- and inter-specific cooperation. Why is this so? One possibility is that partner choice has been overlooked because the traits involved tend to be inconspicuous, such as suppressed secondary sexual characters, or docile behaviour of junior partners. There may also be historical reasons. The dominant theory of cooperation in the recent past has been based on a two-player game and preoccupied with the problem of verification of the partner's behaviour. Obviously, choice cannot play a role in a two-player model and the formation of partnerships remained beyond the scope of theory.

### Market models of sexual selection

We developed our market models in the first place in order to analyse certain aspects of intra-specific cooperation and inter-specific mutualism. The parallels with mating markets and human markets seemed so strong at first glance that we expected to be able to borrow models from sexual selection theory as well as economic theory. Unfortunately we came to the conclusion that neither field could offer us off-the-shelf models that could easily be adapted to cooperation and mutualism. A market philosophy is implicit in the idea that the sex that controls a rare commodity that is important for reproduction can be choosy (e.g. Partridge and Halliday 1984). A theoretical treatment of market mechanisms is lacking, however. For example, as Sutherland (1985, 1987) remarks, little is known about the relationship between the operational sex ratio (Emlen and Oring 1977) and the degree of extravagance of secondary sexual characters, or the amount of pre-mating services rendered to the mate.

As it stands our market model does not represent an alternative theory of mate choice. It can suggest no answers to questions of why certain traits in mates are preferred. Moreover, a typical feature of mate choice is that the genetic basis for a preferred trait and for the preference for that trait become coupled (Fisher 1930; Lande 1981, 1987). Such a mechanism cannot play a role in cooperative and mutualistic systems, with the exception of systems in which parents are assisted by older offspring to raise their young. A market approach might, however, indicate how the present theories of mate choice can be improved and extended. Market models could make explicit the circumstances under which existing preferences will indeed lead to selection for the preferred traits. Behavioural traits, like the provision of nuptial gifts mentioned in the examples above, can represent conditional strategies and therefore allow a more flexible reaction to the market situation than morphological traits.

### A program for empirical research

A dedicated research program is needed to develop market models further and to test their merits. The most important theoretical developments would be to explore models in which both the preference and the preferred trait can vary gradually and models in which both parties exert choice. For empirical studies we see the following opportunities.

1. Relative contributions to intra-specific cooperation. Reyer (1986) in an example of food provisioning by helpers in pied kingfishers, and McGrew (1988) in a study of the infant-carrying behaviour of helpers in cotton-top tamarins, showed that helpers work harder under the pressure of competition with other helpers. This kind of observation could be supplemented by studies that show that the tendency to help can be increased or decreased by (artificial) selection. A note of caution should be issued with respect to studies on cooperation between relatives. It can be in the interest of the dominants (e.g. the breeding pair) to prevent competition among offspring, and it can be in the interest of helpers to lighten the workload of other, closely related helpers. In that case the workload per helper will be negatively, rather than positively correlated with the number of helpers.

2. Selection for preferred characters in inter-specific mutualisms. Mutualisms between ants and nectar-producing counterparts lend themselves for experimentation. A number of authors have shown that the market can successfully be manipulated, e.g. by adding and removing plants infested with phloem-sucking insects (Cushman and Addicott 1989; Cushman and Whitham 1991; Breton and Addicott 1992) or by manipulating the number of ants that have access to the nectar source (Leimar and Axén 1993). Pierce et al. (1987); Fiedler and Maschwitz (1988) and Leimar and Axén (1993) showed that the nectar production of individual lycaenid butterfly larvae can be quantified. Preference of ants for good over bad sugar sources has been shown by many authors, a good example is given by Fiedler and Maschwitz (1989b). Leimar and Axén (1993) showed that individual lycaenid larvae react to the number of ants present, it remains to be shown, however, that the rate of production is sensitive to artificial selection. The ultimate experiment would be to show that selection can also take place through partner choice by the ants.

3. Comparative studies of mutualisms. The same kind of mutualisms as mentioned under 2, for which many different species combinations can be found within taxonomic groups, also lend themselves for comparative studies. Is high production of nectar, honeydew, food bodies and the like correlated with skewed markets? Pierce et al. (1991) remark that high production of lycaenid larvae is coupled with high effort of the ants. Does this resemble "assortative mating" and is it in agreement with market models in which both sides can gradually change the value of their commodity and both sides are choosy?

4. Comparative studies of sexual selection. Similar questions can be answered for reproductive cooperation by comparing closely related species that differ in the operational sex ratio. Is, for example, skew in the mating market correlated with extravagance in secondary sexual characters? Is a skewed adult sex ratio coupled with asymmetrical parental care in species in which remating with the same partner is an important strategy?

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