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2012

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### Recommended Citation

Flemming, TE, Jones, OD, Stoinski, TS, Mayo, L, Brosnan, SF. (2012). The endowment effect in orangutans. *International Journal of Comparative Psychology*, 25(4), 285-298.

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## **The Endowment Effect in Orangutans**

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The endowment effect is the tendency to, seemingly irrationally, immediately value a possessed item more than the opportunity to acquire the identical item when one does not already possess it. Although endowment effects are reported in chimpanzees (Brosnan, Jones, Lambeth, Mareno, Richardson, & Shapiro, 2007) and capuchin monkeys (Lakshminarayanan, Chen, & Santos, 2008), both species share social traits with humans that make convergence as likely an evolutionary mechanism as homology. Orangutans (*Pongo* spp.) provide a unique insight into the evolution of the endowment effect, along with other apparently irrational behaviors, because their less frequent social interactions and relatively more solitary social organization distinguishes them from the more gregarious apes, allowing a test of evolutionary homology. In the present study, we used pairs of both food and non-food objects, as in an earlier test on chimpanzees (Brosnan et al., 2007). We established the apes' preferences in forced-choice tasks, then tested whether they showed an endowment effect in an exchange task, in which subjects were given one of the objects, followed by the option to exchange it for the other. Here, we report the first evidence of the endowment effect in a relatively less social primate, the orangutan. This indicates that this behavior may have evolved as a homology within the primates, rather than being due to convergent social pressures. These findings provide stronger evidence for the hypothesis that at least one bias, the endowment effect, may be common in primates and, potentially, other species.

Humans often exhibit behaviors that seem irrational. For reasons not well understood, we succumb to various cognitive and behavioral biases, some of which may reflect evolved adaptations that are not maximized in all environments, and may lead to seemingly irrational outcomes in less common contexts. One of these, the endowment effect, describes the tendency in humans to value a possessed item – even at the instant of acquisition – more than the opportunity to acquire the same thing when it is not yet possessed (Franciosi Kujal, Michelitsch, Smith, & Deng, 1996; Kahneman, Knetsch, & Thaler, 1990, 1991). For example, people often

Research supported by National Science Foundation Human and Social Dynamics grant (SES 0729244) awarded to Sarah F. Brosnan. All procedures used in the research are in accordance with the Guidelines for the Use of Animals in Research and have been approved by the Institutional Animal Care and Use Committee of Georgia State University (IACUC protocol # A07011) and the Zoo Atlanta Scientific Review Committee. The authors thank all orangutan keepers and care staff at Zoo Atlanta for their assistance in running these studies. Correspondence concerning this article should be addressed to Timothy M. Flemming, Georgia State University, Department of Psychology, Language Research Center, P. O. Box 5010, Atlanta, GA, 30302-5010, U.S.A. (timothy.flemming@reed.edu)

demand considerably more to sell something they have just come to own than they would have been willing to pay to acquire it (Horowitz & McConnell, 2002). This tendency seems inconsistent with standard economic theory because, absent new information or experience, the good itself has not changed in any way that should affect valuation. The endowment effect is important in humans because it can impede otherwise efficient exchanges of goods, and even tradable rights, thereby warping how markets function (Hoffman & Spitzer, 1993; Jones & Brosnan, 2008; Korobkin, 2003). The endowment effect is only one of several behaviors that human and nonhuman primates show that deviate from 'rational' in similar ways [e.g., Gambler's fallacy, availability heuristic (Tversky & Kahneman, 1973), overconfidence (Lichtenstein, Fischhoff, & Phillips, 1982)]. However, no existing theory coherently explains the full suite of irrational behaviors, and only recently have evolutionary connections been posited between irrationalities common in humans and other species (Brosnan et al., 2007; Chen, Lakshminarayanan, & Santos, 2006; Haselton & Ketelaar, 2006; Haselton, Nettle, & Andrews, 2005; Jones, 2001). The endowment effect offers the opportunity to test evolutionary hypotheses for these irrational behaviors using phylogenetic comparisons between related species.

Knetsch (1989) was one of the first to identify the endowment effect in humans. He presented three groups of undergraduates with coffee mugs and chocolate bars. In order to determine the representative ratio of preferences for the group as a whole, participants in one group could choose one of the two items before completing a questionnaire [condition: choice task]. Participants showed approximately equal preference for each object. In another group, participants were given the coffee mug before the questionnaire and then offered the opportunity to exchange it for a chocolate bar upon completion [condition: endowed with mug]. In the final group, the order of the objects was reversed: participants were given the chocolate bar prior to the task and then offered the opportunity to exchange for a coffee mug after completing the questionnaire [condition: endowed with chocolate]. In both of the endowed groups, approximately 90% of participants chose to keep the object with which they were endowed, even though presumably only half of the group would have preferred that item (based on the preference test) if given a choice uninfluenced by ownership. These high refusal rates reflect a strong propensity to retain owned goods (i.e., an endowment effect) despite an equal distribution of preferences for the two objects in the choice condition.

The effect has since been demonstrated in many different situations, including some using cash values (for details see Jones & Brosnan, 2008). But what causes the effect remains a subject of debate. Although various theories have been proposed [such as loss aversion (Tversky & Kahneman, 1991) prospect theory (Tversky & Kahneman, 1992), procedural artifacts (Plott & Zeiler, 2005, 2007)], these theories fail to provide a stand-alone explanation for the function of the behavior (Brosnan et al., 2007; Jones & Brosnan, 2008). For instance, while the endowment effect is undoubtedly linked to loss aversion, this raises the question of why humans are more averse to losing a thing than they are to losing the opportunity to gain the identical thing. In an effort to link disparate but patterned cognitive irrationalities, Jones proposed the 'time-shifted rationality' hypothesis (Jones, 2001) as an explanation of how these behavioral predispositions

leading to irrational cognitive biases may have evolved. He posited that many of the seemingly irrational, but directionally consistent and wide-spread, biases may reflect the disjunction between earlier evolutionary pressures on human cognition and the modern environmental features in which human cognitive abilities play out. On this view, predispositions toward some behaviors that seem irrational today may have evolved as a function of the past benefits that they conferred.

With the endowment effect, for example, relinquishing an item in exchange for another is riskier than keeping it. There are no guarantees that a potential exchange partner will reciprocate; he may instead ‘defect’ upon gaining possession (that is, not provide the object he possesses that was offered in trade). The defection of an exchange partner can yield greater losses than would refusing to exchange, which at least preserves the item possessed, even if it is of lesser value. Modern human societies have dramatically alleviated the problem of defection from exchange interactions through legal and policing systems. Yet the asymmetric risks of exchange likely posed far greater problems for our ancestors, and continue to do so in species that lack (among other things) the ability to use language to mediate interactions and garner support following a defection (Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008).

To test this hypothesis, Brosnan et al. (2007) investigated the presence of the endowment effect in chimpanzees under a series of conditions designed to replicate the choice study by Knetsch (1989). Moreover, they supplemented between-group analyses of group means (enabling comparisons of endowment effect magnitudes among groups, the procedure that is used in human studies) with a within-subjects design that better examined possession tendencies in individuals. Chimpanzees were presented with a series of choices within pairs of foods and pairs of non-food objects. As with the human study, these included a choice condition to establish preferences (between two foods in the one case, and between two non-food objects in the other) and two endowment conditions.

The results provided three key findings. First, they provided the first experimental evidence of an endowment effect in a nonhuman species. Chimpanzees as a group were 15-20% (depending on the item) more likely to keep the food with which they had been endowed than would otherwise be expected on the basis of their group-wide preferences. Second, the prevalence of the effect across individuals was greater for food than non-food items. Specifically, while only 3% of individuals exhibited an endowment effect in the non-food condition, 42% exhibited it in the food condition. Third, the direction of the effect reversed between food and non-food items. Specifically, foods increased the likelihood of refusals to exchange by 15-20% (over expected exchanges on the basis of group-wide preferences). In contrast, the non-food items decreased the likelihood of refusals to exchange by 16-58%. Thus, the chimpanzees’ maintenance of a *less* preferred item indicates an even stronger endowment effect than would be anticipated if the items were equally preferred by the subjects.

Based on these data, and other recent studies finding evidence of an endowment effect (Lakshminarayanan, Chen, & Santos, 2008) and loss aversion (Chen et al., 2006) in capuchin monkeys, and the endowment effect in some of the other apes (Kanngiesser, Santos, Hood, & Call, 2011), evidence is emerging supporting this behavior as a trait in common among primates. However, one

critical component is missing; it is unclear whether the presence of this behavior represents a homology among primates, or a convergence in these species based on some characteristics, such as sociality. Sociality may be important if exchange behavior only emerges in the context of a multitude of rich social interactions. In the present study, we replicate the chimpanzee study in a less gregarious great ape, the orangutan. The orangutan is of particular interest with respect to the endowment effect because it is closely related to the African apes (which include humans), but has a relatively more solitary social organization. Orangutans do maintain some social bonds (van Schaik & van Hooff, 1996), and males form dominance hierarchies with those males in adjacent territories (van Schaik, Preuschoft, & Watts, 2004). Nonetheless, individuals spend a much larger percentage of their time either alone or in mother/offspring pairs, and apparently lack many behaviors that may be related to solidifying social bonds, such as coalitions, cooperative hunting, food sharing and frequent allogrooming (Singleton & van Schaik, 2002; van Noordwijk & van Schaik, 2009; van Schaik, Marshall, & Wich, 2009; although mother-infant food sharing remains common, Jaeggi, van Noordwijk, & van Schaik, 2008). Orangutans typically range either solitarily or as an adult female/offspring pair, or, at a few sites, in small groups (average 2.3 individuals; van Schaik, 1999, 2002), although it is possible that this less socially-dependent lifestyle is the result of recent selective pressures based on habitat loss and destruction, the current pattern of sociality is different from that of the other apes.

Thus, knowing whether the orangutan exhibits an endowment effect similar to that seen in other primates will provide much needed information on the possible factors influencing its evolution. One previous study examined the endowment effect in orangutans, however each of the three orangutans in that experiment showed such a strong preference for one food item (pellets) that they always traded to acquire them, making it impossible to tell whether they showed the effect (Kangniesser et al., 2011; five orangutans tested with non-foods preferred to trade every item they received). For this study, we replicated the earlier chimpanzee study (Brosnan et al., 2007) in seven socially living orangutans to address this issue. We specifically chose to utilize socially-housed orangutans as, despite the possibility that experience in these relatively larger groups could have changed their behavior, we could rule out the possibility that a relatively less social *experimental* environment as compared to the chimpanzees caused a difference in behavior between the two ape species. If rich sociality is critical to the development of endowment effect behavior, these apes may behave differently from the relatively more gregarious chimpanzees and humans. However, if the endowment effect is the result of homology within the apes, or more broadly all primates, we expect the orangutans to behave similarly to the chimpanzees and/or capuchin monkeys.

## Method

### Subjects

Subjects were 7 adult orangutans (3 male; 4 female) from 3 different indoor/outdoor social groups housed at Zoo Atlanta, Atlanta, GA USA. The use of socially housed individuals meant that any differences in behavior were due to species differences, and not any effects of previous lack of social interaction on some individuals. Although this different experience could have changed their behavior, we could also rule out that different housing conditions affected the orangutans' results as compared to the chimpanzees. All animals were familiar with general exchange procedures prior to testing, and had participated in one previous exchange task study (Brosnan et al., 2012). All animals had exchanged both non-food objects and foods as part of regular interaction with keepers. Thus, all animals were both comfortable with exchange and were unlikely to anticipate that exchange was either mandatory or always profitable, since trading history was not consistently associated with reward. Participation was voluntary; subjects were called to the front of their home enclosure and given the opportunity to participate. In rare cases in which subjects chose not to participate, sessions for those animals were postponed until the following day. During testing, animals were separated from the other apes into an area of their indoor environment to minimize distractions. Each session took approximately 5 minutes and each ape completed only one test session per day. Animals were fed their full diet as normal throughout the study. Testing was done prior to morning feedings to ensure that motivation to participate was high.

### Materials

Only food items that were easily passed through caging and were difficult to consume rapidly were chosen. These foods were peanut butter and sugar-free fruit flavored popsicles, both of which were familiar foods to the orangutans. Peanut butter (PB) was placed inside a 6-in length PVC tube along with a small stick for extraction. All subjects were already familiar with obtaining PB in this manner. Likewise, the chosen non-food items were small enough to fit through caging and made of materials that were similar to those used for routine enrichment, again to minimize effects due to novelty. The non-food items were a rope toy and a rubber toy (a "Kong" dog chew toy). All apes in the study were familiar with these toys, as these are common enrichment items with which they routinely interact, but the particular objects used in the study were novel.

### Experimental Procedure

Each subject initially completed a series of six different sessions across two treatments, the food treatment (three sessions) and the non-food treatment (three sessions). No subject ever received more than one session per day. Sessions occurred approximately every other day for the duration of the study. Half of the subjects were randomly assigned to complete food sessions first and the other half to complete non-food sessions first. Within each treatment (food or non-food) subjects completed three sessions in an order that was counterbalanced across subjects.

**Preference sessions.** To determine baseline preferences within each pair (food and non-food, respectively) 16 forced-choice trials were administered for each subject. For this test, the experimenter offered both objects (one in each hand approximately 30 cm apart) approximately 30 cm in front of mesh caging directly in front of the orangutan. The side (left or right) on which the object was offered was counterbalanced between subjects. When a subject gestured at the object, it was given to the subject and the other object was removed and placed out of sight on the researcher's preparation station. In the case of food objects, all subjects typically consumed all of the food in approximately 2 min. In the case of the non-food toy objects, the subjects were allowed to play with and inspect the object for 2-3 min, after which the experimenter requested that it be returned. No food was ever used to solicit the non-food objects or the PVC tubes that contained the PB, to avoid the possibility that subjects would associate the objects with food. When subjects chose not to return the non-food object, they were allowed to keep it until a keeper could obtain it at a later point.

**Endowment Sessions.** The goal of the Endowment sessions was to see if the subject would exchange one object for the other. To accomplish this, in two separate sessions (on different days) the subjects were given one of the objects, then allowed to trade for the other. Each subject was given each object as the endowment only once (one trial per food and non-food object each), and the order

in which foods/objects were presented as the endowed object was randomized and counterbalanced amongst subjects.

For these two sessions, each part of the endowment condition, subjects were initially shown both objects by the experimenter, to make sure that the subjects were aware of their options. Following this, the experimenter passed only one object through the caging to the orangutan. Importantly, the objects were initially shown from a distance, with one being passed to the subject before any gesturing could occur. Immediately upon receipt of the endowed object (i.e., when the object was first in the ape's hand), the experimenter held up the other object and offered to exchange it. No vocal commands were used, to avoid cuing the apes. However the familiar 'exchange gesture' of an outstretched hand was used so that the subjects were aware that exchange was an option. Subjects had to return the first item to the experimenter within 60 s to obtain the other. In the case of foods, subjects were allowed a single lick or bite to verify which food was being offered, but if more than this was taken, the second food item was removed and no exchange was possible. Each of the two endowment conditions for each treatment (food and non-food) were counterbalanced with the choice session for that treatment.

### **Experimental Controls**

After completing these six sessions, all orangutans completed a series of control tests. These control sessions were done following the test sessions, rather than interspersed, to avoid the possibility that the subjects would become satiated with a food item or would become bored with a non-food item. Either of these outcomes would have affected results in the test sessions.

The first control was designed to verify that food preferences between the PB and the popsicle were stable in these orangutans. This was done with a series of four separate sessions (e.g., done on different days), each including four forced-choice trials (16 trials total) in which subjects had to choose between the PB and the popsicle. The side on which each food was presented was alternated between trials, to control for possible side biases.

The second control was designed to determine the degree to which exchanges that occurred were due to the orangutans simply enjoying interacting with the experimenter. For instance, there could arise a preference for exchange across all conditions simply because the act of exchange was a rewarding engagement for the subjects. For this control, each subject was given a single session of four trials. For each trial, each subject received one of the items, followed by the opportunity to exchange for an identical item.

Finally, to verify that the subjects were willing to give up a food in return for another food in at least some situations, subjects completed a final control test in which they could exchange for a highly valued food. Subjects were initially given a popsicle (the same kind as in the study) and then allowed to exchange it for a whole banana. While bananas are of similar shape and size to both the popsicles and peanut butter tubes, they are a highly preferred food (creating a sharp asymmetry in value, which is known to overcome the typical endowment effect in humans). Subjects had up to 5 opportunities to complete the exchange.

### **Statistics**

All statistics were carried out using non-parametric statistics (e.g., chi-squared tests) due to the small number of individuals involved in the test. All *p*-values are 2-tailed.

## **Results**

### **Endowment Effect Magnitude**

We first investigated the orangutan's behavior at the group level, to investigate the magnitude of the response. First considering the food treatment, only 43% of the orangutans preferred the popsicle to PB, yet when endowed with the popsicle, 100% of subjects chose to keep the popsicle, rather than to exchange it for PB, even though PB was the more preferred food. Thus, as a group subjects were approximately 60% more likely to keep the popsicle than would be expected

based on initial preferences (Figure 1:  $Z = 2.00$ ,  $p = 0.046$ ). With PB, the pattern was the same, but the effect was not significant ( $Z = 0.577$ ,  $p = 0.564$ ). However in both of these cases, the group preference between food items is approximately 50% (chance), whereas the tendency to maintain the food item with which the ape had been endowed was between 70% and 100%, or above chance (combining the two conditions:  $Z = 2.41$ ,  $p = 0.013$ ).

In the non-food treatment, the orangutans' exchange behavior did not significantly deviate from their previously established preferences in the group-wise comparisons (see Figure 1: keep rope toy:  $Z = 1.342$ ,  $p = 0.180$ ; keep rubber toy:  $Z = 1.00$ ,  $p = 0.317$ ). Note, however, that the proportion of the group that chose to retain possession of a non-food was approximately 50% (4 of 7 individuals), or chance, in both cases ( $Z = 0.27$ ,  $p = 0.790$ ). This is in contrast to the food condition, in which the orangutans chose to maintain the object with which they had been endowed at least 70% of the time in both cases.

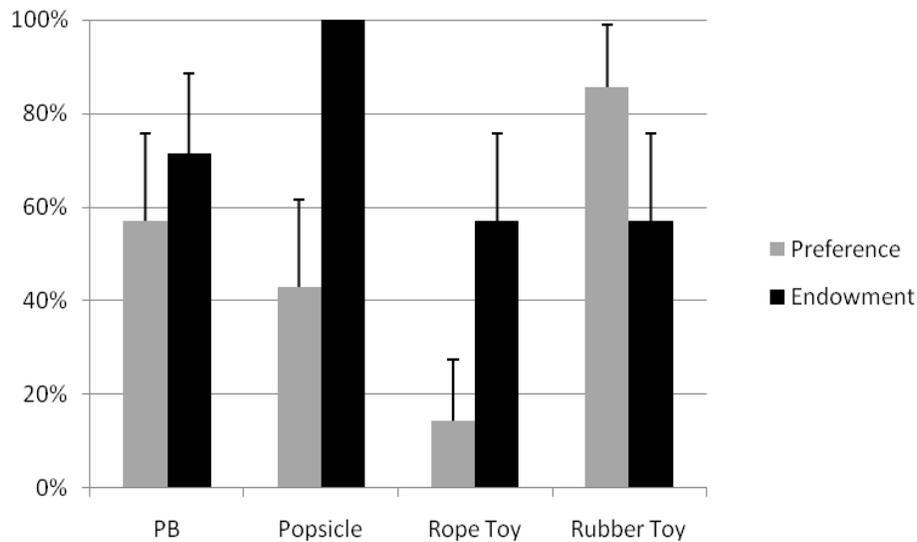


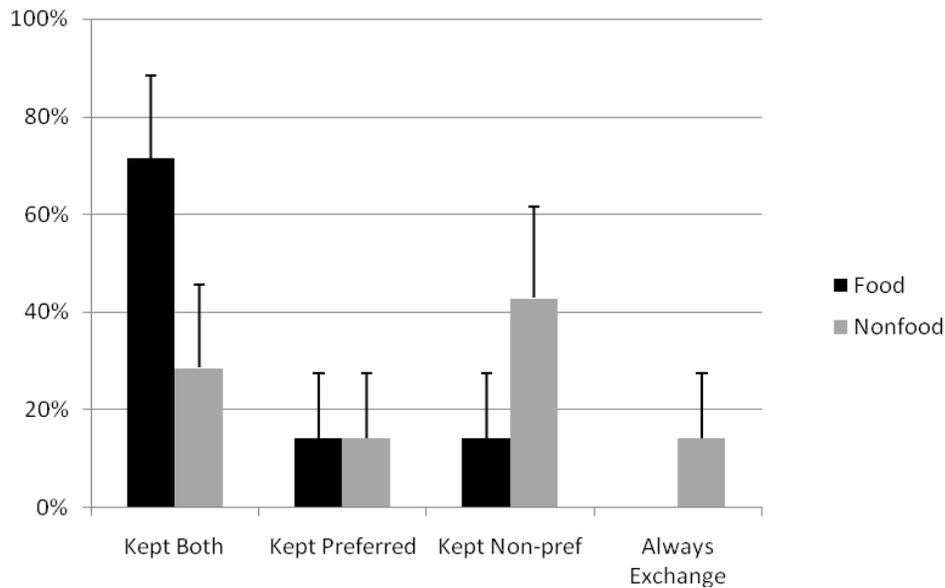
Figure 1. Population-level choices in forced-choice preference tests and endowment-exchange tests. Data are presented as ratio + SE. Grey bars represent the percentage of the population that preferred the object in the choice condition, and black bars represent the percentage of the population that chose to maintain possession of the food or object in the endowment condition when given the opportunity to trade for the other food or object.

### Endowment Effect Prevalence

Individual-level analyses enabled assessment of the prevalence of the endowment effect (i.e., the percentage of the population that, when given opportunities to exchange, keeps both its more-preferred and its less-preferred items). In the food treatment, five individuals (71%) kept both their preferred and their non-preferred foods, where 'preferred' was determined by that individual's choice in the choice condition. That is, even when endowed with their less-preferred food and offered an exchange for the food they preferred, these

orangutans maintained possession of their less-preferred food (Figure 2:  $\chi^2(3, N = 7) = 8.429, p = 0.038$ ). One individual behaved strictly in accordance with his preferences, maintaining possession of only his preferred food when endowed with it, and exchanging his less preferred food when endowed with it. One individual behaved in a manner inconsistent with her previously expressed preference, keeping only her non-preferred food and exchanging her preferred food. Notably, this individual also showed the weakest preference between items in follow-up preference testing. No orangutans exchanged both food items.

For the non-food items we found no significant differences between the four possible individual outcomes ( $\chi^2(3, N = 7) = 1.571, p = 0.667$ ). Only two individuals (29%) kept both their preferred and their non-preferred items, indicative of an endowment effect. One individual behaved in accordance with his preferences, keeping his preferred non-food item and exchanging his least preferred. Four individuals (43%) kept their less preferred non-food object but exchanged their preferred non-food object. Finally, one individual exchanged both items.



*Figure 2.* Choices of individuals in endowment-exchange tests. Data are presented as ratio + SE. Black bars represent food items and grey bars represent non-food toy objects. “Kept both” represents those individuals who chose to maintain possession of both foods or both non-foods rather than exchange; “kept preferred” indicates individuals who chose to maintain possession only of their preferred item, but exchanged for their non-preferred item; “kept non-preferred” indicates individuals who maintained possession of the item they did not typically prefer, but exchanged for this non-preferred item when endowed with their preferred item; “always exchange” represents the one individual who chose to exchange for the other item in both situations.

### Comparing Food and Non-food Conditions

As proposed by Brosnan et al. (2007), there are likely differences between the willingness to exchange foods and non-foods because of the difference in

evolutionary salience between the two classes of objects. To determine if orangutans exhibit this behavioral pattern, as chimpanzees do, we compared the likelihood of exchange for foods and non-food objects. Individuals were significantly more likely to maintain possession of foods (71%), regardless of the opportunity to exchange for another food, than they were to maintain the possession of non-food objects (29%), when given the opportunity to exchange for another non-food item (Figure 2:  $Z = 2.00$ ,  $p = 0.046$ ). Only 1 individual was equally likely to exchange foods and non-food objects, and no individuals exchanged foods more frequently than non-food objects.

### **Ruling Out Other Possibilities**

Our results would be confounded if the food preferences of individuals varied significantly over time. In that case, the ‘endowment effect’ could be due to changing preferences, rather than to an effect of possession. In our consistency controls, 100% of individuals maintained their initial preferences across 16 additional trials in 4 daily sessions of 4 trials each. As a group, subjects preferred the PB to the popsicle 57% of the time in the initial choice session, and the preference for PB stayed consistent, at 53%, across all control sessions. Moreover, each individual showed the same food preference in control trials as in the initial choice session.

Our results would also be confounded if exchange were inherently rewarding to the orangutans (for example, due to pleasurable interaction with the experimenter). To ascertain the level at which exchange was self-rewarding, we performed a control task in which orangutans had the option to exchange for identical objects. We find that in the food treatment, any rewarding aspects of the exchange interaction are overcome by the value of the rewards. No subject ever exchanged a food item for the identical food item. In the case of the non-food objects, however, exchange was more common. Three of seven subjects exchanged the rope for an identical rope and two exchanged the rubber toy for an identical toy. Note that these results are similar to the frequency of exchange in the non-food endowment condition (in which three of the subjects traded away each non-food item). This may indicate that, in contrast to behavior related to the food items, the inherent rewards of exchange were similar in value to the rewards of the non-food objects.

A final control task tested whether orangutans simply maintained possession of food items because they were unwilling to give up a valuable food item under any circumstance, which would also confound an endowment effect. When endowed with a popsicle and offered a banana (a preferred food of approximately the same size) to exchange, three orangutans (43%) traded on the first trial, with all but one exchanging by the fourth trial (85%). This latter individual showed a very strong preference for the popsicle, preferring it to the PB in 100% of trials in the consistency controls, so it is possible that in his case the banana was simply not valuable enough (or the popsicle was too valuable). These results verify that failures to exchange a less preferred food for a more preferred food reflect an active choice to maintain possession rather than a passive resistance to trade.

## Discussion

We find that orangutans exhibit an endowment effect for food items in some contexts, frequently choosing to hold on to less-preferred food items rather than to exchange them for more-preferred foods. The magnitude and prevalence of this effect are generally similar to those that have been seen in other primates, indicating that this is a robust behavior within the taxon. The only notable difference between the orangutans and the chimpanzees is that the chimpanzees prefer to exchange non-food objects more than anticipated based upon their preferences, while orangutans' behavior with respect to non-foods does not deviate from predictions based on their preferences. Our results – which provide evidence of the endowment effect at both group level and individual levels of analysis in the context of food – support the hypothesis that the endowment effect may be the result of homology in the primate lineage, rather than a convergence due to similarities in social cognition amongst humans, chimpanzees, and capuchin monkeys. As discussed in the Introduction, unlike these other primates, orangutans do not engage coalitions, cooperative hunting or even highly regular social interactions commonly observed in other great apes. Although individuals live in overlapping ranges, establish dominance relationships, and may range in small groups when food resources permit, orangutans do not show the level of dependence on others observed in chimpanzees or capuchins (van Schaik, Preuschoft & Watts, 2004). These other species may cooperatively hunt and food share, and also rely on each other for territory maintenance, coalitional support, and other social activities (Brosnan, Freeman, & de Waal, 2006; de Waal, 1997; Fragaszy, Visaberggi, & Fedigan, 2004; Goodall, 1986; McGrew, 1975). If the endowment effect were the result of convergence due to sociality, we might expect to observe it only in those species with similar levels of sociality and social organization. Instead, our observations of the endowment effect in this less gregarious ape, as well as these more social species, indicate that the likelihood that the behavior is a homology among primate species is high.

These data begin to address the open questions surrounding the presence of the endowment effect in humans. There are several potential hypotheses for the presence of the endowment effect in humans. One of these can be ruled out; given that the effect has now been demonstrated in five nonhuman primate species, it is unlikely that the effect arises from uniquely human cultural or genetic phenomena. Moreover, given the differences between the species in which the effect has been demonstrated, it seems most likely to be the result of evolutionary homology.

Unfortunately these data are not yet sufficient to distinguish hypotheses regarding why the effect evolved (i.e., the ultimate reason). One possibility is that the effect is shared across primates as an incidental by-product of some other phenomenon. Our existing data cannot resolve this question, although the selective benefit that would be required for this hypothesized phenomenon to offset the potential cost of the endowment effect as a by-product makes this possibility less likely. Another possibility, which we believe more likely, is that the endowment effect is an adaptation for reducing potential losses that are accrued in exchanges with individuals who may defect. However, this raises the question of why the relatively more solitary orangutan (relative to many other primate species,

including the other great apes) shares this feature. We see three possibilities. First, the endowment effect may have arisen as part of a suite of cognitive processes that humans and other social species have secondarily applied to social situations. This could be tested by examining the endowment effect in a gregarious species that shows fewer cognitive overlaps with primates. Second, this behavior may have arisen in the context of social exchange and been maintained in orangutans despite a subsequent shift away from sociality, perhaps due to the ongoing presence of (albeit limited) food sharing (Jaeggi et al., 2008; van Noordwijk & van Schaik, 2009). Examining other primate species with different social systems would provide evidence for evaluating this hypothesis. Finally, the endowment effect could have emerged in a non-social context. Social exchange is not the only context in which giving something up is risky; for instance, in foraging decisions, an animal may be faced with the option of pursuing a food in the distance when currently in the possession of another food, but choosing pursuit may result in no food (or a much worse one). Thus extractive foragers, who routinely process their foods, may be under selection to maintain the known item rather than pursuing a new one. Examining other species with different foraging strategies may help further evaluate this possibility.

We also find evidence for a future avenue for research in the observed variation in the endowment effect. While we find evidence for an endowment effect with respect to both magnitude and prevalence in the context of food items, the orangutans' behavior does not deviate as widely from expectations based on their preferences with regard to non-food items (in either magnitude or prevalence). Moreover, subjects were more likely to hold on to an item in food than non-food contexts. Perhaps, the perceived value of the non-food objects was low – too low to garner either an aversion to loss or an expectation of the value of the other object being offered. Thus, whether magnitude or prevalence are assessed, we find that the endowment effect is stronger in food than non-food contexts, meaning that individuals are more likely to exhibit the endowment effect when given exchange opportunities that involve what are presumably more evolutionarily salient items. This, too, is the same as was seen with chimpanzees (Brosnan et al., 2007). Future studies might further address this hypothesis through an examination of exchanges with a wider variety of both food and non-food objects (*c.f.* Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012), in order to determine if this is an artifact of the salience of these items to the apes or a phenomenon which deserves additional attention.

One potential limitation of our study is the relatively small sample size. Although previous studies on primates, including some on the endowment effect, have used even smaller samples [e.g.,  $n = 5$  (Chen et al., 2006)], the study on chimpanzees included 33 individuals. The smaller sample means that random fluctuations are more likely to cause variations in the results. For instance, the group preference for one toy was much higher than chance, which may reflect random skew. Importantly, however, our group-level analyses reveal consistencies with both the human and nonhuman primate literature (Brosnan et al., 2007; Chen et al., 2006; Jones & Brosnan, 2008; Knetsch, 1989). Unfortunately, we know of no studies that analyze human behavior at the individual level. Given the variation in the nonhuman primate data, we think that this is an avenue that needs to be

pursued. Nonetheless, our findings with respect to food items are consistent, both within the study and across other studies, indicating that despite the small sample our results are valid. We also note that, in contrast to wild-living orangutans, who typically live either alone, in mother-offspring pairs or, more rarely, in small groups, our orangutans were housed in social situations. This may mean that the observed endowment effect is an artifact of ontogeny, rather than evolutionary history. However, our choice to use socially housed animals as this also ruled out the possibility that any differences between the chimpanzees and orangutans were due to the differences in social housing in the test populations, rather than differences in the species' propensities.

We find that orangutans, like other primates studied thus far, exhibit endowment effects in some food contexts, preferring not to give up foods that are in their possession in exchange for foods they prefer. Given the presence of this phenomenon in other primates with contrasting social structures, the endowment effect is likely a homology within the primate lineage. Future studies should address additional species, both to see if this phenomenon is common outside of the primates and to further test the hypothesis that the behavior varies as a function of evolutionary salience or other cognitive or social constraints.

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