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Essay

Are primates out of the market?

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Biological Market Theory (BMT) has provided an elegant framework to study how commodities are exchanged among individuals. In primates, BMT predicts that individuals exchange grooming with other commodities based on the law of supply and demand. However, BMT still suffers some theoretical and methodological limitations. Our aim in this paper is to discuss some of these limitations, including the lack of consensus over the time frame in which exchanges take place, and over the commodities involved, the cognitive challenges imposed by biological markets (BMs), and the heterogeneity of methods used to test BMT across studies. In particular, we discuss (1) the importance of predetermining both the time frame over which exchanges take place and (2) the commodities that are exchanged in primate BMs, (3) the cognitive skills that primates need to navigate in a BM, and (4) other methodological issues arising when testing BMT. For each of these points, we propose an agenda with possible solutions and we show how the issues raised also apply to BMs in species other than primates.

Biological market theory (BMT) was introduced by Noë and Hammerstein (1994, 1995) to explain how commodities are exchanged among individuals. In biological markets (BMs), classes of traders exchange commodities to their mutual benefit, whenever commodities cannot be obtained by the use of force and are under the exclusive control of one class (or only accessible from alternative sources at high costs). Within the same class of traders, individuals compete with each other over access to partners, by providing more valuable commodities rather than engaging in aggressive behaviour. Therefore, individuals are chosen as partners depending on the value of the commodities they offer, and the choice is made by comparing the offers of all potential partners, similarly to what happens in human markets. As a result, resources with no a priori intrinsic value are exchanged according to the laws of supply and demand, explaining the formation of short and finite relationships between different classes of individuals.

So far, BMT has provided an elegant framework to study social relationships in areas that span from sexual selection, interspecific mutualism and intraspecific cooperation. However, BMT still suffers from a series of theoretical and methodological problems that limit its applicability in some research areas. Our aim in this paper is to discuss these issues and pinpoint possible ways to better address them in the future. We mainly restrict our review to intraspecific exchanges of commodities and, especially, to the primate biological market (PBM). However, at the end of each section, we also assess how the problems raised also apply to BMs in species other than primates. In the following sections, we (1) introduce PBMs, (2) discuss the lack of a clear time frame over which commodities are exchanged, (3) review the commodities exchanged in PBMs, (4) discuss the cognitive challenges imposed by BMs, (5) question the use of heterogeneous methods to test PBMs and (6) draw general conclusions on our actual knowledge of PBMs.

THE PRIMATE BIOLOGICAL MARKET

In most primates, grooming is frequently exchanged among group members. In female philopatric groups, grooming mainly occurs between females with a similar rank, although higher-ranking individuals usually receive more grooming than they give (e.g. Dunbar, 1992; Schino, 2001; Seyfarth, 1980). To explain these consistent findings, Seyfarth (1977) introduced a model assuming that (1) grooming is highly valuable for primates, (2) females are attracted to each other, but especially to higher-ranking individuals, who might provide valuable agonistic support, (3) time to engage in grooming is limited, (4) females compete with each other to reach an optimal ratio between grooming received and grooming given, and (5) higher-ranking individuals outcompete others when trying

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to access the same partner. When these assumptions are met, females groom partners with a similar rank, and higher-ranking females receive more grooming than they give (i.e. females 'groom up the hierarchy'), which is exactly what has been found in most primates (e.g. Schino, 2001).

According to some authors, however, agonistic support is not a common event in primates, and grooming is unlikely to be exchanged for such an uncertain future benefit (Barrett & Henzi, 2006; Henzi & Barrett, 1999, 2007). Therefore, when individuals groom up the hierarchy, they might exchange grooming for rank-related benefits other than agonistic support, such as tolerance over food or other commodities that higher-ranking individuals monopolize and might trade for grooming (Barrett & Henzi, 2006). Moreover, when competition is low and resources cannot be monopolized, dominance gradients are usually shallow and higher-ranking individuals have few commodities to trade for grooming; therefore, grooming should be mainly exchanged for grooming in a reciprocal way (Barrett, Gaynor, & Henzi, 2002; Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Henzi et al., 2003). Consequently, some authors have advocated the need for a more dynamic theory, better able to catch the variety of benefits that may be traded for grooming, and have pointed out that exchanges might be affected by the level of competition in a group and by whether it is possible to monopolize resources. In this respect, BMT was the perfect candidate to improve, although not fully replace, Seyfarth's (1977) model.

The main advantage of applying BMT to primate exchanges is that it offers a richer and more dynamic tool to understand the complexity of primate interactions, as compared to Seyfarth's model. First, BMT offers a more individual-based approach, in which individuals behave differently depending on the commodities traded and the interacting partners (Barrett & Henzi, 2006). Therefore, rather than exerting their control over the partner in dyadic interactions, individuals freely choose their partners among all group members in order to maximize profit (Noë & Hammerstein, 1994). Second, BMT takes into account dynamic changes in the group: supply and demand determine the bartering value of commodities, and the 'value' of each partner changes through time depending on the commodities it can trade (Noë & Hammerstein, 1994). However, if circumstances do not vary, it becomes impossible to test whether exchanges follow the law of supply and demand, since by definition both of these variables remain constant (Barrett & Henzi, 2006). Finally, BMT provides an appealing alternative to the central role played by agonistic support in Seyfarth's (1977) model, which despite being a sort of BM on its own (according to Henzi et al., 2003), failed to consider the wide range of commodities that primates might exchange for grooming (Henzi & Barrett, 1999).

TIME FRAME OF EXCHANGES

One problem of BMT, however, is that we do not know the exact time frame over which exchanges take place. Are commodities exchanged within minutes, hours or even months? Determining the real time frame of interaction is a crucial problem for all studies analysing exchanges among individuals, even when they are not explicitly framed in a BMT (e.g. Gomes & Boesch, 2009; Gomes, Mundry, & Boesch, 2009; see Schino & Aureli, 2010). Although it might be difficult to determine the time frame over which animals exchange commodities, and over which BMT should be tested (Barrett et al., 2002, 1999), understanding this time frame appears a crucial preliminary step to test BMT, rather than 'an important goal for the future' (Barrett & Henzi, 2006, p. 231).

So far, most authors have assumed that primates exchange commodities on a very short-term basis. Barrett and Henzi (2006), for instance, predicted that primate exchanges depend on their current needs and the immediate availability of commodities. The reason for that is that most primates (with the possible exception of great apes: Barrett & Henzi, 2006) would lack the cognitive skills to keep track of the value of multiple commodities over long time frames (see section Cognitive challenges). Even grooming would be traded for grooming within single bouts, and this should be a crucial mechanism to maintain grooming dyads over time (Barrett & Henzi, 2002, 2006; Henzi, Lycett, & Weingrill, 1997). Several studies have provided evidence that grooming given and grooming received are time matched within bouts (e.g. Barrett et al., 2002, 1999; Chancellor & Isbell, 2009; Payne, Lawes, & Henzi, 2003). However, most of these studies only analysed bouts in which both individuals provided grooming (e.g. Barrett et al., 2002, 1999; Chancellor & Isbell, 2009; see Gumert, 2007a, for a similar approach in grooming – sex exchanges). In this way, up to 82% of all grooming bouts are completely dismissed from analyses (e.g. Chancellor & Isbell, 2009). The risk of only analysing bouts that already hint to some form of reciprocation is that different conclusions might be reached (see Manson, Navarrete, Silk, & Perry, 2004). Moreover, if grooming is reciprocated within bouts, why are there so many bouts in which only one individual grooms the other?

Other authors have also observed that primates often fail to reciprocate within bouts, and suggested that primates might exchange goods over an intermediate time frame (e.g. Frank, 2007; Manson et al., 2004; Schino, di Giuseppe, & Visalberghi, 2009; Schino, Polizzi di Sorrentino, & Tiddi, 2007). In bonnet macaques, *Macaca radiata*, for instance, immediately reciprocated bouts account for only 5–7% of the total grooming observed, so that grooming is significantly unbalanced over longer time spans (Manson et al., 2004). In line with this, de Waal (1997) found evidence that grooming is exchanged for (passive) food tolerance within a 2 h time frame. Similarly, Fruteau, Voelkl, Van Damme, and Noë (2009) found that food is exchanged for grooming within 1 h, leading them to talk about 'exchange rates fluctuating from day to day' (Fruteau et al., 2009, p. 12007).

To our knowledge, few studies have specifically analysed the time frame over which primate exchanges occur. Importantly, these studies also included bouts in which exchanges were not immediately reciprocated. Frank and Silk (2009) found that grooming in olive baboons, *Papio anubis*, was more evenly balanced across multiple bouts, rather than within single bouts. Interestingly, most grooming bouts were completely one-sided, and females did not groom up the hierarchy, suggesting that grooming is not reciprocated in the short term, but also not exchanged for other commodities. Two other studies were not explicitly framed in line with BMT, but also found that great apes exchange commodities over long time frames (grooming – grooming: Gomes et al., 2009; sex – meat: Gomes & Boesch, 2009). Gomes et al. (2009), for instance, found that grooming in chimpanzee, *Pan troglodytes*, dyads is reciprocated over a period of 15 months. Similarly, Gomes and Boesch (2009) found that female chimpanzees copulate more with males having shared meat with them over a period of 22 months, but not in the short term. At least in great apes, therefore, exchanges would happen on a long-term basis. Importantly, by extending the time frame over which exchanges take place, these findings would also reconcile BMT (assuming that exchange of commodities drives the formation of short-term finite relationships) with the cumulating evidence of long-lasting social bonds in primates, which appear to be robust through time and crucial for individuals' fitness (e.g. Langergraber, Mitani, & Vigilant, 2007; Lehmann & Boesch, 2009; Mitani, 2009; Seyfarth & Cheney, 2012; Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010).