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Property in non-human primates

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ABSTRACT

Property is rare in most nonhuman primates, most likely because their lifestyles are not conducive to it. Nonetheless, just because these species do not frequently maintain property does not mean that they lack the propensity to do so. Primates show respect for possession, as well as behaviors related to property, such as irrational decision making regarding property (e.g. the endowment effect) and barter. The limiting factor in species other than humans is likely the lack of social and institutional controls for maintaining property. By comparing primates and humans, we gain a better understanding of how human property concepts have evolved.

Property is a concept taken almost for granted among modern Western peoples (at least, until there is a dispute over it). We not only have an intuitive understanding of mine and yours, but also a series of social norms, rules, and governance structures set up to manage the relationships dictated by the presence of property. Yet for all of our focus on property, little is known about how this concept evolved. How did we become the only species on earth to have these complex rules of ownership and succession? It is possible that our sense of property is emergent in humans, a result of our cognitive complexity or advanced culture (e.g. Noles & Keil, this volume; Kalish and Anderson, this volume). On the other hand, it is also possible that these complexities are continuations of the basic property or possession behaviors seen in some other species.

In fact, there are other species which seem to have at least elements of a sense of property (Stake, 2004). Among primates, there is evidence for a sense of property both from observations and from experimental situations. Notably, several primate species behave as though objects in the possession of others belong to that individual (Kummer & Cords, 1990; Sigg & Falett, 1985). Moreover caching species, such as jays and kangaroo rats, hide food items for later retrieval, and may even move them around to avoid snooping competitors (Dally, Emery, & Clayton, 2006; Emery & Clayton, 2001; Preston & Jacobs, 2005). Many of these caching species are phylogenetically quite distantly related to humans, indicating that this behavior emerged in several species based

on similar ecological constraints, known in evolutionary terms as convergence[1], and may be widespread through the animal kingdom.

To understand the emergence of our sense of property, it is useful to explore the behavior both broadly within the animal kingdom and more specifically among other primate species, particularly the apes, as they are our closest phylogenetic kin. Studying how property in these species is different from (or similar to) that of other species, especially in concert with an understanding of the environmental characteristics which may have led to convergences, can help clarify how the human property concept evolved.

1. Defining property

Among humans, the law is the institution perhaps most interested in property, and so a good starting point. The law defines property with respect to the relationship between people that gives rise to the agreement that one object is mine and another is yours (Bentham, 1914). Bentham went so far as to assert that property did not exist before the laws regulating it. However, this definition conflicts with the folk notion of property as a relationship between an object and a person, and denies out of hand the possibility that property could be based on behaviors or concepts present in other species (Stake, 2004).

[1] Convergence is an evolutionary mechanism in which different species evolve similar characteristics (here, property-related behaviors) because of similar environmental constraints. The other mechanism I discuss is homology, in which different species share similar characteristics because both are descended from a common ancestor who displayed the behavior. As a simple example, both blue jays and eagles share wings through homology, because their mutual common ancestor to both species also had wings. On the other hand, blue jays, bats, and butterflies all have wings through convergence; their mutual common ancestor did not have wings. Instead the benefits of taking advantage of an open ecological niche, the air, provided pressure which increased the likelihood of wings developing as the appropriate mutations arose. Note that a close phylogenetic relationship may imply a homologous relationship, but does not guarantee it; the traits could also have arisen independently through convergent processes. While the distinction is critical and often overlooked, for the purposes of this paper it is largely irrelevant whether a particular shared trait evolved through homologous or convergent processes, because we are interested in the presence or absence of property-related behaviors in other species and are not developing a phylogenetic tree based on this data to trace the evolution of these behaviors

There is evidence in favor of this latter position. Children as young as eighteen to twenty-four months of age show inferences about the ownership of property (Fasig, 2000). Such inferences may be due to mechanisms such as following the heuristic that the first possessor of an object is the owner (Friedman & Neary, 2007; Friedman et al, this volume). While even at this early age ideas about ownership could be learned through interactions with adults of the species, this early start indicates the possibility of a predisposition towards property. Moreover, other species seem to have some basic behaviors which are consistent with the idea that a thing can belong to a specific individual. For instance, some species show begging and sharing behavior in relation to food, instead of simply taking by force the food that is desired (e.g. chimpanzees; Goodall, 1986), which indicates that food is seen as having an owner. Several species of nonhuman primates behave as if possession is a special state. In these primates, individuals do not attempt to take objects which are in another's possession, even if the possessor is the subordinate individual (Kummer, 1991; Kummer & Cords, 1990). Interestingly, the United States legal system also prioritizes possession when dealing with property disputes (Stake, 2004). This phenomenon, termed respect for possession, will be discussed in more detail later, but provides strong evidence for a basic sense of property shared between humans and other species.

Thus, it seems reasonable to assume that possession of property is not an emergent property of human institutions, in particular the legal system, and that some precursors to the behaviors and attitudes which led to property as seen in the human sense can be seen in other species. Looking for these precursor behaviors in other species can help to identify the ways in which property evolved and pin down criteria which may be

important for the development of the concept of property. To begin, we first need an operational definition of what is meant by property and which specific behaviors would be evidence for its presence.

In order to maintain property, an individual needs to maintain control over an object which is not a part of its body. Of course, property can be lost, stolen or transferred, so permanent maintenance of access is not a necessary requirement for property. From a biological perspective, there are two different forms of property, that which is physically in one's possession, and that which is maintained despite being outside of one's physical control. For the sake of simplicity, I refer to these, respectively, as possession and ownership.

Maintaining possession is likely the simplest form of property. In this case, an individual maintains an item by keeping that item under its physical control at all times. Functionally, this is defined as the individual touching the item in some way (in an appendage, mouth, beak, etc). Although in the most trivial sense, this form of property is essentially ubiquitous, as any time an individual picks up a piece of food to consume, it is in its possession, possession also extends beyond this. Individuals may maintain possession for more extended periods of time, in which case norms or standards of conduct, for how items in another's possession should be treated may be formed. For instance, among ravens, individuals who possess an item can expect to maintain it, even if a larger or otherwise more dominant individual approaches. These norms are upheld through third-party interactions in which uninvolved third parties will attack those who steal from another raven (Heinrich, 1999). Such norms indicate that possession has a special status in these species.

The second form of property, ownership, is that over which one maintains control even when the item is not in one's possession. This may include such resources as dens, nests, or home ranges, although these are typically group resources which are defended by and shared by all the members of the social group. In a few species, ownership includes another critical resource, food. In species which cache food items, such as squirrels, individuals maintain property without possession, and reclaim those objects when they need them for survival, such as in the scrub jays discussed above. Note that such property need not be due to respect for ownership; in many cases property may remain under the individual's control either because it is hidden from others, or because the individual who has ownership or possession is dominant, so others cannot easily take the items.

What seems to set human property apart from that of other species is the extensive reliance on the goodwill of others to assist in the maintenance of ownership (e.g. property outside of one's possession) through third-party reinforcement. In humans, this takes the form of both institutional structures to maintain ownership rights (police forces, legal systems) and the tendency of humans to respect each other's property ownership. As mentioned above with respect to the ravens, third party norms do exist in other species, but typically only for current possessions, and not with respect to ownership. This may be due to the inability of other species to convey information beyond the immediate, as can be done with language. This means that third-party interventions can only occur in situations in which the transgression was witnessed by a potential supporter (Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008). Moreover, while many of us may resort to the legal system to reclaim property which has been taken from us, the truth is that in a

well-functioning society, this recourse is required surprisingly rarely, particularly with respect to how often property we own is left outside of our immediate possession. People routinely leave their jackets on a seat during the intermission at a play or their grill on the deck of their house or apartment and seem to expect that these items will still be there upon their return. And in fact, they usually are. The question, then, is what is it that makes human property so different?

2. Property in primates

Property in primates is rare, and exists almost exclusively in the form of possession, not ownership. Primates do maintain territories, or home ranges, sometimes individually and sometimes in groups. These can be considered a form of property, although given the frequency of territorial behavior across the animal kingdom, this tells us little specific about the evolution of property. Unlike some other animals, no primate (outside of some humans) relies on caching as a major food source. This is most likely an ecological constraint. Food is the most obvious object for animals to store as property, as it is essential for survival. However, primates typically live in areas where at least some food source is available year-round, allowing them to forage for food as they need it. Moreover, caching is impractical for most primates; they typically eat foods which do not store well, such as fruit, negating the utility of maintaining food for any extended period before consuming it. Thus, the opportunities for food as property, particularly in the form of ownership, are limited.

Primates behave in other ways which are indicative of some concept of possession. One primary manifestation is the remarkable respect for the rights of the possessor of an object shown by some species (Kummer, 1991; Kummer & Cords, 1990). Chimpanzees

show a ‘respect for possession’ which allows individuals to maintain possession of an item, even in the presence of the alpha male (Goodall, 1972). This ability is not limited to the apes, either. Several monkey species show evidence of respect of food possession (Perry, 1997; Sigg & Falett, 1985). Outside of the realm of food, hamadryas baboon males show respect for the females in each other’s harems (Kummer, Götz, & Angst, 1974), not attempting to mate with them or claim them even though these harem units interact with each other on a daily basis.

What qualifies as ‘possession’ varies between species. In some species, even holding an object is not sufficient; individuals must be able to transport the object in order for others to respect possession. In an experimental study, long-tailed macaques respected ownership when the owner had possession and was able to carry the object. Respect for possession broke down, though, even when the owner had possession of the object, in two cases. First was if the possessor could not carry it with them because it was tethered to the floor. Second was if the object had a trailing string (similar to a kite tail) which extended beyond the possessor’s immediate vicinity. In either case, the more dominant individual typically took control of the object. In these macaques, proximity was also not sufficient to maintain possession (Kummer & Cords, 1990).

Not all species have such stringent requirements for possession. Among hamadryas baboons, proximity is sufficient to trigger respect for possession, and in some cases even the memory of a previous possession may be sufficient to trigger this response (Sigg & Falett, 1985; see also Friedman et al, this volume). This variation in experimental outcomes is most likely due to differences in the socio-ecology of the different species. Hamadryas baboons evolved in a situation in which a valuable

possession (e.g. harem females) was in proximity, but not under physical control, widening the concept of possession in this species.

One of the challenges in assessing possession is that it is difficult to determine whether possession is respected as a norm versus for more prosaic self-serving reasons. In many cases, it appears that non-norm based accounts exist to explain animals' interactions over possessions. For instance, food calls may serve to identify possession, which could indicate a norm. On the other hand, the food call may also indicate how likely a challenge is from the possessor. Thus, failure to obtain the food after hearing a food call may be due to non-possessors avoiding a potential fight rather than respect for possession (Gros-Luis, 2004; Krebs, 1982). Similarly, among chimpanzees it has been hypothesized that the intense motivation to keep a food reward is what allows lower-ranking individuals to sometimes maintain possession of a carcass following a monkey hunt, rather than a social norm respecting possession (Goodall, 1986). Finally, it is also likely that 'possession norms' are due at least in part to reciprocity. High ranking individuals may refrain from taking the property of those who rank below them in order to keep those lower-ranking individuals as grooming or mating partners (de Waal, 2005).

These different mechanisms make assessing 'pure' respect for possession difficult. Humans, too, may fail to take resources for many of these same reasons. However, there are some situations in which the evidence does indicate the presence of social norms related to possession. In some species, third party interventions may reduce the frequency with which owners are challenged for their possessions. Although in these cases the non-possessor may not attack for self-serving reasons, the fact that a third party intervenes indicates the presence of possession-related norms. Among long-tailed

macaques, possession was more likely to be challenged for older possessors, who are less likely to scream and, hence, attract support, which the authors propose as evidence of third-party norms supporting possession rights (Kummer & Cords, 1990).

However, none of these studies gets at ownership, or possessions outside of one's immediate control. This is partly due to the lack of situations in which ownership appears in the wild. Thus an alternative approach, which allows for more explicit control, is to investigate these phenomena in the laboratory. In fact, chimpanzees do seem to recognize that they 'own' something beyond their immediate possession in the laboratory. Although in laboratory studies subjects are typically given a food reward for each desired response, chimpanzees are willing to work for rewards (food items or tokens) which collect in a specified location and then are given to the subjects en masse (Wolfe, 1937; Cowles, 1937; Sousa & Matsuzawa, 2001). This indicates that, at least on some level, the chimpanzees understand that the rewards are 'theirs,' even though they are not in their possession. Chimpanzees understand this even if there are several collections of tokens or food, only one of which contains items which are 'theirs.'

As part of another study, chimpanzees were tested in pairs in which each individual could trade tokens for food rewards. These tokens consisted of symbols which represented various foods which were made available in the study; these symbols had been used by each of the chimpanzees since infancy and so had strong associations. The chimpanzees each had a separate food bin, with different food items available to them than were available to their partners. Each could obtain only the foods that were present in their bin by trading the appropriate token for it, despite being able to see their partner's available foods. Moreover, all tokens for foods available for either chimpanzee were

available at all times, so chimpanzees had access to tokens which did not match their available food rewards. The only cost to these incorrect trades was time; the chimpanzees were allowed an unlimited number of exchanges to acquire their foods. Despite this, the chimpanzees learned very rapidly that they could acquire the foods only from their own bin, and did not request the foods from their partners' bins (Brosnan & Beran, 2009). This indicates that that they understood at least on some level that those foods were not 'theirs,' as determined by the experimenter.

Even so, this still does not fully get at ownership, as the human experimenter acted as a mediator. One difficulty with testing property in chimpanzees is that while food items represent the strongest level of motivation, because of this they are also unlikely to hold them for a long period of time without eating them. Thus it is difficult to use food items as part of a study involving property. However, with a little creativity, certain aspects of property may be tested using paradigms which get around the problems inherent in food. For instance, tokens can be used which represent foods (and can later be traded for foods, as in the above study) or food which cannot be consumed immediately can be used. Both of these approaches have been used successfully, as is discussed below.

2.1 The Endowment Effect. The issue of property can be addressed tangentially, by testing for characteristics of property known to be exhibited by humans. One common finding is that humans tend to behave irrationally when making decisions about their property. One way in which this manifests is in a phenomenon referred to as the endowment effect, in which individuals will pay more to keep an item that is in their possession than they would have previously paid to obtain the same item. This implies

that individuals value what is in their possession simply because of that fact, even when there has not been enough time to develop a sentimental attachment to it or additional uses for it (Jones & Brosnan, 2008; Kahneman, Knetsch, & Thaler, 1990).

Chimpanzees, too, increase their preference for items in their possession above and beyond the value they indicated when the object was not in their possession (Brosnan, Jones, Mareno, Richardson, Shapiro et al., 2007). In this study, chimpanzees were given a series of sessions to determine how preferences changed dependent upon possession. One session served to verify their preferences, while additional sessions offered them opportunities to exchange what they were given initially for something else. There was no cost to trading other than the few seconds the trade took. To make sure that the chimpanzees were sufficiently motivated, foods were used instead of tokens representing foods. The chosen foods were difficult to consume rapidly; one item was peanut butter that had to be removed from a PVC tube and the other was a frozen juice stick that subjects preferred not to bite into.

To establish preferences, chimpanzees were asked to choose between the two foods. To determine whether or not the chimpanzees preferred to maintain possession of those items which they had in their possession, chimpanzees were given each of the items individually (in separate sessions) and then immediately offered the opportunity to exchange for the other[2]. As with humans, as a group chimpanzees were more likely to hold onto whichever food item they were given than was expected, based on their preference for the items in the choice session. Individually, almost half of the chimpanzees followed this pattern, choosing to hold onto whichever item they had been

[2] In the experiment itself, the order of presentation of these three sessions were randomized among the 36 subjects to assure that there was no ordering effect influencing responses.

given. All chimpanzees were willing to exchange food items away when something of greater value (a banana) was offered, so their disinclination to exchange cannot be explained by concern about the risks inherent in trading away food or the reliability of the human experimenter.

Interestingly, this holds for foods, but not for other non-food objects with which they interact. When the same study was repeated using two familiar toys, the chimpanzees actually preferred to exchange, perhaps valuing the interaction with the experimenter over the possibilities of the toys themselves (Brosnan, Jones, Mareno, Richardson, Lambeth et al., 2007). This indicates that the endowment effect may hold only for those objects which have great utility to the chimpanzees, such as food, and indicates that even within a concept as basic as property, the context of the interaction matters.

More recently, similar studies have been done with orangutans and capuchin monkeys, indicating that they, too, show an endowment effect (Flemming, Jones, Stoinski, Mayo, & Brosnan, in review; Lakshminarayanan, Chen, & Santos, 2008). Capuchin monkeys also exhibit loss aversion, showing a preference for outcomes framed as a reward over those framed as a loss despite the actual distribution of outcomes being equal (Chen, Lakshminarayanan, & Santos, 2006). This is another 'irrational' behavior which is often linked with the endowment effect. Taken with the results on chimpanzees, it appears that this suite of irrational behaviors occurs in primates in general, supporting the idea that concepts of property are broadly distributed in the primates, and likely throughout the animal kingdom.

2.2 Barter. Another element of property is that it can be used to obtain more or different property through trade and barter. In barter, an individual can trade an object in their possession or under their ownership for another object possessed or owned by someone else. In fact, this, in concert with specialization, is one of the core tenets of economic theory. As such, there has been quite a bit of interest in whether other species can barter. Adam Smith famously quoted that "It [barter, to exchange one thing for another] is common to all men, and to be found in no other race of animals, which seem to know neither this nor any other species of contracts… Nobody ever saw a dog make a fair and deliberate exchange of one bone for another with another dog" (Smith 1776). Barter has not been reported in wild populations, however chimpanzees and other species do share food (e.g. Hockings et al, 2007; Feistner & McGrew, 1989), which is a related behavior. There are also a few captive observations of spontaneous behavior which may indicate the presence of exchange behavior in primates (Paquette, 1992).

Most studies thus far have required subjects to trade a token to a human experimenter for another food item, which both chimpanzees and capuchin monkeys do easily (Brosnan & de Waal, 2004, 2005; Hyatt & Hopkins, 1998). In fact, both of these species also seem to understand the tokens as symbols, and can work with them flexibly (Addessi, Crescimbene, & Visalberghi, 2007; Addessi, Mancini, Crescimbene, Padoa-Schioppa, & Visalberghi, 2008; Savage-Rumbaugh, Rumbaugh, & Boysen, 1978). However, this only indicates that primates can learn associations, but does not require the subject to actually give up something of value to obtain something else. It is this latter, more costly, exchange behavior that we typically consider when discussing barter.

Several studies on barter of food items have found that chimpanzees are not only able to do this, but are very intelligent in how they barter with humans (Lefebvre, 1982; Lefebvre & Hewitt, 1986). In these studies, chimpanzees were rational, trading foods they did not like for those which they did, and trading more readily when the difference in value between the food items was greater. They were also intelligent; the experimenter would take any size food item in exchange for another, and the chimpanzees learned to return very small bits of food, or even just a daub of saliva. This behavior maximized their intake of both foods. A recent study replicated these findings with a larger adult sample of chimpanzees (Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008). In this study, chimpanzees received an endowment of 30 food items (of varying types) and were given the opportunity to exchange those items for other food items. Again, chimpanzees never traded food items for those which were less preferred, and they always traded disfavored foods for much more preferred items. When food items were close in value, subjects typically did not exchange. This behavior, similar to that seen in the endowment effect study discussed above, indicates that chimpanzees are hesitant to give up an item in their possession, possibly because of the risks of trade.

Note that all of the studies on barter discussed above have one significant confound – they all involve trading with humans, rather than a subject of the same species. This makes it difficult to extrapolate their behavior to natural circumstances, due to the difference in the type of relationship between primate conspecifics (e.g. members of the same species) and primates and humans. In the latter, the humans occupy an atypical, omniscient/omnipotent role which may make the monkeys and apes react differently than they would to a conspecific. However, human/primate barter is the norm

because of the difficulty inherent in getting primates to give up a food reward to another individual. Even a well-trained chimpanzee is unlikely to voluntarily trade away a preferred food item in their possession for another. This can be avoided through the use of symbolic tokens, rather than foods.

In a recent study, chimpanzees were given tokens which bore symbols representing foods, rather than the food items themselves (Brosnan & Beran, 2009; also see above). These chimpanzees had trained to use these symbols as infants, and each subject had at least 20 years' experience with them, so they easily understood the token/food associations (controls were run to verify that this was the case). In a series of studies, chimpanzees were given several tokens. Some of these could be exchanged with the experimenter to obtain foods, while others were worthless to them, but could be used by another chimpanzee (their partner). Although chimpanzees initially were hesitant to do so, they ultimately learned to trade tokens amongst themselves prior to exchanging tokens for foods with the experimenter, which maximized the number of foods each chimpanzee could receive. During this time there was experimenter oversight of the interactions; the experimenter would not exchange with either ape until each chimpanzee had traded a token of their choice with their partner (they could simply return the token their partner had given to them). Once experimenter oversight was removed, though, all trade behavior ceased within the first session. Instead, the chimpanzees simply returned all of their tokens to the experimenter, and received many fewer food items than were available.

This test indicates two interesting findings. First, chimpanzees are capable of cognitively understanding trade, and will do so in a way which benefits themselves and

their partner. Second, experimenter control is apparently necessary for successful barter among captive adult chimpanzees. These together indicate that there is significant risk inherent in trading among chimpanzees. This may be due to the lack of recourse if the partner fails to complete the trade. Humans have solved this problem through the introduction of legal and policing systems which can enforce appropriate trade behavior on others, minimizing the risk of any given interaction. Chimpanzees, lacking the ability to communicate beyond the immediate (e.g. narrative language), would have difficulty with third-party reinforcement except in situations in which the third party witnessed the interaction (Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008). Thus it is likely that, despite an apparent lack of cognitive limitations, trading behavior has not evolved due to the high costs inherent in a trading system without oversight and recourse. It is possible that other species, which have less competitive social interactions, may show more of a tendency towards barter behavior, but it is likely that the lack of narrative language limits the development of extensive barter in all species besides humans.

3. Conclusion

Taken as a whole, the evidence supports the idea that, counter to Bentham's assertion, there are biological bases for property. While no other species has developed a system of property ownership as complex and far-reaching as humans have, non-human primates appear to have expectations related to objects, or social norms, which are in their or another's possession. This possession-centered concept of property makes evolutionary sense; not only is it easier to defend property which is in one's possession, but the legal enforcements required for ownership are difficult or impossible to enforce without the development of language.

Norms regarding possession are not the only property-related feature shared between humans and other species. Experimental studies in nonhuman primates have found evidence of behaviors (such as barter) and psychological features (such as the endowment effect) which are seen in human property-related behavior. Perhaps the critical difference between humans and other species is that in other species, individuals may assume that they will need to enforce their right to their property by themselves, without any recourse, while in humans we can rely on others to assist in maintaining our property rights. Even if other species have the necessary cognitive underpinnings, such as third-party enforcement of norms or well developed reciprocity, they still lack the ability to communicate about other individuals' misdeeds. This limits their ability either to request assistance in reclaiming property or to warn others about those who do not respect property, which seriously limits the extent to which these norms may develop.

Thus, the critical development for humans may have been the emergence of two features; first, a norm which indicates that property *outside* of one's immediate possession or control is still property, and should not be taken by others (e.g. ownership; see also Rochat, this volume), and second, the language skills necessary to recruit the support of others in the maintenance of this norm. Together these could have led to the development of formalized legal systems which protect ownership of property even when it is outside of one's immediate control or when an instance of theft takes place beyond the observation of others. Although human property concepts differ from those of other species, this comparative approach sheds light on the biological basis of the emergence of property in humans and other animals.

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