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Forum

Biological markets: theory, interpretation, and proximate perspectives. A response to Sánchez-Amaro and Amici (2015)

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In their review of the applicability of biological markets theory (BMT) to primate exchanges, Sánchez-Amaro and Amici (2015) make numerous valid and important points about theoretical and methodological problems that have so far limited the application of BMT to primates. While we agree with many points of their excellent review, there are a few areas that we feel would benefit from further discussion.

THEORETICAL ORIGINS

Our first point is both historical and theoretically relevant to researchers attempting to make progress in this area. In their review, Sánchez-Amaro and Amici (2015) use Seyfarth's (1977) grooming model as a jumping off point for presenting BMT, describing BMT as an improvement upon Seyfarth's model because it is a more dynamic theory in which a variety of behaviours can be exchanged for grooming based on the levels of within-group contest competition (Barrett, Gaynor, & Henzi, 2002; Barrett, Henzi, Weingrill, Lycett, & Hill, 1999). 'In this respect, BMT was the perfect candidate to improve, although not fully replace Seyfarth's (1977) model' (Sánchez-Amaro & Amici, 2015, p. 52). While we agree that BMT incorporates the consideration of levels of contest competition, which (1) distinguishes it from Seyfarth's model and (2) generates testable predictions about whether like (e.g. reciprocal) or unlike (e.g. interchange) commodities are exchanged, we argue that BMT should be viewed as distinct from Seyfarth's (1977) grooming model. While the authors may not have meant to imply that BMT had its origins in Seyfarth's model, it may be easy for a reader to infer that it did. As such, we would like to point out that BMT was originally conceptualized as a theoretical means to overcome problems associated with classical reciprocal altruism (Trivers, 1971) and the iterated prisoner's dilemma (IPD). In the original formulation of BMT, Noë, Hammerstein and colleagues described at least two aspects of exchanges that IPD-based models fail to address: (1) the existence of inequitable divisions of rewards and (2) opportunities to interact with multiple partners (Noë, 2001; Noë & Hammerstein, 1994, 1995; Noë, van Schaik, & van Hooff, 1991). Like Seyfarth's model, it was inspired by exchange patterns in baboons, specifically coalition patterns used by males to gain access to fertile females. However, it was intended to address the issue of exchange much more broadly than Seyfarth's model. Careful analysis revealed that there was no reciprocal turn taking, the hallmark of reciprocal altruism, between males that provided coalitionary support and those that received support vis a vis gaining access to receptive females (Bercovitch, 1988; Noë, 1990). The baboon data also highlighted the fact that males' opportunities to interact with multiple partners had profound impacts on exchanges. Because males could interact with multiple partners of varying quality, high-quality partners (i.e. 'veto players') were able to extract higher proportions of the rewards. This is an important aspect of exchange that the IPD's delineation of 'cooperate' versus 'defect' fails to predict. As such, Noë's (1990) data with baboons highlighted the power of partner choice: the veto player's involvement in a coalition meant that (1) the probability of success in the coalition substantially increased and (2) the 'veto player' received the majority (actually all in this example) of the postconflict consortships, while his partners received none. By viewing cooperation as an '*n*-player' interaction based on partner choice, BMT was able to explain a suite of exchanges that could otherwise not

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be accounted for by classical reciprocal altruism/IPD. Nor were they explicable in terms of Seyfarth's model, even if/when it was extended to cover variation in within-group competition and exchanges that did not involve grooming.

Although Seyfarth's grooming model should be a part of any discussion of primate exchange, particularly in view of the fact that empirical studies of primates have focused almost entirely on grooming exchanges, we feel that acknowledgment of BMT's origins in broader theoretical models of cooperation is helpful. In particular, doing so more easily encourages consideration of exchanges that do not involve grooming, of varying types of exchanges in a broad range of taxa, and most importantly, the role of *n*-player games involving partner choice. Recognition of the broad scope of BMT via its origins in criticism of reciprocal altruism has led to many important insights in a range of taxa for a variety of exchanges that may not necessarily include grooming, but do critically involve partner choice (e.g. cleaner fish exchanges: Bshary & Grutter, 2002; the protection/nectar exchange between ants and aphids: Fischer, Hoffmann, & Völkl, 2001; or even the nutrient exchange between plants and fungi/bacteria: Werner, Strassman, Ivens, Engelmoer, Verbruggen, Queller, Noë, Johnson, Hammerstein, & Kiers, 2014). Thus it more easily brings primate exchanges into the larger discussion of exchange among organisms in general. To be fair, Sánchez-Amaro and Amici (2015) cite examples of studies of exchanges among primates within the BMT framework that consider partner choice, but do not involve grooming, e.g. embracing for infant access (Slater, Schaffner, & Aureli, 2007) and meat for sex (Gomes & Boesch, 2009), although as they point out, the evidence for BMT for these exchanges, especially meat for sex, remains inconclusive (cf. Gilby, Thompson, Ruane, & Wrangham, 2010). However, the point we want to emphasize here is that recognition of BMT's origins in reciprocal altruism and IPD more effectively conveys that BMT's impact lies not in its ability to incorporate the variable of contest competition, and the subsequent suite of 'commodities that primates may exchange for grooming' (Sánchez-Amaro & Amici, 2015, p. 52; although that is certainly a benefit of BMT), but in the realization that partner choice, which consequently predicts reactions according to supply and demand principles, drives cooperative exchanges. Through '*n*-player' interactions driven by partner choice in contexts in which the value and availability of partners and commodities vary, as they are influenced by contest competition, BMT creates a theoretical foundation whereby exchanges can be conceptualized in terms similar to human markets, i.e. with members (1) 'buying' and 'selling' commodities among one another and (2) pitting potential partners against each other to obtain the fairest 'price'. None of this can be easily conceptualized within the grand scheme of cooperation/altruism theory without recognizing BMT as an outgrowth and improvement upon classical reciprocal altruism.

INTERPRETIVE DEBATES

Our second area of discussion concerns timescale questions, which are also discussed in Kaburu and Newton-Fisher's (2016) response, as well as in Sánchez-Amaro and Amici's (2016) reply. Both articles by Sánchez-Amaro and Amici explain why it is important to determine the time frame over which commodities are exchanged as a preliminary step before testing for BMT, and recommend doing so even in cases where the exchange is not explicitly framed in terms of BMT. They also provide a much needed review of the methodological pitfalls recent studies have encountered when attempting to ascertain time frames of exchange in particular cases. What we would first like to add is a brief discussion of a current debate concerning the theoretical implications of the presence of long-term exchange patterns. As Sánchez-Amaro and Amici (2015, p. 52) note, 'So far, most authors have assumed that primates exchange commodities on a very short term basis'. They do not make this assumption themselves, noting that it has been bolstered by the premise that most primates lack the cognitive skills to keep track of multiple 'accounts' over extended periods of time (Barrett & Henzi, 2001, 2002; Stevens & Hauser, 2004). Consequently, many primate researchers have interpreted evidence for long-term exchanges (Frank & Silk, 2009; Gomes, Mundry, & Boesch, 2009) as evidence against BMT, and rather in favour of reciprocal altruism (particularly one of its many variants: i.e. attitudinal reciprocity), the influence of long-term social bonds (Berghänel, Ostner, Schröder, & Schülke, 2011; Massen, Overduin-de Vries, de Vos-Rouweler, Spruijt, Doxiadis, & Sterck, 2012) or other processes. More recently, several researchers have conceded that there is no theoretical reason to limit consideration of BMT principles to short-term exchanges (Hammerstein & Noë, 2016). Hence, the issue at hand is whether or not observed long-term exchanges are indicative of BMT, or alternative processes.

What Kaburu and Newton-Fisher view as 'misunderstandings', we feel are more reflective of a legitimate theoretical disagreement and empirical challenges. So far, most empirical studies of BMT in primates have not incorporated predictions about long-term exchanges largely because of the difficulties involved in empirically distinguishing BMT from alternative explanations, particularly the influence of long-term social bonds. Sánchez-Amaro and Amici see the influences of BMT and long-term social bonds as distinct processes; they note the difficulty 'of reconciling the co-existence of long-term social bonds and short-term fluctuations, as predicted by BMT' (Sánchez-Amaro & Amici, 2015, p. 56) and suggest that 'BMT largely fails to take into account the interplay of both strategies' (Sánchez-Amaro & Amici, 2015, p. 56). In contrast, strong proponents of BMT, including Kaburu and Newton-Fisher (2016), argue not only that the time frame for BMT-based exchanges can be either short- or long-term, depending on the time frame at which commodities (and partners) change in value, but also that the influence of social bonds can be subsumed under BMT models in which commodity values remain stable over long periods of time. For example, when commodities are stable, partner values can be evaluated via emotional bookkeeping (Aureli & Schaffner, 2002; Schino & Aureli, 2009), based on a series of long-term interactions, a process newly conceptualized as 'attitudinal partner choice' (Fruteau, Voelkl, Van Damme, & Noë, 2009; Hammerstein & Noë, 2016). This difference in perspective not only complicates researchers' ability to distinguish between exchanges that are governed by BMT versus other processes, it shifts attention from the time frame over which commodities are exchanged (emphasized by Sanchez-Amaro and Amici) to the time frame over which the commodity's value changes (emphasized by Kaburu and Newton-Fisher). As rank is relatively stable in most primate groups, commodities intrinsically linked to rank (e.g. agonistic support) typically change over long temporal intervals. At the same time, partner values for these exchanges could concurrently be emotionally mediated by the suite of previous experiences (e.g. one's partner's proclivity to reciprocate in past interactions) and overall benefits received (Evers, de Vries, Spruijt, & Sterck, 2015; Tiddi, Aureli, di Sorrentino, Janson, & Schino, 2011). Conversely, (1) infant access or (2) mating access, especially in seasonally breeding primates, may be examples of more 'volatile' commodities, subjected to shorter-term shifts in the market because the availability of attractive infants and fertile females varies widely over relatively short spans of time.

Are there ways to move past this timescale debate and determine whether or not long-term exchanges are indicative of BMT and/or other processes? Perhaps the potential for long-term