

Article Title: Rethinking the evolution of property and possession: A review and methodological proposition

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Property is a key feature of modern human society; however, identifying the origin of this multifaceted behavior poses a formidable challenge. Here, we explore the methodologies for researching the origin of property. We discuss how an interdisciplinary approach can shed light on how our human ancestors shifted behaviorally from possessing an object to having exclusive property control over it. Possession occurs when social group members only respect an individual's claim to have exclusive access to an object when the individual has physical control over the object. Property occurs when an individual can claim exclusive access to an object, without challenge, regardless of whether the object is in their physical control or not. Researchers across different disciplines have asked what, if anything, distinguishes human property behavior from the behavior of other animals? Further, when and how did this behavior evolve in our lineage? Due to the considerable methodological challenges posed by researching this topic, few studies have been able to directly address these questions. In this review, we explore the challenges involved in defining property and possession and suggest a two-step approach to interdisciplinary definitions. Next, we evaluate four core approaches to the study of property behavior: evolutionary game theory, ethology, comparative cognition, and developmental psychology. Finally, we propose an empirical study, using an ethological approach to test the presence of property and possessive behavior in a natural setting, using our closest living relative, the chimpanzee (*Pan troglodytes*). Overall, we argue that this field of research is at a turning point, where the novel integration of various methods may provide an explanation to the origin of property.

Introduction

Property behavior defines much of modern human life, from the cooperative transfer of land to our laws around thievery. The modern manifestation of property behavior appears distinct from the rest of the animal kingdom. However, research has established that property behavior is derived from possessive behavior, widely documented in nonhuman species.¹ Numerous methodologies have been formulated to understand how possessive behavior could evolve into what we see today in modern humans. Game theoretic modeling has been used to determine the contextual factors in successive competitive scenarios which would lead to property behavior becoming an evolutionarily stable strategy.²⁻⁶ Ethology and developmental psychology have been used to investigate and categorize real-world possessive, and property, behavior in animal and human interactions.^{1,7-10} Finally, comparative cognition has been used to investigate the cognitive abilities and biases of different species and to consider what features are found in species that understand more complex rules of possession, and possibly, property.¹¹⁻¹⁶ There is debate regarding how researchers should define property due to the differing practical requirements of the four key methodologies. In this article, we consolidate and critique these methodologies, and their definitions, with a view to advance the future of property research. We hope to encourage novel, interdisciplinary research which will address the evolution of property behavior with direction and purpose.

Defining possession and property

We define possession as a context in which social group members only respect an individual's claim to have exclusive access to an object when the individual has physical control over the object.^{7,17} Depending on the rank or dominance of the possessor, they may be able to extend their physical proximity and maintain possession of the object.^{1,7,10} Next, we broadly define property by a context in which an individual can claim exclusive access to an object, without challenge, regardless of whether the object is in their physical control or not.¹⁷ Thus, an individual could show either possession or property toward a physically controlled object. However, if an individual maintains exclusive access without physical control, this behavioral outcome is property and not possession. Therefore, property could include a wide range of objects and individuals from territories and fruiting trees, to mates. In line with the two behavioral outcomes above, we would use the following terms to describe the individual and the action they perform: “possessors” performing “possessive behavior” or “property holders” performing “property behavior.” We opt for the term “property holder” rather than “owner” in an attempt to overcome past inconsistencies in the use of the term “owner.”² For other definitions of key terms used in this article, we provide a Glossary.

We propose a two-step approach to interdisciplinary definitions of property. In the first step, we recommend that researchers use a broad, species-neutral definition like the one we have just described. This first step is in line with recent calls for researchers to use more neutral terms.³ Species-neutrality is important because we expect there to be differences between the human, highly derived form of property and the behavior shown by the rest of the animal kingdom. There is a risk of type II error in which research could fail to detect property in other animals if the definitions are too strict and human-specific. For example, it would be overly strict to suggest that property must be rooted in the human institution of language. This would immediately exclude the possibility of many species displaying property behavior.²⁴ Further,

there is no evidence to suggest that property behavior requires formal institutionalization through language.¹ In the second step, researchers can begin to restrict the first-step definition as necessary for their chosen methodology and species. Restrictive definitions can be useful to the point of narrowing research focus and generating ideas for experimental design. Restrictions may be necessary because research requires operational and specific criteria to meet, or not meet, to attain results valued by the field. However, restrictions can also increase the risk of type II error. For example, researchers could choose to define property as social group members defending an absent individual's exclusive access to an object in the case of thievery.¹⁷ Third party punishment of thieves would be a strong case for claiming that property exists in a species but a negative result based on a restrictive definition could be due to type II error. To determine if the third party punishment restriction could feasibly lead to a positive result, researchers can use pilot data testing and the collection of anecdotal evidence. This preliminary work can help researchers to justify why they have applied certain restrictions to their definition of property. Overall, we hope that this two-step approach forms a useful way for researchers to structure the composition of their definitions with the minimal number of restrictions.

The definitions we have provided above relate to the first of the two-step approach. Although we acknowledge that some authors define property as respect for possession, we prefer to separate these terms for both semantic and practical reasons.⁶ Defining property as a respect for possession is too restrictive for our preference. This is because possession is semantically linked to physical control. By extension, physical control cannot adequately capture abstract aspects of property. Practically, we prefer to use two terms rather than using property as a blanket term for the spectrum of behaviors between simple possession and abstract human property. This is because we want to create a useful distinction between the wide ranges of behaviors. Finally, our definitions are broad and species-neutral enough to

mitigate the risk of the separated terms polarizing behavior, and therefore, failing to capture the full range of behavioural variation. For example, a first-step definition which requires a third party punishment system would fail to capture the repertoire of species whose behavior which goes beyond physical control but does not include third party punishment. Thus, we hope to tread the fine line between specific and species-neutral definitions, general enough for us to detect the behaviors, but specific enough to facilitate objective research.

Key Approaches to the Evolution of Property

We discuss four key approaches: evolutionary game theory, ethology, comparative cognition, and developmental psychology (see Table 1). These can be combined to answer Tinbergen's four questions for explaining behavior: function, evolution, causation, and ontogeny.²⁵

| TABLE 1 Summary of key approaches | |
|-----------------------------------|--|
| Approach | How different approaches investigate the evolution of property |
| Evolutionary game theory | This approach looks at how the behavioral outcome of a competitive event can be predicted using theoretical modeling of the possible “decisions” available to players. Using this method, researchers can model the required conditions for property behavior to emerge. Evolutionary game theory helps us to understand how the adaptive value of different behavioural decisions, which ultimately impact fitness, has led to the variety of possession and property behavior we see in the animal kingdom today. This method targets the “function” part of Tinbergen's four questions. ²⁵ |
| Ethology | Using natural behavioral evidence from the animal kingdom, researchers can gather data on social interactions involving access to objects. For |

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|--------------------------|--|
| | <p>example, the analysis of behavioral responses to scent-markings around territories. This data can be used to determine the extent to which outcomes can be explained by property or possession rules. By comparing behavior across species, ethology can help to answer Tinbergen's “evolution” question.²⁵</p> |
| Comparative cognition | <p>Researchers compare the cognitive performances of different species when tested in a controlled environment. For example, researchers can test individuals' memory to investigate their ability to create associations between objects and individuals. This is more often performed in laboratory settings but can also be applied to a field experimental setting. Comparative cognition can inform our understanding of possessive and property behavior on a phylogenetic level, contributing to the question of how the “evolution” of possession and property behavior took place. It can also improve our understanding of the way the brain proximately operates in situations of possession and property, addressing the question of “causation.”²⁵</p> |
| Developmental psychology | <p>By studying the emergence of psychological biases linked with property in human children's development, researchers can suggest which features of property behavior are most likely innate to humans and what may have defined a rudimentary form of human property behavior before the rise of complex cultural institutions. In this way, developmental psychology can answer Tinbergen's “ontogeny” question.²⁵</p> |

Evolutionary Game Theory

Evolutionary game theorists can answer Tinbergen's "function" question by modeling the socioecological contexts, which lead to possessive or property behavior and identifying the differences between them.²⁵ In simplified terms, evolutionary game theory argues that a population of players with a range of available strategies will "evolve" through games, or strategic interactions, over time.²⁶ This is because a strategy may provide a higher payoff to players when it is used against other strategies and itself, under specific conditions. If a population of players adopts this strategy and they do not switch to available alternatives, then it is an "evolutionarily stable strategy."^{2,26,27} Therefore, evolutionary game theory models identify crucial assumptions necessary for possession or property to plausibly emerge as evolutionarily stable strategies.^{26,27} This balance of focus on both possession and property means that some researchers have been able to step away from human-centric definitions of property and call for species-neutral definitions.³ Evolutionary game theorists tend to use less restrictive definitions than ethologists because they begin with a theoretical behavior and generate strategies and contexts based on this behavior. Game theory definitions directly impact the model assumptions and strategies, therefore a minimal number of restrictions are still necessary for model validity and plausibility. On the other hand, ethologists must justify their categorization of recorded behavior. This methodology naturally leads researchers toward more restrictive, species-specific definitions. Therefore, evolutionary game theorists tend toward minimally restricted species-neutral definitions, which we suggest are the crucial bases for every researcher investigating the evolution of property.

Evolutionary game theory has established that possession is often respected because the risk of personal injury is too high. The "Bourgeois" strategy suggests that under certain simple model assumptions, the optimal strategy is to defend an object if you possess it, and not to thief objects possessed by other individuals.^{2,4} This applies when the value of winning the

conflict over the object is less than the cost of losing. The value of winning access to the object relates to an improvement in fitness and ultimately, reproductive advantage.²⁸ These strategies show that respect for possession can plausibly spread through a population as an evolutionarily stable strategy. This model illustrates that possession, a step toward property, can be solved by common sense explanations such as avoidance of costly fights.²⁷ However, “Bourgeois” may not be the evolutionarily stable strategy if conditions change. A higher payoff strategy may become available, such as the assessor strategy in which a player can use an assessment of their opponent's behavior to inform whether they should escalate a fight, flee or attempt to share the resource.² In line with this strategy, recent research has shown that signals which indicate a willingness to defend property can be more effective at maintaining property, than actual prevention.²⁹ In this way, evolutionary game theory models have successfully identified key factors which impact the emergence of both possessive and property behavior. Other models have identified: the costs of competition, the value or fitness advantage of the challenged object, whether objects are plentiful and whether objects are dispersed or clustered.^{5,30}

Evolutionary game theory research has also suggested that property or “privatization” may have been favored by natural selection, as a solution to the tragedy of the commons.^{3,31} The tragedy of the commons occurs when a depletable resource is reduced by individual competition which will reduce the fitness of the group.^{31–34} This “group” could also refer to population or species levels.³² The tragedy is that resources run out quickly when individuals are selfish, whereas if individuals use the resource at a sustainable rate and allow it to replenish, the group as a whole will benefit. Evolutionary game theory research has shown that the tragedy can be solved by privatizing the resource or reducing competitor rivalry by restricting the rate at which they can exploit the resource.³¹ When individuals “privatize,” or show property behavior toward, resources, the pressure on the individual to use up that resource before others do, is removed. Therefore, the tragedy of the commons can be solved by property behavior and

this provides one possible answer to Tinbergen's "function" question for property behavior.²⁵ Further, game theorists have found that privatization is favoured by natural selection at low value of relatedness.³¹ This means that the evolution of property behavior could have occurred in large, highly dispersed populations as well as in smaller, clustered populations.

Recent work has suggested a strategy for the emergence of property, where competitors are of equal strength, with no difference in resource holding potential. The "Restraint with Retaliation" strategy involves retaliating only when someone challenges your access to an object.³ The strategy is evolutionarily stable, under strict model conditions, which incorporate repeated raids over time and winner and loser effects (see Glossary).^{3,23,35,36} Full restraint from raiding, meaning respecting property, would not spread in a population of "unconditional raiders," who will never show restraint. However, "Restraint with Retaliation" could plausibly spread because as population size increases, the presence of additional individuals will increase the likelihood of a raiding individual being raided in return which would increase the costs associated with raiding.³ Thus, an individual in a population of individuals showing "Restraint with Retaliation," will have a higher pay off than individuals in a population of "unconditional raiders."³ Importantly, this model uses an assumption of competitive equality, which suggests that property can emerge without common sense explanations such as the costs of competing. Instead, a more complex explanation might be impacting the players' choices, such as the impact of fights on long-term relationships in terms of status and group hierarchy. Further, this model invites exchange between evolutionary game theory and ethology. By investigating multiple species displaying different strategies, ethologists could test the hypothesis that raiding will decrease when population sizes increase. Ultimately, the population size predictions of the "Restraint with Retaliation" strategy can be used to suggest a plausible time frame for the emergence of property in the human lineage.

Ethology

Ethological research has demonstrated a wide range of animal behavioural traits surrounding the possession of objects. To answer the Tinbergen question of the “evolution” of property behavior, it is important to understand and compare different species' behaviors.²⁵ This method allows us to piece together the evolutionary emergence of property, utilizing both researches on animals displaying the simplest possessive behavior all the way up to complex property behaviour in humans. In addition, ethology is a crucial way in which the field can challenge whether property behavior is unique to humans.

As mentioned, ethologists favor restrictive definitions. This is because the categorization of behavior becomes less subjective if you use stricter criteria. We believe that researchers will benefit from starting research with a broad, species-neutral definition such as those used by game theorists. However, we acknowledge that researchers need to operationalize their definitions in the second of the two-step approach, such that they are relevant for the particular species and context they wish to test. Paradoxically, ethologists need a fairly clear idea of what property and possession would look-like in a particular species to design the test correctly. Historically, researchers have tackled this issue by performing pilot studies. Thus, in line with our preferred method of defining property, ethologists can still restrict their definitions through systematic pilot studies and in-depth research of the zoological literature.

Ethological studies have found that several nonhuman primates show possessive behavior over a broad range of objects, including food, territory, mates, toys, and even tokens representing food.^{1,37-41} In some species, such as long-tailed macaques, *Macaca fascicularis* and hamadryas baboons, *Papio hamadryas*, the outcomes of possession conflicts can be reliably predicted by the rules of proximity and rank (see definitions of these principles in the

Glossary).^{1,7,10} These rules are closely linked to physical control and therefore we have defined them as possessive behavior. These principles illustrate that individuals' physical proximity to a target object, as well as individuals' rank, relative to opponents, are important variables in predicting the outcome of challenges. It seems the proximity rule can often be more important than dominance, with events in which the closest individual to the object will win possession, even if they are of lower rank.^{37,42,43} Similar evidence has been published for brown capuchins, *Cebus apella*.⁴⁴ There are common-sense explanations for why a dominant individual would permit a subordinate to retain possession of an object. As discussed by evolutionary game theorists above, the costs of competition may outweigh the possible benefits.^{44,45} For example, if the target object is of low value and is difficult to move, there are additional transportation costs with potentially low fitness benefits if you win the competition. Thus, ethological research has provided empirical evidence for two key variables likely to affect possession challenges: rank and proximity. This research has demonstrated variation within possessive behaviour in other animals, from simple to complex rules, suggesting a possible evolutionary trajectory towards the complex property behaviour we see in humans today.

Using the breadth of data on possessive behavior in wild species, ethological research has suggested an evolutionary path between from simple possessive interactions to scenarios guided by complex possession rules. Research suggests that behavior progresses from the precedence of power to the precedence of dominance status, and finally to the precedence of prior possession.¹⁰ Hermit crab conflicts demonstrate the precedence of power, in which individuals simply assess relative fighting power and the larger crab aggresses and wins generally.^{10,46} This is effectively a real world example of the assessor strategy, described in the evolutionary game theory section, Page 3. Next, precedence of power becomes precedence of dominance when interactions of power repeat and individuals learn to recognize the status of other individuals without challenging. Precedence of dominance reduces the chance of fighting

along with the associated costs of competition. Finally, precedence of prior possession begins when individuals learn that possessors win over challengers.¹⁰ In precedence of prior possession, physical power is effective only when the challenger is much stronger than the possessor is. Future research can test this phylogenetic hypothesis utilizing quantitative methods and a broad range of species data. By revisiting this proposed model, we can determine what contexts likely triggered key evolutionary changes that led to more complex possession behavior in certain species.

Ethology has already provided important rules that guide many animals' interactions around valued objects but there are still key challenges for those researching wild interactions today. On a grand scale, it is not feasible to attempt to test every species and define how they behave over objects. However, through interdisciplinary collaboration, researchers can suggest which species may be most likely to show possession and property. For example, researchers can achieve this by assessing relevant cognitive abilities in a range of species. Another key challenge is designing property tests for wild behavior so that researchers can rule out any alternative explanations. In the final section of this article, we present an example of how we can test for property behavior in a wild species. In this way, we hope to encourage more researchers to test likely species for property as well as possession. We believe that this targeted approach represents a promising step toward understanding how and why property behavior emerged.

Comparative Cognition

With the benefit of laboratory controls, researchers have identified cognitive abilities and biases of animals, including humans, with regards to possession and property. Here we discuss two main approaches to comparative cognition. First, researchers can test animals for

cognitive skills considered necessary to facilitate property in a social group. For example, X species cannot display property behaviour because they cannot remember associations between an object and an individual beyond an hour. Second, researchers can test animals for cognitive biases that result from acquiring possessions or property. For example, X species only shows biases toward foods that physically exist long enough to require the restraint of group members. These approaches can help us suggest likely species for researchers to test for property behavior.

Researchers can use data on various species' cognitive features relating to property and possession to answer Tinbergen's question of “evolution.”²⁵ Researchers can also use this data set to determine the “causation” explanation to property behavior, as distinct from that of possession.²⁵ In general, researchers design experiments so that the observed behavior can only be explained by a particular cognitive bias or skill. Therefore, comparative cognition favors restrictive definitions of possession and property behavior. As with ethology, we believe that the most useful comparative cognition research will begin with species-neutral definitions and restrict definitions using support from pilot studies.

Within this framework, one species has emerged as exhibiting many of the cognitive skills and biases associated with property: *Pan troglodytes*. This suggests that chimpanzees could be a likely candidate, worthy of further study. Itakura's research on linguistically trained chimpanzees has been highly informative about the extent to which the chimpanzee, our closest living relative, is cognitively capable of property behavior. Ai, a 13-year-old linguistically trained chimpanzee, demonstrated the ability to make symbolic associations between individuals and objects.^{12,13} Ai used bowl color to determine associations between feeding bowls and individuals. In the beginning, Ai showed food demanding behavior toward bowls of all three colors, but over time, her food demanding behavior decreased when the experimenter held a bowl that was not associated with her. Itakura argues that Ai was able to perceive a

symbolic representation of the relationships between objects and individuals. It should be noted that Ai did not reject bowls that were associated with other individuals. Therefore, she did not show full property behavior. However, she was capable of creating and remembering associations between individuals and particular bowls with a high degree of accuracy. Future research could replicate this study with a non-linguistically trained subject to determine if this finding can be applied to wild chimpanzees. This finding suggests that chimpanzees are cognitively able to respond to abstract rules of property with no social group present, based on the memory of associations. Further, there is evidence that chimpanzees have the cognitive skills necessary to understand trade, are able to barter with human experimenters showing rational maximization, and successfully comply with exchange requests when linguistically trained.^{1,37,47,48} Further, chimpanzees recognize working for a reward as establishing exclusive property access.¹⁷ Therefore, comparative cognition has shown that cognitive skills required to facilitate property are present in our closest living relatives.

Cognitive biases associated with possession and property, are originally detected in humans and then experiments are designed to identify if the bias exists in other species. For example, we know that the endowment effect, a bias for valuing objects based on possession, has been found in four great ape species-dependent on context.¹⁴⁻¹⁶ Further, loss aversion, reference-dependence biases, and the endowment effect have been observed in the highly encephalized and proficient tool-user primates of the New World, the capuchins, *Cebus sp.* (see Glossary).^{49,50} These findings suggest that similar cognitive biases toward possessions exist in primate species, other than humans. It seems that evolutionary pressure to secure access to valued possessions may have driven the emergence of similar cognitive biases of both humans and nonhuman primates. It would be useful to investigate what these species share and how they differ from primates who do not show these biases. One similarity which we discuss later, in a case study, is the use of stone tools. Therefore, research into cognitive biases relating

to object access is useful in order to identify species with similar behavioral repertoires to our own.

Overall, comparative cognition plays a key role in understanding the evolution of possessive and property behavior. Species sharing cognitive skills and biases comparable with humans invite further behavioral investigation. Chimpanzees, capuchins, orangutans, bonobos, and gorillas are all on this list.^{1,12–17,38,39,47–50} By understanding the cognitive features of other species, we can generate an evolutionary tree of property behavior. Comparative cognition can also contribute to our knowledge of the causation, or mechanism, of possession and property. Future research could also explore if there are human biases which appear during property, but not possessive contexts.

Developmental Psychology

Developmental psychology provides us with information about the extent to which innate psychological systems are able to explain the modern manifestation of property behavior in humans. In reality, numerous factors may impact the emergence of property in a species, including: the objects targeted by property behavior, psychological propensities toward property, the influences of culture on individual characteristics of adults, and the social context.⁹ Psychological approaches can help us to distinguish which aspects of property behavior are due to innate motivational systems and which aspects are due to culture. Here, we focus on the evidence of the development of property behavior in humans; however, we hope that future research will explore the innate and socially learnt aspects of possessive and property behavior in nonhuman animals.

To answer Tinbergen's “ontogeny” question, developmental psychologists have historically defined the developmental steps between possession and property behavior.²⁵ In

our proposed definition, we call for a species-neutral definition of property, as distinct from possession. In line with this definition, current evidence suggests that humans begin to demonstrate property behavior from the age of 24–30 months, as explored in further detail below. Before this age, humans typically illustrate possessive behavior.⁵¹ Our method of defining possession as distinct from property does not limit development psychologists. Researchers can restrict their definitions of possession into chronological phases before the age of 24–30 months, in the same way that ethologists can restrict their definition to particular species. It should also be noted that studying the increasing complexity in possessive behaviors is just as important as studying the emergence of property behavior. Studies which find the presence of possession at particular ages, rather than property, constitute useful contradictory evidence to proposed landmark ages in the development of property behavior.

Early research attributed the widespread nature of property in humans to a psychological tendency for accepted social practices.^{52–60} Since then, developmental psychology research has established supportive evidence for this tendency in the early and effortless development of abstract property rules.^{61,62} For example, there is an early and consistent use of the first possession rule in human infants (see Glossary).^{8,26,62,63} Across cultures, children are significantly more consistent and decisive in attributing property when one of the potential holders has created the target object: the “creator rule” (see Glossary).^{9,18-}

²¹ There also seems to be general psychological propensities to support property behavior that develop in children, although these propensities require cross-cultural validation. From around 24–30 months, toddlers can: assert and acknowledge property rights recognize and protect their own and others' property communicate property status to others, and act to re-establish the rights of property holders to access their property.⁵¹ Overall, human property behavior is supported by consistently developing property rules and psychological propensities to enforce

norms with third party punishment, to communicate with others to gain support for enforcing these laws and finally to collaborate jointly and with shared intentionality.^{17,64–66}

At the age of three, in the cultures studied thus far, social factors start to play a key role in shaping the development of possession and property behavior. Children begin to experience possession as alienable (i.e., tradeable and negotiable in exchanges) and they are forced to socially evaluate if values in trade are “good,” and to take note of accountability and reputation.^{67–69} Examples of cultural impact on possession are cross-cultural differences in the development of the “first possession heuristic”. For example, there is no evidence of any development of the endowment effect over individually owned objects in the case of the Hadza (see glossary).^{70,71} We suggest that property behaviour may exist in societies like the Hadza, but that cultural factors have transferred individual behavior to the group level, over group-owned property. Cultural factors may also influence individuals determining which abstract possession or property rules are of most importance relevant to the social context. For example, even though we may respect “first possession” as a rule for possession rights, this may be discarded in favor of rules by sex, the length of possession or prior pursuit.⁸ This suggests that the demography, as well as the size, of the group present, plays a key role in determining whether individuals show particularly kinds of possessive or even property behavior.

Developmental psychology plays the key role in indicating the ontogeny of property behavior. This research allows us to make valuable expectations for when modern children typically display this behavior. Further, with an ontogenetic understanding of property, we can determine if property is an inherited part of human behavior. This can be achieved by validating developmental results across many cultures. This will have important implications for designing future research, as we would gear the work of ethology and comparative cognition toward investigating such innate features.

Six steps for an integrated approach

All of the methodologies above are integral to answering Tinbergen's questions, as applied to the evolution of property.²⁵ This approach involves a broad focus on the discipline's progress as a whole. It also calls for an awareness of the current positioning of each methodology and how they can interact with each other. Finally, the approach requires the drive to innovate new research solutions, through engagement with all these methods.

1. Look both at our own species and at the rest of the animal kingdom (prioritizing likely candidates for property, as indicated by comparative cognition) and collate what studies need to be done to fill in the blanks in our knowledge.
2. *Draw on evolutionary game theory*: Evolutionary game theory has explained the factors that control the outcome of raids, such as the value of the object, the strength of competitors, and so on. Collaboration with comparative cognition is helping us to understand how biases affect competition outcomes. Game theory and developmental psychology can look theoretically at how real-world competitions in human children develop toward property behavior. Game theory can produce testable predictions to be tested using ethological research.
3. *Draw on ethology*: Ethology has identified specific rules of possession in a number of animal species. In addition to broadening our understanding of possession rules, ethology also actively tests animal species for property behavior. The selection of likely species to test for property can become more systematic with the collaboration of ethology with comparative cognition and evolutionary game theory. Finally, ethology can apply the methodology of developmental psychology to gain a clearer understanding of the ontogeny of possessive and property behavior in other animals. We suggest this research could begin with species-neutral definitions and progress to

more operationalized definitions of what behavior, we would expect to see in that particular species.

4. *Draw on comparative cognition:* Comparative cognition has tested cognitive skills and biases. This research can help to determine what cognitive characters would be necessary for property behavior to occur. It can then be followed up with systematic and standardized research to confirm if these skills and/or biases exist in a range of animals. The selection and testing of target species would naturally involve collaboration with ethology. Game theory and psychological methods can be used to consider factors such as group composition, including individuals' ontogenetic development.
5. *Draw on developmental psychology:* Developmental psychology has investigated property behavior in children of different ages and cultural backgrounds. This research helps us to understand the extent to which the development of property behavior is innate in humans. It also helps us to identify critical periods of development for the behavior. Developmental research can be validated by cross-cultural investigation. Subsequently confirmed innate features, if confirmed at all, can be compared to other species' development, through integration with ethology and comparative cognition.
6. Integrate the findings from the above-mentioned disciplines in new ways. For example, psychology of human behavior can provide ideas for property and possession biases, which we can test in other animals under experimental settings using comparative cognition. Another example is that comparative cognition can guide ethology with regards to the selection of species.

With clear definitions, direction, and a multitude of methodologies at their disposal, research in this field is at a turning point. At this critical position, interdisciplinary collaborations stand to accelerate our learning about the evolution of property.

A proposition for future empirical research: A quasi-experimental approach centred on the Chimpanzee, *Pan Troglodytes*

To conclude this review, we illustrate an example of how creative approaches, informed by the interdisciplinary findings above, can be used to empirically test for property in wild animal species.³ We suggest that this approach can be used to contribute to Tinbergen's “evolution” and “function” questions. Comparative cognition formed the basis for our species selection and could be used to conduct important follow-up studies, one of which is suggested below. Our selection of target object was guided by the findings of evolutionary game theory and psychology. We also used evolutionary game theoretic models to identify variables to test. Finally, we took consideration of developmental changes in behaviour toward the target object in order to select an appropriate age group for each test. Thus, this approach leverages interdisciplinary findings to generate novel tests for property in a hominin model species in the wild.

One of our closest living relatives, the chimpanzee, shares cognitive skills and biases toward objects with humans (as discussed in the “Comparative Cognition” section above). Our other closest living relative, the bonobo (*Pan paniscus*) does not show respect for possession norms to the same extent as chimpanzees, likely due to lower punishment costs.⁷² Chimpanzees are more manipulative with objects than bonobos, which we suggest makes chimpanzees more likely to illustrate property behaviors in the wild.⁷³ In addition, chimpanzees are a suitable model species for stone tool using hominins that may have had a patriarchal, rank based society. Therefore, a chimpanzee model allowed us to indirectly test whether early hominins could have shown property behavior, without requiring complex language, formal institutions or a level of cooperation existent in modern humans.

Evolutionary game theory and psychology findings have identified a list of factors which may affect whether an object will be a target for property behavior.⁹ Research into the psychology of property suggests that a target object are likely to be: durable, controllable, of functional utility, capable of creation (in the sense that you can find one and create a functional purpose for it), and necessary to access high energy resources.⁹ Evolutionary game theory research highlights the importance of object value, availability, and distribution.³⁰ We selected stone tools as our target object. Stone tools are functional, valuable objects that enable chimpanzees to access high energy nuts. Stone tools are durable, can be shaped or “created” and are controllable. Stone tools are not so easily available and dispersed, that individuals would not compete for them. On the other hand, they are not so rare, valuable or clustered that one high-ranking individual would simply horde them. This means that individuals in a chimpanzee population could have repeated strategic interactions over the same stone tools for relatively long period of time. Therefore, we selected stone tools as a target object because they are plausible and testable targets for property behaviour in wild chimpanzee populations.

Ethologists testing for possession or property behavior in any land-dwelling species would benefit from the example set by the wild laboratory, set up by Matsuzawa and colleagues in Bossou forest, Guinea, in 1988.⁷⁴ This method captures natural chimpanzee behavior, in a context which allows researchers to manipulate a quasi-laboratory context. The laboratory is a natural clearing (7 m by 20 m), situated at the top of Mount Gban, and chimpanzees voluntarily visit the so-called “outdoor laboratory” (7 390 N, 8 300 W) to crack nuts, among other activities. Therefore, we suggest that the wild laboratory would be the ideal location for this novel approach.

Next, we needed to assess that this combination of species, target object and further, specific population, were worthy of investigation. We created simple hypotheses for chimpanzee tool use behavior, assuming that they did not display possession or property. Then,

we applied available data from Bossou to determine whether the chimpanzee behaviour could be explained without possession or property behavior (see Table 2).

Having confirmed that these explanations do not dismiss a possession or property explanation a priori, we considered what observable behavior would be sufficient to constitute evidence for possession and beyond this, property. We formed three testable hypotheses for possession and property behavior (Table 3). The first two hypotheses test for support or rejection of the existence of property behavior over stone tools in chimpanzees. The variables used in these hypotheses reflect the importance of signals and the number of individuals present, as suggested by evolutionary game theory findings.^{3,29} These hypotheses contribute to Tinbergen's "evolution" question.²⁵ The third hypothesis targets a possible evolutionary advantage for the selection of property behavior over stone tools: the increase of tool skill, specifically efficiency, due to increased time spent with particular tools, which may lead to increased energetic intake. Therefore, this hypothesis contributes to Tinbergen's "function" question.²⁵

| TABLE 2 Alternative hypotheses for stone tool use reuse at Bossou, Guinea | | |
|---|---|---|
| Hypotheses | Predictions | Preliminary analysis |
| (1) Chimpanzees do not have stone tool preferences, they use what is available. | They will use toolsets (hammers and anvils) at random, based on availability. | A chimpanzee will use a less preferred, but available stone tool rather than go hungry. Nevertheless, there is evidence that they use the same toolsets more than expected by chance. ⁷⁵ |

| | | |
|--|--|---|
| <p>(2) Chimpanzees do not defer to others' preferences for stone tools beyond proximity and/or rank.</p> | <p>Respect for possession exists only if the property holder is within arm's reach of the object. Respect for possession is also dependent on the respective ranks of the two "players." When the property holder is absent and their stone tool becomes available, individuals with less efficient stone tools will use them.</p> | <p>As they grow, juveniles are given harsher punishments than infants, if they try to use other individuals' tools while they are present. This indicates that individuals are encouraged to find and use their own preferred tool. They are discouraged from using others' tools even if they available. A new study shows that juveniles are the main tool "recyclers" and this affects their tool-use efficiency.⁷⁶</p> |
| <p>(3) Due to associative mechanisms between food and tools, chimpanzees prefer particular tools simply out of familiarity. They have no real sense of property.</p> | <p>With newly introduced tools, individuals will show no preference, as they are not familiar with the tools.</p> | <p>At Bossou, new tools were introduced in 2008 and preferences emerged quickly. This is an anecdotal report; however, it makes clear that familiarity is not the only factor driving use patterns. Further, an associative explanation is not necessarily mutually exclusive to a property explanation.</p> |

| TABLE 3 Possession and property hypotheses testing using chimpanzee stone tool behavior | |
|---|---|
| Hypotheses | Predictions |
| (1) Looking and taking: length of observation and number of adults present in a party explains the occurrence of takeover events. | The likelihood of an individual taking a tool from another individual— a “takeover event” - increases with (a) time spent monitoring the individual before the “takeover” and (b) with a lower number of individuals present capable of punishing the “thief” (i.e., adults), compared to instances when takeover events do not take place following the abandonment of toolsets. |
| (2) The presence of possession and property norms explains the severity of punishments given, including third party punishment. | Punishment will last longer and will be more severe when the punished individual is using the “preferred tool-set” of another individual. this rule will apply even when the punishing individual is a third party. |
| (3) Higher reutilization of the same stone-tool set explains higher individual efficiency. | Efficiency of nut-cracking increases when individuals use a very limited number of toolsets and a negative correlation should appear between toolsets used and efficiency. |

Test 1: Looking and taking: Investigating observation, group presence, and takeover events

A test of how much time adults spend observing conspecifics during nut-cracking, without “taking over” toolsets, could illuminate whether or not adults are monitoring conspecifics' preferences, relating to respect for stone tool property norms.⁷⁷ Stone tools preferred by highly skilled individuals may be more subject to “takeovers” because individuals prefer to observe the most proficient nut-crackers of the group as observers get older.⁷⁸

If possessive or property behavior is present, the likelihood of a departure event being followed by a “takeover event” will be higher with increased monitoring. This is because individuals, who are about to takeover a toolset, should monitor the user carefully, so that they use the object out of sight of the possessor/property holder, to avoid direct punishment. Second, in property behavior, but not in possession behavior, individuals should be wary of third party punishment. Therefore, takeover events will negatively correlate with group size. Takeover events may be more likely in smaller groups because the risk to the “thief” of being punished would be reduced (for operational definitions, see Table 4).

| TABLE 4 Operational definitions for Test 1 “Looking and taking: investigating observation, group presence and takeover events” | |
|--|--|
| Term | Definition |
| Departure events | An event in which an individual, who had been cracking nuts, ceased using its tools and moved away from the objects, leaving the nut-cracking area. ⁷⁶ |
| Highly skilled adults | Individuals who, on average, crack nuts with three strikes or less. ⁷⁷ Previous research uses the number of blows to crack a nut. ⁷⁸ |
| Takeover events | During the subsequent 60s to departure event, another individual begins to use the abandoned tools. ⁷⁶ |
| Observation | An event in which a group member approaches another group member within a distance of 1m and remains with fixed gaze upon the target individual's face or hands for 3 or more continuous seconds. ⁷⁹ |
| Group presence | Third party presence is established by the number of adults present at the moment of a departure event. This excludes infants and juveniles because relative to a “thief,” they present a low punishment threat. |

Test 2: Norm violation: Comparing different punishment contexts

Adults, even third party individuals, begin to punish infants as they grow into juveniles when the juvenile attempts to “takeover” adults' stone tools.⁷⁷ This could suggest the presence of a social norm regarding either possession or property. We would test the prediction that third parties, with no preference for the stone toolset involved, will punish individuals more severely, and for longer periods of time, in contexts where the stone toolset is the preferred toolset of another individual compared with stone toolsets that are preferred by no individual. This test targets property behavior because this goes beyond a possessor maintaining physical control over the target object. We would need to control for two variables in this test: the ID of the punisher and whether the punished individual is alone or not. The first variable controls for individual differences in the severity of the third party's punishment. The second variable controls for the explanation that individuals who are found nut-cracking alone at the outdoor lab are punished by arriving group members simply because the individual is accessing the nuts before others. The focus of the test would be to understand if the “status of the toolset used” can explain a significant amount of variation in a composite measure of punishment severity (for operational definitions, see Table 5).

| TABLE 5 Operational definitions for Test 2 “Norm violation: comparing different punishment contexts” | |
|--|---|
| Term | Definition |
| Punishment events | A punishment event starts when an individual or groups of individuals initiate(s) an agonistic interaction with another individual. |
| Punishment severity | Severity multiplied by punishment length (in seconds). Severity is defined as 1 (0 contact made), 2 (1 or 2 contacts made), or 3 (3 or more contacts made). |

| | |
|-------------------|--|
| Status of toolset | <p>The last five uses of the toolset in question are recorded. A use is defined as an individual nut-cracking with the stone tool set or one of the stone tools for 10 or more continuous seconds.</p> <p>The toolset is defined as “own or unused” if:</p> <ol style="list-style-type: none"> 1. The toolset has not been used before 2. OR the punished party has been the “user” for at least three of the last five uses 3. OR the toolset has been used by various individuals, with no individual using the toolset more than twice. <p>The toolset is defined as “other's” if:</p> <ol style="list-style-type: none"> 1. Another individual has used the toolset for three or more of the last five uses. |
|-------------------|--|

Test 3: Efficiency and toolset repertoire: Testing an adaptive explanation

If property behavior, or rather restraining the use of absent individuals' tools, were to be favored in hominin evolution, there may have been an adaptive benefit for doing so. Property behavior toward stone tools may benefit individuals through improved knowledge and efficient use of their particular tool or toolset, which can translate into higher energetic gains. Property behavior may also help individuals to avoid punishment by property holders or by group members enforcing punishment for reneging on property norms. If property behaviour were to confer an adaptive advantage, we should expect individuals who limit their tool repertoire, rather than using other individuals' preferred tools, to be the most efficient tool users. Therefore, a supportive result would be a significantly negative association between toolset repertoire and skill (for operational definitions, see Table 6).

| TABLE 6 Operational definitions for Test 3 “Efficiency and toolset repertoire: testing an adaptive explanation” | |
|---|--|
| Term | Definition |
| Toolset repertoire | Divided into three categories: “Diverse toolset user” individuals that use more than four toolsets, “toolset user” individuals that use three or four toolsets and “limited toolset user” individuals that use only one or two toolsets. |
| Skill | The average number of blows the individual performs to crack a nut. ⁷⁸ Skill is categorized into four levels: (0) 10 or more blows, (1) 7–9 blows, (2) 4–6 blows, and (3) 1–3 blows. The higher the category the more skilled the individual. ⁷⁸ |

These three tests described above illustrate that researchers should not be dissuaded by initial challenges of designing tests for researching property behavior in wild species. Here, we have selected a species and target object based on interdisciplinary findings and evidenced that the problem of operational definitions is surmountable. In addition, we illustrate an empirical way to test a hypothesis for a significant catalyst in the evolution of property: the use of stone tools by a model species. This single case study is not the answer to the evolution of property, but it is a starting point toward methodology designed to capture natural behavior.

Like any realistic example there are limitations to this methodology, and awareness of this fact enables us to be constructive. Pilot studies would be carried out, to test if operational definitions being coded successfully capture the intended behavior and thus, to avoid the risk of type I and type II errors. For example, in the “Looking and taking” test, there is a risk of false negative results because the operational definition for an observation event is strict; subjects may be performing more inconspicuous observations that are not captured by the definition. Further, follow up studies would be important. For example, if a relationship were found between repertoire size and skill in Test 3, this would prove an association, but not

causation. Laboratory research could help to confirm or reject a causal relationship between toolset repertoire and efficiency. In this way, we hope that this realistic methodological example evidences the value of the interdisciplinary approach throughout the research process.

Conclusions

Overall, we hope to have demonstrated that this field is at a crucial point. Creative approaches to the study of possession and property in nonhuman species represent a major step forward for the discipline.³ To illustrate this point, we have presented an example of how the interdisciplinary approach can be used to test for property behavior in a hominin model species in the wild. Contemporary researchers have clear terminology at their disposal and a broad range of methodologies with which to expand knowledge of this subject. This represents a turning point in the discipline, a clear opportunity for interdisciplinary, creative research to systematically fill in the gaps of our evolutionary knowledge of the origin of property.

| Glossary | |
|------------------|--|
| Barter | In barter, an individual can trade an object or service for another which is possessed or owned by another individual. ¹⁷ |
| Creator rule | Property holder status is given to the individual or individuals who created or modified the object. ¹⁸ Empirical examples of this rule include individuals feeling ownership toward their own work, their organization, the products they create and their jobs. ^{9,11,19–21} |
| Endowment effect | The overvaluing of an object due to possession and/or property exhibited by an individual or group of individuals. For example, in trade for the same two |

| | |
|---------------------------|--|
| | objects, a seller may attach higher sentimental, and thus economic, value to an object in their possession and/or property compared with an identical item which is not in their possession/property. |
| First possession rule | Property holder status is given to the first possessor of the object as shown in developmental studies and throughout the animal kingdom. ^{4,8,17} |
| Loss aversion | Preference to avoid losses rather than acquire gains, even when the variable of object value is held constant. |
| Proximity principle | Respect for possession is dependent on the physical proximity of the possessor to the object. |
| Rank principle | Respect for possession is dependent on hierarchy and correlates with the relative ranks of the present possessor and prospective possessor. |
| Reference dependence bias | Individuals evaluate outcomes relative to a reference point, leading to context-specific gain and loss classification. ²² |
| Winner and loser effects | Individuals are more likely to win raids (such as those over possessions or property) at time T, based on victories at time T-1, T-2, and more likely to lose at time T, based on losing at time T-1, T-2. ²³ |

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