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Forum

Markets misinterpreted? A comment on Sánchez-Amaro and Amici (2015)

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In a recent essay, Sánchez-Amaro and Amici (2015) reviewed evidence in support of biological market theory (BMT) in primates. Since the pioneering work by Noë (1990, 1992; Noë, van Schaik, & van Hoof, 1991), and Barrett and colleagues (Barrett, Gaynor, & Henzi, 2002; Barrett, Henzi, Weingrill, Lycett, & Hill, 1999), several studies have looked for and found evidence of BMT in a variety of primate species, from lemurs (Norscia, Antonacci, & Palagi, 2009; Port, Clough, & Kappeler, 2009) to monkeys (Fruteau, Lemoine, Hellard, van Damme, & Noë, 2011; Gumert, 2007; Tiddi, Aureli, & Schino, 2012) and apes (Kaburu & Newton-Fisher, 2015a, 2015b; Koyama, Caws, & Aureli, 2012; Newton-Fisher & Lee, 2011). With an increasingly large number of studies, a review such as the one by Sánchez-Amaro and Amici (2015) would be warmly welcome as a timely summary of the evidence for BMT, and an indication of future directions. The authors identify four areas of interest and usefully highlight some potential issues with BMT, for example where free trading is compromised by extortion or the need for comparable methods across studies. However, while their aims may be laudable, we feel there are particular flaws in some of their arguments and some misrepresentation of cited literature that we would like to correct:

TIME FRAMES

One of the strengths of this review is to highlight our general ignorance regarding the time frame over which animals exchange or reciprocate behaviour. However, the authors misunderstand BMT in suggesting that it predicts only 'short and finite relationships between different classes of individuals' (p. 51), and in arguing that it is difficult to reconcile such short-term interactions with the evidence of long-term relationships in primates. While the authors are right when they state that 'so far, most authors have assumed that primates exchange commodities on a very short-term basis' (p. 52), this itself was not due to a prediction of BMT but instead was a practical solution to a lack of a priori knowledge of the relevant time frame for reciprocation. This is why many studies have looked at grooming reciprocity within bouts (Barrett et al., 1999; Manson, David Navarrete, Silk, & Perry, 2004; Newton-Fisher & Lee, 2011). However, this does not mean that the presence of unreciprocated bouts cannot be explained under a BMT framework (by definition, grooming that is traded for some other commodity is not reciprocated in kind), or that BMT predicts only within-bout grooming reciprocity, as Sánchez-Amaro and Amici (2015) suggest. The authors further conflate the time frames over which exchanges occur with the contingencies that influence variation in such exchanges: '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' (p. 53). Although Sánchez-Amaro and

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Amici (2015) imply that only exchanges based on economic considerations (as proposed by BMT) are contingent, they neglect to recognize that those driven by 'bonds' or 'relationships' (under a relationship model) would also be contingent: 'contingent' does not mean 'short term', but 'dependent upon'. In this one sentence, the authors also appear to conflate grooming frequency with degree to which it is reciprocated, and to equate either or both of these measures of grooming with 'bonds' that are otherwise undefined, leaving the contrast between 'bonds' and exchanges described by BMT, which we presume they intend to draw, difficult to interpret.

BMT does not, in fact, make any specific predictions on how fast variation in supply and demand occurs. A social group could, for example, display a structurally despotic organization or exploit food that remained monopolizable (so only a few individuals can provide rank-related commodities such as agonistic support and tolerance in a feeding context: Barrett et al., 1999; Kaburu & Newton-Fisher, 2015a) for an extended time period. In turn, this could lead to long-term exchanges of grooming and other commodities between subordinates and dominants. While we would agree that determining the time frame for reciprocal or other exchanges is clearly important, it is not a 'crucial preliminary step' (p. 52) for testing BMT: what really matters for a markets model is the time frame over which the value of commodities changes (some commodities are volatile while others are more stable) in order to identify whether behavioural strategies are sensitive to shifts in market conditions. BMT offers clear and explicit predictions in this regard: (1) behaviour should change in a specific direction in response to a shift in supply and demand of whatever particular commodity is exchanged; (2) differences in behaviour should be apparent when groups under different market conditions are compared.

COGNITIVE CHALLENGES

There are two points that need to be addressed here. First, the authors take considerable pains to suggest that the cognitive demands of record keeping and tracking the market value of partners would be excessive, implying that BMT cannot apply to primates as 'it is still unclear which level of cognitive complexity is required for primates to trade in BMs, and whether all primates possess these skills' (p. 56). In their discussion of time frames, the authors appear to indicate a preference for a relationship-based, or social-bond, model to explain primate grooming exchanges, but it is not immediately clear that this would be any less cognitively demanding, given that it requires tracking of third-party relationships, with each relationship a product or abstraction of a history of interactions (Hinde, 1976). For species in which individuals spend time apart in different subgroupings (most obviously chimpanzees, *Pan troglodytes*, but to an extent in others such as baboons, *Papio* sp.), this would require some kind of cognitive mechanism to interpolate unseen interactions in order to properly evaluate third-party relationships, unless, of course, this is achieved using some form of emotional book keeping ('attitudinal partner choice': Fruteau et al., 2009): but why then are the authors so quick to dismiss emotion as a mechanism for the operation of biological markets? Second, and more critically, BMT is a functional theory, that is, a model of the action of natural selection on behavioural strategies; it does not postulate a particular mechanism, whether that be emotional, rule of thumb or complexly cognitive, and can be applied across taxa (recent examples include microbes and mycorrhizal fungi: Werner et al., 2014; Wyatt, Kiers, Gardner, & West, 2014). Thus, while it might be ideal to be able to determine the particular mechanism at work (and this may well differ between taxa), our ignorance or otherwise is not relevant to determining the usefulness of BMT for understanding cooperative exchanges. This part of their review is essentially a red herring. If primates behave as if they have to employ strategies that take into account market value in choosing social partners, then BMT provides us with insights that we would not otherwise have. This apparent failure by the authors to recognize that BMT is a functional theory is also present in their discussion of infant handling. Sánchez-Amaro and Amici (2015) argue here that grooming may serve to calm mothers as an alternative to a markets-based explanation. However, this is a mechanistic explanation and thus complementary to a functional explanation (Tinbergen, 1963) such as that offered by BMT. The suggestion that females need more calming when infants are rare because they are harassed more frequently, as proffered by the authors (and previously by Barrett, 2009; Henzi & Barrett, 2002) may well be correct, but it is not incompatible with a markets' explanation that selection has shaped grooming strategies to be sensitive to variation in either mothers' demands (how much calming they need) or the supply of infants, with the result that more grooming must be provided to access infants when they are a rare commodity.

BIOLOGICAL MARKETS THEORY VERSUS SEYFARTH'S (1977) MODEL

In their essay, the authors suggest that BMT is 'the perfect candidate to improve, although not fully replace, Seyfarth's (1977) model' (p. 52). They then list some aspects that make BMT an improvement of Seyfarth's (1977) model, such as the possibility of accounting for the dynamics of a primate population (and thus a variation in market forces) and allowing individuals to 'behave differently depending on the commodities traded and the interacting partners' (p. 52). However, as we laid out in a recent article (Kaburu & Newton-Fisher, 2015a), these are different models that generate different predictions (Henzi et al., 2003). The most crucial difference between BMT and Seyfarth's model is that the latter posits that grooming distribution is limited by dominance rank (dominant individuals have the priority in partner choice), while BMT assumes that individuals are, in principle, free to trade with any group members (R. Noë, personal communication). Although Sánchez-Amaro and Amici (2015) state that under a BMT framework 'predictions are not always straightforward and easy to test' (p. 57), this distinction between BMT and Seyfarth's model offers a clear opportunity to test different predictions for each model and so better understand how primates distribute a service, such as grooming. More specifically, in Seyfarth's model, the majority of grooming (and not just reciprocity) should be largely directed to individuals close in rank to the actor, while under BMT, grooming should be distributed across all dyads, with only reciprocity being more pronounced between individuals close in rank (Henzi et al., 2003); we found that the distribution of grooming was a better fit for the BMT prediction than the prediction from Seyfarth's model (Kaburu & Newton-Fisher, 2015a). This leads to another crucial point that Sánchez-Amaro and Amici (2015) missed, namely that evidence in support of BMT should not be based exclusively on whether the provision of a service (e.g. grooming) is predicted by the receipt of the same or another commodity (e.g. agonistic support). Support for BMT should also be sought by looking at how individuals distribute their commodities. It is at this point that the indices that Sánchez-Amaro and Amici (2015) dismiss as 'complex' and 'whose rationale is not always evident' (p. 57) actually come in useful. More specifically, the Shannon – Weaver index is a particularly valuable tool that has been used repeatedly in the primate literature to examine how individuals distribute grooming across their partners (i.e. whether they direct grooming to a specific clique of partners or they distribute grooming more or less equally across their group members).