INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2018, 31
Charles Abramson
Special Issue Editor
Peer-reviewed

The Importance of a Truly Comparative Methodology for Comparative Psychology

Mackenzie F. Smith [1,2], Julia Watzek [1,2], and Sarah F. Brosnan [1,2,3,4]

[1] Georgia State University Language Research Center, U.S.A.
[2] Georgia State University, Department of Psychology, U.S.A.
[3] Georgia State University, Neuroscience Institute and Center for Behavioral Neuroscience, U.S.A.
[4] Georgia State University, Department of Philosophy, U.S.A.

Comparative research has taught us much about the evolution and development of human and animal behavior. Humans share not just physical and biological similarities with other species, but also many behavioral traits and, in some of these cases, the psychological mechanisms behind them. Comparing behavior and cognition across multiple species can help scientists to pinpoint why and when in phylogenetic history a behavior may have evolved, how it evolved, and what the mechanisms behind it are (Tinbergen, 1963). While the comparative approach has proven quite effective in addressing these questions, comparing behavior across multiple species is not as easy and straightforward as it may initially seem. Rigorous methodology and careful interpretation of results is crucial to answering any of these questions definitively. The focus of the current article is on the comparative methodology and the important factors that need to be addressed in order for comparative research to be effective. We first discuss the benefits and importance of comparative research, followed by the challenges that need to be overcome in good comparative work. We then discuss experimental economics as one "model system" for comparative work that has proven particularly good at addressing such issues, and comment on other approaches. We conclude with future directions for comparative research with an eye on important methodological and theoretical considerations.

Comparative psychology is often synonymous with the study of animal behavior, including the study of animals in order to better understand humans (Dewsbury, 1989). While this is one aspect, it does not adequately encompass the true nature or foundation of the comparative approach. Broadly speaking, the comparative approach utilizes similarities and differences in the behavior and cognitive processes of different species (including humans) to make inferences about the evolutionary history and adaptive significance (or not) of characteristics and behaviors (Greenberg & Haraway, 1998). Comparative studies give us an unprecedented view into the process and history of evolution. Fossil records have provided invaluable information about the evolution of physical and morphological characteristics, but they tell us less about behavior (although see Martin, 2014).

Comparative psychology is fundamentally tied to the theory of evolution. A proper understanding of key evolutionary processes is therefore necessary in order to draw meaningful conclusions from species comparisons. Because closely related species descend from common ancestors, they share at least some, if not many, biological characteristics, depending on the degree of the relationship. Since evolution can only involve characteristics that were already present, the comparative approach can help us understand how the common ancestor of a collection of species may have looked and behaved, by considering similarities among the species being compared. In addition, looking at the differences helps us determine what the selection pressures for and building blocks of a distinct or novel behavior may have been.

Please send correspondence to Mackenzie Smith Georgia State University Atlanta, GA 30302, U.S.A. (Email: mfsmith018@gmail.com) https://doi.org/10.46867/ijcp.2018.31.01.12

Similarities between species can arise from homology or convergence (analogy). Homology refers to the existence of a shared characteristic in two (or more) species as a result of its presence in a common ancestor of those species. For example, lactation and (at least some level of) maternal care are homologies across the entire mammalian order, due to their presence in the common ancestor to all mammals. Convergent evolution reflects the process whereby two (or more) species independently evolve a similar characteristic, not as the result of phylogenetic relatedness, but due to similar environmental and selective pressures. For example, tool use in primates and corvids independently evolved in the different taxa without a shared common ancestor that used tools (for review see Sanz, Call, & Boesch, 2013; although tool use can take different forms and there is debate about how this influences our understanding of the phylogeny of tool use Crain, Giray, & Abramson, 2013). Corvids and primates are fairly distant phylogenetic relatives, but even relatively closely related species can have analogous behaviors evolve via convergence rather than homology. For example, we can study the convergence of tool use within the primate order, since tool use has been demonstrated in a range of primate species that, so far as we know, lack a tool using common ancestor (i.e., nut-cracking in chimpanzees and capuchin monkeys). Such close convergences allow us to better identify the similar ecological pressures that may lead to such behaviors, such as environments with less easily available food (Seed & Byrne, 2010), while better controlling for factors that are the result of homology than is possible when comparing more distant taxa.

Studying the differences among species can be just as informative as considering similarities. When we study divergent evolution, we are looking at the differences between species that have emerged since their last common ancestor. Particularly with divergence in closely related species, we may be able to pinpoint specific ecological differences, and therefore the potential differing selective pressures, that may have led to the diverging characteristics. For example, to test the hypothesis that social complexity can be a selective force behind some advanced cognitive abilities, such as transitive inference (useful for tracking social relationships within group), researchers have compared two species of lemurs (*Lemur catta* and *Eulemur mongoz*) and two species of corvids (*Gymnorhinus cyanocephalus* and *Aphelocoma californica*) that differ predominantly in their levels of sociality. Discovering the capacity for transitive inference in both the social lemurs and social corvids, but not their less-social relatives, implicates sociality as a driving force behind this behavioral divergence (Bond, Kamil, & Balda, 2003; Maclean, Merritt, & Brannon, 2008).

The examples given thus far demonstrate how the comparative approach can address questions about the phylogenetic history and adaptive function of behavior. These are both *ultimate* explanations about the evolutionary processes that lead to the behaviors, however the comparative approach can also provide *proximate* explanations for the immediate mechanisms and development of a behavior. True understanding of a behavior comes from answering all four of Tinbergen's questions about the phylogeny and function (ultimate level) and mechanisms and ontogeny (proximate level) of a behavior (Tinbergen, 1963). For example, researchers of bird song now know the phylogenetic lines in which specific song features appeared, they have discovered that the current utility of songs is to both attract mates and ward off rivals, the neurological circuitry that produces singing is well understood, and we know there is a sensitive period in development when birds learn songs from conspecifics (Bateson & Laland, 2013). While few behaviors have been studied and understood at each level of Tinbergen's questions in this way, an enhanced understanding of behavior comes from trying to address multiple levels of questions within individual studies and across projects and research programs. Indeed, birdsong provides a prime example of this approach; our current understanding required numerous studies from many different laboratories, and it is the additive results from these research efforts that allow us the comprehensive understanding of this behavior.

Of course, the comparative approach is entirely dependent upon the ability to make meaningful comparisons among species, such that we can assume that they are an accurate reflection of nature, and not differences in the experimental procedures. While this seems an obvious assumption, there are many theoretical and practical considerations to take into account when making species comparisons. With all types of research (field or laboratory, observational or experimental), research design and methodology can severely impact whether and how widely comparisons can be accurately made. We address experimental work in particular, both because the added level of control means that we are better able to address possible solutions to these challenges and because the primary work in our laboratory is experimental, so we are most familiar with this set of challenges.

Challenges of Comparative Research

A key challenge to comparative research is making sure that any differences (or similarities) discovered reflect true species differences (or similarities), rather than differences in the procedures. This requires that we use, to the degree possible, identical procedures across the species tested. In an ideal situation, you design a paradigm that can be conducted identically across all of the species in question. You would also assume that the different species all interpreted your identical procedure in the same way. If each step is identical, then you could, in this ideal world, assume that any similarities and differences are truly reflective of similarities and differences among the species tested.

Of course, in the real world that we all inhabit, creating identical procedures that fairly assess abilities across species is challenging and, in some cases, virtually impossible. You need to design a procedure that is both physically possible for all the test species and that they all interpret similarly. Considering the former, given the diversity of body plans in the animal kingdom, it is often the case that only fairly closely related species can be given a truly identical paradigm. As a result, we often rely on analogous procedures (i.e., a primate grabs a target while a corvid pecks it), which may or may not have the same underlying mechanism or reflect the same understanding by the animal. Considering the latter, species may have biological differences in sensory or perceptive modalities that influence how they perceive a task (Plotnik et al., 2013; Plotnik, Shaw, Brubaker, Tiller, & Clayton, 2014). While tasks may be designed to rely differentially on vision, olfaction, audition, etc., in some cases it may be difficult to design analogous procedures across modalities. Moreover, even if the species perceive it similarly, differences in cognitive architecture, experience, and environment may influence how they interpret it.

What this means is that scientists often must adapt paradigms from one species for use with another. While such adaptations can be necessary, they also present a different problem because they may inadvertently favor one species. For instance, if the task is adapted identically without considering some key feature of the second species (i.e., preferring the auditory to visual cues; Maille & Roeder, 2012), then the second species is disadvantaged and may appear to be less able as compared to the former. On the other hand, in an effort to equalize the tasks, the experimenter may add training steps or simplify procedures and thereby inadvertently favor the second species, making it appear more able than the former. In an ideal situation, multiple permutations of the task would be run on each species, but doing so may be impossible due to resources, time, or number of subjects.

While these may be the two most critical fundamental issues for comparative work, there are other more prosaic ones as well. An incomplete list includes: differences in the physical test setup, differences in housing, differences in how captivity affects behavior, differences that preferentially cue one species to the behavior of interest, differences in the amount of training or exposure to the test, differences in general exposure to training or cognitive testing, etc. The latter two issues are particularly important when considering cognitive studies, where experience may influence outcomes, and some individuals, particularly in long-lived species such as cetaceans and non-human primates, may become test-savvy. Differences in life histories should be considered when directly comparing species, as it is known that experience influences at least some cognitive tests (Brosnan et al., 2011). Considering the former issues, even seemingly minor differences in experimental design can greatly influence results, which we describe a few examples of below.

One of the most common reasons for null results in comparative work is the failure to design a study that animals understand the way that the experimenter intended. Tasks need to be designed so that they are intuitive to the animals. To give an example, Chalmeau and colleagues (Chalmeau, Visalberghi, & Gallo, 1997) tested whether capuchin monkeys (*Cebus [Sapajus] apella*) would cooperate by simultaneously pulling bars to activate a switch that released a reward. The capuchins were able to get the rewards, but pulled at similar rates whether a partner was present or not, indicating that the successful outcome was the result of unintentional coordination rather than intentional "cooperation." On the basis of this study alone we would conclude that capuchin monkeys do not understand cooperation. However, in a similar task in which subjects jointly pulled on bars to bring in a counterweighted tray, capuchin monkeys showed evidence of understanding the role of their partner (Mendres & de Waal, 2000). What led to these conflicting results? A key difference between these two studies was that in the latter study, the bars directly pulled a platform that visibly brought the rewards towards the subjects as they pulled, and provided kinesthetic feedback when a partner was or was not helping (i.e., it got too heavy if the partner let go). In contrast, in the former study, the physical disconnect between the bar and the reward meant that these cues were absent. Indeed, when the successful barpull monkeys were tested in a situation similar to Chalmeau and colleagues (1997), in which they had to push levers to activate a juice apparatus, the subjects failed, despite their previous experience working together (reported in Brosnan & de Waal, 2002). Thus, a relatively minor methodological tweak completely changed the ability of the monkeys to understand the task. Indeed, we think a take-home message from these particular studies is that animals often do best with paradigms that are based entirely on physical principles that they can see, experience, and understand. Complicated apparatuses involving hidden (to the animals) components may allow for more flexibility, but can mask the contingency for an animal between their behavior and its effect.

Even with identical paradigms, how the task is presented can be critical. For years, it was believed that apes could not solve the trap tube task, a test of casual understanding in which subjects must push a food reward in the appropriate direction (or choose an appropriate tube lacking a trap) to avoid losing it in a "trap", or pit in the tube, that keeps subjects from obtaining the food (Limongelli, Boysen, & Visalberghi, 1995; Povinelli, 2003). Later, however, Call and colleagues performed a series of studies demonstrating that apes avoided the trap just fine, in the right circumstances. For instance, they can solve the task if they can rake a reward towards themselves, but not if they have to push the reward away (Mulcahy & Call, 2006). They also do better when they are given a single tool that they then must insert in one of the tubes (i.e., make an active choice which tube to use the tool in), rather than tools being present in both tubes when they start the experiment (Girndt, Meier, & Call, 2008). Finally, they succeed when there is no tool needed at all (Seed, Call, Emery, & Clayton, 2009) or when the trap is part of a platform rather than a tube (Martin-Ordas, Call, & Colmenares, 2008).

Even whether food is visible or hidden can cause differences in results. For example, early experiments on prosocial behavior gave subjects the option to provide food to their partner at no cost to themselves. Results indicated that, among other species tested, capuchin monkeys were prosocial but chimpanzees (*Pan troglodytes*) were not (Jensen, Hare, Call, & Tomasello, 2006; Lakshminarayanan & Santos, 2008; Silk et al., 2005). In these studies, the rewards for both the subject and their partner were always visible, and it has been hypothesized that this may induce competitive tendencies in the chimpanzees, who have a less relaxed feeding ecology than capuchins, reducing their prosocial behavior (Cronin, 2012). Indeed, when chimpanzees were re-tested in contexts in which food was not visibly displayed, they showed prosocial behavior (Horner, Carter, Suchak, & de Waal, 2011; but see; Amici, Visalberghi, & Call, 2014).

Finally, even when procedures are identical, animals' ecologies or cognitive architecture may make them more sensitive to some cues than others. An excellent example of this point is a recent set of studies exploring how ecology influences which cues are relevant to different species. Initial work, using a procedure that was specific to cleaner fish (*Labroides dimidiatus*), showed that these fish were much better at solving a foraging task than capuchin monkeys, chimpanzees, or orangutans (*Pongo spp.;* Salwiczek et al., 2012). However, adapting the cues to be more specific to monkeys allowed them to do almost as well as the fish (Prétôt, Bshary, & Brosnan, 2016a, 2016b), indicating that it was not the task that was the problem, but it might instead be that the primates were unfamiliar with the cues and therefore had to learn what cues to use before they could subsequently solve the task. Interestingly, we then back-tested the monkey adaptations on cleaner fish, and found that they did just as well as they had previously. This result could indicate that the fish can use a broad set of cues, or simply that their general intelligence has been underestimated (Brown, Laland, & Krause, 2011; Bshary, Gingins, & Vail, 2014). Such findings emphasize the need to look for "smart" behaviors in species other than the large-brained megafauna, as all species may develop complex behaviors in response to their environmental pressures. Studying these behaviors may help uncover convergent processes that have shaped cognition.

In comparative work, it is key to "back-test" paradigms modified for a different species on the original species, to ensure that the modified task generates the same results as anticipated. Failure to do so can result in incorrect conclusions, and may be particularly problematic when adapting human tasks to non-human species, because they are often so dramatically altered. For example, one study that tested for framing effects, a cognitive bias whereby subjects respond differently to the same decision if it is presented as a loss versus a gain, resulted in behavior indicating the bias in capuchin monkeys (Lakshminarayanan, Chen, & Santos, 2011). However when researchers in another laboratory tested the modified procedure on humans, they found no evidence of the bias (Silberberg et al., 2013). Thus, the result in capuchins may have been a similar looking behavior resulting from a different underlying mechanism. Conversely, several studies exploring the so-called ultimatum game in chimpanzees found that changing the procedure changes humans' behavior, but in ways that reflect the chimpanzees' responses. In a typical version of this game, an anonymous proposer offers a split of an experimenter-provided jackpot and a responder either accepts it, and both get their portion, or refuses, in which case neither gets anything. In several different adaptations, chimpanzee responders, unlike typical humans, never refused an offer, no matter how unequal (Jensen, Call, & Tomasello, 2007; Kaiser, Jensen, Call, & Tomasello, 2012; Proctor, Williamson, de Waal, & Brosnan, 2013). However, two additional tests of the adapted paradigms with humans showed that they, too, never refused in this procedure (Proctor et al., 2013; Smith & Silberberg, 2010). Moreover, in both humans and chimpanzees, there were far fewer unequal offers made by proposers than in the typical game (Proctor et al., 2013). This may be due to the fact that, unlike in the typical human study, in which the partners are anonymous strangers in a one-shot interaction, the chimpanzees and children in this latter study were in a repeated interaction with a known member of their social group, which presumably alters both humans' and chimpanzees' behavior (Milinski, 2013).

Back-testing the paradigm is not the only issue that is of particular importance when testing humans. One obvious difference between human and animal research is the use of language. In almost all research conducted with humans, participants are given verbal instructions or even pre-tests to ensure that they respond in the expected manner. The directions, explanation of the experiment, training procedure, or even just the experimental set-up may cue a participant or inadvertently shape their behavior towards a specific outcome.

Animals do not receive verbal instructions of the same sort, which introduces an inequality of experience (although they typically do receive training on some aspects of the task, and experimenters must work hard to ensure that the training does not bias their behavior). One way to equalize the situations is to present little or no verbal instruction to humans in at least one condition, possibly compared to a condition with traditional instruction. In fact, in research where humans are presented with the same non-verbal task as animals, their behavior is more similar to the animals' (Jensen et al., 2007; Smith & Silberberg, 2010). One caveat, however, is that you do not avoid problems entirely by avoiding language; without language, it may be more difficult to ensure that the subjects interpret the task the way that the experimenter intended. This could even be a larger problem for humans, who are accustomed to active instruction.

Another factor that can contribute to different results between humans and animals is that humans are always tested with conspecific experimenters (other humans), while animals are typically tested with heterospecifics (human experimenters). Thus, humans have an inherent advantage in their ability to 'read' the experimenter's behavior and make assumptions about the study, which has been shown to impact the results of experiments on social learning (Call, Carpenter, & Tomasello, 2005; Call & Tomasello, 1994; Nagell, Olguin, & Tomasello, 1993), instrumental helping (Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007), and cueing (Essler, Schwartz, Rossettie, & Judge, 2017). These issues could be compounded when multiple experimenters are involved (either at the same time or rotating). It is possible to avoid some of these issues by training conspecific models in animal studies, and computerized testing removes the experimenter altogether (at least during the actual study), which may additionally reduce instances of inadvertent cueing, or relieve stress for individuals that are nervous around humans.

We also note that it is sometimes difficult to interpret results because, while authors present the details of the experiment, they do not always provide sufficient information about subjects' histories or the surrounding context. Two key details that are overlooked surprisingly often are the subjects' social histories and the relationships among the individuals being tested. These are particularly critical in tests of social behavior, but because we know that rearing history influences many aspects of cognition, this should be reported in all cases (i.e., were they mother reared? Isolation housed at any point? Subject to invasive procedures in the past?). Ideally, subjects should be socially competent individuals with well-established long-term social bonds, and the relationships among the individuals should be documented. It is also important to know subjects' housing and testing conditions. For instance, are subjects ever food or water restricted? This may cause them to make different decisions than sated subjects who are working for treats above and beyond their daily caloric or liquid needs. How familiar are subjects with the testing apparatus or testing facility? Is their failure to learn lack of experience with the task, or lack of ability? How are subjects oriented relative to one another? Can they easily perceive each other's actions and rewards? Finally, a key issue is whether testing is truly voluntary, or if subjects are restricted in some way other than physical restraint or food restriction (i.e., cannot go to an outside yard or favored part of the enclosure, cannot have treats, or do not receive their day's meal unless they participate). Subjects who are participating freely may be more motivated to pay attention and choose carefully than those who just want to get through the task so they can get past the imposed restriction.

Finally, we end by pointing out that whereas interpreting comparative results can be difficult when there are variations in procedure across species, and we therefore should strive to use identical procedures, sometimes you do not *want* strictly identical methodologies. Indeed, completely equalized procedures will not take into account the unique aspects of each species that might also be important. Therefore, we recommend that whenever possible, comparative work be embedded in a program that uses identical procedures to develop a framework, and then tests the hypotheses that are generated based on the results by developing species-specific designs that may be more naturally intuitive or better account for species-specific ecological or morphological considerations. If the hypotheses are correct, you should be able to predict how species-specific differences will influence results on the task. Comparative experimental economics provides an example of a program designed to address this first level, beginning with identical comparisons across species, and then adapted to more species-specific designs.

Comparative Experimental Economics as a Model System

Economists face the same suite of issues as comparative psychologists, attempting to understand and explain complex phenomena that are difficult to study in their natural context. One way that economists have addressed this challenge is with the development of game theory and experimental economics, which distill complex decision-making scenarios into very simple, often dichotomous-choice tasks (Smith, 1987, 1991; see also the closely related field of behavioral economics; Allison, 1983; Camerer, 2003, which explores when and why decision-makers deviate from rational choice predictions, and similar work that was developing in behavioral ecology at the same time, using game theory to better understand animal contests; Maynard-Smith, 1982). This simplification allows economists to compare results across contexts in very standardized ways, which is key for the utility of experimental economics as an approach for comparative work. These simple tasks can be easily instantiated in animals, even in multiple formats, allowing us to directly compare decision situations across species and contexts (Brosnan, Beran, Parrish, Price, & Wilson, 2013). The games are designed to capture key components of more complex decision-making phenomena that occur in real-world settings, such as cooperation, competition, and trust. Although this approach sacrifices some ecological validity, it is effective for discovering the mechanisms behind decision-making. The simplicity also allows for the manipulation of specific variables within the paradigm, to assess how behavior changes under a variety of circumstances.

The basic setup of dichotomous economic games revolves around a 2 × 2 decision matrix, whereby each player makes a choice between two options and their *joint* decision determines the outcome. This dichotomous choice paradigm has been used to look at animal behavior in a variety of scenarios ranging from cooperation to competition, using adaptations of economic games such as the Assurance Game (Brosnan et al., 2011; Parrish, Brosnan, Wilson, & Beran, 2014), Hawk-Dove Game (Brosnan et al., 2017), Snowdrift Game (Sánchez-Amaro, Duguid, Call, & Tomasello, 2016), Matching Pennies Game (Martin, Bhui, Bossaerts, Matsuzawa, & Camerer, 2014; Sanabria & Thrailkill, 2009), and the famous Prisoner’s Dilemma Game (Clements & Stephens, 1995; Haroush & Williams, 2015; Stephens, McLinn, & Stevens, 2002; Tian & Uchida, 2015).

Here, we use the first (and simplest) experimental economics game used in our laboratory[1] to illustrate how these games can be adapted for truly identical procedures across species (Brosnan et al., 2011). The Assurance Game (AG), or Stag Hunt Game, models the decision about whether to coordinate hunting; players choose to either hunt a hare alone or hunt together for a stag. Sharing the stag results in the most benefit, but it requires joint action for success. Hunting hare is relatively easy and there is high success alone, however the reward is smaller than a stag. In the dichotomous choice game, on each turn players choose between *Stag* and *Hare*. If both players choose *Stag*, they receive the highest payout (food rewards for the non-human primates, and monetary rewards for the humans), whereas any player who chooses *Hare* receives the smaller reward

---

[1] The payout matrixes and procedures used for these games have been documented in several publications (Brosnan et al., 2011, 2017; Brosnan, Wilson, & Beran, 2012).

regardless of what their partner does, making it the less risky strategy. The worst outcome is choosing *Stag* when your partner chose *Hare,* because you receive no payout at all. There are two coordinated Nash equilibria (NE) in the AG (strategies where a player can do no better by changing their strategy so long as their partner's choice remains constant; Fudenberg & Tirole, 1991), the higher-paying *Stag* and the lower-paying, but safer, *Hare*. The payoff structure of the AG makes it a good game to begin with, because coordination on *Stag* is the obvious choice for pairs who understand the payoffs. As a result, we can (presumably) determine whether the subjects understand the way in which the game is played, which is important for future games that lack an obvious 'best' response.

We tested socially-housed chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), capuchin monkeys (*Cebus [Sapajus] apella*), and humans on multiple versions of the AG (Brosnan et al., 2011; Brosnan, Wilson, & Beran, 2012). Chimpanzee and capuchin monkey pairs were drawn from long-term, well-established mixed sex social groups, and pairs consisted of individuals who voluntarily separated together. Rhesus monkeys were tested with the compatible partner with whom they were housed. Human subjects typically never meet one another, because studies are anonymous (or, in psychology studies, the "partner" may well be a computerized player), but in our study, humans were together in the waiting room prior to the study and interacted during testing. An important aspect of our design was to test humans using identical procedures to those used with the non-human primates (importantly, without verbal instruction). As mentioned above, such "back-testing" is a vital aspect of the research program, as finding a result similar to the existing literature helps to validate the adapted procedure, and deviations indicate that the paradigm needs adjustment to get at the behavior of interest.

An additional benefit of the experimental economics paradigm is that it can be adapted in multiple ways. For example, when possible, we tested our species on multiple versions of the game with the same basic structure and payoffs. One version was a manual exchange task, in which subjects chose which of two tokens to return to the experimenter, and the other task was a computerized version, in which subjects chose one of two icons on a computer screen. The greater control of the computerized task also allowed us to test our subjects on both a synchronous version of the task (similar to typical economic game play, in which neither partner knew what the other played when they made their decision) and an asynchronous version, where the second responder could see what their partner had chosen and adjust their behavior (or not) accordingly (this form of game play is potentially equivalent to a sequential game in game theory terminology, assuming the second mover sees the first mover's response). As we discuss below, there is no one best procedure, but each offers unique opportunities.

Using the manual version of the task, we found that at least some pairs within all species that we tested were able to find the payoff dominant NE (*Stag-Stag*; Brosnan et al., 2011). Capuchins did the least well, with only one pair consistently finding the payoff dominant NE. Chimpanzees were better able to find the NE than the capuchins, however chimpanzees' performance was highly correlated with prior experience with cognitive testing. Those with an extensive testing background found the payoff-dominant NE, whereas those with less testing experience settled into stable patterns of play, but not the payoff-dominant NE. One of the more important findings of this manual version was the surprising behavior of humans. Only about 20% of our human pairs settled on the payoff-dominant NE, 40% settled on *Hare-Hare*, and the rest did not establish a stable strategy. Further analysis revealed that those pairs who settled on the *Hare-Hare* NE never experienced the best-paying *Stag-Stag* outcome. In other words, they did not fully explore the parameter space and so did not realize that there was a higher-paying option (post-game debriefing supported this conclusion).

To further understand how species' behavior varies across multiple contexts, we additionally tested capuchin and human subjects on a computerized version of the task, and added rhesus monkeys (we did not have sufficient computer trained chimpanzees available to test; Brosnan et al., 2012). The computerized version allowed for a much higher trial count (because trials were shorter), a shorter interval between choice and reward (computers react faster than human experimenters), and both synchronous and asynchronous versions of the task (because on the computer we can control what is visible on the screen). These results painted a somewhat different picture. The capuchin monkeys did much better on the computerized task, with seven of the eight pairs settling on the payoff-dominant NE in the asynchronous task. However, they were never able to do so in the synchronous version, even after finding the NE in the asynchronous version (i.e., it was apparently not dependent on experience). Rhesus monkeys were able to find the payoff-dominant strategy in both the synchronous and asynchronous versions. Humans also did much better on the computerized version. All 27 pairs settled on a stable strategy, with nearly 80% of them playing the payoff-dominant strategy. Why they did so much better than in the manual task is likely related to language. In the manual task, the experimenter was present in the room and, presumably because of this, subjects never spoke to one another (at no time were there instructions regarding talking, or not). In the computerized task, the pair was alone in a room, and all pairs talked to one another. Interestingly, the pairs that settled on the lower paying *Hare-Hare* strategy were the only pairs that did not speak about the game.

Although our procedures were isolated from the species' ecologies, our results may shed some light on the impact of ecology on the evolution of these species' decision-making. For example, capuchins, who only solved the task when they could see their partner's choices, live in small social groups where they are rarely out of view of one another, and thus may not have been under selective pressure to remember about interactions with absent individuals (Fragaszy, Visalberghi, & Fedigan, 2004). On the other hand, chimpanzees and rhesus monkeys live in much larger groups (or fission-fusion groups, in the case of chimpanzees) where they are frequently out of sight of one another and, in the case of chimpanzees, coordinate when out of view of one another (i.e., when hunting monkeys or going on territorial patrols in groups, Boesch & Boesch, 1989; Mitani & Watts, 2005). Therefore, these primates may have been selected to remember partner's patterns of behavior even when the partner is out of view.

This experimental economics model system also demonstrates the importance of running multiple versions of a paradigm, to give each species as many opportunities to succeed as possible. Indeed, there is no one ideal approach, and using different approaches allowed us to benefit from the advantages and work around the disadvantages for each. Manual tasks are more ecologically relevant (there are no computer systems in the wild!), and can be tweaked to take advantage of species-typical propensities. While we have used exchange-based approaches to study economic games, researchers in other laboratories have tested the same payoff structures using even more ecologically relevant approaches with chimpanzees. One took advantage of the context upon which the Assurance Game was originally conceived, with a simple foraging task in which subjects could work alone to get a small reward or commit to coordinating on a larger one (Bullinger, Wyman, Melis, & Tomasello, 2011; Duguid, Wyman, Bullinger, Herfurth-Majstorovic, & Tomasello, 2014). Adaptations such as these may not allow for as wide of a comparison across species, but offer a very high level of ecological validity. More broadly, manual tasks may avoid the challenge of a procedure that the animals do not understand, because they (presumably) can more easily follow the causality of their behavior than they can with computerized paradigms or electronic switches that trigger rewards. On the other hand, the inability to use electronic or computerized systems limits the available manipulations, and because manual tasks rely on a human experimenter controlling the procedure, there are fewer trials (because each takes longer), a longer interval between choice and reward, more opportunities for mistakes when coding responses (and a bigger time investment if data are coded from video), and, of course, the ever-present risk of cuing by the experimenter.

We have already discussed the primary disadvantage of computerized tasks, the lack of ecological validity. In addition, computerized systems are more expensive[2], there is a level of abstraction necessary between behavior and outcomes that is not present in the more intuitive manual tasks, and, depending on the apparatus, may require a substantial investment in training prior to any experiments. Nonetheless, once trained, subjects can effectively use computerized tasks to answer a wide variety of behavioral and cognitive questions (Beran, Evans, Klein, & Einstein, 2012; Inoue & Matsuzawa, 2007; Martin, Biro, & Matsuzawa, 2017; Prétôt et al., 2016b). Moreover, there are obvious benefits, including increased trial counts, automated data recording, and the ability to do manipulations that are impossible in manual tasks that are inherently limited by the physics of the real world (i.e. things can appear suddenly, change, disappear, etc.). Additionally, there is a much tighter contingency between behavior and outcome (this and increased trial counts are both known to enhance learning; Wolfe, 1934), and the elimination of human bias or cues. Finally, if a goal is to compare animal behavior to that of humans, computerized testing is the predominant testing modality for human studies, so results are more directly comparable to the existing literature.

Future Directions

Comparative psychology has led to a much improved understanding of both human and animal behavior, and in particular its evolution and underlying mechanisms, but there is more to do. One additional area of future research that we believe will be particularly fruitful is moving controlled laboratory experiments away from the dyad and towards the social group. Such studies have already been done to great effect (Burkart & van Schaik, 2013; Hall, Lambeth, Schapiro, & Brosnan, 2015; Watzek, Rossettie, Raines, & Brosnan, 2015). The majority of work on social behavior to date has used experimenter-determined pairs, for the very practical reason that it is difficult to interpret results that aren't tightly controlled. Thus, understanding dyadic behavior provides a framework that allows us to better interpret messy natural social interactions. However, these messy interactions could be more informative. Collecting data within the broader social group allows subjects to participate more naturally, choosing when, if, and with whom they want to participate. We are currently applying this approach to a variety of economic games, which we hope will provide additional insight into how social dynamics influence decision-making. We are eager to see how social dynamics impact behavior and cognition in other areas, such as cooperation or prosocial behavior.

Moreover, while we study primates, and therefore rely on examples from these taxa, one critical component of comparative psychology is to be as taxonomically broad as possible. While primates are frequently studied due to their close relationship with and similarity to humans, they represent a minority of the animal kingdom. Analyses that include wider ranges of species will create more powerful hypotheses (Silk, 2007). Moreover, while comparative researchers who are interested in the evolution of complex cognitive abilities typically study species such as primates, elephants, cetaceans and, more recently, corvids (Byrne, Bates, & Moss, 2009; Schusterman, Thomas, & Wood, 2013), recent research points to the utility of studying more diverse taxa, such as the social fishes and other birds (Bshary et al., 2014; Emery, 2006). We second the encouragement to comparative researchers to look beyond the mammalian order and include taxa that may demonstrate informative convergences in the evolution of behaviors and cognitive abilities.

---

[2] Although with recent technological developments in the form of microcontrollers, computerized testing systems can be both cheap and portable (Varnon & Abramson, 2013), allowing researchers to reduce costs as well as bring these advantages (like tight temporal contingencies and no direct human interaction) to the field as well.

We also encourage comparative researchers to take a cue from cultural anthropologists and psychologists and look at differences between populations of the same species. In particular, in light of our earlier discussion of the impact of housing and experience with testing, it would be interesting to know the full scope of how prior life experiences (such as participation in cognitive tasks) affects behavior on future tasks. Is it a result of expanded cognitive abilities due to a lifetime of cognitive enrichment, or is there a simpler explanation, such as a better understanding of what the task is asking? We may also find instances in which ecological pressures lead to different behaviors or cognitive abilities within the same species (Ménard & Vallet, 1997; Robbins et al., 2016; Whiten et al., 1999). On a related note, there can be variation in how representative an individual, or even a population, is of the species as a whole (Hodos & Campbell, 1969). This can be due not only to natural variations in cognitive ability and behavior, but also to differences in experience or training. While the obvious solution is to test as many subjects as possible from multiple and diverse populations (Bramblett, 1978), when this ideal cannot be reached researchers can still report individual data (as well as inferential statistics and group means; Craig & Abramson, 2015) along with complete subject histories so that future researchers can consider the effects of specific experiences on behavior.

In conjunction with our last point, we encourage researchers to incorporate more fieldwork into comparative research (Janson & Brosnan, 2013). Fieldwork and laboratory work are complementary, and should be considered together. Field studies offer more ecological validity and an opportunity to see how behaviors and cognitive abilities are actually being used by the animals. Moreover, observations, particularly in the field, may uncover hitherto unknown behaviors (Boesch & Boesch, 1989) and thereby not only advance our understanding of the species, but provide new hypotheses to be tested. Laboratory work complements this by providing the opportunity for tightly controlled experiments that are essential for teasing apart causality, which are often infeasible in the wild. Moreover, finding an unexpected cognitive ability may alert field researchers to consider why such an ability may have evolved and where it could be utilized in the animals' natural world. Although it is typically difficult for one individual to do both field and laboratory work (although see; Fragaszy et al., 2013; Hayashi, Mizuno, & Matsuzawa, 2005; Inoue-Nakamura & Matsuzawa, 1997; Sabbatini et al., 2014), researchers can collaborate or, at the very least, read each other's' literatures and incorporate each other's ideas.

While it is easy enough to call for the incorporation of more diverse species in comparative research and the connection of laboratory and fieldwork, both can be quite challenging in practice. As we have discussed, access to species and resources are limited, and time is finite. Identical procedures across numerous species are more challenging when species differ in body plan, sensory modality, cognitive architecture, and more. Despite these challenges, however, we hope that more scientists make the effort to design their studies to be directly comparable to other's results, or to set up collaborations to do so explicitly. It is well worth the rewards to be able to not only directly compare species to one another, but also to gain an understanding of how the unique aspects of their ecology and social system may be shaping a species' behavior. In so doing, we will do the most to advance our understanding of animal behavior and cognition.

References

Allison, J. W. (1983). *Behavioral economics*. New York, NY; Praeger.

Amici, F., Visalberghi, E., & Call, J. (2014). Lack of prosociality in great apes, capuchin monkeys and spider monkeys: Convergent evidence from two different food distribution tasks. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 22.

Bateson, P., & Laland, K. N. (2013). Tinbergen's four questions: an appreciation and an update. *Trends in Ecology & Evolution, 28*, 712–718. https://doi.org/10.1016/j.tree.2013.09.013

Beran, M. J., Evans, T. A., Klein, E. D., & Einstein, G. O. (2012). Rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) remember future responses in a computerized task. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*, 233–243. https://doi.org/10.1037/a0027796

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, *78,* 547–573. https://doi.org/10.1002/ajpa.1330780410

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, *65*, 479–487.

Bramblett, C. A. (1978). Is the concept of "control group" valid? A quantitative comparison of behavior of caged baboon groups. *American Journal of Physical Anthropology*, *49*, 217–226. https://doi.org/10.1002/ajpa.1330490210

Brosnan, S. F., Beran, M. J., Parrish, A. E., Price, S. A., & Wilson, B. J. (2013). Comparative approaches to studying strategy: Towards an evolutionary account of primate decision making. *Evolutionary Psychology*, *11*, 606–627.

Brosnan, S. F., Parrish, A., Beran, M. J., Flemming, T., Heimbauer, L., Talbot, C. F., … Wilson, B. J. (2011). Responses to the Assurance game in monkeys, apes, and humans using equivalent procedures. *Proceedings of the National Academy of Sciences*, *108*, 3442–3447. https://doi.org/10.1073/pnas.1016269108

Brosnan, S. F., Price, S. A., Leverett, K., Prétôt, L., Beran, M., & Wilson, B. J. (2017). Human and monkey responses in a symmetric game of conflict with asymmetric equilibria. *Journal of Economic Behavior & Organization*, *142*, 293–306. https://doi.org/10.1016/j.jebo.2017.07.037

Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature*, *13*, 129–152. https://doi.org/10.1007/s12110-002-1017-2

Brosnan, S. F., Wilson, B. J., & Beran, M. J. (2012). Old World monkeys are more similar to humans than New World monkeys when playing a coordination game. *Proceedings of the Royal Society of London B: Biological Sciences*, *279*, 1522–1530. https://doi.org/10.1098/rspb.2011.1781

Brown, C., Laland, K., & Krause, J. (2011). *Fish cognition and behavior* (2nd ed.). Oxford, UK: Blackwell Publishing.

Bshary, R., Gingins, S., & Vail, A. L. (2014). Social cognition in fishes. *Trends in Cognitive Sciences*, *18*, 465–471. https://doi.org/10.1016/j.tics.2014.04.005

Bullinger, A. F., Wyman, E., Melis, A. P., & Tomasello, M. (2011). Coordination of chimpanzees (*Pan troglodytes*) in a Stag Hunt Game. *International Journal of Primatology*, *32*, 1296–1310. https://doi.org/10.1007/s10764-011-9546-3

Burkart, J. M., & van Schaik, C. (2013). Group service in macaques (*Macaca fuscata*), capuchins (*Cebus apella*) and marmosets (*Callithrix jacchus*): A comparative approach to identifying proactive prosocial motivations. *Journal of Comparative Psychology*, *127*, 212–225. https://doi.org/10.1037/a0026392

Byrne, R. W., Bates, L., & Moss, C. J. (2009). Elephant cognition in primate perspective. *Comparative Cognition & Behavior Reviews*, *4,* 65–79. https://doi.org/10.3819/ccbr.2009.40009

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition, 8,* 151–163. https://doi.org/10.1007/s10071-004-0237-8

Call, J., & Tomasello, M. (1994). The social learning of tool use by orangutans (*Pongo pygmaeus*). *Human Evolution*, *9*, 297–313. https://doi.org/10.1007/BF02435516

Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.

Chalmeau, R. , Visalberghi, E., & Gallo A. (1997). Capuchin monkeys (*Cebus apella)* fail to understand a cooperative task. *Animal Behaviour*, *54*, 1215–1225.

Clements, K. C., & Stephens, D. W. (1995). Testing models of non-kin cooperation: Mutualism and the Prisoner's Dilemma. *Animal Behaviour, 50*, 527–535. https://doi.org/10.1006/anbe.1995.0267

Craig, D. P. A., & Abramson, C. I. (2015). A need for individual data analyses for assessments of temporal control: Invertebrate fixed interval performance. *International Journal of Comparative Psychology*, *28*. Retrieved from https://escholarship.org/uc/item/847557dt

Crain, B. J., Giray, T., & Abramson, C. I. (2013). A tool for every job: Assessing the need for a universal definition of tool use. *International Journal of Comparative Psychology*, *26*. Retrieved from https://escholarship.org/uc/item/3qg3h7pd

Cronin, K. A. (2012). Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour*, *84,* 1085–1093. https://doi.org/10.1016/j.anbehav.2012.08.009

Dewsbury, D. A. (1989). Comparative psychology, ethology, and animal behavior. *Annual Review of Psychology*, *40*, 581–602.

Duguid, S., Wyman, E., Bullinger, A. F., Herfurth-Majstorovic, K., & Tomasello, M. (2014). Coordination strategies of chimpanzees and human children in a Stag Hunt game. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*, 20141973. https://doi.org/10.1098/rspb.2014.1973

Emery, N. J. (2006). Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*, 23–43. https://doi.org/10.1098/rstb.2005.1736

Essler, J. L., Schwartz, L. P., Rossettie, M. S., & Judge, P. G. (2017). Capuchin monkeys' use of human and conspecific cues to solve a hidden object-choice task. *Animal Cognition*, *20*, 985–998. https://doi.org/10.1007/s10071-017-1118-2

Fragaszy, D. M., Liu, Q., Wright, B. W., Allen, A., Brown, C. W., & Visalberghi, E. (2013). Wild bearded capuchin monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. *PLOS ONE*, *8*, e56182. https://doi.org/10.1371/journal.pone.0056182

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: The biology of the genus Cebus* (1st ed.). Cambridge, UK ; Cambridge University Press.

Fudenberg, D., & Tirole, J. (1991). *Game theory*. Cambridge, MA: MIT Press.

Girndt, A., Meier, T., & Call, J. (2008). Task constraints mask great apes' ability to solve the trap-table task. *Journal of Experimental Psychology: Animal Behavior Processes*, *34*, 54–62. https://doi.org/10.1037/0097-7403.34.1.54

Greenberg, G., & Haraway, M. M. (Eds.). (1998). *Comparative psychology: A handbook*. New York, NY: Garland/Taylor & Francis.

Hall, K., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2015). *Chimpanzees respond differently to inequity based on relative food values*. Paper presented at the 38th Annual Meeting of the American Society of Primatologists, Bend, Oregon.

Haroush, K., & Williams, Z. M. (2015). Neuronal prediction of opponent's behavior during cooperative social interchange in primates. *Cell*, *160*, 1233–1245. https://doi.org/10.1016/j.cell.2015.01.045

Hayashi, M., Mizuno, Y., & Matsuzawa, T. (2005). How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. *Primates*, *46*, 91–102.

Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review*, *76*, 337.

Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences*, *108*, 13847–13851. https://doi.org/10.1073/pnas.1111088108

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, *17*, R1004–R1005.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*, 159.

Janson, C. H., & Brosnan, S. F. (2013). Experiments in primatology: From the lab to the field and back again. In M. Blair, E. Sterling, & N. Bynum (Eds.), *Primate ecology and conservaton: A handbook of techniques* (pp. 177–194). Oxford, UK: Oxford University Press.

Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum game. *Science*, *318*, 107–109. https://doi.org/10.1126/science.1145850

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1013–1021. https://doi.org/10.1098/rspb.2005.3417

Kaiser, I., Jensen, K., Call, J., & Tomasello, M. (2012). Theft in an ultimatum game: Chimpanzees and bonobos are insensitive to unfairness. *Biology Letters, 8,* 942-945. https://doi.org/10.1098/rsbl.2012.0519

Lakshminarayanan, V. R., Chen, M. K., & Santos, L. R. (2011). The evolution of decision-making under risk: Framing effects in monkey risk preferences. *Journal of Experimental Social Psychology*, *47*, 689–693. https://doi.org/10.1016/j.jesp.2010.12.011

Lakshminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology*, *18*, R999–R1000. https://doi.org/10.1016/j.cub.2008.08.057

Limongelli, L., Boysen, S. T., & Visalberghi, E. (1995). Comprehension of cause-effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *109*, 18–26.

Maclean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social complexity predicts transitive reasoning in prosimian primates. *Animal Behaviour*, *76*, 479–486. https://doi.org/10.1016/j.anbehav.2008.01.025

Maille, A., & Roeder, J. J. (2012). Inferences about the location of food in lemurs (*Eulemur macaco* and *Eulemur fulvus*): A comparison with apes and monkeys. *Animal Cognition*, *15*, 1075–1083. https://doi.org/10.1007/s10071-012-0531-9

Martin, A. J. (2014). *Dinosaurs without bones: Dinosaur lives revealed by their trace fossils* (1st ed.). New York, NY: Pegasus Books.

Martin, C., Biro, D., & Matsuzawa, T. (2017). Chimpanzees spontaneously take turns in a shared serial ordering task. *Scientific Reports*, *7*, 14307. https://doi.org/10.1038/s41598-017-14393-x

Martin, C. F., Bhui, R., Bossaerts, P., Matsuzawa, T., & Camerer, C. (2014). Chimpanzee choice rates in competitive games match equilibrium game theory predictions. *Scientific Reports*, *4*, 5182. https://doi.org/10.1038/srep05182

Martin-Ordas, G., Call, J., & Colmenares, F. (2008). Tubes, tables and traps: Great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition*, *11*, 423–430. https://doi.org/10.1007/s10071-007-0132-1

Maynard-Smith, J. (1982). *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*, 1405–1413. https://doi.org/10.1098/rspb.2010.1735

Ménard, N., & Vallet, D. (1997). Behavioral responses of Barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. *American Journal of Primatology*, *43*, 285–304. https://doi.org/10.1002/(SICI)1098-2345(1997)43:4<285::AID-AJP1>3.0.CO;2-T

Mendres, K. A., & de Waal, F. B. M. (2000). Capuchins do cooperate: The advantage of an intuitive task. *Animal Behaviour*, *60*, 523–529.

Milinski, M. (2013). Chimps play fair in the ultimatum game. *Proceedings of the National Academy of Sciences*, *110*, 1978–1979. https://doi.org/10.1073/pnas.1222132110

Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*, 1079–1086. https://doi.org/10.1016/j.anbehav.2005.02.012

Mulcahy, N. J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition*, *9*, 193–199. https://doi.org/10.1007/s10071-006-0019-6

Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *107*, 174–186.

Parrish, A., Brosnan, S. F., Wilson, B. J., & Beran, M. J. (2014). Differential responding by rhesus monkeys (*Macaca mulatta*) and humans (*Homo sapiens*) to varibale outcomes in the Assurance Game. *Animal Behavior and Cognition*, *1*, 215–229. https://doi.org/10.12966/abc.08.01.2014

Plotnik, J. M., Pokorny, J. J., Keratimanochaya, T., Webb, C., Beronja, H. F., Hennessy, A., … Getz, D. (2013). Visual cues given by humans are not sufficient for Asian elephants (*Elephas maximus*) to find hidden food. *PLOS ONE*, *8*, e61174. https://doi.org/10.1371/journal.pone.0061174

Plotnik, J. M., Shaw, R. C., Brubaker, D. L., Tiller, L. N., & Clayton, N. S. (2014). Thinking with their trunks: elephants use smell but not sound to locate food and exclude nonrewarding alternatives. *Animal Behaviour*, *88*, 91–98. https://doi.org/10.1016/j.anbehav.2013.11.011

Povinelli, D. J. (2003). *Folk physics for apes: The chimpanzee's theory of how the world works* (2nd ed.). New York, NY: Oxford University Press.

Prétôt, L., Bshary, R., & Brosnan, S. F. (2016a). Comparing species decisions in a dichotomous choice task: Adjusting task parameters improves performance in monkeys. *Animal Cognition*, *19*(4), 819–834. https://doi.org/10.1007/s10071-016-0981-6

Prétôt, L., Bshary, R., & Brosnan, S. F. (2016b). Factors influencing the different performance of fish and primates on a dichotomous choice task. *Animal Behaviour*, *119*, 189–199. https://doi.org/10.1016/j.anbehav.2016.06.023

Proctor, D., Williamson, R. A., de Waal, F. B. M., & Brosnan, S. F. (2013). Chimpanzees play the ultimatum game. *Proceedings of the National Academy of Sciences*, *110*, 2070–2075. https://doi.org/10.1073/pnas.1220806110

Robbins, M. M., Ando, C., Fawcett, K. A., Grueter, C. C., Hedwig, D., Iwata, Y., … Yamagiwa, J. (2016). Behavioral variation in gorillas: Evidence of potential cultural traits. *PLOS ONE*, *11*, e0160483. https://doi.org/10.1371/journal.pone.0160483

Sabbatini, G., Manrique, H. M., Trapanese, C., De Bortoli Vizioli, A., Call, J., & Visalberghi, E. (2014). Sequential use of rigid and pliable tools in tufted capuchin monkeys (*Sapajus spp*.). *Animal Behaviour*, *87*, 213–220. https://doi.org/10.1016/j.anbehav.2013.10.033

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., … Bshary, R. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging task derived from cleaner – client reef fish cooperation. *PLOS ONE*, *7*, e49068. https://doi.org/10.1371/journal.pone.0049068

Sanabria, F., & Thrailkill, E. (2009). Pigeons (*Columba livia*) approach nash equilibrium in experimental matching pennies competitions. *Journal of the Experimental Analysis of Behavior*, *91*, 169–183. https://doi.org/10.1901/jeab.2009.91-169

Sánchez-Amaro, A., Duguid, S., Call, J., & Tomasello, M. (2016). Chimpanzees coordinate in a snowdrift game. *Animal Behaviour*, *116*, 61–74. https://doi.org/10.1016/j.anbehav.2016.03.030

Sanz, C. M., Call, J., & Boesch, C. (2013). *Tool use in animals: Cognition and ecology*. Cambridge, UK: Cambridge University Press.

Schusterman, R., Thomas, J. A., & Wood, F. G. (2013). *Dolphin cognition and behavior: A comparative approach*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Seed, A., & Byrne, R. (2010). Animal tool-use. *Current Biology*, *20*, R1032–R1039.

Seed, A. M., Call, J., Emery, N. J., & Clayton, N. S. (2009). Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology. Animal Behavior Processes*, *35*, 23–34. https://doi.org/10.1037/a0012925

Silberberg, A., Parker, S., Allouch, C., Fabos, M., Hoberman, H., McDonald, L., … Wyatt, L. (2013). Human risky choice in a repeated-gambles procedure: An up-linkage replication of Lakshminarayanan, Chen and Santos (2011). *Animal Cognition*, *16*, 907–914. https://doi.org/10.1007/s10071-013-0623-1

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 539–559. https://doi.org/10.1098/rstb.2006.1994

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., … Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, *437*, 1357–1359. https://doi.org/10.1038/nature04243

Smith, P., & Silberberg, A. (2010). Rational maximizing by humans (*Homo sapiens*) in an ultimatum game. *Animal Cognition*, *13*, 671–677. https://doi.org/10.1007/s10071-010-0310-4

Smith, V. L. (1987). Experimental methods in economics In J. Eatwell, M. Murray, & P. Newman (Eds.), *The new palgrave: A dictionary of economics* (pp. 241–248). London, UK: Palgrave Macmillan.

Smith, V. L. (1991). *Papers in Experimental Economics* (1st ed.). Cambridge, UK: Cambridge University Press.

Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an iterated prisoner's dilemma. *Science*, *298*, 2216–2218. https://doi.org/10.1126/science.1078498

Tian, J., & Uchida, N. (2015). Monkeys in a prisoner's dilemma. *Cell*, *160*, 1046–1048. https://doi.org/10.1016/j.cell.2015.02.049

Tinbergen, N. (1963). On aims and methods of ethology. *Ethology*, *20*, 410–433.

Varnon, C. A., & Abramson, C. I. (2013). The propeller experiment controller: Low-cost automation for classroom experiments in learning and behavior. *Comprehensive Psychology*, *2*, 7–8. https://doi.org/10.2466/07.08.IT.2.2

Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *PLOS Biology*, *5*(7), e184. https://doi.org/10.1371/journal.pbio.0050184

Watzek, J., Rossettie, M. S., Raines, A. R., & Brosnan, S. F. (2015). *More for me, less for you: Capuchin monkeys (Cebus apella) responses to inequity in a group setting*. Paper presented at the 52nd Annual Conference of the Animal Behavior Society, Anchorage, Alaska.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*, 682–685. https://doi.org/10.1038/21415

Wolfe, J. B. (1934). The effect of delayed reward upon learning in the white rat. *Journal of Comparative Psychology*, *17*, 1–21.

Financial conflict of interest: SFB was funded in part during the writing of this manuscript by NSF SES 1425216.
Conflict of interest: No stated conflicts.

Submitted: *January 30, 2018*
Resubmitted: *March 21st, 2018*
Accepted: *April 7th, 2018*