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.

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**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...
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 primate exchanges, 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 dynamics 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, 2006). 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 primate exchanges 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, 2007, 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 Noé (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 chimpanzees, 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).
Determining the real time frame over which exchanges take place is clearly a hard task, especially in primates, the species of which differ significantly in terms of ecology, demography and social structure. First, different species may use different time frames, reflecting their ability to keep track of values and exchanges over longer periods (see section Cognitive challenges). Second, even dyads belonging to the same group and species might exchange over different time frames. In chimpanzee dyads, for instance, providing grooming increases instances of food sharing in the following hours, but the effect is stronger for those dyads rarely grooming each other (de Waal, 1997; but see Colmenares, Zaragoza, & Hernández-Lloreda, 2002; Leinfelder, De Vries, Deleu, & Nelissen, 2001). This suggests that individuals with looser bonds (e.g. rarely grooming each other) might show more contingency-based exchanges, while individuals with stronger bonds might reciprocate over longer time frames, because their relationship quality allows them to better tolerate unbalanced exchanges and reciprocate over longer time frames (see Cheney & Seyfarth, 2012). Third, individuals might discount commodities provided over a long time frame: primates are known to prefer immediate over delayed rewards (e.g. Stevens, Hallinan, & Hauser, 2005), so that grooming provided today might not be the same as grooming received tomorrow. How should researchers take this into account when analysing data? Fourth, the amount of data collected might affect the time frame over which exchanges of commodities correlate. When observations of particular events are scarce, power is low and reciprocity might be revealed over longer time frames (e.g. Gomes & Boesch, 2009). Therefore, simply increasing the hours of daily observations might lead to very different results (see Campenni & Schino, 2014). If grooming is provided randomly, for instance, rates of grooming given and received tend to balance over long periods of observation, providing another explanation as to why exchanges of commodities balance over several months, and casting doubt on the existence of PBMs with long-term time frames (e.g. Frank & Silk, 2009; Gomes & Boesch, 2009; Gomes et al., 2009).

Overall, these considerations cast doubt on the existence of a general time frame of interaction over which primate exchanges take place. Therefore, although BMT provides no guideline to solve this issue, it is evident that we need to make clear, justified, specific a priori predictions on the exact time frame of exchanges, which presumably varies according to the species, individuals and currencies involved. Even if it were feasible to predict that chimpanzees exchange sex for meat in 22 months (Gomes & Boesch, 2009) but grooming for food in 2 h (de Waal, 1997), which would be the biological significance of our prediction? In their brilliant review, Gilby, Thompson, Ruane, and Wrangham (2010) noted how surprising it is that meat sharing predicts long-term, but not short-term mating frequency in Gomes and Boesch’s (2009) study. Why should males give meat to oestrous females who will only reciprocate with mating within 22 months? Finally, consistency in the interpretation of results is needed. When analyses are limited to immediately reciprocated exchanges (because exchanges would happen in the short term), longer-term consequences should not be inferred. If it is assumed that exchanges happen in the same bout, for instance, one should not conclude that grooming that is not immediately reciprocated in a bout might be reciprocated over a longer time frame (Chancellor & Isbell, 2009). Similarly, if grooming is predicted to be exchanged for sex in the same bout, there is no reason to infer that grooming might also secure more sexual opportunities after the bout (Comert, 2007a).

In the future, experimentally controlled studies should be implemented to improve our understanding of the time frame over which exchanges take place. One possible approach could be to test captive populations (where confounding variables are easier to control) with a protocol similar to that used by Frutet el al. (2009). In their study, exchanges of grooming were regularly monitored across three phases: (1) a baseline phase, in which no experimental manipulations were introduced; (2) the experimental phase, in which one individual allowed group members access to food; (3) a subsequent phase, in which more individuals provided food access to group members. Comparisons of grooming across phases allowed the researchers to see whether food access was exchanged for grooming, and the time frame over which these exchanges took place. By carefully keeping other commodities constant across phases (e.g. no infants are born, no females are in oestrus, no other food sources are monopolized), one could use this approach to test whether and when individuals are groomed in exchange for food access. Importantly, by varying the commodity monopolized by individuals (e.g. access to food, outdoor areas, oestrous females, mothers with infants), we could understand whether different commodities are exchanged across different time frames. If we could determine an exact time frame for exchanges, we could question its biological significance (e.g. why would primates exchange some goods within the very same bout, but others within months?); the mechanisms allowing these exchanges (see section Cognitive challenges) and the validity of using the same time frame across different contexts and populations.

Determining the time frame of exchanges appears to be a key issue in studies of primates, but might be less crucial in other species. In a series of studies by Bshary, for instance, cleaners and client fishes interacted according to BMT (Bshary, 2001; Bshary & Grutter, 2002: Bshary & Grutter, 2002: Bshary & Schaffer, 2002). However, the time frame over which commodities were exchanged was not a real issue, as interactions (once established via partner choice) always involved the contextual exchange of the same two commodities. In contrast to primates, individuals in other species might simply lack the chance to engage in exchanges over longer time frames, by not living in the same cohesive long-lasting social group in which exchanges may be reciprocated over long time frames. Probably, the same issues raised for primates will instead concern BMs in other species living in cohesive long-lasting social groups, such as social carnivores or marine mammals.

**COMMODITIES EXCHANGED**

Grooming is highly valuable for primates, serving multiple functions: it might strengthen social bonds (Dunbar, 1984), cement coalitions (Seyfarth & Cheney, 1984), produce endorphins (Keverne, Martensz, & Tuite, 1989), serve a hygienic function (Hutchins & Barash, 1976; Saunders & Hausfater, 1988; Tanaka & Takefushi, 1993; Zamma, 2002), modulate immune system changes (see Gust, Gordon, Brodie, & McClure, 1996) and reduce tension (Aureli, Preston, & de Waal, 1999; Schino, Rosati, & Aureli, 1998). According to BMT, grooming is thus both a valuable commodity and a currency to exchange for other commodities (Barrett & Henzi, 2001; Barrett et al., 1999). However, the intrinsic costs and benefits of grooming are still debated (see Kaburu & Newton-Fisher, 2015; Russell & Phelps, 2013; Schino, Ventura, & Troisi, 2003), and its multiple functions might make grooming ambiguous to interpret (see Colmenares et al., 2002; Metz, Klump, & Friedl, 2007). For example, grooming might have a different value across species (see Barrett & Henzi, 2006; Manson et al., 2004), and ‘not all instances of grooming need represent market trading’ (Barrett & Henzi, 2006, p. 216), meaning that some grooming might not be traded for other commodities. However, the effect of these variables cannot be easily predicted or quantified. Furthermore, according to BMT, grooming is largely exchanged for other commodities when hierarchies are steep (and higher-ranking individuals manipulate commodities), and is highly reciprocal when hierarchies are
swallow (and commodities cannot be monopolized; Barrett et al., 2002, 1999; Henzi et al., 2003). However, all individuals exchange grooming with each other and grooming is thus always partly reciprocal, regardless of the dominance gradient (Barrett & Henzi, 2006). For instance, grooming might be traded for grooming also when hierarchies are steep and conditions ‘stressful’ (Balasubramaniam, Berman, Ogawa, & Li, 2011, p. 1269), or if ‘the sole benefits that grooming itself offers’ are enough (Henzi & Barrett, 1999, p. 54). Consequently, the steepness of the hierarchy provides only partially reliable indications of the commodities that individuals would exchange.

If grooming can be traded for different commodities (e.g. grooming, food, tolerance at feeding or drinking sites, access to infants, preferential mating, agonistic support), which percentage of grooming given should we correlate with the amount of each commodity received, when testing BMT? Correlating grooming with more than one commodity is no solution: if grooming is a currency paid in exchange for some commodity according to the law of supply and demand, the same amount of grooming cannot be exchanged for more than one commodity (e.g. Carne, Wiper, & Semple, 2011). In turn, commodities might be exchanged with each other. For instance, different studies have shown that grooming is traded for sex (e.g. Gumert, 2007a), sex for food (e.g. Gomes & Boesch, 2009) and food for grooming (e.g. Fruteau et al., 2009). How can we predict the complex ways in which all these commodities might be exchanged with each other? Note that the problem is not solved by analysing only those bouts in which two commodities are exchanged: first, commodities might be exchanged with each other also across bouts (see section Time frame of exchanges); second, some grooming in a grooming bout might not represent ‘market trading’; and third, even within the same bout individuals might exchange more than two commodities.

Another approach is to analyse how grooming is distributed among group members: if grooming is not exactly reciprocated, and higher-ranking individuals receive more grooming than they give, it is assumed that grooming is traded in exchange for commodities that only higher-ranking individuals can provide (Barrett et al., 1999; Henzi et al., 2003). Meta-analyses, for instance, have shown that primates often groom up the hierarchy, suggesting that grooming is exchanged for rank-related benefits (Schino, 2001; Schino & Aureli, 2008). However, this is not always the case, even when dominance hierarchies are steep and individuals should groom up the hierarchy (e.g. Balasubramaniam et al., 2011; Colmenares et al., 2002; Leinfelder et al., 2001; Schino et al., 2003). Moreover, grooming up the hierarchy is per se no proof of BM, as this explanation also fits Seyfarth’s model. To prove BMT, one would also need to show that there is really an exchange taking place, and that this exchange happens according to the laws of supply and demand, by, for instance, being stronger in groups with a steeper dominance hierarchy. What evidence do we have so far for exchanges of commodities following the laws of supply and demand in primates?

**Grooming for Tolerance, Agonistic Support, Aggression**

Primates can trade grooming for increased tolerance over food (e.g. Barrett et al., 2002; Carne et al., 2011; Richter, Mveis, Malaviyijitnond, Schüßke, & Ostner, 2009; Tiddi, Aureli, Polizzi di Sorrentino, Janson, & Schino, 2011; Ventura, Mojolo, Koyana, Hardie, & Schino, 2006; de Waal, 1997; but see Frank, 2007; Fruth & Höhmann, 2002; Kaburu & Newton-Fisher, 2015; Molesti & Mojolo, 2015; Stevens, Vervaecke, de Vries, & van Elsacker, 2005; Surbeck & Höhmann, 2014; Vervaecke, De Vries, & Van Elsacker, 2000; Watts, 2002). They may also trade grooming for agonistic support (e.g. Carne et al., 2011; Koyama, Caws, & Aureli, 2006; Schino, 2007; Schino et al., 2007; but see Silk, Alberts, & Altmann, 2004; Stevens, Vervaecke et al., 2005), although this might require planning skills that most primates would lack (Barrett & Henzi, 2006; see section Cognitive challenges). Some studies have also found a positive correlation between grooming provided and aggression received (e.g. Gumert & Ho, 2008; Port, Clough, & Kappeler, 2009; Schino, Ventura, & Troisi, 2005; Xia et al., 2012, 2013): some individuals might ‘extort’ grooming by the threat of force, and partners might groom them more to reduce aggression (e.g. Barrett & Henzi, 2006; Schino et al., 2005). However, the risk lurking in this elegant explanation is that any result can be a posteriori interpreted as evidence of BM: If A provides food to B, B will groom A in exchange (e.g. Fruteau et al., 2009); but if A is aggressive to B, B will also groom A in exchange (e.g. Schino et al., 2005). Moreover, how can we know how much of the grooming provided is paid in exchange for some commodity (e.g. agonistic support, tolerance) and how much serves an appeasement function, being exchanged for a commodity that we cannot measure (e.g. lack of aggression)? In the end, given that PBM should be a free market in which individuals do not compete aggressively over resources (Noë & Hammerstein, 1994; but see Bshary, 2001; Clutton-Brock & Parker, 1995), the mere possibility that some individuals might be aggressive to ‘extort’ other commodities might be seen as a distortion of market forces and used to explain negative results that otherwise would not fit BMT (e.g. Balasubramaniam et al., 2011; Gumert, 2007b; Kaburu & Newton-Fisher, 2015). Importantly, these findings also cast doubt on the possibility of realistically considering primate groups as BMs: primates generally appear to aggressively compete to access partners and resources (i.e. partner control), in contrast to the assumption of BMT, according to which individuals would freely choose their partners depending on the commodities available on the market (e.g. Noë & Hammerstein, 1994).

Furthermore, some studies have shown that primates reciprocate grooming to a lesser extent when the hierarchy is steep, as predicted by BMT, but have failed to provide evidence that grooming is exchanged for other rank-related commodities (e.g. Balasubramaniam et al., 2011; Stevens, Vervaecke et al., 2005). Recently, Kaburu and Newton-Fisher (2015) failed to find evidence that chimpanzees with a steeper hierarchy trade grooming for agonistic support, while chimpanzees in more egalitarian groups groom more reciprocally. Instead of concluding that grooming reciprocity was not affected by hierarchy steepness and that their study thus provides no evidence of a BM, they argued that ‘grooming is sufficiently valuable to male chimpanzees that they will continue to trade for it when other services are available and for which they also trade’ (Kaburu & Newton-Fisher, 2015, p. 68). Moreover, they argued that by providing benefits to reproductive rivals, grooming should be given in a limited amount. Of course, it makes sense to consider grooming as a valuable commodity. The question is whether we can find a priori a reason why grooming should be a highly valuable commodity in some chimpanzee groups, and thus always be reciprocally exchanged (Kaburu & Newton-Fisher, 2015), but not in baboons (e.g. Barrett & Henzi, 2006), or whether we are once again running the risk of making our findings fit BMT with a posteriori interpretations.

**Grooming for Access to Infants**

It is also controversial whether primates trade grooming for access to infants. According to BMT, if infants are a valuable commodity, females should groom mothers to access their infants, and should do that more when the number of infants decreases (Fruteau, van de Waal, Van Damme, & Noë, 2011; Gumert, 2007b;
Henzi & Barrett, 2002; but see Fruteau et al., 2011, for reasons why giving an infant is also good for mothers). In most studies, however, the amount of grooming provided to access infants did not fluctuate depending on the law of supply and demand (Frank & Silk, 2009; Lazaro-Perea, de Fátima Arruda, & Snowdon, 2004; Payne et al., 2003; Slater, Schaffner, & Aureli, 2007; Tiddi, Aureli, & Schino, 2010). Interestingly, affiliative behaviours might be simply provided to mothers as a signal of benign intent, having no market value (Slater et al., 2007; Tiddi et al., 2010). This would also explain why mothers need to be groomed longer when few infants are available (Tiddi et al., 2010), or when they are higher-ranking individuals (Gumert, 2007b; Henzi & Barrett, 2002): more grooming would be needed to calm down mothers (and access their infants) when infants are scarce and mothers might be more frequently harassed, or when mothers are higher-ranking individuals and thus potentially more dangerous to approach.

**Meat for Sex**

Even more controversial is the existence of a BM in which males trade meat with females in exchange for mating opportunities (Stanford, 1996). Few studies have provided evidence that male chimpanzees are more likely to hunt when oestrous females are available (Stanford, Wallis, Mpongo, & Goodall, 1994; but Gilby, Eberly, Pintea, & Pusey, 2006; Gilby & Wrangham, 2008; Mitani & Watts, 2001), and preferentially share meat with oestrous females (Teleki, 1973; Watts & Mitani, 2002; but Gilby, 2006; Gilby et al., 2010). Similarly, some authors have shown that mating rates increase after meat has been shared (Gomes & Boesch, 2009; Stanford, 1998; but Gilby, 2006; Gilby et al., 2010; Mitani & Watts, 2001; Watts & Mitani, 2002). However, positive evidence of a BM is scant and has important limits. Theoretically, for instance, there is no reason why female chimpanzees would need meat as an incentive to overcome a reluctance to mate, given that promiscuous mating might have several benefits (see Gilby et al., 2010). Moreover, female mate choice probably plays a very minor role in chimpanzees (Feldblum et al., 2014; Muller, Emery-Thompson, Kahlenberg, & Wrangham, 2011), so that males could hardly increase their reproductive success by exchanging meat for sex (see Gilby et al., 2010). Methodologically, these studies are also problematic, by using too broad a definition of ‘oestrous’: Stanford et al., 1994; of ‘sharing’: Teleki, 1973) or failing to compare findings with baseline controls (e.g. Stanford, 1998; Watts & Mitani, 2002). Even Gomes and Boesch (2009) found no evidence of short-term exchanges of meat for sex, and no dyadic correlation between the amount of meat shared and the number of copulations. While convincing evidence remains scant in the short term, it is possible that sharing and mating are not causally linked in the long term, and males skilled at obtaining and sharing meat are preferred sexual partners for reasons other than meat sharing (see Gilby et al., 2010). There is, therefore, still no conclusive evidence of a BM in which males share meat in exchange for mating opportunities.

**Grooming for Sex**

Finally, some researchers have investigated whether grooming is exchanged for sex. Some studies, for instance, have shown that males groom oestrous females more frequently than anoestrous ones (e.g. Colmenares et al., 2002; Hemelrijk, VanLaere, & van Hooff, 1992; Norscia, Antonacci, & Palagi, 2009; but Cooper & Bernstein, 2000). More relevantly for BM, in Gumert’s (2007a) study, male crab-eating macaques, *Macaca fascicularis*, groomed females in exchange for sex, and grooming duration was linked to the availability of females around the interaction. This last study, however, raises several methodological issues, including the exclusion of all those grooming and mating instances that did not happen in the same bout (see section Time frame of exchanges), the use of a questionable proxy of female availability (see section Cognitive challenges), and the analysis of grooming given and received as if they were two completely independent measures (see section Methodological issues). Therefore, more evidence is needed to claim that grooming is exchanged for sex according to BMT.

Overall, there is no convincing evidence for the existence of a PBMs in which individuals exchange meat or grooming for sex, or grooming for infant handling or social tolerance. There are several reasons why researchers might have failed to consistently detect BMs for these commodities: exchanges might have involved other/multiple commodities, they might have happened in another time frame, or they might have simply not followed the law of supply and demand. In some cases, it is possible that other contingent effects altered the value of commodities (e.g. grooming might be more valuable after a stressful event). In other cases, the changes in circumstances (required to detect BMs: Barrett & Henzi, 2006) might have simply not been salient enough to trigger a change in partners’ value. In this respect, it is possible that only especially rare commodities are salient enough to alter long-term bonds, which are based on the long-term reciprocal exchange of frequent commodities (e.g. grooming). However, it is clear that the frequency of commodities probably varies across species/populations and through time, so that if grooming and tolerance may be generally considered a frequent commodity, for instance, frequency of infant handling strongly depends on the species’ reproductive characteristics.

In the future, more experimentally controlled studies are needed to understand which commodities are exchanged according to BMT. Experimentally manipulating the frequency of certain commodities (e.g. providing access to common versus rare food) might provide insight as to whether commodities are exchanged according to BMT only if their frequency falls below a certain threshold. After predetermining the time frame of exchanges (see section Time frame of exchanges), experimental manipulations like those implemented by Fruteau et al. (2009) should assess BMs when individuals can only exchange two commodities (e.g. when no infants are born, no females are in oestrus and no other food sources can be monopolized). Once there are baseline results on the way two commodities are exchanged (e.g. grooming for food access), some of the tested individuals should be provided with a further commodity to trade (e.g. sex, when females go into oestrus), to monitor how PBMs are affected by the availability of more commodities and how interactions vary when individuals are confronted with these changes. Importantly, experimental manipulations should be replicated in the same population regardless of the identity of the individuals involved, as well as across conspecific populations and over time. Supply and demand being equal (e.g. number of individuals per food provided, number of oestrous females per adult male), results should be consistent over time and across individuals and populations, if exchanges really depend on the law of supply and demand. On the other hand, if primate exchanges depend on the existence of social relationships resistant to contingent changes in resource availability, we would expect no consistent patterns across individuals and populations, as well as temporal fluctuations independent of variations in supply and demand. Finally, a meta-analytical approach could be used to detect patterns of similarities across studies and construct an intervening variable better capturing the network of causal connections among independent and independent variables in BMs (see Aureli & Whiten, 2003).

Some of the concerns expressed for PBMs do not apply to other species, simply because these might have fewer commodities to
trade. Cleaner fishes, for instance, can only offer removal of ectoparasites to their clients, while their clients can only offer food transport to the cleaner’s territory, resulting in an easier form of BM (see Bshary, 2001). In contrast, testing BMT in cooperative breeders might imply similar challenges to primates. In meerkats, Suricata suricatta, for example, the majority of individuals do not reproduce, but help female breeders to raise their offspring: according to BMT, the more helpers are available, the fewer the commodities helpers should receive from breeders in exchange for their help (e.g. Kutsukake & Clutton-Brock, 2010). However, as in primates, commodities traded can be multiple (e.g. infant protection, tolerance or access to resources by helpers, in exchange for tolerance, lack of aggression or access to resources by breeders), making predictions unclear and BMT harder to test.

COGNITIVE CHALLENGES

In contrast to Seyfarth’s (1977) model, partner choice plays a crucial role in BMT (Nee & Hammerstein, 1994). Rather than a series of long-term dyadic interactions in which one subject exerts control over the other, BMT envisions primate relationships as a series of short-term polyadic interactions in which individuals continually choose the best available partners depending on the offer and demand. This approach poses several problems, in that evidence of long-term relationships in primates is abundant (e.g. Langergraber et al., 2007; Lehmann & Boesch, 2009; Mitani, 2009; Seyfarth & Cheney, 2012; Silk et al., 2003, 2009, 2010), and it is no easy task to reconcile the coexistence of long-term social bonds and short-term fluctuations as predicted by BMT. Similarly, although social relationships are probably a combination of both dyadic partner control and polyadic partner choice, BMT largely fails to take into account the interplay of both strategies. Another major problem is that in order to select the best partner, individuals must not simply keep track of previous exchanges with every partner, but also be able to track and compare the relative value of the different commodities available from each potential partner, and the number of potential competitors (although the effects of demand on the exchange of commodities have not yet received similar attention to the effect of supply).

In dyadic interactions, emotions might help primates keep track of resources and maintain cooperative exchanges through time, without requiring complex cognitive skills (Brosnan & de Waal 2002; Schino & Aureli, 2009; de Waal, 2000). While emotional book keeping might well work at the dyadic level, helping primates to keep (emotional) track of past relationships, it is harder to imagine that emotional book keeping might be a useful tool when the value of different commodities, potential partners and competitors should be assessed and compared in the complex way of PBMs. Gumert (2007a), for instance, explained how emotional book keeping would work in a BMT: grooming would alleviate stress/fear involved in social interactions, facilitating the trade of commodities. Similarly, the other ‘parameters of the social market may trigger physiological states that modulate how motivated males and females are to cooperate depending on the abundance of potential partners and competitors’ (Gumert, 2007a, p. 1666). Possibly, when competition over a resource is high, other individuals may also feel the urge to compete over the same resource (maybe via emotional contagion), increasing the commodity offered in exchange (so that the value of commodities increases when there are more competitors). Although this hypothesis deserves attention, operationalizing it is no easy task should different psychological states be triggered by the number of potential partners, by the ratio of potential partners per competitors, or by an approximation of this ratio, as in Gumert (2007a)?

Alternatively, some authors have tried to reduce the cognitive complexity of PBMs by assuming that all exchanges are based on their current needs and the immediate availability of commodities (Barrett & Henzi, 2002, 2006; Barrett et al., 1999). This assumption, however, is problematic. First, it limits the BM to a series of immediate exchanges, in which primates are blind to the past and the future (see Gilby, 2013). Second, it might mislead researchers to only take into account behaviours that are immediately exchanged in the very same bout, excluding relevant amounts of data (see section Time frame of exchanges). Third, it disregards the fact that other researchers have found exchanges to happen over longer time frames (see e.g. Schino & Aureli, 2010; section Time frame of exchanges), or with commodities such as agonistic support that are not always immediately available (see section Commodities exchanged). Fourth, some authors have found that individuals groom in anticipation of future need, by for instance grooming in exchange for future tolerance at feeding sites (de Waal, 1997). Finally, this assumption does not drastically reduce the cognitive challenges of PBMs, in that primates would still need to be able to assess (although just in the immediate present) the number of potential competitors and partners, and thus the relative value of the different commodities to be exchanged. Therefore, it is still unclear which level of cognitive complexity is required for primates to trade in BMs, and whether all primates possess these skills.

In the future, research will need to better assess whether emotional book keeping can alone account for the complex exchanges predicted by PBMs, involving multiple commodities and partners over long time frames. If primates navigate across potential partners and commodities by cognitively tracking previous exchanges with other partners, tracking and comparing the relative value of the different commodities available and the number of potential competitors, they will need enhanced cognitive skills, for instance in terms of memory and ability to quantify. If future studies find convincing evidence of PBMs in primates that fail to show these skills (as tested in the laboratory with ad hoc cognitive tasks), further support would be provided for the hypothesis that primates rely on emotional book keeping to navigate in BMs.

In other species, BMs are necessarily limited to a series of immediate exchanges. In cleaner — client fish relationships, for instance, exchanges of commodities happen in the short term, drastically reducing the cognitive complexity of such a BM. When exchanges happen over a longer-term frame, as in the case of cooperative breeders, the same issues raised for primates apply: if exchanges are not based on current needs and immediately available commodities, emotional book keeping might provide a cognitively less challenging tool to efficiently navigate in BMs.

METHODOLOGICAL ISSUES

A much less theoretical problem is that most studies have used very different methods to test BMT. This does not facilitate comparisons across studies, and raises questions on whether the appropriate methods are always used. In most studies, for instance, grooming is included as the main currency being exchanged. However, different criteria are used to quantify grooming. In some studies, grooming is measured in terms of frequency of grooming bouts (e.g. Stevens, Vervaecke et al., 2003), while in others in terms of duration of grooming (e.g. Kaburu & Newton-Fisher, 2015). If grooming is a currency exchanged for other commodities, however, it seems plausible that grooming duration should be a more reliable measure: why should primates prefer being groomed twice for a total of 2 min, for instance, rather than just once for 5 min? On the contrary, the fact that the frequency of grooming bouts or the categorical occurrence of grooming (rather than its duration)
sometimes predicts exchanges with other commodities might suggest that the function of grooming is to communicate benign intent to partners and facilitate exchanges (see e.g. Tiddi et al., 2010), rather than to serve as a currency to be exchanged according to the law of supply and demand.

Interestingly, there is not even a consensus on the definition of a grooming bout. While some studies consider grooming bouts to end when grooming is suspended for more than 10 s (e.g. Barrett et al., 1999; Henzi & Barrett, 2002; Tiddi et al., 2010), others consider grooming bouts to end after 20 s (Fruteau et al., 2009), 30 s (e.g. Fruteau et al., 2011; Gumert, 2007a), 1 min (e.g. Chancellor & Isbell, 2009; Manson et al., 2004), 2 min (e.g. Payne et al., 2003) or even 5 min (e.g. Port et al., 2009). In other studies, no information is provided on when grooming bouts are considered to end (e.g. Balasubramaniam et al., 2011; Koyama, Caws, & Aureli, 2012; Norscia et al., 2009). Although practical issues linked to the visibility of primates and the socioecology of species might partly explain methodological differences, such inconsistencies must surely affect the analysis of data, especially if analyses only include exchanges happening in the same bout or use frequencies of grooming bouts as the dependent variable (but bouts are defined in different ways).

Similarly, observations are often done using different techniques: spanning from focal sampling (e.g. Carne et al., 2011; Clarke, Halliday, Barrett, & Henzi, 2010) to ad libitum sampling (e.g. Gumert, 2007b), combinations of ad libitum and focal sampling (e.g. Fruteau et al., 2011), and combinations of scan and focal sampling for shorter (e.g. Barrett et al., 1999; Henzi et al., 2003) or longer observation sessions (e.g. Kaburu & Newton-Fisher, 2013). Of course, the choice of observation techniques largely reflects socioecological aspects of the group and species studied, but as all these studies aim to test the same hypothesis (e.g. whether primates exchange commodities according to the law of supply and demand), such a variety of approaches is partly unjustified. Another important aspect is the difference in the number or duration of observations across studies. Some studies, for instance, provide no exact information on the number of observation hours that have been implemented (e.g. Gumert, 2007b) or on the hours of grooming observed (e.g. Barrett et al., 1999). This is not as trivial as it might seem, given that more observations provide more power to the analyses, so that reciprocity might be detected over shorter time frames when observations are more frequent (see section Time frame of exchanges).

Furthermore, grooming bout frequency/grooming duration can undergo different transformations before being analysed. Some studies, for instance, have analysed the exchange of grooming given with other commodities, without controlling for grooming received (e.g. Gumert, 2007a). This method, however, can be problematic, because grooming given might fluctuate within dyads depending on grooming received, and independently of other commodities available in the BM. In other studies, therefore, grooming given and grooming received within each dyad are analysed as a ratio, which might be a more informative measure of the grooming relationship between individuals (e.g. Fruteau et al., 2009; Payne et al., 2003; Port et al., 2009). If it is true that grooming is always partly reciprocal (e.g. Barrett & Henzi, 2006; Henzi & Barrett, 1999), exploring the relation between grooming given and other commodities received, while controlling for grooming received, might be the safest approach. However, grooming given and grooming received have often been linked using complex indexes, whose rational is not always evident (e.g. Barrett et al., 2002; Henzi et al., 2003; Kaburu & Newton-Fisher, 2015). Similarly, grooming given should also be controlled for association time between subjects. If two individuals spend little time together, but most of this time is spent grooming, their relationship probably has a higher quality than that of two individuals grooming as long, but being often in proximity without grooming.

Finally, analyses of data also largely differ across studies. Some studies, for example, include all instances in which specific behaviours have been observed, while others only include behaviours observed during reciprocal bouts (e.g. Barrett et al., 2002, 1999; Chancellor & Isbell, 2009; Gumert, 2007a). As already discussed (see section Time frame of exchanges), however, this might lead to the exclusion of very large portions of data (e.g. Chancellor & Isbell, 2009). Knowing at least how many data points have been excluded might be extremely informative about the strength of results, but this information is not always included (e.g. Gumert, 2007b).

Primates species differ strongly in their biology and socioecology. Therefore, a general agreement on the methodological approach to be used is not always possible or desirable (e.g. in terms of observational techniques chosen or length of grooming bouts). However, there is no reason why different approaches are used for the same species. Even across different taxa, the number of observation hours should not be the casual result of practical contingencies, but have a strong ecological justification, as it might significantly affect the results of analyses. Similarly, regardless of the species tested, it would be important to avoid excluding large parts of data sets, by also including nonimmediately reciprocated bouts, and to refrain from a posteriori explanations, which might bias the interpretation of negative results according to BMT. Unless explicitly justified, future studies should use duration instead of frequency of grooming, while controlling grooming given for grooming received and association time.

Similar considerations apply to species other than primates. Whenever possible, the use of similar methodological approaches facilitates comparisons and strengthens findings. The number of observation hours should be ecologically justified, data should not be excluded, and commodities should be quantified in a consistent way, taking into account association time and the interdependence of multiple commodities whenever needed.

Conclusion

To date, BMT is still one of the most comprehensive theories explaining the complex exchanges of commodities among classes of individuals. In a variety of research areas, it has proved a reliable tool to predict social interactions across conspecifics and members of different species (e.g. Barclay, 2013; Cowden & Peterson, 2009; Schwartz & Hoeksema, 1998). Even in primates, the BTM has often been used to explain the complex exchanges of commodities that characterize this taxon. The main strength of the PBM is its complexity: multiple variables interact flexibly and predict exchanges among individuals, largely reflecting the complexity of real social interactions. In contrast to other theories, for instance, BMT recognizes the central role played by partner choice, introduces new resources that primates can exchange for grooming, acknowledges temporal variation in the value of commodities, and accepts the existence of high interindividual variability in the way primates exchange commodities.

Ironically, however, this complex, dynamic, individual-based approach is also the main weakness of BMT: predictions are not always straightforward and easy to test, and when results fail to match them, several alternative explanations may be proposed to explain results in a BMT framework (e.g. aggression might have distorted market forces, grooming might not be that valuable for a certain species, some instances of grooming must have been exchanged for other commodities or in other time frames, and so on). If individuals really balance costs and benefits of commodities across partners and bouts (e.g. Schino et al., 2003), depending on the social characteristics of conspecifics (e.g. Gumert,
2007b), on the relative value of the different commodities and on the number of potential competitors (e.g. Carne et al., 2011), then complexity is so high and exchanges affected by so many variables, that predicting and testing them all might be simply impossible. How can we test whether an excess of meat in exchange for sex, for instance, has not been paid back (in a different time frame) by asking for less grooming to handle infants? Perhaps not surprisingly, the most convincing examples of BM to date are those involving species other than primates, in which few commodities can be exchanged over a very short time frame (e.g. Becker & Grutter, 2005; Hellmann et al., 2015; Wyatt, Kiers, Gardner, & West, 2014).

Although we see no clear solution to the excessive complexity of PBMs, we have provided some possible solutions that might help address the main issues raised in this essay: the time frame over which exchanges take place, the commodities exchanged in PBMs, the cognitive challenges imposed by PBMs and consistency in the methodological approach. Only after addressing these issues shall we be able to understand whether primates can still be considered ‘to be in the market’. Although the largest majority of studies have so far provided no convincing support to the existence of PBMs, only more systematic studies addressing the theoretical and methodological issues reviewed here might provide us with reliable conclusions on the realistic applicability of BMT to primates. Our hard task for the future is to transpose the complexity of real social interactions into a series of clear predictions which can be easily tested and interpreted. To date, the complex interactions of multiple factors might often allow an exaggerated flexibility in the interpretation of results. Of course, all hypotheses might be true, but a theory that does not allow clear testable predictions has probably lost much of its utility.

Acknowledgments

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