Markets carefully interpreted: a reply to Kaburu and Newton-Fisher (2016)

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In our recently published essay (Sánchez-Amaro & Amici, 2015) we aimed to discuss the literature on primate biological markets (BMs) by drawing attention to the problems that, in our view, affect most primate studies endorsing the existence of BMs. In this way, we aimed not only to warn of conclusions based on dubious methodological approaches, but also to provide some possible new avenues to more efficiently test biological market theory (BMT) in primates. Finally, we hoped to stimulate debate with experts in BMT, including primatologists working in the field, to critically discuss the points we raised in our essay and find new ways to collaboratively improve empirical work on primate BMs.

In this respect, we are very happy about the Forum article by Kaburu and Newton-Fisher (2016, in this issue), which clearly supports our view that BMT is an essential theory explaining exchanges of commodities among individuals, whose details are still highly debated. Although we clearly disagree with most of the issues raised by the authors, we appreciate the opportunity to better explain some of the points raised in our essay. Furthermore, we hope that our answer to their Forum article will further contribute to the debate on how to best test BMT in primates. Given that some of the issues we raised are also more generally relevant to the study of exchanges among individuals, regardless of whether these are explicitly framed in a BMT, we hope that our response will also provide some useful hints to researchers working in fields other than BMT.

In our response, we first remark on the importance of some of the issues raised in our essay, whose relevance, we believe, Kaburu and Newton-Fisher (2016, in this issue) have failed to recognize. Subsequently we proceed with a discussion of some studies on primate BMs considered by Kaburu and Newton-Fisher (2016, in this issue) as convincing evidence in support of primate BMs, by specifically warning against a posteriori interpretations of results. Finally, we defend our personal view of the general methodological approach that should be used to study primate BMs by explicitly highlighting the way our view differs from that discussed by Kaburu and Newton-Fisher (2016, in this issue), and advancing some ideas to further improve the study of primate BMs.

TAKING OUR CRITIQUES FOR WHAT THEY ARE: CRITIQUES

In their Forum article, Kaburu and Newton-Fisher (2016, in this issue) tried to reduce most of the problems raised in our essay to...
our failure to understand BMT. Here, we try to clarify why we believe that the issues we raised are indeed fundamental for the study of BMs in primates, and how Kaburu and Newton-Fisher (2016, in this issue) misinterpreted most parts of our essay (and failed to acknowledge the soundness of the rest).

First of all, Kaburu and Newton-Fisher (2016, in this issue) state that we ‘misunderstand BMT in suggesting that it predicts only ‘short and finite relationships between different classes of individuals’’. In our essay, however, we never state that BMT only predicts short and finite relationships. Indeed, we strongly criticize the fact that this approach has often been used with primates (e.g. Barrett, Gaynor, & Henzi, 2002; Barrett & Henzi, 2002, 2006; Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Chancellor & Isbell, 2009; Gumert, 2007; Henzi, Lycett & Weingrill, 1997; Payne, Lawes, & Henzi, 2003) without conducting any preliminary analyses as to what the time frame of exchanges really is. Although determining the real time frame over which primates exchange commodities may be no easy task, there are surely creative ways to address this problem (see below).

Kaburu and Newton-Fisher (2016, in this issue) first attribute to us an assumption that we never made (i.e. primates exchange commodities on a very short-term basis), then criticize us for making this assumption and a few lines later stating that this assumption themselves (i.e. exchanges happen within bouts), as ‘a practical solution to a lack of a priori knowledge of the relevant time frame for reciprocation’. As clearly discussed in our essay, analysing only exchanges happening within the same bout (e.g. Barrett et al., 2002; Barrett & Henzi, 2002, 2006; Barrett et al., 1999; Gumert, 2007; Henzi et al., 1997; Payne et al., 2003) can lead to up to 82% of bouts being completely dismissed from analyses (e.g. Chancellor & Isbell, 2009). The arbitrary selection of different time frames of interaction and the dismissal of large parts of the data set can lead to too few grounded conclusions (see e.g. Campenni & Schino, 2014; Manson, Navarrete, Silk, & Perry, 2004, for an interesting discussion). When reviewing the literature for our essay (Sanchez-Amaro & Amici, 2015), we found it puzzling that some researchers claimed to have found evidence of BMT by disregarding all exchanges that did not happen in the very same bout (Barrett et al., 2002, 1999; Chancellor & Isbell, 2009; Gumert, 2007), while others made exactly the same claim for exchanges that happened not only in different bouts, but also over long periods of time (Manson et al., 2004; Schino, di Giuseppe, & Visalberghi, 2009; Schino, Polizzi di Sorrentino, & Tiddi, 2007). As BMT sensibly makes no general prediction as to the time frame of exchanges (plausibly because it can vary depending on the species and other contextual factors), a convincing test of BMT should imply that researchers, among other things, first try to determine the plausible time frame of exchanges through exhaustive observations (e.g. combining traditional sampling methods with video-camera recordings), and only then test whether these exchanges happen according to the laws of supply and demand, carefully avoiding circular arguments (see below).

Second, Kaburu and Newton-Fisher (2016, in this issue) claim that ‘by definition, grooming that is traded for some other commodity is not reciprocated in kind’. However, we fear that the authors missed our main point: the fact that grooming is traded either for another commodity, found no evidence for that and then concluded that maybe grooming is after all simply reciprocated with grooming, still providing support to BMT. If we want to test whether primates exchange grooming for other commodities, we think we should have a priori a set of clear predictions, as to which commodities should be taken into account, and why in a certain population grooming might still be mainly traded for grooming, regardless of other commodities being available (see below for further discussion).

Third, according to Kaburu and Newton-Fisher (2016, in this issue), we would ‘imply that only exchanges based on economic considerations (as proposed by BMT) are contingent’, thus neglecting ‘to recognize that those driven by ‘bonds’ or ‘relationships’ (under a relationship model) would also be contingent’. Once more, Kaburu and Newton-Fisher attribute to us a statement that we instead aimed to criticize. As repeatedly stated throughout our essay, we think that bonds and relationships might play an important role in BMs: if different dyads trade over different time frames depending on the quality of their relationships (as some studies would suggest: e.g. de Waal, 1997), for instance, this variability needs to be taken into account. In this respect, the approach used in many studies appears over-simplistic, by reducing analyses to within-bound exchanges (and thus disregarding notable amounts of data: e.g. Barrett et al., 2002, 1999; Chancellor & Isbell, 2009; Payne et al., 2003; Gumert, 2007), or increasing the hours of observations instead of trying to determine the plausible time frame over which these exchanges happen according to the laws of supply and demand) is enough to support BMT, even if we do not know the time frame over which the value of commodities changes is essential for a market model, as Kaburu and Newton-Fisher (2016, in this issue) state. But before we can test ‘whether behavioural strategies are sensitive to shifts in market conditions’, we also need to know the time frame over which these should be assessed. Do we need to observe animals for 2 h or 6 months, to detect these shifts? Or should we observe them until we find significant evidence that any two commodities are exchanged and thus be able to provide some positive evidence for BMs? Different studies have used very different approaches, and the reason why usually remains unclear, at least in our opinion. As we have discussed in our essay, some authors have discarded exchanges happening in different bouts (e.g. Barrett et al., 2002, 1999; Chancellor & Isbell, 2009; Gumert, 2007), others have calculated complex indexes, whose rationale is not always evident (e.g. Barrett et al., 2002; Henzi et al., 2003; Kaburu & Newton-Fisher, 2015). This variety of approaches does not help to objectively test BMT, and calls for a more standardized approach to the study of primate BMs. Although the theoretical predictions of the BMT are ‘clear and explicit’ (and we do indeed applaud them, and especially their application to other taxa: e.g. Barclay, 2013; Cowden & Peterson, 2009; Schwartz & Hoeksema, 1998), we think that the methodological approach that has been used to test these predictions in primates has often been unclear.

The issue is not as trivial as it seems. The following example might better explain why we disagree with Kaburu and Newton-Fisher (2016, in this issue) when they suggest that detecting a shift in primate exchanges (according to the laws of supply and demand) is enough to support BMT, even if we do not know the time frame over which these exchanges happen. Consider this example: if I want to buy a car, the price I will pay might depend on how demand and offer change through time. If you are an external observer willing to assess whether this is the case, it might be useful to know the price I am paying for the car. If I am paying 20 monthly rates of 1000 euros each, but you only observe me for 1 month, you might wrongly conclude that the car cost me just 1000 euros. According to Kaburu and Newton-Fisher (2016, in this issue), instead, there would be no need to conduct observations for the whole time of exchanges (e.g. 20 months): shifts in the monthly rates alone will be informative of the existence of a market (e.g. single rates will decrease when the demand decreases) regardless
of the overall time frame of interaction. However, this argument relies on the untested (and dubious) assumption that rates are all equal (i.e. that the frequency of exchanges is constant through time). In contrast, I might be free to pay the price on just one occasion, or at different rates, with the condition that rates have overall been paid after 20 months. Just monitoring what happens over a shorter time frame, therefore, might provide a partial picture, in which the ‘key payments’ are missing, or are overestimated, and the shifts that an observer detects could just reflect this problem and have nothing to do with BMs.

This is similar to what happens with primates, who do not exchange commodities constantly through time (i.e. grooming rate probably varies across bouts, hours, days and weeks, even if the market remains constant). In a baby market, for instance, handlers and mothers may tend to balance their grooming over the 2 months before infants are born. Therefore, if they are only observed the week before and the week after the infant is born, shifts in grooming ratio may not necessarily be due to a shift in the supply and demand of infants. Instead, the shift may just reflect the fact that too few data have been collected, and we have missed the key grooming bouts ‘restoring’ the initial grooming ratio. If exchanges do not happen with a constant frequency (and this is what we should assume), monitoring what happens over a shorter time frame might provide a partial picture which has nothing to do with BMs.

Other researchers disagree with us. One referee of this article, for instance, suggested that to prove the existence of a primate BM it is sufficient to first detect an overall exchange between two commodities (by detecting a correlation between two behaviours at the group level), and then, if this exchange exists, to identify a context in which this trading could potentially be altered by a shift in the supply and demand ratio. However, these are not sufficient prerequisites to prove a BM. Gumert (2007), for instance, found a shift in the grooming received by mothers as a function of the number of infants in the group (i.e. mothers received more grooming when there were fewer babies in the group). This may prove the existence of a BM, as the author postulates, but it may also simply reflect a shift in the grooming ratio because exchanges have been observed for much too short a period of time, so that ‘key payments’ are missing or are overestimated. For instance, simply taking into account exchanges of commodities outside the reciprocal bouts might have completely changed the pattern of results. In other words, while we agree with the referee that these steps are necessary, we do not think that they suffice in proving the existence of a BM.

Thus, in our view, it is not enough to detect a shift in primate exchanges to conclude that there is a BM: this is only true if the commodities involved are exchanged with a constant frequency throughout bouts, hours, days and even months. If this is the case, then surely a shift is a good enough hint for the existence of BMs. However, it is highly unlikely that exchanges happen with a constant frequency across time (e.g. that I groom you twice as much as you groom me in every bout, day, week and month). Much more likely, there will be ‘unbalanced’ exchanges, but overall, within a certain time frame, these exchanges will tend to ‘balance’. Therefore, a more reliable approach to test BMT might be to predetermine this time frame in which dyadic exchanges tend to ‘balance’, i.e. the minimal unity of time in which the ratio between commodities given and received within dyads is not significantly changing, when supply and demand are held constant. This means that before testing whether primates exchange grooming for baby handling, for instance, one should predetermine not only how grooming is distributed in the community when there are no babies at all, but also the time frame over which the ratio between grooming given and received within dyads becomes constant. This ratio, for instance, might vary across days, but it might not differ between the first and second week, or between the first month and the second month, and therefore a week, or a month, should be used as the time frame over which to test the occurrence of shifts, because this is the time span over which individuals ‘balance’ their exchanges. Considering a different unit of time would be wrong, and would lead us to detect shifts when there are none.

Once we have predetermined this time frame, a shift in exchanges may surely become symptomatic of a BM. We consciously use the conditional: in our opinion, a shift in exchanges demonstrates the existence of a BM only if one can contextually demonstrate a shift in the commodity acquired. For instance, we do not believe that a shift in grooming exchanges demonstrates that grooming is being exchanged for ‘something else’, if we do not predetermine what this ‘something else’ might be, and/or we do not detect any shift in the commodity that should have been acquired through grooming (see e.g. Norscia, Antonacci, & Palagi, 2009, and Koyama, Caws, & Aureli, 2012, showing a shift in grooming exchanges in favour of oestrous/swollen females, but not a shift in male copulation rates).

Fourth, in our section on cognitive challenges, we briefly explain why both short- and long-term tracking of exchanges in BMs might be cognitively too complex for primates, which we discuss emotional book-keeping as a possible alternative mechanism to navigate in primate BMs. To date, for instance, cooperative relationships are largely believed to be facilitated by oxytocin, which probably plays a role in keeping track of social interactions in primates (e.g. Crockford et al., 2013). As we explicitly state in our essay, therefore, emotional book-keeping is a plausible mechanism that primates may use to track exchanges in BMs. However, we believe that some researchers have failed to convincingly operationalize it when studying BMs, providing no clear a priori reasons as to why certain specific factors should trigger the psychological states required by emotional book-keeping. For instance, we would have found Gumert (2007) much more convincing if he had argued a priori (or even better: if he had first provided sound experimental evidence) that psychological states are triggered by an approximation of the ratio of potential partners to competitors (and not simply by the number of potential partners, for instance) and only then tested BM with this solid knowledge. Psychological states in primates can be affected by several factors (see e.g. Engelhardt, Heistermann, Hodges, Nürnberg, & Niemitz, 2006; Engelhardt, Hodges, Niemitz, & Heistermann, 2005) and it is compelling to determine them a priori, before testing BMT. Kaburu and Newton-Fisher (2016, in this issue) failed to appreciate that, claiming instead that we ‘dismiss emotion as a mechanism for the operation of biological markets’. On this point, they further argue that, BMT being a functional theory, it is not so important to know which mechanism allows exchanges to happen. But there is more to that: according to Kaburu and Newton-Fisher (2016, in this issue), if we find evidence of BMT in primates implying that primates make use of complex strategies to navigate in BMs, we should also be free to assume that primates do have the cognitive or emotional skills to employ these strategies. In our essay, we pinpoint multiple inconsistencies and flaws in the methodological approach used so far to test BMT in primates; if on top of this we have a nice functional theory assuming that primates need to do things they might not be able to do (or for which we have no evidence so far), it is really hard to digest that (1) ‘several studies have looked for and found evidence of BMT in a variety of primate species’, as instead stated by Kaburu and Newton-Fisher (2016, in this issue), and that (2) these findings also provide evidence of complex emotional or cognitive strategies in primates, which have never been proved in any other way.

Fifth, according to Kaburu and Newton-Fisher (2016, in this issue), we would find it ‘unreasonable’ that grooming value should
differ between species. In contrast, we repeatedly argue that ‘different species may use different time frames’, and we cast doubt on ‘the existence of a general time frame of interaction over which primate exchanges take place’. Of course, the value of grooming might also vary across species, and as far as we know, even across populations and dyads (see e.g. de Waal, 1997), for instance because grooming might be valuable for a certain individual or in a certain location. However, we need to have a priori predictions, as to why this should be the case, and possibly even experimental evidence (independent of BMT, to avoid circular arguments as in Kaburu & Newton-Fisher, 2015: see below). If we do not start having some clear frames to study BMT in primates, we run the serious risk that ‘the complex interactions of multiple factors might often allow an exaggerated flexibility in the interpretation of results’. In this respect, it might be useful to initially shift the focus from mere observational to more controlled set-ups, in which experimental manipulations are implemented and assumptions tested, as has already been proven in some recent studies (Borgeaud & Bshary, 2015; Fruteau, Voelkl, Van Damme, & Noe, 2009). However, it is important to note that replicability across species and populations is not always high. Therefore, predetermining the time frame of interaction, as explained above, should be done whenever it is practically possible before testing BMs. In their Forum article, Kaburu and Newton-Fisher (2016, in this issue) admit that ‘whether and to what extent grooming varies in value remains to be determined’ but do not recognize it as a priority. Of course, we do not want to say that BMs do not exist in primates, or that in the future there will be no way to find a proper way to convincingly test BMT while taking into account this huge variability across species, populations, individuals and contexts; all we want to do is highlight that convincing evidence is so far extremely scant. Surely, all previous studies have significantly contributed to our better understanding of BMs, even when they raise serious methodological concerns: somehow, they paved the way to better approaches. However, efforts need to be made in the future to find better experimental solutions to the problems we raised.

Sixth, Kaburu and Newton-Fisher (2016, in this issue) find it ‘unsustainable’ when we argue that using aggression to compete over resources contrasts with the predictions of BMT. However, as the authors surely know, the literature in the past has been clear in stating that aggressive competition within the same class is contrary to BMT, and that resources exchanged according to the law of supply and demand cannot be exerted (Noë & Hammerstein, 1994). If we accept that resources can also be taken by force, as claimed by Kaburu and Newton-Fisher (2016, in this issue), then we might wonder: how many of these resources are exerted, and how can we quantify them and account for this when assessing how resources are traded with each other? Does it also mean that, in the very few cases in which clear evidence of primate BMs was found, we were dealing with a very special population living in the ideal world we envisioned, in which no competition happens, resources are not exerted and BMs are not altered? After the publication of our essay, Hammerstein and Noë (2016) have tried to address this issue, suggesting that the use of force might happen in some cases, without in any way affecting the general applicability of BMs. How exactly this happens, however, remains unclear. Moreover, while we surely applaud any attempt to develop BMT in such a way that it better reflects the complexity of primate exchanges, we think that this complexity should not lead to a lack of clear predictions.

Finally, the authors had problems with our following sentence: ‘As a result, resources with no a priori intrinsic value are exchanged according to the laws of supply and demand, explaining the formation of short and finite relationships between different classes of individuals’. We did not mean that individuals in BMs exchange worthless resources: if they are resources, they clearly need to have some value. Instead, we meant that valuable resources are exchanged among individuals, but the exact value of these resources is not determined a priori, fluctuating in the BM as a function of the laws of supply and demand. We hope that, with this clarification, the authors will not have to puzzle further over this sentence.

**Lack of Evidence is Not Evidence**

At the beginning of their Forum article, Kaburu and Newton-Fisher (2016, in this issue) report a series of studies that would provide convincing evidence that BMs exist in a variety of primate species (e.g. Fruteau, Lemoine, Hellard, van Damme, & Noe, 2011; Gumert, 2007; Kaburu & Newton-Fisher, 2015; Koyama et al., 2012; Newton-Fisher & Lee, 2011; Norscia et al., 2009; Port, Clough, & Kappeler, 2009; Tiddi, Aureli, & Schino, 2012). We think that this might be misleading for those readers who are not very familiar with the literature on primate BMs. With a few exceptions (Fruteau et al., 2011; Port et al., 2009), the studies cited in the Forum article do indeed fail to provide convincing evidence of BMs (or only provide some partial evidence that may support the BMT). In particular, the studies cited by Kaburu and Newton-Fisher (2016, in this issue) either present serious methodological flaws and inconsistencies, as we discussed in our essay (e.g. Gumert, 2007; Kaburu & Newton-Fisher, 2015), or they provide completely different conclusions to those reported by Kaburu and Newton-Fisher (2016, in this issue). Tiddi et al. (2012), for instance, provide clear and sound experimental evidence of grooming exchanges following Seyfarth’s (1977) model, but make no conclusions whatsoever about the existence of BMs. Similarly, Norscia et al. (2009) provide evidence that males groom oestrus females more frequently than anoestrous females. These results suggest that oestrus females might be more valuable than anoestrous females to males, but do not provide any evidence as to whether males get sex in exchange for grooming, nor whether commodities fluctuate depending on the law of supply and demand (i.e. they do not yet provide evidence for the existence of a primate BM). In the same line, Koyama et al. (2012) provide evidence suggesting that males groom swollen females more often than non-swollen females, and that the amount of grooming provided to swollen females depends on the number of swollen females present. However, they fail to show the existence of a BM, in that females receiving more grooming did not copulate more often with those males. Of course, it is possible that these patterns reflect the existence of BMs, but to fully claim the existence of primate BMs some more evidence is required (for a more convincing approach, see e.g. Fruteau et al., 2009; Pansini, 2011; Borgeaud & Bshary, 2015).

This approach becomes especially misleading when Kaburu and Newton-Fisher (2016, in this issue) discuss the existence of baby markets. Although they make a good effort to divide mechanistic and functional explanations, they nevertheless fail to acknowledge that the large majority of studies on baby markets did indeed fail to find any evidence supporting the existence of a BM in which grooming is exchanged for baby handling according to the laws of supply and demand (Frank & Silk, 2009; Lazaro-Perea, de Fátima Arruda, & Snowden, 2004; Payne et al., 2003; Slater, Schaffner, & Aureli, 2007; Tiddi, Aureli, & Schino, 2010). Therefore, we think there is no reason to advocate the coexistence of a mechanistic and a functional explanation, at least unless more evidence is collected to support the functional explanation defended by Kaburu and Newton-Fisher (2016, in this issue). To date, on the basis of the experimental evidence we believe that affiliative behaviours are simply provided to mothers as signals of benign intent (similarly to submissive displays, to be clear), and not as a quantifiable currency which is exchanged according to the laws of supply and demand. This explanation is presented and discussed with intellectual
honesty by Slater et al. (2007), and Tiddi et al. (2010), as clearly acknowledged in our essay. Similarly, as it concerns the existence of a BM in which sex is exchanged for food or grooming (which according to Kaburu and Newton-Fisher should be supported by experimental evidence), we instead refer to our essay and especially to Gilby, Thompson, Ruane, and Wrangham (2010), who provided a very detailed and thoughtful critique on the topic.

In their Forum article, Kaburu and Newton-Fisher (2016, in this issue) specifically argue that they have provided convincing evidence of primate BMs, in that chimpanzees with a steeper hierarchy groom more for agonistic support, while chimpanzees in more egalitarian groups groom more reciprocally (Kaburu & Newton-Fisher, 2015). In contrast, in our essay we argued that their study fails to provide this evidence, and in their Forum article Kaburu and Newton-Fisher (2016, in this issue) concluded that we misrepresented their work. However, in their paper they state that they have ‘found no statistically significant difference between communities in the degree to which male chimpanzees reciprocated grooming effort’ (Kaburu & Newton-Fisher, 2015). Later, they confirm these findings by stating that ‘the analysis using LMM confirmed that for males in both communities the amount of grooming given was predicted by the amount of grooming received’ (Kaburu & Newton-Fisher, 2015). In what way should we have misrepresented their work, when stating in our essay that in their study ‘grooming reciprocity was not affected by hierarchy steepness’? Moreover, if grooming given and received were reciprocated in both communities, how could that same grooming also have been used in exchange for agonistic support (at least in one of the two communities)? This is explicitly recognized by the authors in the Discussion of their paper: ‘Our finding that grooming reciprocity persists in the face of variation in hierarchy steepness is contrary to the grooming-trade model, which suggests that grooming reciprocity should be weaker when grooming can be traded for alternative services (Barrett et al., 2002, 1999)’. We therefore believe that, if ‘grooming reciprocity was not influenced by hierarchy steepness’, their study failed to provide evidence for the existence of a BM in this community (at least, not when these commodities and time frame are considered).

In our essay, we also discussed how problematic it is to assume that grooming might be exchanged for a reduction in aggression (i.e. some individuals might ‘extort’ grooming by the threat of force, and partners might groom them more to receive less aggression). If we assume that grooming can be exchanged for different commodities, for instance, it is hard to test how much grooming is provided in exchange for some measurable commodity (e.g. agonistic support) and how much for a commodity that we cannot really measure (e.g. reduced aggression). Kaburu and Newton-Fisher (2016, in this issue) disagree with us, and argue that it is enough to find a negative relationship between grooming given and aggression received, in order to prove that subordinates exchange grooming for dominants’ reduction in aggression. The existence of such a negative relationship (and not positive, as we wrongly stated in our essay, incorrectly using ‘positive’ as a synonym for ‘significant’) has indeed often been used to postulate the existence of a primate BM, in which grooming is traded for a reduction in aggressions (e.g. Barrett & Henzi, 2006). This argument, however, is weak for several reasons. First, a significant correlation between two variables might prove the existence of an exchange, but does not alone prove the existence of a BM (which, as Kaburu and Newton-Fisher surely know, also implies that the exchange happens according to the laws of supply and demand). Second, aggression serves multiple essential functions in group-living primates (e.g. de Waal, 1996; van Schaik & Aureli, 2000), and it might be seriously misleading to just consider it as functional to BMs: if ever, it is plausible that only some aggression will be ‘repressed’ in exchange for grooming, but how much should that be? Moreover, even if providing grooming decreased the frequency of aggressions received, we would need a baseline for each dyad as to which would be the standard amount of aggression received, were grooming not provided. However, this seems unfeasible. Alternatively, we would need to detect an exchange with a commodity other than grooming. Thus, we could establish a baseline level of aggression prior to the introduction of the targeted commodity, to study whether aggression levels fluctuate as a function of the commodity introduced. Finally, it might be possible that a negative relationship across individuals between grooming given and aggression received simply reflects a high-quality relationship between pairs of individuals with strong affiliative bonds and few resources over which they compete (i.e. favourite partners may be groomed more and attacked less frequently).

A QUESTION OF METHODOLOGICAL APPROACH

Kaburu and Newton-Fisher’s (2016, in this issue) Forum article also provides us with the chance to discuss more in general what we believe should be the right methodological approach to the study of BMs. While we ideally view scientific research as a series of clear a priori hypotheses and precise testable predictions which need to be corroborated by strict experimental evidence, Kaburu and Newton-Fisher (2016, in this issue) seem to propose a more flexible approach, in which hypotheses might be added a posteriori and assumptions made without necessarily testing them, if this might be ‘a practical solution’ (see below). First, we think that predictions should be clear and results detailed enough to provide an exhaustive test of the hypotheses. Although it is true that the theoretical predictions of BMT are relatively clear, the way these predictions have been tested are often not straightforward. Kaburu and Newton-Fisher (2016, in this issue), for instance, argue that ‘support for BMT should also be sought by looking at how individuals distribute their commodities’, and not ‘be based exclusively on whether the provision of a service is predicted by the receipt of the same or another commodity’. However, we think that the fact that grooming is ‘distributed across all dyads, with only reciprocity being more pronounced between individuals close in rank’ cannot per se be considered a sufficient satisfactory proof of BM. BMT makes clear predictions as to what we should expect from a BM, and testing BMT should try to provide evidence that these expectations are indeed met. Surely, analysing the distribution of grooming across individuals might be a necessary first step. However, as we make clear in our essay, there is other essential evidence that needs to be provided to make a convincing argument in favour of BM in primates: if grooming distribution better fits the BMT prediction, what is grooming being exchanged for, and in which time frame, and which mechanisms are primates using to do that? We believe that simply dismissing all these arguments not only makes BMT useless, but also less credible.

In our essay, we often emphasize that in order to test BMT (and especially, whether commodities are exchanged according to the laws of supply and demand) we should first experimentally test a series of assumptions that are now simply taken for granted, including the exact commodities being exchanged, and the time frame over which these commodities are exchanged (see above). Kaburu and Newton-Fisher (2016, in this issue) see it differently, and suggest that there is no need to be so strict about determining these parameters before testing BMT, as new statistical tools (e.g. mixed model analysis) would now provide us with the chance to directly address these problems during data analyses (e.g. to see the extent to which grooming provided is explained by the receipt of one or more commodities). Of course, the use of modern statistical tools is always beneficial, in science. However, we think that
Kaburu and Newton-Fisher’s view is simplistic. First, most previous studies could not take advantage of these statistical tools to analyse their data. Therefore, although the authors of these studies surely cannot be blamed, it is evident that their studies could not use statistics to take into account the problems we raised. Moreover, it is important to note that better statistical tools can improve only our understanding of the data we have collected, but not that of the data we should have collected. If we want to know the extent of grooming exchanged for other commodities, for instance, we should make sure to have collected data about all these other commodities, and to have done it over the right time frame. Once we have collected partial information, for the wrong period of time, there is nothing that statistics can do, no matter how good the analysis is. Needless to say, most of the studies that the authors cite in this paragraph as providing evidence of BMs in primates, ‘despite the variety of methods used’, are not decisive, in our view, either because of serious methodological flaws/inconsistencies (e.g. Barrett et al., 1999; Gumert, 2007; Kaburu & Newton-Fisher, 2015; see our Essay for more details), or because the results were much more complex than suggested by Kaburu and Newton-Fisher (2016, in this issue), thus providing no clear evidence of primate BMs (e.g. Balasubramaniam, Berman, Ogawa, & Li, 2011).

Furthermore, our essay highlighted the importance of collecting data with a consistent, well-justified methodological approach. Throughout our Methodological Issues section, we pointed to numerous inconsistencies in data collection and data analyses, which included things like lack of clear criteria to quantify grooming, differences in observation techniques, varying duration of observations, use of different indexes and dismissal of some parts of the data set. Although Kaburu and Newton-Fisher (2016, in this issue) carefully avoid discussing these issues, which seem not to undermine their trust in the existence of primate BMs, we do think that these issues can crucially challenge the solidity of most of the results so far provided in support of primate BMs. Needless to say, our essay and this reply are not intended to diminish the previous valuable efforts made to study primate BMs. Our aim was instead to review the extensive number of studies that have been done on the topic and provide a constructive critique on the aspects that we have found most problematic, fostering discussion and providing new ideas for future research.

Finally, the authors claim ‘the importance of a posteriori interpretations’, which in their opinion would be formally hypothoses. Surely, it is possible to have clear hypotheses, thoroughly test them, find no evidence supporting them and propose new ones that will have to be tested in future studies, with a new data set. In this respect, we clearly agree with Kaburu and Newton-Fisher (2016, in this issue) about the importance of a posteriori interpretations, as a means to stimulate future research. However, we strongly criticize a very different methodological approach that has often been used to test BMT in primates, and which Kaburu and Newton-Fisher (2016, in this issue) seem to defend: when there is no evidence supporting the original hypotheses, a posteriori interpretations can be added and the same data used to ‘test’ the new hypotheses. It comes as no surprise, therefore, that Kaburu and Newton-Fisher (2016, in this issue) can find ‘evidence of BMT in a variety of primate species’, even when evidence is completely lacking (e.g. because the authors tested something completely different: Tiddi et al., 2012), or when it has been built on a posteriori interpretations (e.g. Barrett & Henzi, 2006; Kaburu & Newton-Fisher, 2015).

CONCLUSIONS

Paradoxically, we completely agree with the conclusions by Kaburu and Newton-Fisher (2016, in this issue), in that BMT is a valuable theory with a huge potential. In our conclusions, we stated that ‘BMT is still one of the most comprehensive theories explaining the exchange of commodities among classes of individuals’, and that it has reliably and convincingly predicted social interactions in taxa ‘in which few commodities can be exchanged over a very short time frame’. With our essay, we do not think that we have missed a valuable opportunity to provide a constructive critique of BMT as applied to primates, as stated by Kaburu and Newton-Fisher (2016, in this issue). Instead, we think we have raised numerous empirical issues that need to be addressed in the future, and that have been largely ignored in the study of primate BMs, seriously undermining the credibility of this theory. While we clearly acknowledge the need for ‘a complex, dynamic, individual-based approach’, as is implied by BMT, we also want to remark that such a complex theory needs more systematic studies addressing the theoretical and methodological issues reviewed in our essay, to avoid exaggerated flexibility in the interpretation of results. As the authors also state, we need ‘more detailed studies and more refinement of particular applications of BMT to tease apart the complexities in primate social behaviour’, something that, so far, despite the authors’ claims and few good exceptions, we think has not always been done.

Throughout our essay, we have tried to contribute what we believe might be reasonable practical solutions to address the two main weaknesses of most studies on primate BMs, and preliminarily determine (1) the plausible time frames over which exchanges should occur and (2) the most meaningful commodities we should take into account when testing BMT. As we have already discussed, the only approach we envision is to preliminarily conduct more experiments in well-controlled environments. Understanding the time frames over which commodities are exchanged is the primary step to further investigate how (1) the introduction of new commodities and (2) quantitative or qualitative changes affect how familiar commodities are exchanged according to the laws of the supply and demand. In this way we will not simply obtain information on the time frame over which the value of commodities changes (i.e. ‘what really matters for a markets model’, according to Kaburu & Newton-Fisher, 2016, in this issue), but we will also set the a priori foundations to understand whether commodities are indeed exchanged with other commodities, according to the laws of supply and demand. We are aware, as other researchers have suggested, that ‘life is shorter and PhD studies even more’ (Hammerstein & Noë, 2016), and we are also aware that we are far from providing an exhaustive list of solutions to all the problems we have raised. None the less, we hope that coordinated efforts across departments and disciplines will allow researchers to credibly address the issues we raised and find creative solutions to finally provide a solid experimental approach to the study of primate BMs.

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