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How do biological markets compare to the markets of economics?

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Abstract

After an introduction to biological markets written for non-biologists, I explore whether and to what extent natural markets, i.e. markets on which non-human traders exchange goods and services with members belonging to their own or to other species, can be compared to human 'economic' markets, i.e. the markets analysed by economists. Biological Market Theory (BMT) borrows jargon and ideas from economics, but was at least as much inspired by sexual selection theory, a collection of models of 'mating markets', including human mating markets. Here I ask two main questions: (1) Is there more than only a superficial resemblance between both types of markets? (2) Can the analysis of one yield insights about the other?

First, I consider the different forms of human trading and markets and propose some biological ones to which these can best be compared, e.g. companies trading goods in markets shaped by 'comparative advantage' to underground nutrient exchange markets between plants and rhizobial bacteria and mycorrhizal fungi; job and retail markets with pollination, seed dispersal and protection markets between plants and insects; 'embedded markets' with grooming markets in non-human primates and so forth. Then I look at some phenomena that are considered to be exclusive to human markets, such as common currencies and binding contracts, and ask whether these are indeed that exclusive. Finally I look at the common ground: negotiations that take place on several types of markets, natural or not; the honesty of advertisements, which is recognised as a major problem for both human and non-human clients; the biological equivalent of the market – firm dichotomy and the importance of the costs of partner choice, which are known to economists as 'transaction costs' and to sexual selection theoreticians as 'search costs'. I conclude that there are several good reasons to have a closer look at those properties that set human and biological markets apart, but certainly also at those features that make them comparable to each other.

Keywords: cooperation, mutualism, trade, biological markets, mating markets, embedded markets, sexual selection, partner choice, currency, binding contract, negotiation, bargaining, honest advertisement, transaction costs, search costs, market – firm dichotomy

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Introduction

Biological Market Theory (BMT) was developed as an alternative to those models of the evolution of cooperation in non-human organisms that assume 'cheating' to be the pivotal problem for the stability of cooperation and 'partner control' to be nature's principal solution (Bshary and Noë 2003; Hammerstein and Noë 2016; Noë 2001; Noë and Hammerstein 1994, 1995; Noë et al. 1991). Frequently discussed control mechanisms include abandoning the partner, punishment and harassment. BMT instead emphasizes the central role of partner choice. When some agents choose among a number of potential partners, the latter will try to ensure being chosen by offering higher quality goods and/or better service and/or demanding less in return for those commodities. When agents are able to discriminate among (potential) partners on the basis of their own net gain from interactions with those partners, then their choice behaviour will result in selection against cheaters as a side-effect. Phenomena such as partner choice, outbidding competition and the resulting adaptation of exchange rates of commodities to changes in supply-demand ratios are reminiscent of interactions on human markets with face-to-face trading and bartering. Such markets are obvious sources of inspiration for models of non-human trading, in the form of both intra-specific cooperation and inter-specific mutualism. Through the eyes of a biologist 'trading' is identical to 'cooperation', since both are interactions in which all agents involved, as a rule, end up with a net gain. Sexual Selection Theory (SST), which describes 'mating markets', has been another important source of inspiration during the development of BMT (reviewed in: Andersson 1994).

I start with an introduction to biological markets for non-biologists in which I describe some of the best studied examples. These include a wide spectrum of species from fungi and plants, to fish and primates and strategies implemented by highly cognitive mechanisms in some cases and by biochemical processes in others.

Then I look at a number of phenomena that are typical for human markets and ask whether drawing parallels with non-human markets is both warranted and scientifically productive. Such phenomena include, among others, bartering and negotiation, the use of currencies and the conclusion of binding contracts. Finally, I pay special attention two questions. (1) Is the distinction between markets and firms valid and useful in the case of biological markets? (2) Is the treatment of 'transaction costs' in economics equivalent to the treatment of 'search costs' in both BMT and SST?

Biological Markets for non-biologists

The eternal problem of the evolution of cooperative behaviour

Countless introductions of papers on the evolution of cooperation will start by telling the readers about an enigma that already puzzled Darwin: why would individuals invest in others without a guarantee of net returns? Which mechanisms guarantee net returns, or at least make it more likely? There is a long list of recent review papers that the reader can check for details of the many mechanisms proposed in the literature (Bergmüller et al. 2007; Noë 2006; Queller and Strassmann 2006; Sachs et al. 2004; West et al. 2011; West et al. 2007a; West et al. 2007b). Here I will quickly skim over

enough of the basics to give readers less familiar with evolutionary biology a fair chance to follow the rest of the chapter.

Before listing the most common mechanisms, I have to explain my choice of terms (for details see Noë 2006). “Cooperation” for me is the umbrella term that includes intra-specific cooperation, inter-specific mutualism and symbiosis. These labels are commonly used in ecology, but other disciplines use the same or similar labels in all kinds of different ways; a cacophony of terms reminiscent of the Tower of Babel (Noë 2006). The term cooperation describes the result of an interaction between two or more agents from which all participants profit. In biological terms: their fitness increases compared to the situation before the interaction. An economist may prefer to replace ‘fitness’ with ‘utility’.

Cooperation as such is not an entity under direct natural selection. Natural selection does not act at the level of interactions between individuals, but on the individuals themselves. Natural selection ‘sees’ individuals as packages of genes that are all in the same boat: either there will be more boats of the same type in the next generation, or the boat sinks. What IS under natural selection here is the behaviour of the agents or, more specifically, the behaviour that makes it likely that interactions lead to net benefits for the actors. In a review written a decade ago (Noë 2006) I labelled such behaviour “cooperative investment” to stress both the idea of risky investment (net returns are not guaranteed) and the most likely outcome (benefit for all). Others use labels such as “altruism”, “Altruistic behaviour”, “cooperative behaviour”, or even, incorrectly, “cooperation”. I am fine with “cooperative behaviour” too, but for some it may be difficult to imagine investments made by the likes of plants and fungi as resulting from behaviour.

When I talk about ‘cooperation’ in this chapter, I think of the kind of interaction in which one or more ‘commodities’, used here as a ragbag for all kinds of goods and services, are transferred between two agents. These agents may be part of networks of many agents and may interact with other agents at other occasions or even simultaneously, but the standard interaction is a dyadic affair. In other words, I don’t refer to forms of cooperation in which multiple agents have to take coordinated action in order to arrive at a beneficial outcome for all participants. No social dilemmas, common goods, collective actions or whatever one wishes to call these instances of n-agent cooperation.

Models of the evolution of cooperation roughly fall in five categories, depending on the assumed mechanisms promoting selection for cooperative investment in dyadic actions:

1. **Kin selection models.** An explanation of cooperation among closely related individuals, which obviously will be members of the same species. When individuals can somehow discriminate between closely related individuals and others, invest preferentially in those relatives, and do so only when the cost for the investor is small relative to the gain by the beneficiary of the investment, then such ‘altruistic’ investment behaviour can thrive. By promoting the fitness of its close relatives, an actor increases the chances that the genetic information that instigated him to show the cooperative behaviour is better represented in the next generations. The idea behind this is simple: the closer the relative, the higher the chance that the relative carries the same genetic information as the actor, including the ‘genes’ prompting the carrier to behave in a cooperative way.

2. **Green beard models.** This is a bit technical and beyond the scope of this chapter. The basic idea is that the genetic information that leads to cooperative behaviour, as mentioned under point 1, is now coupled to a signal, a 'green beard', that can be perceived by the actor (Dawkins 1976). By only investing in folks wearing green beards, the actor promotes the propagation of the 'cooperation genes' in future generations. This is kin selection without kinship, i.e. without the necessity of being closely related at the level of the whole genome (for an example see: Queller et al. 2003).
3. **Partner control models.** These models were proposed to explain cooperation among unrelated agents. The basic idea is that each individual attempts to control the behaviour of each agent (s)he interacts with in such a way that at the end of each interaction or series of interaction the actor enjoys net gain. There are many ways to control others, for example: defection (simply stop interacting when it costs more than it pays); harassment (annoy the other during the other to such an extent that (s)he changes his/her behaviour in favour of the harasser); punishment (hit the other over the head between interactions). The game-theoretical paradigm most used as a basis for models is the iterated prisoners' dilemma (IPD) in which players have the choice between 'cooperate' and 'defect'. Partner control models got mighty popular after the publication of some early theoretical papers (Axelrod and Hamilton 1981; Trivers 1971) and a few empirical ones that at first seemed to support these models, (Fischer 1988; Packer 1977; Seyfarth and Cheney 1984; Wilkinson 1984). However, the early empirical support all but crumbled under close scrutiny. This was followed by decades of research in which a great number of theoretical papers were published, but no empirical studies that showed the use of strategies that are indeed contingent on the actions of one partner only, such as tit-for-tat and reciprocal altruism. It was not before 2008 that a paper was published reporting a convincing example of an IPD in animals (Bshary et al. 2008) and one more that could well pass the test too (Krams et al. 2008). These papers, and a few more that followed, couldn't prevent the hot air balloon of partner control from deflating further, however.
4. **Partner choice models.** There is nothing wrong with the idea that one can slap an unprofitable partner on the wrist just by abandoning him, but it is unlikely that most agents will simply sit on their hands, as far as they have any, after that. A much more likely action after abandoning one partner is searching for another. And the abandoned partner may of course also go looking for a new friend. Rare are the organisms that have no choice among potential partners at all. Partner choice, or partner switching, is a potent force in the evolution of cooperation and central to what Peter Hammerstein and I have labelled 'biological markets' (Noë and Hammerstein 1994, 1995). First of all, partner choice can be a selective force promoting certain characteristics in partners that are profitable to the agents exerting choice, just like female choice (i.e. mate choice exerted *by* females) can select for all kinds of fancy secondary sexual traits in males. Partner choice can also drive competition by outbidding, resulting in relatively better exchange rates for the choosing party. This causes momentary adaptations to fluctuations to supply-demand ratios; hence the market-like character of these cooperation arenas. Partner choice can thus drive a form of natural selection that we dubbed 'market selection' (Bshary and Noë 2003) in evolutionary time and can drive agents to adapt to fluctuations in the markets they participate in on a time scale of an individual's life time or even shorter. Obviously, both forms of adaptation are closely linked, but

market selection will often be a weak or even unnoticeable force even in organisms that react strongly to supply and demand fluctuations. Market selection is notably hard to detect when it runs counter to sexual selection, such as in birds in which female choice selects for bright colours in males, but dominant males prefer male partners with dull colours (Greene et al. 2000; Noë and Hammerstein 1994).

5. **Group selection models.** I mention group selection only to complete the picture here. There is little controversy around the idea that natural selection operates at multiple levels, notably alleles ('genes'), individuals (i.e. packages of genes), groups (i.e. packages of individuals of the same species, ecosystems (i.e. packages of individuals belonging to different species etc. (Queller and Strassmann 2009). There is much controversy, however, about the relative impact of selection at those different levels (Leigh Jr 2010). I am firmly in the camp of the individualists and use the term 'agent' here as synonym to 'individual'. Since the effect of partner choice at the level of individual agents forms the main topic of this chapter, group selection is hardly relevant here. It can be a major force, however, in the evolution of forms of cooperation that are under cultural (rather than natural) selection, which are ubiquitous in human societies (Richerson and Boyd 2005; Richerson et al. 2003; Smaldino 2014).

Properties of biological markets

- *Trader classes*

An archetypical biological market has trader classes that offer class-specific goods or services ('commodities'). In most cases the roles are fixed, such as in plants and pollinators, cleaner fish and their clients, but agents can also be temporary members of a class and switch classes. For example, baboons may provide access to food patches when dominant, but offer grooming to gain access to food patches when subordinate (Barrett et al. 1999). More than two trader classes can be found in various complex forms of mutualisms, as for example in leaf-cutter ants that protect the fungi they grow for food (on the pieces of leaves they cut from trees) against fungus parasites by inoculating their fungus gardens with antibiotics producing bacteria (Currie et al. 2006; Currie et al. 1999).

- *Commodities*

Traders on biological markets exchange 'commodities', which are either tangible goods (examples: nutrients, such as nectar or phosphorus, and domatia, housing structures provided by plants to mutualistic insects) or 'services' (examples: protection of plants or aphids provided by ants, grooming provides by monkeys, removal of ecto-parasites provided by cleaner fish)

- *Partner choice*

Preference for trading partners is based on expected net gain. Expectations can be based on past interactions, ongoing interactions, 'advertisements' (signals correlated with the commodity offered), or a combination of these. Choosing a new partner may follow abandoning or being abandoned by a partner and hence may also be described as 'partner switching'.

- *Outbidding competition*

Competition over access to preferred partners takes the form of outbidding competition, i.e. improving offers by changing the exchange rate in favour of the partner. Competition by use of force may often play a role too, but should be seen as a

factor constraining the market rather than shaping the market, comparable to the effect of robbery and theft on human markets.

- *Supply and demand*

Exchange rates of commodities are primarily determined by supply – demand ratios. The *direction* of changes in exchange rate after changes in supply and/or demand should be predictable, but it is hard to imagine how exact exchange rates could be predicted for biological markets. Economists also have problems predicting exact prices, even when the values of all commodities can be expressed in a common currency, a component lacking on virtually all biological markets (see next point).

- *The lack of common currencies*

With few possible exceptions, which I'll discuss below, there are no equivalents of common currencies. The 'currency' of evolutionary biology is fitness, which is a measure of reproductive success relative to the reproductive success of conspecifics. It is comparable, with some restrictions, to 'utility' in economics. Units of fitness cannot be converted from one species to the next, so the gains and losses of members of different species can certainly not be expressed in fitness units on a single scale.

- *The lack of binding contracts*

Nonhuman traders cannot conclude 'binding contracts' verbally, in writing, or otherwise, before engaging in interactions and there are no justice-like or police-like external institutions to enforce contracts. For some actors on biological markets the profitability of interactions can be guaranteed by mechanical means, e.g. a bumblebee can hardly avoid taking up pollen when reaching for the nectar offered by a flower.

- *Negotiation*

Even if supply and demand ratios dictate a certain exchange rate, the question will be: which mechanisms translate this market-wide parameter into an exchange rate between two individual agents? These mechanisms are in general species and interaction specific, but some of these can be lumped together under the heading 'negotiation'. During exchanges in which a commodity is delivered piecemeal, the receiving trader can obtain information about the likelihood that the partner will continue its delivery by observing the attitude of the partner. The attitude of the partner is determined by past interactions with the same and other agents acting on the same market. It is not necessarily in the interest of a trader to reveal its attitude, however, and this may become visible only after a challenge by its partner. The process reminds of the 'raising the stakes' strategy proposed in the context of partner control models (Roberts and Sherratt 1998; Sherratt and Roberts 2002). An example of negotiation during grooming in vervet monkeys given below may clarify what I mean by negotiation processes on biological markets.

- *Advertising*

Partners may be selected directly on the basis of the (relative) quality or quantity of the commodity they offer, but in many cases this cannot be assessed before the actual exchange begins and hence first investments have been made. One partner may reduce those initial investments, as well as search costs (see next item) for the other party by 'advertising' the commodity on offer, e.g. the petals of a flower form a kind of billboard advertising the presence of nectar to potential pollinators. Obviously there are pitfalls: flowers may also attract nectar robbers and advertisements may be exaggerated or utterly dishonest (Fraser 2013).

- *Search costs*

Finding a partner and starting an exchange doesn't come for free. The 'search costs' to be paid form a threshold between living without a partner and finding one, or between the present partner and an alternative one. Time and energy spend for the search are obvious components of search costs, but so are increased predation risks during searches and investments in the assessment of the potential partners. Search costs were ignored in some early sexual selection models, resulting in some rather unrealistic predictions (Andersson 1994). When the search costs prevent both agents from switching to a better partner, but cooperation remains potentially profitable for both, the agents are de facto condemned to deal with each other. In such a case partner control mechanisms prevail.

A few examples of non-human markets

- *Cleaner fish markets*

There are quite a few marine fish and shrimp species that feed on ecto-parasites found on the skin and in the gills and mouths of, usually larger, fish. Some are facultative cleaners, some only do it in their youth only, while for others it is a full time job. The cleaner fish – client mutualism was listed as an example of reciprocal altruism by Bob Trivers (1971), but was not well studied till Redouan Bshary started working on the cleaner wrasse *Labroides dimidiatus*, an obligate cleaner, in the mid-nineties (reviewed in: Bshary 2001; Bshary and Noë 2003).

The natural history of cleaning in a nutshell: Cleaner wrasses defend small territories on corals, called 'cleaning stations'. All kinds of fish visit them to get rid of their ecto-parasites, which usually infect them in great numbers overnight, but also of dead and infected skin. Individual cleaners can have more than 2000 interactions per day and may reduce the parasite density on clients by a factor of 4–5 (Grutter 1999). The interaction is considered mutualistic, because the cleaner profits from food delivered at home and the client from getting cleaned. However, *L. dimidiatus* prefer the mucus, scales and skin of the client over their ecto-parasites (Grutter and Bshary 2003), a potential cause of discord in the mutualistic transaction. Clients can also harm cleaners, but some more than others: predators can attempt to eat the cleaner. Non-predatory species can chase the cleaner around when they are big enough, as most are.

Market processes become apparent when two groups of clients are compared: 'residents' and 'floaters'. Residents have small home ranges that contain only a single cleaner station, while floaters are either fish with big ranges containing multiple stations, or pelagic fish that visit the reef occasionally. Residents have no choice and the cleaner is therefore in a monopolistic position. Floaters can visit multiple stations and play off cleaners against each other by returning only to those that provide the best service, i.e. they don't have to wait and are not bitten (Bshary and Schäffer 2002). The difference is most evident when both client types approach the cleaner simultaneously: the cleaner invariably serves the floater first. Floaters are on average bigger species than residents, so in principle their larger body surface and hence higher number of ecto-parasites could also explain the difference. However, when residents are compared to same-size floaters, the latter are still served longer and get bitten less (Bshary 2001).

- *Baby markets*

Most, if not all, primate females love cuddling the babies of other females. This is not necessarily a by-product of their love for their own infants, but a way of getting to know new members of their group. For young females it may also important in learning to

handle infants, as the mortality of first-borns tends to be higher than the mortality of subsequently born infants (Cheney et al. 2004; Koyama et al. 1992; Smuts and Nicolson 1989). Only new-borns, which in most primate species have a distinctly coloured natal coat, attract strong attention. For the following story it is irrelevant, however, why female primates want to handle other females' infants so desperately. Fact is that they do and that they usually have to groom the mother first, before the latter allows touching her infant.

Peter Henzi and Louise Barrett reasoned that if indeed would-be infant handlers 'pay' for access to infants by grooming the mother, the price paid for access would depend on the number of infants in a group (Henzi and Barrett 2002). Data they collected on chacma baboons in South-Africa, which are brown as adults and black as babies, indeed confirmed this hypothesis: the more black infants there were in the group, the shorter was the grooming time needed to gain access to them. As always, the 'grooming-up-the-hierarchy' effect was visible too: for the same number of infants handlers subordinate to the mother had to groom longer than handlers dominant to the mother. The idea of a 'baby market' has been confirmed for several other species since (Fruteau et al. 2011; Gumert 2007; Schaffner and Aureli 2005; Slater et al. 2007; Wei et al. 2013).

The mother's anxiety level may well turn out to be part of the proximate mechanisms behind all this: lower ranking mothers are likely to be more reluctant to relinquish control over their infant than higher ranking ones and mothers may feel more pressure the more would-be handlers are vying for their infant. The step from a simple 'stress level' story to an explanation based on supply and demand is made when mothers actively use infant scarcity to exact more grooming by the handlers beyond the point that they became relaxed enough to hand over their costly offspring. A hint that they actually do this is in the 'negotiation moves' (Waal et al. 2013) mothers often make: they shield their infants and offer fresh body parts to groom, thus inducing the handler to groom longer. If reducing stress was the whole story, we would expect mothers slowly thawing during the grooming bout, but not seeing them actively ask for more grooming.

- *Partner value in vervet monkeys*

We could show that vervet monkeys quickly adapt to changes in partner value in an experiment in which first one and then two low-ranking females were experimentally enabled to produce food for their whole group by opening a remote-controlled food container filled with pieces of apple. When only one food provider was present, the grooming ratio between her and her group members shot up to her advantage, but dropped quickly again, roughly half-way back to base level, within a few trials after a second provider was introduced (Fruteau et al. 2009).

- *Underground nutrient exchanges*

Great examples of partner choice and adaptation to supply-demand ratios come from mutualisms between plants and microbial organisms. Among the many different mutualisms of this type, the most intensely studied are the interactions between legumes and both arbuscular mycorrhizal fungi and soil bacteria of the rhizobia-group. In both cases nodules are formed in which nutrients are exchanged: the plants offer carbohydrates they acquire through photosynthesis in the chloroplasts found in all green tissues, but notably leaves. The fungi and bacteria, respectively, offer essential nutrients that they take up from the soil, notably phosphorus and nitrogen (reviewed in: Bücking et al. 2016; Friesen 2012; Kiers and van der Heijden 2006; Simms and Taylor 2002; Werner and Kiers 2015; Werner et al. 2014; Wilkinson 2001). One reason for the

interest in these nutrient exchanges is their enormous economic importance: about 85% of all plant species, among which virtually all plants important in agriculture, depend on them.

The big advantage of these systems is that they can be experimentally manipulated and the amounts of nutrients exchanged can be accurately quantified. One essential difference between the two mutualisms is that mycorrhizal fungi grow long filaments that can make contact with multiple hosts, while rhizobia live in contact with or in the direct vicinity of the roots of a single host. Fine-tuned adaptation to changing supply-demand ratios, resulting from partner choice going both ways, has been shown in several experimental studies, for example between plants and rhizobia (Friesen 2012; Gubry-Rangin et al. 2010; Heath and Tiffin 2009; Simms and Taylor 2002) and between plants and arbuscular mycorrhizal fungi (Argüello et al. 2016; Bever 2015; Bever et al. 2009; Fellbaum et al. 2014; Franklin et al. 2014; Grman et al. 2012; Kiers et al. 2011; Verbruggen et al. 2012). The mechanisms involved in nutrient exchanges seem at first sight fiendishly complex and far removed from the simple bartering of goods, but a recent model based on basic principles from cell biology showed that plants and arbuscular mycorrhizal fungi may well be seen as traders reacting to changes in supply and demand in a straightforward way while maximizing their private net gain (Schott et al. 2016). Underground markets have also been used as empirical touchstones in the development of sophisticated market models of more general interest (Wyatt et al. 2014, 2016).

Partner choice

I use 'partner choice' as an overarching term for the exertion of preference for a subset among potential partners on the basis of expected net gain from future interactions. Preferences can be based on a comparison of both known and unknown individuals. This implies that I consider 'partner switching' also as a form of partner choice, i.e. an individual that abandons a known partner in order to form a relationship with a new one, does so on the basis of information about the profitability of interacting with either one. The term 'partner switching' has also been used otherwise, namely as a process by which a relationship is started with a random new partner after the break-up of an existing partnership (Wubs et al. 2016). The latter definition seems more relevant to agent-based simulations than to real-life organisms.

Partner choice comes in many disguises. There are probably as many mechanisms that play a role in discriminating between potential partners as there are species involved in one or the other form of cooperation. I illustrate some general principles with a few specific biological examples and comparisons to human trading behaviour.

- *Unidirectional vs bidirectional choice*

Partner choice on biological markets can be largely unilateral, comparable to clients choosing among shops or restaurants, or go both ways, comparable to universities selecting students that have chosen to apply for certain universities and companies choosing among applicants for a certain job. Insects visiting flowers and transporting the plant's pollen in exchange for nectar will be an example familiar to most. The pollinators unilaterally choose the flowers they want to visit, while the plants do their best to outcompete surrounding plants. It would be a mistake to think that organisms cannot choose because they are immobile, however. Both trader classes on the underground markets in which plants exchange nutrients with mycorrhizal fungi (see above 'Underground nutrient exchanges') can exert choice (Fellbaum et al. 2014; Kiers

et al. 2011). Immobile traders will, as a rule, exert choice after the first contact has been made and eventually commodities have been exchanged (see next point).

- *Choice before or after investments in the partner are made*

Depending on the number of partners needed for an optimal result, a trader can select the best partner, or a few high-quality partners, out of many, or only eliminate the worst ones. Sessile and slow moving organisms, such as plants and corals, are limited in their choice options by their low mobility. Plants tend to trade simultaneously with (very) large numbers of much smaller organisms, such as insects, fungi and bacteria. One can imagine that picking individual bacteria is a bit tedious, so a good alternative strategy is to accept large numbers of partners and eliminate those that do not deliver a net gain. This choice strategy has at some point been labelled 'sanctioning' (Denison 2000), a term that makes sense since in many cases the negative choice by the large partner results in the demise of the small ones. The drawback of this strategy is that a certain investment in low-quality partners has been made before sanctions can be inflicted, opening the door to free-riding. The term 'sanctioning' was introduced in the context of the nutrient-exchanges between plants and rhizobia (see above 'Underground nutrient exchanges'), but there is some debate whether choice by the plants is exerted only by sanctioning mechanisms or also by positive choice before any investment is made (e.g. see Gubry-Rangin et al. 2010). Choices that require low or no investment can only be made on the basis of signals sent by the chosen class of traders that somehow show correlation with the quality and/or quantity of the commodity on offer. The problem of honest advertisements looms large here (Fraser 2013; see also 'Honest advertising' below), but this is a can of worms I don't want to open too widely in this review.

- *Cognitive vs non-cognitive mechanisms*

It is one question which kind of strategy traders use; another is how they implement it. When one thinks of trade among humans, or perhaps among primates or vertebrates in general, one is inclined to expect quite a bit of cognitive power to be used in processes such as partner choice, outbidding a competitor and negotiating for a better exchange rate. This is likely to be largely correct too, although one shouldn't underestimate the share of non-neuronal mechanisms, such as changes in hormone titres and so forth, in social decision making. It would be wrong to think, however, that equivalent strategies are not being used just because the traders involved lack neurons. Rather sophisticated partner choice mechanisms have, for example, been reported in microbes (reviewed in Bever 2015; Bücking et al. 2016; Werner and Kiers 2015; Werner et al. 2014).

- *Periods over which partners are evaluated*

In recent years a somewhat sterile discussion has emerged among primatologists about the time period over which the profitability of partnerships is measured, which is assumed to be the basis on which partners are chosen. Some stress the value of long-term 'bonds' for primates (Dunbar 2010) – others stress that tracking short-term fluctuations is typical for primate grooming markets (Barrett and Henzi 2001; Barrett et al. 1999; Sick et al. 2014). In my eyes, both camps are neither right nor wrong. It all depends on the nature of the commodities exchanged.

The impact of market effects is most obvious when traders react quickly to changes in supply and demand, as in the vervet food provider experiment (Fruteau et al. 2009) described above. In 'baby markets' (also described above), the amount of grooming mothers receive also changes quickly when a new-born arrives, but when the infants age and their attractiveness diminishes, the mothers receive less and less grooming. In

other primate grooming-based trading, the value of a partner can be rather stable over long periods, however. Support in conflicts, for example, is only valuable when given by an individual that is dominant over one's opponent. High-ranking animals are therefore much sought-after partners and in the case of primates this can be the same individuals for many years. High-ranking protectors should therefore not be chosen on the basis of the outcome of few interactions, but rather based on the average outcome of long series of interactions with some rate of discounting the further back these interactions are. Grooming them to keep them ready and willing to lend support should be done regularly, since one never knows when one will be attacked by some young rascal. Tolerance in rich food patches is another commodity that can only be provided by animals high in the hierarchy. It is therefore good to have a good relationship with them over the long run, even though the value of access to food patches itself, and thus the amount of grooming invested, may vary with the time of the day (Sick et al. 2014) and the season (Barrett et al. 2002). My message for primatologists is thus: BMT is about fluctuations in supply and demand, but these fluctuations are not necessarily over short time-frames only, but rather over time frames that correspond to the variation in supply and demand of the commodities at hand. Short-term effects indeed dominate the BMT literature, but that has practical grounds: such effects are easier to observe and quantify and PhD-projects are short.

- *Bookkeeping*

Some kind of bookkeeping is necessary to determine the (relative) value of partners on the basis of past interactions. It is rather unlikely that any non-human animal does this on the basis of adding absolute values in any form ('calculated bookkeeping'), if only because the only relevant currency for such calculations would be the fitness effects on the calculating individual due to each interaction. Biologists find it notoriously difficult to measure fitness effects. 'Fitness' is optimized in the course of evolution via selection on proximate mechanisms that, on average, promote higher fitness (notably lower mortality and/or higher reproductive output per time unit). A plausible kind of mechanism underlying bookkeeping of fitness gains due to interactions with various partners, is based on variation in the titres of a number of (neuro)hormones that are involved in positive and negative feelings towards those partners (McCall and Singer 2012). To give a caricatured example: the titre of oxytocin of individual X can be a bit higher in reaction to seeing partner Y than before the previous interaction with Y when Y helped X in a fight with Z. This mechanism has been baptised 'attitudinal partner choice' (Fruteau et al. 2009) in an attempt of doing justice to the term 'attitudinal reciprocity' introduced earlier as an alternative mechanism to 'calculated reciprocity' (de Waal 2000). "Emotional bookkeeping" (Schino and Aureli 2009) is, however, both a more general and more intuitive label for basically the same concept. It is possible that different hormones, different combinations of hormones, or a combination of hormonal and neuronal mechanisms are behind short-term and long-term changes in attitude towards partners, but this is not the place to discuss neuro-endocrinological mechanisms in any detail (see for reviews: Glimcher 2003; McCall and Singer 2012; Rilling and Sanfey 2011).

Sexual selection and mating markets

Biological market theory borrows jargon from economics, but sexual selection theory actually provided us with more information and inspiration. 'Reproductive cooperation' can be seen as a special form of cooperation between two (sometimes more) unrelated individuals. From Darwin onwards it has been clear that the dynamics of reproductive

pair formation can only be understood against the background of the ‘mating market’, although oddly enough that specific term only recently became *in vogue* in biology. Sexual selection theory is much older and much better developed than BMT, so the latter has little to add to the former. Nevertheless there are a few cases in which the explicitly economic thinking in terms of supply and demand helped spotting aspects that would have escaped our attention otherwise. To explain this, I start with a rather peculiar example involving green nests and red bishops.

- *Green nests and red bishops*

This story is based on a paper by Metz and colleagues (2007). Male red bishops, a southern African weaver bird, construct elaborate nests in colonies, often in a single tree, that are inspected at length before being accepted or rejected by females looking for a place to breed. When she likes the nest, the female will mate with its builder. Building nests costs considerable time and effort and the males will adapt their investment to the number of females in demand. The females base their choice not only on the shape and sturdiness of the nest, but also its freshness. The plant material from which the nest is built has anti-parasitic effects as long as it is fresh and green, but this fades once the material gets dry and brown. The availability of fresh building material is dependent on rainfall, which can be erratic in the region. When females are scarce, the males are forced to work harder in order to outcompete the other males in the same colony. The choosiness of females on the mating market of the red bishop is therefore determined by the ratio green nests in supply and females in demand for nests, rather than on the Operational Sex Ratio (OSR), the ratio between males and females ready to reproduce at any time, which is the classical parameter of the strength of sexual selection (Emlen and Oring 1977).

- *Human mating markets*

Human mating markets are of interest here for two reasons: Firstly, they show great cultural variation in the way ‘biological’ and ‘economical’ partner choice mechanisms mix. Secondly, they provide some good examples of the added value of paying attention to the effect of changes in supply and demand other than through simply changes in the Operational Sex Ratio (OSR).

A considerable literature about the economic aspects of human partner choice exists. There is a bewildering variety of cultural norms concerning bride wealth and dowry payments, showing that mate choice either way is strongly influenced by economic considerations, be it by the bridal couple itself or their families. Although the variation is probably largely due to cultural evolutionary processes, the practise of adding wealth to the new household, one way or the other, is likely to have direct reproductive consequences by way of increased fertility and reduced mortality of mother and child (for reviews and references see: Buss and Schmitt 1993; Gangestad and Simpson 2000; Grossbard-Shechtman 1993; Testart 2013). These effects become notably apparent, if one analyses data from pre-industrial societies with no access to contraceptives. One of several nice examples is the study of Eckart Voland and colleagues of the 18th and 19th century population of the Krummhörn region in north-west Germany (Voland 1995; Voland and Dunbar 1995; Voland and Engel 1990). In a nutshell: the more land a man has, the younger his bride will be. Access to land in men and age at marriage in women are both closely correlated to reproductive success. This form of ‘assortative mating’ is typical for mating markets in which both sexes exert preference and both have several partners to choose from simultaneously.

Interesting in the present context is the effect of real-time ('life-time') adaptations, as opposed to changes detectible at an evolutionary time scale only, to local differences or short-term changes in supply and demand ratios on mate choice on human mating markets. An early example was reported by Bogusław Pawłowski and Robin Dunbar on the basis of an analysis of so-called 'lonely hearts' advertisements in newspapers, a study obviously conducted before most of the action shifted to the internet (Pawłowski and Dunbar 1999, 2001). By quantifying the number of characteristics desired in the partner and the number of potentially desirable characteristics of the advertiser, the authors showed that advertisers are sensitive to their own relative value in the market. A similar result was also found in a framing study in which subjects looked at soap opera-like sequences with high and low OSR among the actors, respectively (Taylor 2013). Fine-tuning to local supply and demand ratios was found in two studies that analysed mating markets in different regions with marked differences in OSR. In a study using data from the US, women married men of higher socio-economic status when there were relatively fewer women on the local marriage market (Pollet and Nettle 2008). In another study of a polygynous society in Uganda, the same authors found that in general men that owned land were more likely to be polygynous than landless men, as can be expected, but this effect was stronger in regions in which relatively fewer women on the marriage market (Pollet and Nettle 2009). Finally, market-thinking that goes beyond classical sexual selection theory also proved its worth in explaining the variation in reproductive success in older men in various pre-industrial populations on the basis of the resources older men control (Vinicius and Migliano 2016).

To what kind of human markets do biological markets compare?

Commodity swaps vs currency-based trade

If one seeks inspiration from human ('economic') markets to understand natural ones, then one should select the right kind of human markets to compare with. Comparing to highly complex global trade in shares in which transactions are decided in nanoseconds by computer algorithms makes little sense. Human individual trading behaviour should remain visible, since we are talking about trading strategies at the individual level here. This also excludes the use of macro-economic models in which individual behaviour has been averaged out in utility functions and the like. Markets of interests in the present context are those with face-to-face trading. The next question is whether one should limit to direct bartering of goods and services or whether one could compare to markets on which the values of commodities are converted in a common currency too. I think that one can in some exceptional cases, but I'll return this below under 'Currencies'.

Trader classes

A direct comparison between biological and economical markets is most straightforward when both have two distinct classes of traders, e.g. shopkeepers and clients, plants and pollinators etc. Partner choice, i.e. the preference for the best partner and the most profitable deal, drives markets both in nature and in human societies and in both cases one finds uni-directional and bi-directional partner choice (see above).

Embedded markets

Paying attention to the individual relationships of the traders has been well-accepted in sociology and economic anthropology ever since Mark Granovetter published his

seminal paper on ‘embedded markets’ in 1985 (Granovetter 1985), but the basic ideas go back to Karl Marx and Karl Polanyi (Lie 1991). A trader on an embedded market will not follow the rational strategy of *Homo economicus* when trading, but will take all kinds of long terms relationships, friendships, family ties and a host of social norms into account. In some markets, it is simply not done to buy from shop A if one is a regular customer of shop B, even if A’s price for the same product is lower. Inversely, it is not done to charge prices well above the market average from a regular customer (Alexander and Alexander 1991; Frenzen and Davis 1990; Le Velly 2002; Simpson and McGrimmon 2008; Varman and Costa 2008).

As far as I can see from my outsider’s vantage point, the problem with the literature on embedded markets, is that it remains stuck in a descriptive mode without generalisation, theoretical modelling and hypothesis testing. In evolutionary biology this is considered unacceptable since decades - a nice example of the evolution of norms in fact. What we can nevertheless learn from the embedded market literature is that proper market models should reflect all relevant parameters that have influence on a deal between traders. In a game-theoretical model this would mean that norms, friendships, reputations etc. should be reflected in the payoff structure, a job not very likely to be accomplished with simple two-player, two action matrix games. Fortunately, many of the parameters that would be relevant to our understanding of trading in a bazaar, can be safely left out in models of biological markets. But that does not mean that there are many biological markets simple enough to build models assuming just two classes of traders each offering just one easily quantifiable commodity. The underground nutrient exchange markets discussed above may seem to come pretty close, even though the devil is in the rather complicated mechanisms involved in the implementation of partner choice and trading (but see Schott et al. 2016, as discussed above). Primate grooming markets, to give an example from the other end of the cognitive spectrum, tend to be rather messy, because many different goods and services are traded against each other; few, if any, of those can be quantified using a common ‘currency’; trading takes place in the context of kinship ties and relationships that often last for many years, and so forth. The art of modelling, as always, is stripping away as much as possible without distorting the core of the system beyond recognition. This demands intensive communication between theoreticians and empiricists. A good example of that is a recent paper by Wyatt and colleagues (Wyatt et al. 2014). Perhaps the modelling of human embedded markets can move forward too after we get a handle on various biological markets first (see section ‘Common ground’ below).

How different are biological and economical markets?

Two universal differences between human ‘economic’ markets and biological markets seem obvious: the lack of currencies and binding contracts in the latter. However, with a few examples I will argue that even these differences are better seen as different shades of grey rather than black and white. Something similar can be said of two further phenomena that I’ll discuss in this section: negotiation and honest advertisement.

Currencies

In the following I will use the term ‘currency’ as interchangeable with ‘money’, even though some people would perhaps enjoy hotly debating the difference. For me

anything goes, as long as it consists of uniform entities that are recognised by multiple traders as something that can be exchanged against multiple goods or services.

According to the classical definitions of Aristotle a currency has the following properties: (1) medium of exchange; (2) unit of account; (3) store of value and (4) mode of payment (Guyer 2012). The last property is generally assumed to be subsumed under the first three, so I will only ask whether any examples of items with one or more of the first three of Aristotle's characteristics can be found on biological markets. In fact I will simplify the question by concentrating on one specific example: grooming in non-human primates, a well-studied and easily quantifiable behaviour and known to be exchanged against a number of different commodities in a large number of different primate species. The alternative would be using different examples for each of Aristotle's properties, but that risks requiring further extensive explanations for readers not familiar with the natural history involved. I also happen to be a primatologist and some familiarity with the example used certainly helps.

- *Is grooming a medium of exchange?* Consider the following: (1) Almost any group member with the exception of the youngest infants, can provide grooming at any time as long as other activities don't prevent animals from sitting peacefully together. (2) Grooming can be exchanged, in the short or long run, against sex, support in conflicts, protection against predators, tolerance in food patches, food items, access to infants and other group members and perhaps a few more commodities important to non-human primates, including grooming itself. (3) Grooming can be used to equalize unbalanced trade, levelling the 'inefficiencies of barter' in exchanges of other commodities, such as meat-for-sex. So Aristotle will perhaps not turn in his grave when I submit that grooming qualifies as a medium of exchange.
- *Is a unit of grooming time a unit of account?* Obviously, not all minutes of grooming have the same value. In a grooming bout there will be diminishing returns, making the last minute less valuable for the groomee than the first minute, and probably also more costly to provide for the groomer when his hands get tired and opportunity costs rise, for example. The value of grooming may also depend on who supplies it. A minute of grooming will therefore not always give the same amount of 'pleasure', or in other words, will not always have the same utility, but the same is true for *any* currency, as far as I can see. We can ask a more specific question: Can grooming be used to convert the value of tolerance in food patches to gaining access to an infant? Consider the following fabricated, but plausible, story:
 - a) *Subordinate S grooms dominant D for 10 min*
 - b) *D then tolerates S in a food patch*
 - c) *... allowing S to forage 15 min shorter*
 - d) *... and instead groom mother M for 7 min*
 - e) *M's then allows S to hold her infant for 4 min*

Has some amount of 'tolerance' now been converted to some amount of 'access to infants' by expressing both in grooming time units? Perhaps Aristotle would even have accepted that grooming is a unit of account of sorts.

- *Is grooming a store of value?* No, obviously one cannot stack it in the shed or bring it to the bank. However, as stated above, everybody has it handy almost all of the time in quantities limited only by other activities. The latter limitation should not be underestimated, by the way (Dunbar 2010).

Comparing grooming to fiat money used in human societies obviously is a bit of a stretch, but one can ask the legitimate question whether other currencies used by humans come closer. Two categories come to mind: commodity currencies and community currencies.

- *Commodity currencies.* There is an almost endless list of items that have been used, or are still used, as currencies: salt, beads, cloth, arrow heads, cigarettes, barley, shells etc. (Guyer 2012). Their transitoriness (e.g. barley) and the variability of the exchange value of units, makes some of these a bit more grooming-like than fiat money. In Cameroun, for example, bundles of small iron strips were used, but the amount of produce one could buy with a bundle varied considerably with time and location (Guyer 2012). Contrary to grooming, however, most commodity currencies can be stored, but certainly not all – at least not for longer periods.
- *Community currencies.* Some local communities use, or used, so-called community currencies (also known as LETS – Local Exchange Trading Systems). Examples are: time banking (UK, Australia and several other countries), time dollars (US), the Ithaca Hours System (US), noppes (The Netherlands) and so forth (Collom 2011; Richey 2007; Seyfang 2004). The common, rather utopic, idea behind most LETS is that one invests a certain amount of time in some activity for another member of the community (or several members, or even the whole community) and is paid back by another member of the community with activity time as the unit of account. Everybody can invest by using skills (s)he excels in and get paid back in services (s)he is not that good at. For example, plumber A fixes the wastepipes of cleaning lady B for half an hour; lady B cleans the surgery of dentist C for half an hour, where after dentist C fools around in the teeth of A for half an hour. In other words, all activities are considered having the same value as long as they take the same investment in time. Some communities issue vouchers, loyalty cards, locally printed money-like bills etc. to keep track of things. Other communities have a central administration of services delivered and received. The reason why I find it more interesting to compare primate grooming with these community currency systems rather than with fiat money is the fact that value is measured in time units and that transactions take place in closed communities in which people know each other and control each other socially rather than relying on enforcement by third parties. ‘Embeddedness’ is more prominent here than in the formal fiat money-based economies of western societies. Obviously, major differences with grooming remain: bookkeeping in centralised, rather than tracked by each individual, and value generated can generally be stocked for a long time.

Binding contracts

Another feature that is, on first sight, rather unlikely to be found in nature is contracts made binding under the threat of third-party punishment. It would seem improbable that there are institutions in the animal, floral, fungal, bacterial, or whatever non-human kingdom guaranteeing that agents stick to a contract concluded in advance of a cooperative interaction. The creation and maintenance of institutions in human societies that back up contracts, such as police and courts of justice, requires solving complex second-order social dilemmas (Henrich and Boyd 2001; Oliver 1980; Yamagishi 1986).

An agent can also be prevented from breaking a contract without interference by third parties, when he is vulnerable to direct bodily harm inflicted by the partner. But, in such cases one can ask why the partner wouldn't use force to extort the commodity in the

first place? Yet another way of making the breaking of a contract costly is depositing a guarantee in the form of goods that can be seized at any time by the partner. When those goods represent less value than the cooperative investment agreed upon under the contract, there is no reason to fulfil the contract, however. When the goods are worth more, then there is no reason why the partner would not seize the guarantee rather than the investment under contract. Hence, the only effect a deposit of goods has in the context of dyadic cooperative interactions, is reducing the risk for the receiving party. The only fool-proof way of guaranteeing the fulfilment of contracts in nature is, to my knowledge, making the delivery of a commodity inevitable upon the reception of the commodity for which it is traded. An example: a bumblebee cannot enter a flower and suck nectar without getting pollen stuck all over its body and hence transporting it to the flowers visited next. Rather elaborate structures have evolved in flowers to guarantee the transfer of pollen to and from the pollinators' bodies (e.g. Dellinger et al. 2014). Whether or not one would like to compare such mechanisms to binding contracts is a matter of definitions and taste. And it does not prevent occasional nectar-robbers, which usually come in the form of specialised 'parasitic' species, from taking the flower's nectar without transporting any pollen.

There is one example that has been compared to concluding contracts in the literature and worth considering in more detail: the mutualism between bobtail squids and bioluminescent bacteria. The natural history of this mutualism has been studied and described in great detail by Margaret McFall-Ngai and her colleagues (Davidson et al. 2004; McFall-Ngai 2008a, b; McFall-Ngai 2014; McFall-Ngai et al. 2012; McFall-Ngai 2000; Visick and McFall-Ngai 2000; Wang et al. 2010). The term 'contract' is used by McFall-Ngai and colleagues (e.g. in Visick and McFall-Ngai 2000), but the use of contract theory in the context of mutualisms, using the bobtail mutualism as the main example, was worked out in more detail by others (Archetti 2011; Hammerstein and Noë 2016; Weyl et al. 2010).

The natural history is as follows: The squid have light organs that emit light produced by bioluminescent bacteria living in the light organ. The main function of these light organs is to light up the squid from below, so that their silhouettes are less visible from below against the background of the surface. The bacteria benefit from living in the light organ, but they can also live free-floating in the ocean. Most bacteria (90 – 96 %) are expelled every day and the light organ is filled again by the remaining population. A fast-growing bacterial population produces more light than a stable one. The partner choice event of interest here, however, is when the young squids recruit light-emitting bacteria, which make up less than 0.1 % of the bacterial population in ocean water, in their virgin light organs for the first time. How do they select the right bacteria that indeed emit light and how do they keep their organs free from free-riding or even pathogenic bacteria? The solution is producing an anti-bacterial poison, which kills all bacteria except the bio-luminescent ones that have an antidote. The poison – antidote interaction inevitably leads to light production. Glen Weyl and colleagues (Weyl et al. 2010) and Marco Archetti (Archetti 2011) compare the problem of the squid to the problem of companies that want to recruit new employees without having any reliable information about the candidates. Employers that want to avoid costly probation periods can offer contracts with an 'entrance fee', e.g. an amount of money that a skilful employee can easily gain back within a few months, but scares off weak candidates. The logic is that of 'honest signalling' (see below). The bacteria may not sign binding contracts with squids, but the squids can be pretty sure they pay the rent.

Negotiation

Further central questions of BMT concern the propagation of exchange rates through the market and the way in which pairs of traders arrive at exchange rates at or near the level momentarily dictated by the market. To pose a more down-to-earth question based on a concrete example again: how do a young female monkey and the mother of the baby she would like to cuddle know what the momentary price for access to infants is and how do they arrive at a grooming time in accordance with that price? In a first attempt to answer this question, we have done a bit of work on ‘negotiation’ over grooming in vervets (Waal et al. 2013). Negotiation over grooming is nothing very complex. During resting periods of the group one monkey approaches another and it is pretty obvious to both animals (and the observer) that grooming is called for. The question is who starts and who grooms for how long.

In most primates studied grooming goes ‘up the hierarchy’, i.e. the dominant of the pair will receive relatively more grooming than the subordinate. This is generally interpreted as the price paid for services only dominants can provide, e.g. tolerance in food patches and support in conflicts (Barrett and Henzi 2001; Carne et al. 2011; Henzi et al. 2003; Port et al. 2009; Sick et al. 2014; Watts 2010). We start therefore with a baseline asymmetry in almost any pairs of monkeys. In our vervets an approaching female was a bit more likely to start grooming than the one she approached, but the difference was not great. The approachers were a bit more motivated to groom and the stationary ones ready to doze off, probably. What grooming monkeys do is stopping at times to see how the other reacts. The latter can do one of three things: ignore the groomer, start grooming in turn, or present a body part that hasn’t been groomed yet. The latter gesture is very effective: there is a 50% change that a groomer resumes grooming after a new body part has been presented compared to only a few percent if her partner does nothing. As a result grooming bouts last longer when more body parts are presented. So groomers try to groom as little as possible hoping that the other is willing to take over, but they can be persuaded to continue for longer. Sooner or later, though, grooming will stop and when that is depends on the groomer’s motivation and the groomee’s persuasion.

Now imagine a young female grooming a mother with a baby in the hope of being allowed to hold the baby for a while. She will stop grooming once in a while and try grabbing the infant, but the mother will give her a clear sign by shielding off the baby and presenting a new body part, if she thinks she can insist on more grooming. On how much grooming she can insist will, however, depend on the local grooming market. The motivation of the groomer to persist will depend on the alternative options she has, i.e. the number of equally interesting other infants in the group. Mothers will thus soon notice when they are asking too much, because the groomer walks off instead of continuing the groom. I hypothesise that the market-wide price is set through the action of multiple females negotiating with all mothers present in the group.

Honest advertisements

The problem of the honesty of signals was recognized by economists and other students of human behaviours following the lead of Veblen ((1899) and Spence (Spence 1973). They recognised that a signal can be honest, i.e. correlates well with the qualities of the signaller, when it is costly and hence cannot be produced by individuals that lack the means of producing it. The basic idea was re-invented in biology by Zahavi (1975, 1977) under the label ‘handicap principle’, which after initial scepticism (Maynard Smith 1976,

1978), followed by rehabilitation (Grafen 1990), lead to considerable activity, both in the form of theoretical models as well as empirical tests.

The honesty of advertisements is an issue in some, but not all biological markets. In some cases, notably with few big organisms going into a mutualistic relationship with many members of a small species, e.g. plants with rhizobia or figs with fig-wasps, the big partner will initially accept any small partner that presents itself, but will end the relationship with all partners that turn out not to be profitable. A plant expels badly performing rhizobia from its roots (Denison 2000); a fig aborts figs that contain too many fig wasp larvae, even though it needs fig wasp females born in its figs to ensure the transport of its pollen to other figs (Bull and Rice 1991). Expelling small partners, of which a number of examples exist and a variety of mechanisms has been described, is nowadays often called 'sanctioning', as mentioned above (section 'Choice before or after investment'). For the big partner this usually doesn't mean the end of benefits from cooperation, but just a few partners less. For the small partner it may be the end of the road; a strong form of selection through partner choice indeed. In systems with sanctioning partners involved, partner choice is based on the actual net gain assessed during ongoing relationships and honesty is therefore normally not an issue.

In other cases, mechanistic solutions have evolved that make the mutual profitability of a cooperative interaction virtually guaranteed, once both parties have chosen to engage in it. The mutualism between bobtail squid and bio-luminescent bacteria, mentioned above, is an example. I also mentioned some rather complicated structures in flowers that ensure the transfer of pollen to the pollinator in that context. However, the pollination of flowering plants also stands for a mutualistic interaction in which the honest advertisement problem looms large. Flower petals are like billboards advertising the presence of flowers at a distance and before the visiting pollinator has got any nectar, he has already invested some time and effort by visiting the flower. Flowers that are permanently empty exist (Bell 1986; Gilbert et al. 1991), but most are at least temporarily empty after pollinators removed all nectar from it. Some flowers will replenish the nectar reward again, but that takes some time, while others will go out of business after a first successful visit. So it is no surprise that an arm's race has evolved between flowers that try to lure pollinators with little reward and pollinators that got very good at sensing the presence of nectar at great distances or sometimes the secondary signals, such as changes in humidity and electric fields that betray the recent visit of a competitor (e.g. von Arx et al. 2012). Plants that have sent and/or received the pollen they want, have no interest in attracting pollinators any more, since these are likely to do more harm than good. All kinds of flower signals evolved therefore, e.g. changes in colour, signalling that a reward is no longer available. For a further discussion of these issues see a chapter by Ben Fraser (2013).

One last remark: I prefer to avoid suggestive terms such as 'cheater', 'free-rider' or 'parasite' in this context. It is sometimes useful to have a label that is easy to remember, but charged labels risk causing bias against alternative explanations. More importantly, BMT stresses the fact that partners can bestow a net gain and nevertheless be rejected in favour of even more profitable ones. Only in systems that function under the adagio 'the more partners the better', will partners be expelled or aborted because they yield zero net benefit or even incur costs. In such cases the label 'cheater' may be warranted, even though it doesn't add much to our understanding.

Common ground

The history of biology and economics is full of re-invented wheels. Most, if not all of these wheels were invented in economics first, I must admit. Well-known examples are 'honest signalling', as mentioned above, and the re-invention of game theory (von Neumann and Morgenstern 1944) and the especially Nash equilibrium (Nash 1951) by John Maynard Smith (Maynard Smith 1974, 1982; Maynard Smith and Price 1973). In Maynard Smith's evolutionary game theory the Nash equilibrium resurfaces as one of two conditions for an 'evolutionary stable strategy' (ESS), a notable example too of biologists re-inventing, but also improving and extending an economical concept.

Here I focus on two, mutually interdependent, parallels specific to biological markets: the biological equivalent of the 'markets - firms' dichotomy and the comparison of 'transaction costs' in economic models and 'search costs', also known as 'costs of choice', in sexual selection and partner choice models.

The equivalent of the 'markets - firms' dichotomy

Economists make a distinction between markets and firms. According to 'transaction cost theory' (Coase 1937) traders tend to escape from market forces by getting organised in firms when the costs of obtaining a commodity on the open market are higher than the costs of producing the commodity within a closed unit. In a broad sense a firm can be defined as any entity that reduces the costs of acquiring a commodity by producing it cheaper by better internal organisation: a firm can be a commercial company, a medieval guild, an association etc. I will avoid burning my biological fingers on definitions of markets and firms, but instead start with two citations from Coase's classic paper: On p. 388 he writes: *"Outside the firm, price movements direct production, which is co-ordinated through a series of exchange transactions on the market. Within a firm, these market transactions are eliminated and in place of the complicated market structure with exchange transactions is substituted the entrepreneur-co-ordinator, who directs production. It is clear that these are alternative methods of co-ordinating production."* Followed on p. 389 by: *"... the distinguishing mark of the firm is the supersession of the price mechanism."*

Obviously, the dichotomy between firms and markets isn't as clear cut as Coase originally suggested: cartel formation between firms and other mechanisms distort the idealized price-setting of friction-free markets, firms, notably large ones, can suffer from internal competition and often have internal transaction costs too (Walker and Weber 1984). The question where exactly the firm ends and the market starts is reminiscent of the discussion about the levels of adaptation in biology (also known as the 'levels of selection' problem, but see Gardner and Grafen (2009) for an explanation of why adaptation, rather than selection, is the crucial issue): which unit is coherent enough to act, in practise as well as in evolutionary modelling, as a packet of genes on which natural selection acts as if it is a single unit?

Units of adaptation, and hence biological equivalents of firms, can in principle be found at many different levels of organisation. In fact the 'Major Transitions in Evolution' (sensu Maynard Smith and Szathmáry 1995) can be compared to mergers of smaller firms into bigger ones, reducing the forces of the free market more and more in the process. Thus, any individual is a biological firm, since it consists of packages of genes that reproduce in a largely coordinated fashion. Notably the eukaryotic genome

resembles a construction kit assembled from DNA originating from many different species. Eukaryotic individuals are not only gene-packages, but also units including vertically inherited symbionts, such as mitochondria and chloroplasts, which originated from independently living organisms. Groups of individuals resemble firms if they are somehow well-organised, for example due to kin structure and/or strong leadership. Groups can have reduced internal competition, notably due to a hierarchical organisation based on dominance relationships. Group may communally produce commodities more efficiently than is possible for solitary-living individuals, for example by defending common territories and resources, by reducing the risk of predation and so forth.

Those that like the idea of comparing groups to firms should not forget, however, that group-living in most species is explained by the reduction of predation costs in the form of lower mortality, but also of shared vigilance. This is achieved at a price of increased competition over resources compared to a solitary life-style (Alexander 1974; van Schaik 1983; van Schaik and van Hooff 1983). The improved access to resources due to the strength of the group compared to competing groups is unlikely to compensate for the increase in the costs of competition due to group-living. Living in a group implies indirect scramble competition as well as direct contest competition with one's worst competitors: conspecifics. Dominance relationships dampen the ill-effects of contest competition over resources, but the competition of many mouths eating the same food remains. If a group of animals is a biological firm, then it is one with inefficiencies due to internal competition. Eusocial groups, such as found in bees, wasps, ants, termites and several other species, including mammals such as naked mole-rats, may be better organised firms with division of labour by morphologically different castes, but they still harbour quite a bit of conflict (reviewed in Davies et al. 2012, Chpt 13).

Better biological examples of entities resembling firms are obligate mutualisms in which host organisms inherit endosymbionts from their parents. The relationship host-symbiont is notably tight when the symbiont is inherited intracellularly, i.e. as an organelle living the cells of the host and transferred to the next generation in the gametes of one or both parents. With this mode of inheritance the mutualistic entity is comparable to a single organism, whereby the contours of the 'organism' concept become blurred (Queller and Strassmann 2009). The latter authors define an organisms 'a unit with high cooperation and very low conflict among its parts' (p. 1344) and earlier on the same page they indeed compare organisms thus defined with firms. Cooperation and conflict between host and symbiont is at a level comparable to the cooperation and conflict among the genes of a single organisms in the 'parliament of genes' (Leigh 1971). As is true for real parliaments, however, the genome is full of conflicts too (Strassmann and Queller 2010).

Host – symbiont mutualisms in which the symbionts are 'horizontally transmitted', i.e. acquired through partner choice by the host, provide good biological examples of markets, as argued above. In some cases the symbionts are acquired only once at the start of the life cycle of the host, e.g. in the bobtail squid – bioluminescent bacteria mutualism described above, or they are recruited throughout the hosts life-cycle, as in the plant – rhizobia mutualism, also described above. Companies, consisting of sets of individuals working together in the common interest of their firm, compete with other companies on the market. However, the composition of the work force of a company is the result of market forces on the labour market and promotions may invoke fierce internal competition, so employees that work together as a closed firm at one moment

compete with each other on open markets at another. The cyclic alternation of firm-dominated and market-dominated phases is even more obvious in universities that go through a yearly ritual of selecting students all at the same time, all selecting from the same pool of high school absolvents that all of which apply for overlapping sets of universities. Such firm – market cycles can also be recognised in many a mutualism in which horizontally acquired endo-symbiotic partners: the life cycle starts with the recruitment of partners, followed by a period during which host and symbionts have their eggs in the same basket. In many cases such recruitment phases return periodically, interspersed with periods during which interests are aligned again. This may even be the case in vertically, but extracellularly transmitted symbionts in which horizontal transmission occurs occasionally, i.e. once in many generations (Kaltenpoth et al. 2014). Thus within the big host – small symbiont type of mutualisms, we find examples that resemble firms, examples that resemble markets, and examples that resemble either depending on the phase in the life-cycle of the host.

Other examples of alternating market-like and firm-like phases are found in the life-cycles of numerous socially living micro-organisms ('social microbes'). Examples include various *Volvox* species, which are green algae that form complex colonies; *Dictyostelium* slime moulds, amoebae that go through free-living phases as well as various forms of aggregations such as slugs that move around as a single entity and fruiting bodies and *Myxococcus xanthus*, bacteria that form biofilms and feeding swarms that act like hunting packs in carnivores (Queller and Strassmann 2009).

Transaction costs compared to the costs of partner and mate choice

When the transaction costs are very low, the market has very little friction, supply and demand are in balance, the price is at equilibrium and the markets 'clear' (= Say's law). Ronald Coase did not use the term 'transaction costs' yet, but wrote about the concept as early as 1937 (Coase 1937), but the concept is perhaps better known via the work of Coase's fellow Nobel laureates Oliver Williamson (Williamson 1979, 2005) and Douglass North (North 1990).

One equivalent of transaction costs in biology is the 'costs of mate choice' in sexual selection models (Real 1990, 1991). Early models of sexual selection overlooked these costs, which led to ill fits with empirical data (discussed in Andersson 1994, Chpt 2). Since we were familiar with these developments (Hammerstein and Parker 1987) and assumed that our fellow biologists would share this knowledge too, Peter Hammerstein and I considered the costs of partner choice and partner switching to form an essential element of any biological market model from the start without much further ado.

High transaction costs/costs of partner choice causes a lot of friction in the market up to a point at which market mechanisms no longer work. At that point cooperation will be better described by partner control models, such as those based on two-player IPDs, than by partner choice models, such as BMT. The cooperating dyad becomes a small firm of two and the question is how they reduce production costs within their firm.

Conclusion

A comparison between human and natural markets can easily get bogged down by nit-picking about definitions of what 'markets', 'currencies', 'contracts' and other core

features are and whether these have equivalents in nature. This would, however, obscure the, to me at least, obvious fact that there is a lot of the common ground, which can be put to good use and inspire new questions and hypotheses in both directions.

My main interest is not to search for historical continuity in the evolution of markets or trading behaviour. Strategies of non-human and human traders may resemble each other, but the mechanisms by which these strategies are implemented, and hence the actual items sensitive to natural selection, are unlikely to show much continuity between species as far apart on the tree of life as bacteria, fungi, plants, insects and vertebrates. Those specifically interested in the evolutionary roots of human trading behaviour should probably look no further than the non-human primates or eventually group-living vertebrates in general. The 'origins' question is in any case better phrased as one about the evolution of cooperation.

Recognizing common properties and using those as reference points of common theoretical models, notably based on game theory and agent-based modelling, can lead to the cross-fertilization in several ways:

- Insights from economics can inspire hypotheses about biological markets, e.g. an understanding of why commodities are produced within the firm as opposed to purchased on the market can inspire hypotheses about the evolution of symbioses and notably about the issue of 'vertical' acquirement of symbionts by heritage versus 'horizontal' acquirement from the environment.
- Insights in the effect of the cost of partner choice and partner switching from both economics ('transaction costs') and sexual selection theory ('search costs'), can help understanding why and under which circumstances partner control mechanisms eclipse partner choice mechanisms on biological markets.
- Some biological markets can serve as models for human 'economic' markets. The art is in finding the right matches. I could, for example, imagine using nutrient exchange markets, such as between rhizobia and plants or mycorrhizal fungi and plants, as testing grounds for 'comparative advantage'-based trading between firms. Biological markets on which sessile organisms such as plants, have to attract mobile partners to ensure the transport of their pollen or their seeds, or to protect themselves against herbivores, can be used as model systems for job markets, retail markets and education markets, all of which have few sessile actors (employers, shops, universities etc.) and many mobile ones (employees and applicants, customers, students etc.). 'Embedded markets' may find their parallels in the grooming-based markets of non-human primates.
- There is something to learn about the question of honest advertisement in economics from the insights about honest signalling in biology. After being introduced elsewhere (see above), our insights have been advanced considerably by developments, both empirically and theoretically, in biology. A lot of signalling occurs in market-like contexts in which less mobile traders signal to attract more mobile partners.
- The differences between natural and human markets can also be exploited to understand how crucial and 'uniquely human' phenomena, such as verbal negotiation, the conclusion of binding contracts and the use of universal currencies, really are. Do these lead to qualitatively different markets or rather to more efficient markets at quantitatively larger scales?

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