1 Title: **Markets misinterpreted?, a comment to Sánchez-Amaro, A.**
2 **and Amici, F. (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), ~~Hemelrijk (1994)~~, 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 (Gumert 2007; Tiddi, Aureli, & Schino 2012; [Fruteau, Lemoine, Hellard, van Damme & Noë, 2011](#)) and apes (Koyama et al., 2012; Newton-Fisher & Lee, 2011; Kaburu & Newton-Fisher, 2015a, 2015b). With an increasingly large number of studies, a review such as the one by Sánchez-Amaro and Amici (2015) is 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. Their aims are laudable, but we feel there are particular flaws in some of their arguments and some misrepresentation of cited literature that we would like to correct:

Time frame of exchanges

One of the most troublesome aspects of Sánchez-Amaro & Amici (2015)'s review is the (wrong) idea that BMT predicts only short-term interactions: in the very first paragraph (p.51) they state that under BMT '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'. The authors then argue that it is difficult to reconcile these short-term interactions with the evidence of long-term

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relationships in primates. However, while it is unclear how resources cannot have intrinsic value (making us question their definition of 'resources'), the authors are also wrong in thinking that there can be only short-term relationship in the market model: BMT does not make specific predictions on how fast the variation in supply and demand occurs. In other words, a social group can display a structurally despotic organization or food can remain monopolizable (and thus only few individuals can provide rank-related commodities, such as agonistic support and tolerance in feeding context; Barrett et al., 1999; Kaburu & Newton-Fisher, 2015) for an extended time period. This in turn can lead to long-term grooming interactions between subordinates and dominants. 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), but this was not a prediction of BMT, but a practical solution to the fact that it is not possible to determine a priori the relevant time-frame of reciprocation. This explains why many studies have looked at grooming reciprocity within bout (Barrett et al., 1999; Manson, Navarrete, Silk, & Perry, 2004; Newton-Fisher & Lee, 2011). However, this does not mean that the presence of non-reciprocated bouts cannot be explained under a BMT framework, or that BMT predicts only within-bout grooming reciprocity, as the authors suggested. Sánchez-Amaro and Amici (2015) say, for instance, that 'the risk of only analysing bouts that already hint to some form of reciprocation is that different conclusions might be reached (see Manson et al., 2004)' (p. 52). However, this would lead to a bias resulting in erroneous support for partner control (e.g. reciprocal altruism), rather than BMT. Grooming that is not traded for itself within bout can actually be traded for other commodities, or exchanged for grooming received on a long-term basis (Gomes et al., 2009). The key issue of non-

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reciprocated bouts is whether this grooming is actually reciprocated over a longer time-frame, or rather bouts are independent from each other. However, determining this time frame can be a hard task for which the authors do not provide any practical solution. Oddly, the authors indicate that experimental work similar to the one implemented by Fruteau et al. (2009) should be used to have a better understanding of the time frame of commodities exchange (p. 53). Here we would like to make two points: first, that it is not the time frame of commodities exchanged what really matters in a markets model, but it is the time frame over which the value of commodities changes, as some commodities have volatile values and other rather stable ones. Second, that what is really relevant in Fruteau et al. (2009)'s experiment is not that female monkeys exchange commodities within a 1-hr time frame

but rather that the value of a food provider shifts in relation to the number of food providers present in the group, which is what BMT predicts. Additionally, the fact that Fruteau et al. (2009) found that food is exchanged for grooming during their daily hour of observation, does not necessarily mean that everything happened within that hour.

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

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91 this would be any less cognitively demanding, given that it requires tracking of third
92 party relationships, with each relationship a product or abstraction of a history of
93 interactions (Hinde, 1976). For species where individuals spend time apart in different
94 sub-groupings (most obviously chimpanzees, but to an extent in others such as baboons),
95 this would require some kind of cognitive mechanism to interpolate unseen interactions
96 in order to properly evaluate third party relationships. Unless, of course, this is achieved
97 using some form of emotional book-keeping (or ‘attitudinal partner choice’: Fruteau et
98 al., 2009), but why then are the authors so quick to dismiss emotion as a mechanism for
99 the operation of biological markets? Second, and more critically, BMT is a functional
100 theory. That is, a model of the action of natural selection on behavioural strategies; it
101 does not postulate a particular mechanism, whether that be emotional, rule of thumb or
102 complexly cognitive. Thus, while it might be ideal to be able to determine the particular
103 mechanism at work (and this may well differ between taxa), our ignorance or otherwise is
104 not relevant to determining the usefulness of BMT for understanding the cooperative
105 exchanges of non-human primates. This part of the review is essentially a red herring. If
106 primates behave as if they have to employ strategies that take into account market value
107 in choosing social partners, then BMT provides us with insights that we would not
108 otherwise have, including for those species less cognitively developed such as microbes
109 (Werner et al., 2014). Remarkably, the authors appear to confuse proximate and ultimate
110 functions also in other points of their essay. In their discussion of the trading of grooming
111 for infant handling, for instance, Sánchez-Amaro and Amici (2015) argue that ‘affiliative
112 behaviours might be simply provided to mothers as a signal of benign intent, having no
113 market value[...] more grooming would be needed to calm down mothers (and access

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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' (p. 54). However, the calming effect of grooming is a *not* an alternative to BMT, but a proximate mechanism, that can explain why grooming fluctuates following the market forces of supply and demand (Barrett, 2009; Barrett & Henzi, 2001).

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Biological Markets theory vs Seyfarth's (1977) model-

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In the 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 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 with 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 predicts that individuals are 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). In contrast, 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) dismissed as 'complex' and 'whose rational 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 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).

2) *Misrepresentation of our work*

—In Kaburu & Newton-Fisher (2015a), following up earlier work testing specific predictions of BMT in a single chimpanzee community (Newton-Fisher & Lee, 2011), we analysed the possible trading of grooming for other commodities (i.e. agonistic support, tolerance and meat) between adult male chimpanzees in two communities that exhibited dramatic differences in the steepness of their dominance hierarchy. From BMT, we predicted that grooming should be traded for rank-restricted commodities among

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159 chimpanzees in the community where rank relationships were steep, but not in the
160 chimpanzee community with a more structurally egalitarian hierarchy. We were surprised
161 to see Sánchez-Amaro and Amici (2015) claim that Kaburu & Newton-Fisher (2015a)
162 ‘failed to find evidence that chimpanzees with a steeper hierarchy trade grooming for
163 agonistic support, while chimpanzees in more egalitarian groups groom more
164 reciprocally’ (p 54) when in fact, we *did* find evidence that male chimpanzees living
165 under a despotic dominance hierarchy traded grooming for agonistic support: (1)
166 dominant males provided more agonistic support than subordinates; (2) males directed
167 grooming up the hierarchy; (3) high-ranking males received more grooming than they
168 gave; and (4) individuals gave more grooming to partners from whom they received more
169 support. Critically, and matching the prediction from BMT, we did not find these results
170 in the more structurally egalitarian community. Given the concerns that Sánchez-Amaro
171 and Amici (2015) raise about comparable methodologies, we note both here and in the
172 paper that we collected data in both communities using the same protocols and
173 definitions, and analysed it using the same techniques. Our study provides an explicit test
174 of BMT, and provides evidence that the market forces of supply and demand shape the
175 exchange of commodities in chimpanzees. Furthermore, and explicitly contrary to
176 Sánchez-Amaro and Amici’s (2015) suggestion that we did not conclude that ‘grooming
177 reciprocity was not affected by hierarchy steepness’ (p. 54), we found that male
178 chimpanzees of both communities reciprocated grooming, stating that ‘grooming was
179 reciprocated regardless of hierarchy steepness’ and, contrary to their implication that we
180 forced our findings to fit BMT a posteriori (p. 54), we appreciated that this finding was
181 ‘contrary to the grooming-trade model’ (Kaburu & Newton-Fisher, 2015a, p. 68). Given

this conclusion, we sought to explain our results in the light of chimpanzee social system, where individuals ‘continue to trade for it when other services are available and for which they also trade’ (p.68). Similarly, in presenting results that both supported and refuted specific predictions of BMT, Newton-Fisher & Lee (2011) used the opportunity to discuss modifications to BMT that would be needed to make sense of the results from a markets perspective.

Sánchez-Amaro and Amici (2015) also state that ‘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, 2015a), but not in baboons (e.g. Barrett & Henzi, 2006)’ (p. 54). Here they attribute to us a suggestion that grooming should only be valued in some, but not other groups of chimpanzees (a hypothesis we have not advanced) and imply that it is unreasonable that its value should differ between species. The authors have failed to grasp that the supposition of low-value grooming is part of the grooming-trade model ([i.e. grooming is traded for itself only when alternative commodities are not available](#)) – the application of BMT to primate grooming – developed for and tested in female cercopithecine monkeys. All we state in our work is that this assumption appears unwarranted for male chimpanzees, given the persistence of grooming reciprocity across communities with differing degrees of dominance hierarchy steepness. Whether and to what extent grooming varies in value remains to be determined, although it is worth noting that male chimpanzees have different social dynamics from female baboons: the latter [exchange grooming almost exclusively in an unidirectional form \(one individual grooms a partner: Barrett et al., 1999\)](#) and gain grooming and agonistic support primarily

from close maternal kin (Gouzoules & Gouzoules, 1987), while the former [engage often in mutual grooming \(both individuals groom one other: Kaburu & Newton-Fisher, 2013; Machanda et al., 2014\)](#)—and have to seek the benefits of both from their closest reproductive rivals (Newton-Fisher, 2014). On this basis alone, we should probably expect some differences in the patterns of their behavioural exchanges.

3) *Trading of commodities*

On p. 54, the authors claim that the positive correlation between grooming given and aggression received found in some studies is often seen in the light of BMT as subordinates' attempt to appease dominants by 'buying' tolerance. The authors criticize this approach by arguing that 'any result can be a posteriori interpreted as evidence of BMT' (p. 54), and that 'appeasement' is not a commodity 'we can measure (e.g. lack of aggression) (p. 54)'. However, we argue that it is possible to assess whether subordinates try to 'appease' dominants by measuring rates of aggression received (Gumert & Ho, 2008; Kaburu & Newton-Fisher, 2015a; Xia et al., 2013). Within a Biological Markets framework, if subordinates use grooming as a 'currency' to appease dominants, then we expect a *negative* relationship (rather than positive) between grooming given and aggression received. Accordingly, to our knowledge, all the studies that found evidence of grooming for tolerance/appeasement showed that grooming given was negatively predicted by aggression received (Gumert & Ho, 2008; Xia et al., 2013) Even Schino et al. (2005), cited by the authors, did not argue that the positive relationship between grooming and aggression was due to subordinates' attempt to reduce aggression from dominants, but probably resulted from dominants' extortion of grooming, with this

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operating as a ‘distorting factor that may significantly alter the possibility of free trading of biological commodities’ (p. 209). When it comes to coercion, the authors wrongly claim that it is an assumption of BMT that commodities should be exchanged when they cannot be taken by force (p. 54). However, the lack of coercion is *not* an assumption of BMT, but a necessary condition in which market forces can operate and be measured. Furthermore, –Sánchez-Amaro and Amici (2015) wonder ‘how can we know how much of the grooming provided is paid in exchange for some commodity [...] and how much serves an appeasement function [...]?’ (p. 54). Yet we do have statistical tools, such as mixed model analysis, that offer us the opportunity to test to what extent the provision of grooming is best explained by the receipt of one or more commodities. In our own analysis of the grooming-trade model in chimpanzees, we ran linear mixed models (LMM) in which grooming given was set as dependent variable while grooming, aggression, meat and support received were all considered as independent variables in a single model while controlling for repeated observations of the same individuals. We found that, in a despotic community, grooming given was best predicted by both grooming and support received, with grooming received exerting the strongest effect. The use of LMMs also addresses the issue the authors raised on p. 57, namely ‘exploring the relation between grooming given and other commodities received, while controlling for grooming received’. Given that LMMs are becoming an increasingly popular statistical tool in the study of BMT (Carne et al., 2011; Fruteau ~~et al., Lemoine, Hellard, van Damme & Noë,~~ 2011; Kaburu & Newton-Fisher, 2015a, 2015b), it is surprising that Sánchez-Amaro and Amici (2015) do not mention the use of this powerful statistical method to explore the trading of commodities in biological markets. While Sánchez-

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250 Amaro and Amici (2015) criticize the lack of consistency across studies investigating
251 BMT in primates they do not take into account how over the past two decades new
252 statistical analyses, such as LMM, have become available in familiar and easy to use
253 statistical packages such as R and SPSS. Yet, despite the variety of methods used, such as
254 regression (Barrett et al., 1999), correlation (Gumert, 2007), matrix correlation
255 (Balasubramaniam, Berman, Ogawa, & Li, 2011; Ventura, Majolo, Koyama, Hardie, &
256 Schino, 2006), and LMM (Kaburu & Newton-Fisher, 2015a, 2015b), most of these
257 studies have found evidence of trading in primate groups, providing compelling evidence

258 in support of BMT. Overall, we feel like the authors missed a fundamental aspect of
259 BMT: unlike what the authors state, the issue is not whether individuals exchange a
260 service for another one (e.g. 'which percentage of grooming given should we correlate
261 with the amount of each commodity received, when testing BMT?" p. 54), but rather
262 whether this exchange is sensitive to the variation in supply and demand (Barrett et al.,
263 2009; Fruteau et al., 2009; Kaburu & Newton-Fisher, 2015a).

264 Missing references

265 Sánchez-Amaro & Amici (2015) argue that, in order to test the time-frame of the
266 exchange of commodities, researchers should employ a 'protocol similar to that used by
267 Fruteau et al. (2009)'(p.53). However, the authors missed some relevant experimental
268 work: a recent experiment in vervet monkeys (*Chlorocebus pygerythrus*), for instance,
269 showed that dominant females tolerated and supported more low-ranking females who
270 had recently groomed them more (Borgeaud & Bshary, 2015). Additionally, although not
271 explicitly set up in the light of the BMT, Hemelrijk (1994) showed that, by

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272 experimentally inducing grooming and aggression in captive long-tailed macaques
 273 (*Macaca fascicularis*), females were more likely to support partner who had been
 274 grooming them in the 10 minutes before, than partners that had not groomed them.
 275 Moreover, while Sánchez-Amaro & Amici (2015) mention almost exclusively cleaner
 276 fish as a example of non-primate species in which BMT has been tested, they completely
 277 ignore a broad literature providing evidence in support of BMT, in a wide variety of
 278 species, from the delayed plumage coloration in birds (Greene et al., 2000), to the
 279 mutualistic interaction between mycorrhizal fungi and rhizobia (Werner et al., 2014) or
 280 human fairness (André & Baumard, 2011).
 281 Finally, we note that in concluding that “there is no convincing evidence for the existence
 282 of a PBM in which individuals exchange meat or grooming for sex” (p. 55), Sánchez-
 283 Amaro and Amici (2015) do not discuss Koyama et al.’s (2012) evidence for supply and
 284 demand influencing male chimpanzees’ grooming of swollen (‘oestrus’) females,
 285 although they cite the paper elsewhere in their essay, and/or Norscia et al. (2009)’s work
 286 on sifakas (*Propithecus verreauxi*) showing that male-to-female grooming matched
 287 female-to-male grooming only during the pre-mating season, while male-to-female
 288 grooming correlated with female mating during the breeding season. They have also
 289 missed our finding of precisely an exchange of grooming for mating in one of our two
 290 study communities: a mating market in the absence of effective coercive aggression by
 291 males (Kaburu & Newton-Fisher, 2015b). While we agree with Gilby et al. (2010) that
 292 our finding is puzzling, if not downright odd given what is known about female
 293 chimpanzee mating strategies, the result appears to be robust and suggests that there is
 294 more to be learned about the mating strategies employed by female chimpanzees.

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295 In conclusion, although we applaud the authors' effort in putting together a review of the
296 work to date investigating biological market theory in non-human primates, we feel that
297 there are areas of their essay that misinterpret or misrepresent aspects of both the theory
298 and the studies that have been conducted to test its application to primate grooming
299 exchanges.

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