

Economics in Nature
Social Dilemmas,
Mate Choice and
Biological Markets

Edited by

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Modelling interspecific mutualisms as biological markets

Introduction

Mutualistic interactions between species are diverse and widespread, and are becoming well documented empirically (Bronstein 1994b). The partners involved in mutualistic interactions range from bacteria to fungi to plants and animals. Early mathematical models of mutualisms predicted that they should be rare in nature (e.g. May 1973). Since then, modellers of mutualisms have focused on defining conditions and mechanisms that could account for the prevalence of mutualistic interactions in nature. Recently, mutualisms have been modelled as biological markets (Noë & Hammerstein 1994, 1995; Schwartz & Hoeksema 1998).

Mutualisms are characterised by complexity and variation, with multiple, varying individuals and species on both sides of the interaction, species engaged in multiple types of mutualism simultaneously, and costs and benefits of the interaction changing over time and space. Biological market models address this complexity in a number of ways, and as such may be appropriate for modelling many types of mutualistic interactions. The central mechanism of market models is that the price of trade is negotiated, with individuals choosing partners who are offering the best price. This partner-choice mechanism incorporates variation among potential partners in a mutualism, and recognizes that mutualisms operate in a complex community context.

Many mutualisms may be best seen as interactions in which individuals of one or both species exploit individuals of the other species, but that none the less result in net benefits to each of the individuals involved (Thompson 1982; 1994; Futuyma & Slatkin 1983; Janzen 1985; Herre & West 1997). A modelling approach that explicitly outlines the costs and benefits of the interaction to the individuals or species involved, such as

Box 8.1 The economic law of comparative advantage

Classical western economists of the late eighteenth and early nineteenth centuries were primarily concerned with economic growth, in particular trying to understand the influences on the 'wealth of nations' (Leighton 1970). Adam Smith, in his well-known treatise by this title in 1776, emphasised the role of free trade among nations in increasing the wealth of all nations, stating that 'it is a maxim of every prudent master of a family never to attempt to make at home what it will cost him more to make than to buy. What is prudence in the conduct of every private family, can scarce be folly in that of a great kingdom' (Smith 1937). This analogy between international trade and the workings of a family illustrates the idea of 'absolute production advantage', which hypothesises that if one nation produces commodity A better than commodity B, and another nation perceives the opposite production possibilities, then the total wealth of two nations will be increased if they each specialise in production of the commodity that they produce more efficiently, and then trade for the other commodity. The achievement of economist David Ricardo, in the early nineteenth century, was to show that trade is advantageous for both nations even if one nation is better at producing both commodities than the other nation. The only requirement for trade to be beneficial is that the two nations perceive different ratios of costs of the two commodities, i.e. they perceive different relative costs of the two commodities. Trade will always benefit both nations as long as the exchange rate for the two goods lies between the ratio of costs that each country experiences individually. The economist John Stuart Mill reformulated Ricardo's theory to make specific predictions about the mechanisms determining the international exchange rate for two commodities. This principle worked out by Ricardo and Mill has been termed the 'law of comparative advantage'. The history of the development of these economic principles is well detailed by Ellsworth and Leith (1975). The law of comparative advantage, and its associated graphical depiction of the market conditions of two countries potentially engaging in trade, forms the basis of the biological market approach to modelling species interactions

presented in this chapter and previously (Schwartz & Hoeksema 1998). Many of the graphical tools and terms we employ in the biological market approach have direct counterparts in the basic literature of the economics of international trade (e.g. Leighton 1970; Ellsworth & Leith 1975; Grubel 1977). For example, our 'isolation acquisition isocline' corresponds directly to the classic 'production possibilities curve'. Similarly, our 'optimal consumption vector' is equivalent to the economist's set of 'consumption indifference curves'. We suggest that the basic economic principles of international trade are useful in understanding the specialisation and trade that may occur between two interacting biological species.

the biological market approach discussed here, is useful in analysing these types of mutualisms (Keeler 1985; Thompson 1986; Addicott & Tyre 1995; Connor 1995; Joshi & Thompson 1995; Pellmyr *et al.* 1996; Herre & West 1997; Pellmyr 1997). Such models will be useful for making predictions about conditions under which benefits of an interaction outweigh the costs.

We have previously presented a biological market model to analyse the specific situation in which two species in a mutualistic interaction both require the same two resources (Schwartz & Hoeksema 1998). The economic principle that is the basis for this model is relatively simple. Classic economic theory tells us that nations can benefit by specialising in production of certain goods and trading with other nations rather than producing all commodities themselves (Mill 1877; Ricardo 1891; Box 8.1). The biological equivalent of this theory is that individuals or species that are more efficient than others at one aspect of resource capture (e.g. carbon fixation) ought to specialise and trade with others for other resources (e.g. soil water and macro-nutrients). Specialising individuals acquire their resource at a discount relative to other trading partners and can trade the surplus for more of other resources than they could acquire on their own. The principle of increasing total resource acquisition through specialisation and trade, however, can be extended beyond *absolute* production advantage to include *relative* production advantage. In this case, an individual may be less efficient than its trading partner at the production of all commodities and still benefit from trade as long as it is more efficient at the production of one commodity than it is at another (Ricardo 1891).

Basic model of specialisation and trade

Individuals of two species (A and B) require both of two resources for growth, and experience a tradeoff in acquisition of these resources. The tradeoff in resource acquisition is described by a resource acquisition isocline representing the maximum annual amount of the two resources individuals of each species can acquire in isolation (Fig. 8.1a,b, solid lines). This *isolation acquisition isocline* intercepts the axes at the maximum amount of resources each species could obtain in a year if the species completely specialised in acquisition of one resource (R_{max}). The negative of the slope of the isolation acquisition isocline is equal to the resource cost ratio (the *isolation cost ratio*, or I). We allow individuals to choose to acquire resources at any point along their isolation acquisition isocline.

We define an individual's fitness to be maximised for a specific combination of acquired resources. The set of points defining this specific combination of resources is a straight line, beginning at the origin, that lies in the plane of the relevant resources. We call this line the *optimal consumption vector*. In the absence of resource exchange, a species optimises its fitness by acquiring resources at the intersection of the isolation acquisition isocline and the optimal consumption vector (points 1 in Fig. 8.1a,b).

Example 1: Simple trade between a plant and a mycorrhizal fungus

We illustrate the simplest application of this model by analysing a common mutualism, that between a plant and a mycorrhizal fungus. In this example, individuals of species A (a vascular plant) are more efficient than those of species B (a mycorrhizal fungus) at acquiring both of two resources (phosphorus and carbon). Individuals of species A perceive an isolation cost ratio of 1:1, while B perceives an isolation cost ratio of 4:1 (Fig. 8.1). Thus, the fungus is less efficient at acquiring either resource than the plant, but is better at acquiring phosphorus (R2) than carbon (R1) (Fig. 8.1b). In reality, fungi are likely better at acquiring phosphorus than plants; however, for illustrative purposes we assume plants are more efficient at acquiring phosphorus than fungi.

The principle illustrated by this simple model is that, if the poorer resource competitor perceives a lower isolation cost of one resource than the other resource, it will always benefit by specialising (with respect to acquisition) on the resource that it acquires more efficiently and trading for the other resource. By trading, individuals of both species experience a more favourable cost ratio than without trade. Thus, they are able to

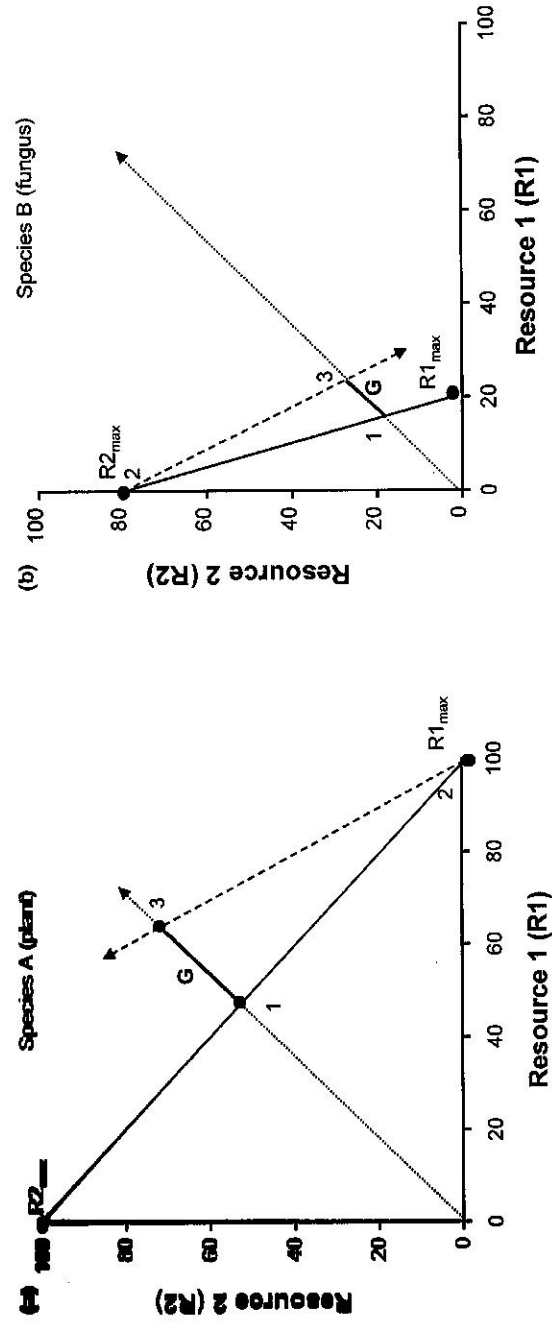


Fig. 8.1 Market conditions for a simple model of resource specialisation and trade between two species (species A, a plant, and species B, a mycorrhizal fungus). Each have an optimal consumption vector (.....), which represents combinations of resource 1 and resource 2 that maximise individual fitness, and an isolation acquisition isocline (- - -), which represents the maximum combined amount of resources 1 and 2 that can be acquired without trade. In the absence of resource exchange (trade), the optimum resource acquisition is represented by point 1. With trade, species B specialises on acquisition of resource 1 (phosphorus; b, point 2, $R1_{max}$), which it acquires more efficiently than resource 2 (carbon). Species A, in turn, specialises in acquisition of resource 2 (carbon; a, point 2, $R2_{max}$). Each species then trades a portion of one resource for the other required resource to end up along a trade acquisition isocline (- - -). The optimum resource acquisition with trade, for each species, is represented by point 3. The gain from trade (G) is the distance along the optimal consumption vector between its intersections with the isolation acquisition isocline and the trade acquisition isocline.

acquire additional resources along a new *trade acquisition isocline*, which is analogous to the isolation acquisition isocline introduced earlier, except that it represents all possible combinations of the two resources that a species can acquire with specialization and trade (Fig. 8.1a,b). The negative of the slope of this line is the *trade cost ratio* (T). Under conditions of resource specialisation and trade, individuals will acquire resources at the intersection of this trade acquisition isocline and the optimal consumption vector (points 3 in Fig. 8.1a,b). We can define the *gain from trade* (G) to be equal to the distance along the optimal consumption vector from its intersection with the isolation acquisition isocline to its intersection with the trade acquisition isocline. An individual's fitness is assumed to be greater the more resources it can acquire, and thus the further away from the origin it is along the optimal consumption vector. Therefore, it is to the advantage of all individuals to specialise in the acquisition of the commodity for which they experience an acquisition advantage relative to potential trading partners. This result holds even under the condition that, in isolation, individuals of one species obtain both resources more efficiently than those of the other species, and perceive no difference in the cost of obtaining the two resources (Schwartz & Hoeksema 1998). Under any conditions where the trade cost ratio (T) lies between the isolation cost ratios (I) for the two trading partners, trade will be beneficial to both partners (Schwartz & Hoeksema 1998). Graphically expressed, the intersection of the optimal consumption vector and the trade acquisition isocline will always be farther from the origin than the intersection between the optimal consumption vector and the isolation acquisition isocline (Fig. 8.1).

Applicability of the biological market approach

The market model described above, based on the example of mycorrhizal interactions, involves two species requiring the same two resources, and the benefits exchanged involve costs to both species. In nature, however, many mutualisms do not fit this description. Often, the benefits exchanged between two species are services (e.g. seed- or pollen-dispersal), rather than resources. Furthermore, the benefits in mutualisms are often by-products of selfish actions (e.g. pollen movement among plants by a flower-feeding herbivore, Connor 1995) and as a result involve little or no cost to the organism giving the benefit. The following example illustrates the applicability of market models of mutualisms by showing how the market model framework can incorporate the exchange of services, as well

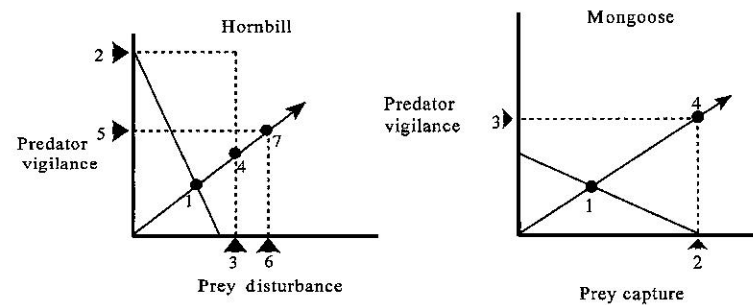


Fig. 8.2 Market model representation of a mutualism involving hornbills and the dwarf mongoose. Dashed lines represent trade acquisition isoclines, solid arrows represent optimal consumption vectors, and other solid lines represent isolation acquisition isoclines. (a) Market conditions of the hornbill where: (1) represents the amount of vigilance and prey disturbance experienced by the hornbill in isolation; (2) represents the amount of vigilance by a hornbill when in association with the mongoose; and (3) represents the amount of prey disturbance received from the mongoose in exchange for vigilance against shared predators. In this case, when hornbills are not vigilant against mongoose-specific predators, they experience (4) with specialisation and trade. If, however, hornbills are also vigilant against mongoose-specific predators, they are slightly less vigilant against their own predators (5), but receive more prey disturbance (6) from the mongoose in exchange for vigilance against shared predators. (b) Market conditions of the mongoose where: (1) represents the amount of vigilance and prey capture experienced by the mongoose in isolation; (2) represents the amount of prey capture when the mongoose specialises in prey capture; (3) represents vigilance received from hornbills in exchange for hornbill prey disturbance. Thus, under specialisation and trade the mongoose experiences increased vigilance and prey capture (4).

as benefits that are by-products. As in the first example above, we employ a graphical approach. The mathematics behind this graphical approach is simple algebra and is detailed elsewhere (Schwartz & Hoeksema 1998).

Example 2: Mixed-species foraging flocks

Rasa (1983) describes an interesting mutualistic association between the hornbill (a bird) and the dwarf mongoose. The two species form mixed foraging flocks, in which each performs a service that benefits the other. The hornbills take advantage of prey disturbed by the feeding activities of the mongoose, while the mongoose benefits when the hornbill warns of predators. This interaction is described by a market model when we consider the hornbill to require both prey disturbance and predator vigilance (Fig. 8.2a). Similarly, the mongoose needs both prey capture and predator vigilance

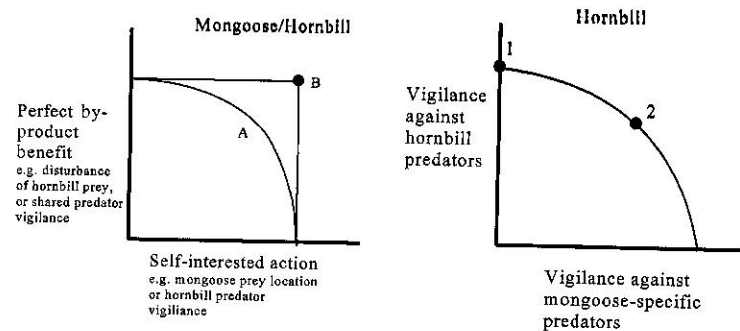


Fig. 8.3 By-product relationships for hornbill and mongoose resources and services. (a) Mongoose prey location results in prey disturbance for hornbills as a perfect by-product. Similarly, hornbill predator vigilance of shared predators results in a perfect by-product benefit of vigilance for the mongoose. (b) Market conditions of hornbill, in which vigilance against mongoose-specific predators is perceived as a partial by-product of vigilance against all hornbill predators because vigilance against additional predators may reduce the efficiency of vigilance against hornbill predators. Hornbills may, in theory, choose to be (1) vigilant specifically against hornbill predators, or (2) vigilant against both hornbill and mongoose predators.

(Fig. 8.2b). In isolation both species must expend energy on both activities. The hornbill could be considered to perceive vigilance against predators that prey on both the mongoose and the hornbill as a perfect by-product of vigilance against only its own (hornbill) predators, since, in watching for all of its own predators, the hornbill is also watching for some of the mongoose predators. Similarly, the mongoose perceives disturbance of hornbill prey as a perfect by-product of foraging for its own food. We can model these by-product relationships between commodities by changing the shape of the acquisition isoclines from the straight line used in the basic model above. We use a convex acquisition isocline (Fig. 8.3a, line A) when the acquisition of one resource is partially a by-product of the acquisition of the other resource. When acquisition of one resource is a perfect by-product of the acquisition of another resource, the isocline is square (Fig. 8.3a, line B). As discussed above, if the acquisition or production of one resource results in a by-product that is not needed by the acquiring species, then all of that by-product resource or service may be available for trade.

This situation favours hornbills that specialise in vigilance, and trade mongoose predator vigilance for disturbance of its prey by the mongoose. The situation also favours the mongoose that trades disturbance of hornbill prey to the hornbill for vigilance against predators. With specialisation

and trade, both the hornbill and the mongoose perceive trade acquisition isoclines that are more favourable than their isolation acquisition isoclines (Fig. 8.2). These new trade isoclines are not straight sloped lines because in each case, individuals are trading perfect by-products to receive benefits, and thus do not need to give up important resources. The point of intersection of the trade acquisition isocline with the consumption vector is determined by the amount of benefit received for the by-product traded.

Connor (1995) suggests that if the hornbills warn about predators that do not prey on hornbills, they are 'investing' in by-product benefits received from the mongoose. This investment is described by our model if we consider the hornbill to perceive vigilance against mongoose-specific predators to be a partial by-product of vigilance against all of its own predators (Fig. 8.3b). Such a hornbill may be slightly less vigilant against its own predators, but can trade vigilance against all mongoose predators for more prey disturbance by the mongoose (Fig. 8.2a). It is important to point out that we are not hypothesising that the organisms involved are consciously 'trading'. Further, it may be difficult to quantify specific values of services rendered. We are instead suggesting that a market model is a useful context for describing interactions in which two organisms both provide services for the other that have little cost to themselves.

As Connor (1995) discusses, by-product benefits are important in many abundant present-day mutualisms, including such well-studied examples as pollination and seed-dispersal. Furthermore, present-day interactions that do not involve by-product benefits may well have evolved from interactions that began as by-product mutualisms or commensalisms. Despite the potential importance of by-product benefits, models of mutualisms have not considered them explicitly. As we show here, by-product benefits are conceptually straightforward to model, and can affect the predictions of mutualism models in significant ways.

Discussion

Mutualisms are increasingly being understood as mutually exploitative interactions that happen to result in net benefits to both species involved (Thompson 1982, 1994; Futuyma & Slatkin 1983; Janzen 1985; Herre & West 1997). The interaction is considered a mutualism if the benefits and costs involved add up to a net benefit for both species. From this perspective, market models are useful for understanding mutualisms, since they are explicit about the specific costs and benefits being exchanged. This feature allows us to make specific predictions about the conditions required for mutualism.

Bronstein (1994a) pointed out that mutualisms are not static, but rather they commonly change over space and time depending on a number of factors. One example is that of resource availability. Changing resource availability has been shown to strongly change the nature of the mycorrhizal mutualism, with the relationship being less favourable for the plant at higher soil nutrient availability (e.g. Johnson 1993). Market models are useful for modelling such changes in mutualistic interactions, since they are explicit about how the market conditions of the interaction change as supplies and demands of the the benefits involved change (Schwartz & Hoeksema 1998).

The first example of a market model presented here, that of resource trade between a plant and a mycorrhizal fungus, suggests how exchanges of goods or services between species will be favoured in many situations. The economic principle of specialisation and trade forms the basis for this idea. The model shows that some type of trading relationship is favoured as long as the two species involved perceived different ratios of acquisition costs of two resources. The second example presented here, that of the hornbill and mongoose mixed foraging flocks, shows how the market approach can incorporate mutualistic benefits that are services rather than resources. It also demonstrates how the degree to which one resource or service is a by-product of another can be modelled explicitly in the biological market approach.

It should be remembered that specific conditions are required for the functioning of a market mechanism in nature. Most importantly, mutualistic interactions may be less likely to function as biological markets if access to a partner's benefits is determined forcibly by those receiving the benefits, rather than by a choice of the giving partner (Noë & Hammerstein 1994). It would be useful to quantify the extent that partner-choice determines the distribution of benefits in mutualisms. That type of data would suggest the extent to which biological market models can be applied usefully to natural systems.

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