



Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

Using an evolutionary approach to improve predictive ability in the social sciences: Property, the endowment effect, and law

Sarah F. Brosnan^{a,*}, Owen D. Jones^{b,*}^a Departments of Psychology & Philosophy, Neuroscience Institute, Language Research Center, Center for Behavioral Neuroscience, Georgia State University, Atlanta, GA, USA^b Departments of Law and Biological Sciences, Weaver Family Program on Law, Brain Sciences, and Behavior & Evolutionary Studies Initiative – Vanderbilt University, Nashville, TN 37203, USA

ARTICLE INFO

Keywords:

Cognitive heuristics and biases
Endowment effect
Loss aversion
Prospect theory
Evolutionary salience
Evolution

ABSTRACT

From the perspective of other disciplines, evolutionary approaches more often provide explanation and coherence than they help to solve discrete problems. We believe that more examples of the latter sort will help both with disciplinary synthesis and with the advance of knowledge. Here we describe a 20-year arc of research to demonstrate the problem-solving utility of an evolutionary perspective by focusing, as a case study, on a particular cognitive bias – the endowment effect – that has implications for law. Legal systems often assume that humans make decisions that are substantively rational, consistent, and aimed at maximizing their own wellbeing. But prevalent cognitive biases disrupt this, showing that humans consistently make decisions that seem to violate rationality and/or their own best interests. And despite decades of research, there has been little progress in understanding why these biases exist. We are among the scholars who have converged on the idea that many cognitive biases may have evolved as adaptations to pre-modern conditions, the evolutionarily sudden changes from which often leave them mis-matched to current conditions, prompting us to situationally irrational outcomes. Here, we discuss our data testing hypotheses derived from this perspective in both humans and non-human primates and consider how it has advanced our understanding of both the endowment effect narrowly and cognitive biases generally – including those relevant to law and policy.

1. Introduction

Despite decades of conceptual advances, methodological innovations, and empirical successes, the acceptance of evolutionary perspectives into traditional social science fields remains limited. Some of this doubtless stems from continued resistance in large segments of society to evolution, generally. Some stems from the historical and still too-common lack of cross-disciplinary integration, which limits the influence of every field on all others. And some stems from deep misunderstandings about what evolutionary perspectives do (and don't) entail.

We believe something else is also at work. On one hand, evolutionary perspectives often provide powerful, deep, and elegant logical and conceptual coherence, tying together the proximate (mechanistic) and the ultimate (evolutionary and historical) causal pathways by which life's many physical and behavioral features emerge. Those perspectives have often made compelling sense of existing data and successfully predicted new findings. On the other hand, evolutionary perspectives far less frequently

have tackled specific, discrete problems that have long-stymied the social sciences and provided a roadmap, more broadly, for a way forward.

We think more examples of the latter sort are necessary to make a compelling case for the *utility* of evolutionary perspectives. Therefore, we here describe a 20-year arc of research of that kind. It is our hope it may help serve the evolutionary community by providing a case study of how an evolutionary perspective can help to solve problems in a way that is simultaneously powerful and useful. Specifically, we describe how an evolutionary perspective on a phenomenon known as *the endowment effect* can help to surmount a long-standing impediment to predicting how that effect will vary. This simultaneously, thereby, illustrates the much larger point that evolutionary perspectives can help unite under a single theoretical approach many of the cognitive phenomena, known as *cognitive biases*, that are still often treated in the social sciences as having independent origins.

The endowment effect is not only theoretically interesting, but also of practical importance. It names the finding that the minimum price

* Corresponding authors.

E-mail addresses: sarah.brosnan@gmail.com, sbrosnan@gsu.edu (S.F. Brosnan), owen.jones@vanderbilt.edu (O.D. Jones).<https://doi.org/10.1016/j.evolhumbehav.2023.01.001>

Received 31 December 2021; Received in revised form 1 January 2023; Accepted 2 January 2023

1090-5138/© 2023 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

people will accept to part with an item they have just acquired (here, the “Sell Price”) often greatly exceeds the maximum price they would have paid to acquire it (“Buy Price”) (Knettsch & Sinden, 1984). The effect can be a major impediment to the efficient operation of markets, and therefore to the legal systems that support and facilitate them, which typically assume the absence of such an effect. Of course, the legal system writ large is a behavioral intervention, focused almost entirely on influencing human behavioral decision-making (Jones & Goldsmith, 2005). For this reason, cognitive biases – which slant perception, decision, and behavioral outcomes in often unexpected and problematic ways – have immediate, concrete, and important implications for human psychology, behavior, and law, as well as for the many socially and economically important issues at their intersection.

Below, we first describe cognitive biases and how they can be understood through an evolutionary lens. We then examine the endowment effect, to illustrate but one of the cognitive biases, and describe our evolutionary approach to understanding it. We focus initially on how the evolutionary approach allowed us to address theoretical questions. We then end by noting the practical implications, which we hope will make clear why this evolutionary approach is so broadly useful, beyond the progress it makes toward understanding the origins of and patterns in this one particular bias.

2. Cognitive biases meet evolutionary perspectives

One model of how people make decisions stems from *rational choice theory*, which posits that, by and large, people use their self-interests to make choices that will provide them with the greatest benefit. Against this background, Daniel Kahneman and Amos Tversky are generally credited with sparking the serious study of patterned deviations from rational-choice decision-making, which they called *cognitive biases* (Kahneman, Slovic, & Tversky, 1982). These biases are unconscious and are generally believed to result from a series of “errors in thinking” that impact our behaviors in ways that look, on the surface, wholly irrational. These include some well-studied biases, such as the framing bias (by which identical information can yield different decisions, as a function of how the information was presented) or the availability bias (by which examples that come readily to mind are assumed to be more representative than they are), that have substantial real-world impact.

Cognitive biases are important because the vast bulk of our legal, economic, and social policies are rooted in the idea that people will, for the most part, behave in substantively rational ways (using “rational” in the economic sense, which focuses on the *outcome*, rather than in the deliberative sense, reflecting the *process*). Thus, to the extent that cognitive biases are widespread, their very existence suggests that people’s perceptions are skewed in ways that can lead to decisions – and thereby to behaviors – that are substantively irrational (Corr & Plagnol, 2018; Kahneman, 1991; Kahneman et al., 1982; Sunstein, 2000). From a practical perspective, and relevant to the law, where there are disjunctions between the assumptions underlying policies, on the one hand, and behavioral outcomes, on the other, policies will be misguided, wrong, inefficient, or ineffective, and sometimes even counter-productive.

Put simply, cognitive biases have real-world consequences. And they confound policy-makers, including those in law, who must confront, predict, and work around irrational behavior of the governed. Two examples will illustrate. First, people appear to have tendencies to irrationally discount the future. That is, they often prefer to buy a slightly less expensive but energy-guzzling appliance instead of a slightly more expensive appliance that is less costly to run – even when the difference in cost between the two machines can be earned back in energy savings in a short time (Ainslie, 1991). This has important implications for law and government policies on things as disparate as protecting the environment and encouraging the accumulation of retirement savings. Second, people tend to mistakenly assess probabilities. That is, they will make very different choices between functionally equivalent options that present the same risks in different ways (Slovic, Fischhoff, &

Lichtenstein, 1982). For instance, they will fail to recognize that a 0.7 risk of death (when phrased in the language of probabilities) is the same thing as saying that 7 out of 10 similarly-situated people will die (when phrased as a frequency distribution). This has important implications for risk regulation through the mechanisms of law.

Traditional approaches do not easily explain the origins of or patterns in these biases. And this is despite significant research efforts in psychology, economics, and behavioral economics that have gone into documenting and attempting to explain them. However, these approaches either assume that people are consistently making mistakes (and failing to learn to correct them), examine each bias in isolation, or both. Eventually, some scholars with training in evolution posited that very rapid changes in conditions – such as the vast social, economic, legal, medical, and technological changes humanity has experienced in a mere few thousand years – can lead to a “mismatch” between physical and cognitive adaptations to deep ancestral conditions, on one hand, and modern circumstances, on the other. That perspective was initially focused on individual biases (e.g., Kacelnik, 1997). But not long thereafter, and within a couple months of each other, Gigerenzer (2000), Haselton and Buss (2000), and one of us (Jones, 2001) independently published proposals that large swaths of cognitive biases might all derive from such evolutionary mismatches. The ensuing decades have seen significant progress in demonstrating the value of the evolutionary approach to cognitive biases (e.g. Daly & Wilson, 2005; Gigerenzer, 2006; Haselton et al., 2009; Jackson & Willey, 2011; Wang, 2011), including by the ABC Research Group at the Max Planck Institute for Human Development (directed by Gerd Gigerenzer).

This perspective on cognitive biases, especially when discussed within the evolutionary literature, has been called *evolutionary mismatch*, *ecological rationality*, *adaptive rationality*, or *error management theory*. We prefer, and will here use, the term “time-shifted rationality” (Jones, 2001), as we believe it is best for conveying the core notion to a cross-disciplinary audience that thinks principally in the binary terms of rationality and irrationality. The core notion of time-shifted rationality is that some cognitive biases can be seen as functionally rational if one simply shifts the time period at which one makes that assessment. But, whatever one calls it, the key value this evolutionary perspective adds to the cognitive bias literature is that it not only grounds these biases on a common theoretical foundation, drawing deeper connections between them, but it can also make entirely novel and testable predictions. We next demonstrate the prediction point, focusing on the endowment effect for illustrative purposes. Thereafter, we apply the evolutionary perspective more broadly to cognitive biases as a whole.

3. Test case: the endowment effect

The endowment effect describes the seemingly irrational and often immediate flip, as if of a switch, by which a person suddenly values something just acquired at more than that same person valued that same item a moment ago. And it is important to keep four things in mind.

First, “endowment” should be read to mean “ownership,” the meaning most common in law and in economics. It should not be confused with the meaning of “endowment” in the life sciences, in which an organism’s phenotypic features often reflect, in part, its genetic endowment. Indeed, we acknowledge that the term “endowment effect” is clunky, and arguably misleading (Plott & Zeiler, 2007; Zeiler, 2018). But because it is the term most scholars use, we use it here as well. Second, the endowment effects has nothing to do with the acquisition of new information about a newly-owned thing (which might lead one to value it more highly); that’s a totally separate phenomenon. Third, the endowment effect also has nothing to do with developing memories of using a thing (which might lead one to sentimental attachments, which could in turn lead one to value it more highly). Fourth, it is crucial to note that the effect does not describe the universal – and rational – phenomenon that people would prefer to sell an item for more than they paid for it, and hence to make a profit. Instead, the endowment effect

describes a purer form of seemingly instantaneous changes in valuation, which pivot solely (it appears) on the fact of ownership.

To our knowledge, the endowment effect was first proposed as a mismatched adaptation in Jones, 2001, as one of several likely examples of evolved cognitive biases. We chose to make the endowment effect our test case of a time-shifted rationality approach to cognitive biases for three reasons. First, the effect has large legal and policy implications, making it important to understand the underlying causes. Second, it is amenable to study in cross-species experiments that enable a clear test of the evolutionary perspective on cognitive biases. Finally, its causes (and even existence) remain hotly debated (Morewedge & Giblin, 2015; Zeiler, 2018), making it an ideal bias to explore in other species, for whom some of the extant hypotheses (such as those focused on human language used in experiments) do not apply.

Of course, if the endowment effect did not have a powerful impact across a wide variety of domains, it would be irrelevant. But the endowment effect has immense practical importance. As more than 1000 published articles have argued (per Arlen & Tontrup, 2015), society suffers, by way of economic inefficiencies, whenever the ratio of a person's Sell Price to that person's Buy Price is not 1 to 1 (Ericson & Fuster, 2014; Kahneman, Knetsch, & Thaler, 2008). Specifically, the endowment effect causes wide-ranging market inefficiencies in real-world transactions, such as those involving laws and policies regarding real property, contracts, intellectual property, employment, and consumer debt, as well as in allocations and trades of various legal rights, such as property rights.

To see this, consider that the Coase Theorem (Coase, 1960) posits that when the costs of transacting are lowered, goods and services will migrate through the market into the hands of the people who value them most. The policy implication – which is widely influential in real-world situations – is that governments should work through legal stratagems to reduce transaction costs (the sum of all costs incurred when buying or selling a good or service) so that society can reap the benefits of goods and services so migrating. The problem is that a key assumption underlying the Coase Theorem, and therefore underlying the policies it affects, is that people will value goods and services rationally. So whenever and wherever humans exhibit the endowment effect, reliance on the Coase theorem, unmodified by real-world irrationalities, is misplaced.

Specifically, in the presence of the endowment effects goods and services will tend to stick longer, sometimes forever, to those hands that first received them, impeding efficient flow and distribution of resources (Arlen & Tontrup, 2015; McDermott, Fowler, & Smirnov, 2008). Because efficient markets are a big deal to countries, economies, and people, endowment effects are a big deal to policy-makers (Jones & Brosnan, 2008; Zeiler, 2018). For instance, in the presence of widespread endowment effects, the end distribution of legal rights will be far more sensitive than is commonly assumed to the initial distribution, meaning that far more attention needs to go into determining the initial allocation than is currently the case.

3.1. Illustration: you've just bought a watch

Although endowment effects can exist on scales large enough to impede markets, they are most relatable – and easier to understand – on small ones. So, here's a small-scale example, exaggerated for emphasis. Suppose you want to buy a nice watch for yourself. You are seated across from a jeweler, with the watch in question between you, in the middle of a table. You've already given some thought to your budget, and to the question of how much you like this particular watch, compared to how much you like something else that you could do with the money it might cost you to buy it.

You've decided the maximum you would pay for the watch (your Buy Price) is \$500. You'd be thrilled to buy it for less, and will try to do so. But by setting your private internal maximum price at \$500 you necessarily must value \$501 in cash more than you value the watch. Fortunately, you and the jeweler after some negotiation agree on a price of \$450 for the watch. You pay that sum on the spot in cash. The watch –

though it hasn't moved – is now yours. You own it.

Now suppose that someone new enters the store, sees and likes that watch, learns that it is yours, and offers you \$750 in cash for it – on a credibly *take it or leave it* basis. What would you do? Economists predict that you *must* take the money. Refusing to do so would be irrational, for the simple reason that if the watch wasn't worth \$501 to you a moment ago, it can't possibly be worth more than \$750 to you now.

Whether or not you personally would take the money or keep the watch, here's the key thing to know. Many hundreds of studies that probe buying and selling behavior suggest that a surprisingly large proportion of people would refuse to sell the watch for sums greater than \$500, even though they would not have paid \$501 to buy it. And even though they have not even touched the watch, or in any way gained value through use or sentimental attachment. That often holds true even when offers are many multiples of the Buy Price (not just 50% more, as in our example).

To get our terms straight, one can say that whenever the (maximum) Buy Price and (minimum) Sell Price are not effectively identical that reveals the *existence* of an endowment effect. And the ratio of the two provides a measure of the *magnitude* of the effect. For instance, 1:5 is a larger endowment effect magnitude than is 1:2. From a practical perspective, any time the ratio is not 1:1, human behavior is throwing sand in the gears of how goods and rights are distributed in society. That adversely affects not just the individuals involved, but all populations immediately downstream – and then further downstream from that. Not just watches, but goods and rights generally acquire a stickiness – or an inertia, if you will – that makes them less likely to move in the marketplace in the direction of the people who value them most. And scholars believe that this creates very widespread and costly market inefficiencies, locally and globally, both minor and massive.

4. The evolutionary perspective on the endowment effect

Of course, the larger question is what causes people to so consistently make a decision that looks so inefficient. There are hundreds of studies of the endowment effect in economics, psychology, and behavioral economics. But there are only a handful of ideas about what causes the effect, which would also help us understand why the magnitude differs so substantially across contexts. Unfortunately, many of these proposals are more descriptive than predictive (Jones, 2018; Klass & Zeiler, 2013; McCaffery, 1994). For instance, some have argued that the endowment effect is caused by loss aversion (Kahneman, Knetsch, & Thaler, 1990, 1991), which features in theories of reference dependence (Koszegi & Rabin, 2006), such as prospect theory (Kahneman & Tversky, 1979). Others more recently have attributed the phenomenon to self-association (Gawronski, Bodenhausen, & Becker, 2007), psychological inertia (Gal, 2006), or value construction (Johnson & Busemeyer, 2005).

Back in 2001, one of us (Jones) proposed that the endowment effect evolved because for vast swaths of evolutionary time it was inherently very risky for a member of a social species to give up an item in hand for the chance to exchange it for something that might, potentially, be slightly better. Giving up one thing for another risked having neither in the end. In turn, natural selection would therefore have favored any predisposition to discount the value of an item in another's possession that might be acquired through trade, compared to the value of what one already possessed. Importantly, this latter point describes an evolved propensity, not a cognitive appraisal, so it does not require that the individual be consciously aware of, or reflecting on, the relative risks. As long as individuals acted *as if* they understood the risks, then there could be selection pressure on that behavior, irrespective of what they understood.

Returning, then, to the core idea that connects evolutionary perspectives to cognitive biases, these biases (or many of them, at least) may reflect a mis-match between a human cognitive adaptation and relatively sudden novel environmental changes. This could explain not only the existence and persistence of the bias, but why, when people behave 'irrationally', their irrational behavior is typically directional, rather than random. Jones argued that a psychological leaning to favor

what one has over what one could acquire was substantively rational (in the economic sense) across all but the most recent periods of human history, despite predisposing us to irrational outcomes in modern, evolutionarily novel environments, because in almost all of primate and hominid history we lacked the modern inventions of abstract and tradeable property “rights” and reliable third-party mechanisms – including robust legal institutions – to enforce trade (Jones, 2001). Indeed, while primates have some possession norms (Brosnan, 2011; Kummer, 1991; Sigg & Falett, 1985), they lack property rights in the same way as is seen in humans, most likely due to the challenge of third-party enforcement without language (Brosnan & Beran, 2009).

The evolutionary perspective offers great explanatory potential. But we were interested in predictive power. So we set out, together with many colleagues along the way, to test whether the endowment effect was an example of a cognitive bias reflecting time-shifted rationality. Over a 20-year period we have made a series of evolutionarily-informed step-wise predictions, none of which are generated by any other theory for why the endowment effect exists.

1. We predicted we would find a trade-based endowment effect in non-human species;
2. We predicted that the size of the effect in non-human primates (hereafter, primates) would vary across certain categories of items;
3. We predicted that we could, again in primates, vary the size of the effect for the very same item by manipulating the context; and
4. To bring this full circle back to humans, we predicted that variation in the evolutionary salience of items in question would predict some of the variation in the magnitude of endowment effects in humans, for a novel set of items.

We address each of these in turn.

4.1. Prediction: presence in other species

If time-shifted rationality explains the presence of an evolved predisposition that results in an endowment effect in humans, then it is unlikely that *only* humans exhibit that bias. Indeed, even in quite complex behaviors in humans, such as language (Fitch, Huber, & Bugnyar, 2010; Pollick & de Waal, 2007), culture (Wrangham, Mc Grew, de Waal, & Heltne, 1994; Frigaszy & Perry, 2003), and morality (Brosnan, 2014; Flack & de Waal, 2000), we see either the behaviors, or precursors to these behaviors, in other species (Sapolsky, 2017). Consequently, we predicted that we would find evidence of the endowment effect in other species. When looking in this way, there are two approaches. First, is to look in phylogenetically close species (i.e., those that share a relatively close common ancestor), on the assumption that these species are more likely to also share behaviors in common. Second, is to look in species that share in common some key characteristic hypothesized to be related to the trait of interest (i.e., a convergence; see Brosnan, this issue, for a more detailed discussion). In our case, we were interested specifically in whether other primates shared the trait, which would suggest that it evolved in humans from an existing tendency among the non-human primates. We began in the great apes, deploying a modified version of an early endowment effect procedure by Knetsch, 1989, to test for the presence of the endowment effect in chimpanzees, orangutans, and gorillas (Brosnan et al., 2007; Flemming, Jones, Mayo, Stoinski, & Brosnan, 2012; Drayton, Brosnan, Carrigan, & Stoinski, 2013; others pursued related phenomena in these and other species around the same time, e.g., Kanngiesser, Santos, Hood, & Call, 2011; Lakshminarayanan, Chen, & Santos, 2008).

The basic protocol by Knetsch took advantage of the fact that there is no reason to believe that different groups of humans would value the same object differently. Thus, in the classic early experiment, two groups of students were either given a coffee mug or a chocolate bar, then an irrelevant questionnaire (distractor task), and finally the chance to trade their endowed item for the other one. Their trade preferences were compared to a third group who were simply given a choice

between the mug and the chocolate bar. From the perspective of classical economics, the preferences of the first two groups for mugs should match each other and the preferences of the third group. Yet despite the preference for mug over chocolate being essentially chance in the third group, in both groups that could trade, 90% of subjects preferred to keep what they were initially endowed with. Thus, despite having had no opportunity to learn about the items, nor gain sentimental attachment, subjects developed sharply opposite preferences, suggesting that this was an endowment effect because nothing had changed about the mug/chocolate except the fact of ownership.

With our ape subjects, we used a similar scenario, providing them with one item and allowing them to keep it or trade it back for another (trading, even food, is relatively easy for apes; Brosnan & Beran, 2009; Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008), and then comparing their preferences to those under a free-choice condition. We did make a change from the Knetsch protocol; food and non-food items should, from an evolutionary perspective, be treated very differently because of the necessity of food for survival, which makes it a highly salient resource. (That is, it contributed historically to evolutionary fitness.) In addition, apes do not generally seek out non-food items, with few exceptions such as tools, and so are likely to be less motivated by non-food items. Thus, we had two conditions, one food condition and one object (non-food) condition, each with the same three trial types; endowed with A (option to trade for B), endowed with B (option to trade for A), and free choice. Each subject got one of each of the six trials, but on different days, to avoid confounding later choices with what food they had experienced earlier in the day, with half experiencing the Food condition first and half the Object condition first (see Brosnan et al., 2007 for more details on the Methods).

Considering just the Food Condition for the time being, because we used a within-subjects design, we were able to compare each subject's preference between the two foods, when given the choice, to their tendency to maintain possession in order to evaluate whether the subject was behaving rationally or (from the perspective of neoclassical economics) irrationally in the two trade conditions. Under this definition, if the subjects are behaving rationally, then when given their more-preferred food they should refuse to trade it for their less-preferred food; likewise, when given their less-preferred food, they should trade it for their more-preferred food. Whenever a subject was given their less-preferred food and yet did *not* trade it for their more-preferred food, we counted that as evidence consistent with the presence of an endowment effect. Controls ensured that subjects: 1) were willing to trade with the experimenter (that is, they did not think that if they gave it up, they would not get anything back); and 2) did not always trade with the experimenter.

Not surprisingly, across chimpanzees (Brosnan et al., 2007), orangutans (Flemming et al., 2012), and gorillas (Drayton et al., 2013), subjects given their more-preferred food essentially always kept it when offered a trade for their less-preferred food. More importantly, however, many subjects *also* tended to keep their *less*-preferred food when they could have traded it for their *more*-preferred food, suggesting that our primate relatives also exhibit an endowment effect. This experiment (Brosnan et al., 2007) provided the first trade-based evidence of an endowment effect in a non-human species.¹

¹ Some readers may be aware of a butterfly study, in which butterflies appeared to defend sunspot territories more vigorously when they were the territory holder (Davies, 1978). This is often cited outside the biological literature as evidence of the endowment effect, on the hypothesis that defenders saw the territories as ‘their’ possessions. Less known, however, outside of biology, is that subsequent experiments demonstrated that the findings were more likely explained by a difference in fighting ability between warmer butterflies (who had possession of the sunspots and were therefore being warmed by the sun) and the cooler butterflies (who were trying to take over those sunny territories) (Stutt & Willmer, 1998).

4.2. Prediction: variation in magnitude, between items high and low in evolutionary salience

Not all items that might be lost in trade have equal impacts on evolutionary fitness (i.e., surviving, thriving, and reproducing). Consequently, if the endowment effect evolved as a time-shifted rationality, then it is likely to vary with the changing costs, to an individual, of losing an item to a defecting trading partner. Consequently, we predicted that endowment effects would be greater for items that are high-salience from an evolutionary perspective (such as foods, which provide necessary energy for survival and reproduction) than for items that are low-salience from an evolutionary perspective. As noted above, our studies therefore included both Food and Object Conditions, allowing us to test this directly. To emphasize, this prediction is not based on whether subjects *prefer* food to toys (clearly, they should and do), but rather that the endowment effect should be stronger for food than for toys, because primate species evolved in an environment in which food was essential, and is therefore quite salient, whereas no non-food objects are essential to primates.

As predicted, we found across chimpanzees, orangutans, and gorillas (Brosnan et al., 2007; Drayton et al., 2013; Flemming et al., 2012) that the endowment effect was much less strong, or even absent, for non-food items as compared to foods. In chimpanzees, for example, subjects were far more likely to keep their less-preferred food item when they could have traded it for their preferred food item than they were to keep their less-preferred toy when they could trade it for their preferred toy. Indeed, this result highlights the necessity of an evolutionary perspective; without it, these two sets of results would seem mutually incompatible and might easily lead us to conclude that the effect is either absent, the result of experimental quirks, or a particularly fragile effect. However, with the evolutionary perspective, we identify an effect that varies according to the category of item, in a predictable direction, across categories of items, highlighting the utility of the evolutionary approach.

4.3. Prediction: variation in magnitude, for same item, by utility

If time-shifted rationality biases behavior in a way sensitive to the varying risk of losing an item in a failed trade with a defecting trading partner, then it follows that the effect might also vary as a function of the immediate utility, or lack of utility, of the item in question. This is also a stricter test of prediction 2, because by changing the salience of the same item, we can avoid any possibility that the effect arises because they simply like some objects (foods) better than others (toys). To test this, we used a tool, an item that varies in whether it is immediately useful depending on whether the object it is to be used upon is currently available. We predicted that subjects would be more likely to exhibit an endowment effect for a tool that could be used to obtain food when it could be used immediately – that is, when the food was present and available – than when the food was either absent or present but unavailable.

As we did previously, for this experiment (Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012) we elicited subjects' preferences between two familiar tools (used as part of their regular enrichment) and their trading behavior when one was initially endowed. This time, however, we tested across three different situations: a) when there were no foods on which to use the tools; b) when both foods were present and visible, but out of reach; and c) when both foods were both available and in reach.

There was a strong effect of context. The tools elicited no endowment effect (i.e. chimpanzees almost always traded both more preferred and less preferred tools) when the foods they could extract were either absent or out of reach. This was very similar to how they responded to the toys in Brosnan et al., 2007. However, when the food was within reach, subjects exhibited a robust endowment effect for the tools, at the same magnitudes as they showed for foods in the earlier work. That is, the endowment effects were considerably larger in contexts that rendered

tradable items immediately useful to acquire food, even though the items themselves were not foods, demonstrating that it is the salience of the item that mattered, not simply that it was an effect of the presence of preferred foods.

4.4. Prediction: evolutionary salience score will predict variation in magnitudes, across a large set of novel items

Hundreds of studies have shown that the magnitude of the endowment effect varies considerably across various items (Horowitz & McConnell, 2002; Plott & Zeiler, 2007; Sayman & Öncüler, 2005; Tunçel & Hammitt, 2014; Zeiler, 2018). In one study, for instance, participants in a buying condition would pay no more than \$25 for a hunting permit, while those in a selling condition, who had just acquired a permit, would not part with it for less than \$172 (Heberlein & Bishop, 1986). In a different study, participants in a buying condition wouldn't pay more than \$17.94 for a book, while those in a selling condition would not part with it for less than \$18.65 (Chapman & Johnson, 1995).

There have been a handful of studies finding different endowment effect magnitudes for different categories of items (e.g. Chapman & Johnson, 1995), but most studies investigate the effect for just one or two items (e.g. Maddux et al., 2010; Morewedge, Shu, Gilbert, & Wilson, 2009). Crucially, prior to the publication described here (Jaeger, Brosnan, Levin, & Jones, 2020) – and to our knowledge since – there have been no other published studies that attempt to *predict* – across a large set of novel items – any of the *variance* in the magnitudes of endowment effects. We attribute this deficit to the fact that studies lacking an evolutionary perspective on why we behave in the ways that we do, and how we tend to behave in those ways rather than others, lack any framework for seeing a broader motif in the data. That is, without the conceptual understanding that these biases exist for a particular reason, it is difficult to see or even look for an underlying pattern that allows for the generation of testable predictions about variations in magnitudes. The time-shifted rationality perspective, however, allows us to predict at least some of the variance in the magnitude of the endowment effect, based on how salient items are for evolutionarily relevant categories.

In practice, if we were to take a series of items, and for each one separately quantify an evolutionary salience score, on the one hand, and the endowment effect magnitude, on the other, we should see that the evolutionary salience score for that item does a significant amount of the work in predicting the endowment effect magnitudes for that item. To do this, we – together with our colleagues Christopher Jaeger and Daniel Levin – developed a tool that objective third-party raters could use for quantifying evolutionary salience. Raters provided a 1 to 9 score for each of 6 different factors (related to health, attractiveness to dates, social status, basic human needs, value, and tangibility), with each factor intended to probe the relevance for an item to a person's thriving, surviving, and reproductive success. To establish a salience score for each, we selected a set of 24 items that we anticipated would provide a range of evolutionary salience from high (such as an entitlement to the best available healthcare, for life, for free) to low (such as a half-pound of styrofoam packing peanuts). Participants recruited through Amazon Mechanical Turk used the tool to score the items.

Next, we established an endowment effect magnitude for each item with a *separate* set of participants, again through Amazon Mechanical Turk. For this, we used the standard endowment effect tests, using the standard between-group paradigm, adapted from Chapman and Johnson (1995). Specifically, we assigned participants randomly to one of two conditions. We instructed those in the Sell Price condition to assume that they currently possessed each item and to indicate (in U.S. dollars) the minimum amount of money that they, personally, would accept to sell the item. We instructed those in the Buy Price condition to assume that they did not currently possess each item, and to indicate (in U.S. dollars) the maximum amount of money that they, personally, would pay to buy the item (for a more detailed description of our Methods, see

Jaeger et al., 2020). Although this approach does not have participants make real-world exchanges for these items, scholars have previously noted that gaps between Sell Price and Buy Price are comparable, between real-world and hypothetical exchanges (Horowitz & McConnell, 2002; Morewedge & Giblin, 2015). As hypothesized, the evolutionary salience scores collected from one set of participants predicted a great deal of the variation in endowment effect magnitudes manifested by the other set of participants. In fact, evolutionary salience scores predicted fully 52% of the variation.

5. Conclusion

Our research on the endowment effect contributes to a large and growing body of work that suggests that many of the cognitive biases we see reflect adaptive decisional/behavioral predispositions that only became irrational when human environments changed in ways that render the predispositions less beneficial. The rapidity of those changes, from an evolutionary perspective, has left predispositions that were once rational now irrational (i.e., they reflect time-shifted rationality). To study those irrationalities in the present, without the chronological context that evolutionary analysis provides, reduces our ability to understand how and why these traits evolved and to develop a predictive science around them. Indeed, many cognitive biases likely arose as cognitive adaptations, as a function of evolutionary processes adapting our brains to their then-current environments, which has important implications for psychology, economics, and behavioral economics, generally (Jones, 2018; Jones & Goldsmith, 2005).

Of course, there are other factors influencing the endowment effect. For instance, we know that there are effects of culture, with individuals who are more integrated into markets apparently showing stronger magnitude effects (Apicella, Azvedo, Christakis, & Fowler, 2014). Undoubtedly other cultural effects will also emerge. However, it is important to note that these are influences *on* the endowment effect, not explanations of how it arose in the first place. Another recent proposal models the endowment effect assuming inherent uncertainty about the value of objects (Bruner, Calegari, & Handfield, 2019). Indeed, we fully agree; arguably the reason that humans have been selected to value what they have is uncertainty about the value of what others possess (i.e., what might be available as a possible trade), not to mention uncertainty about the likelihood of the trade going through. But again, while this explains the psychological context in which the endowment effect emerged, it cannot explain the variation in *magnitude* that is seen across contexts and items, unless we assume that people are consistently more uncertain about the value of some items than others. What the time-shifted rationality approach can explain is where these magnitude differences come from.

Evolutionary perspectives trace the origins of some currently irrational cognitive biases to evolved psychological adaptations that were beneficial in our evolutionary past while being, often, irrational now, in modern environments. This is important for three reasons.

First, the evolutionary approach is the only one to date that has generated a step-wise series of interconnected and testable predictions about the endowment effect. As described above, we have thus far tested a series of four predictions and found strong empirical support for each. These included predictions that other primates would also have endowment effects, that these effects would be larger for evolutionary salient goods than other goods, and that the effects – for the very same object – could predictably vary by context. Then, circling back to humans, the evolutionary perspective generated the first successful prediction of variation in *magnitudes* of endowment effects across a large and novel set of items. Together, these results can provide a grounded theoretical foundation for beginning to explain and predict patterns in where and how the magnitude of endowment effects will vary in policy-relevant human conditions.

Second, the success of this arc of research adds strong support to the notion that a wide variety of cognitive biases may – despite their

diversity – stem from common evolutionary pathways, rather than independently-arising quirks. These biases include, for instance, hyperbolic discounting, availability heuristics, biases in optimism and pessimism, status quo bias, inconsistent preferences, mistaken assessments of probabilities, framing effects, base rate fallacies, and illusory correlations. Each of these creates problems for the legal systems that seek to incentivize, encourage, and shape pro-social and economically efficient behavior. Thus all are subject to potentially useful predictions about the circumstances under which the various biases are most and least likely to manifest.

Third, and more broadly, this arc of research provides a very concrete example of how integrating an evolutionary approach into human psychological and behavioral domains can help clarify, explain, and resolve problems that tend to remain stuck without it. We do not wish to exaggerate the significance of this line of research. But the fact remains that, using basic perspectives from evolutionary biology, we were able to make a successful string of novel, connected, step-wise predictions, which no other extant theory predicts, either singly or together. We believe this serves as a testament to the power of integrating evolutionary perspectives generally, and to the concrete utility in doing so.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Sarah F. Brosnan was funded during the writing of this manuscript by NSF grants BCS 2127375, SES 1919305 and SES 1658867. Owen D. Jones acknowledges support from the Weaver Family Program in Law, Brain Sciences, and Behavior. The authors gratefully acknowledge the Evolutionary Studies Initiative at Vanderbilt University and Victoria Schmit in the preparation of this manuscript.

References

- Ainslie, G. (1991). Derivation of “rational” economic behavior from hyperbolic discount curves. *American Economic Review*, 81, 334–340.
- Apicella, C. L., Azvedo, E. M., Christakis, N. A., & Fowler, J. H. (2014). Evolutionary origins of the endowment effect: Evidence from hunter-gatherers. *American Economic Review*, 104, 1793–1805.
- Arlen, J., & Tontrup, S. (2015). Does the endowment effect justify legal intervention? The debiasing effect of institutions. *The Journal of Legal Studies*, 44, 143–182.
- Brosnan, S. F. (2011). Property in nonhuman primates. *New Directions for Child and Adolescent Development*, 2011(132), 9–22.
- Brosnan, S. F. (2014). Why an evolutionary perspective is critical to understanding moral behavior in humans. In M. Bergmann, & P. Kain (Eds.), *Challenges to moral and religious belief* (pp. 195–219). Oxford University Press.
- Brosnan, S. F., & Beran, M. J. (2009). Trading behavior between conspecifics in chimpanzees, pan troglodytes. *Journal of Comparative Psychology*, 123(2), 181–194.
- Brosnan, S. F., Grady, M., Lambeth, S., Schapiro, S., & Beran, M. J. (2008). Chimpanzee autarky. *PLoS One*, 3(1), Article e1518.
- Brosnan, S. F., Jones, O. D., Gardner, M., Lambeth, S. P., & Schapiro, S. J. (2012). Evolution and the expression of biases: Situational value changes the endowment effect in chimpanzees. *Evolution and Human Behavior*, 33, 378–386.
- Brosnan, S. F., Jones, O. D., Lambeth, S. P., Mareno, M. C., Richardson, A. S., & Schapiro, S. J. (2007). Endowment effects in chimpanzees. *Current Biology*, 17, 1704–1707.
- Bruner, J., Calegari, F., & Handfield, T. (2019). The evolution of the endowment effect. *Evolution and Human Behavior*, 41, 87–95.
- Chapman, G., & Johnson, E. J. (1995). Preference reversals in monetary and life expectancy evaluation. *Organizational Behavior and Human Decision Processes*, 62(3), 300–317.
- Coase, R. (1960). The problem of social cost. *Journal of Law and Economics*, 1, 1–44.
- Corr, P., & Plagnol, A. (2018). *Behavioral Economics*. New York: Routledge.
- Daly, M., & Wilson, M. (2005). Carpe diem: Adaptation and devaluing the future. *The Quarterly Review of Biology*, 80(1), 55–60.
- Davies, N. B. (1978). Territorial defence in the speckled wood butterfly (pararge aegeria): The resident always wins. *Animal Behaviour*, 26, 138–147.
- Drayton, L. A., Brosnan, S. F., Carrigan, J., & Stoinski, T. S. (2013). Endowment effects in gorillas (gorilla gorilla). *Journal of Comparative Psychology*, 127(4), 365–369.

- Ericson, K. M., & Fuster, A. (2014). The endowment effect. *Annual Review of Economics*, 6, 555–579.
- Fitch, W. T., Huber, L., & Bugnyar, T. (2010). Social cognition and the evolution of language: Constructing cognitive phylogenies. *Neuron*, 65(6), 795–814.
- Flack, J., & de Waal, F. B. M. (2000). "Any animal whatever": Darwinian building blocks of morality in monkeys and apes. *Journal of Consciousness Studies*, 7(1–2), 1–29.
- Flemming, T. M., Jones, O. D., Mayo, L., Stoinski, T., & Brosnan, S. F. (2012). The endowment effect in orangutans. *International Journal of Comparative Psychology*, 25, 285–298.
- Fragaszy, D. M., & Perry, S. (2003). *The biology of traditions: Models and evidence*. Cambridge University Press.
- Gal, D. (2006). A psychological law of inertia and the illusion of loss aversion. *Judgment and Decision making*, 1, 23–32.
- Gawronski, B., Bodenhausen, G. V., & Becker, A. P. (2007). I like it, because I like myself: Associative self-anchoring and post-decisional change of implicit evaluations. *Journal of Experimental Social Psychology*, 43(2), 221–232.
- Gigerenzer, G. (2000). *Adaptive thinking: Rationality in the real world*. Oxford and New York: Oxford University Press.
- Gigerenzer, G. (2006). Bounded and rational. In R. J. Stainton (Ed.), *Contemporary Debates in Cognitive Science* (p. 129). Blackwell.
- Haselton, M. G., Bryant, G. A., Wilke, A., Frederick, D., Galperin, A., Frankenhuys, W. E., & Moore, T. (2009). Adaptive rationality: An evolutionary perspective on cognitive bias. *Social Cognition*, 27(5), 733–763.
- Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind-reading. *Journal of Personality and Social Psychology*, 78, 1–11.
- Heberlein, T. A., & Bishop, R. C. (1986). Assessing the validity of contingent valuation: Three field experiments. *Science of the Total Environment*, 56, 99–107.
- Horowitz, J. K., & McConnell, K. E. (2002). A review of WTA/WTP studies. *Journal of Environmental Economics and Management*, 44, 426–447.
- Jackson, R. E., & Willey, C. R. (2011). Evolved navigation theory and horizontal visual illusions. *Cognition*, 119(2), 288–294.
- Jaeger, C. B., Brosnan, S. F., Levin, D. T., & Jones, O. D. (2020). Predicting variation in endowment effect magnitudes. *Evolution and Human Behavior*, 41, 253–259.
- Johnson, J. G., & Busemeyer, J. R. (2005). A dynamic, stochastic, computational model of preference reversal phenomena. *Psychological Review*, 112(4), 841–861.
- Jones, O. (2001). Time-shifted rationality and the law of law's leverage: Behavioral economics meets behavioral biology. *Northwestern University Law Review*, 95, 1141–1205.
- Jones, O. (2018). Why behavioral economics isn't better, and how it could be. In J. C. Teitelbaum, & K. Zeiler (Eds.), *Research Handbook on Behavioral Law and Economics* (pp. 476–504).
- Jones, O., & Goldsmith, T. (2005). Law and behavioral biology. *Columbia Law Review*, 105, 405–502.
- Jones, O. D., & Brosnan, S. F. (2008). Law, biology, and property: A new theory of the endowment effect. *William & Mary Law Review*, 49, 1935–1990.
- Kacelnik, A. (1997). Normative and descriptive models of decisionmaking: Time discounting and risk sensitivity. In G. R. Bock, & G. Cardew (Eds.), *Characterizing human psychological adaptations*. Chichester (United Kingdom): Wiley.
- Kahneman, D. (1991). Judgment and decision making: A personal view. *Psychological Science*, 2, 142–145.
- Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1990). Experimental tests of the endowment effect and the Coase theorem. *Journal of Political Economy*, 98, 1325–1348.
- Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1991). The endowment effect, loss aversion and status quo bias. *Journal of Economic Perspectives*, 5, 193–206.
- Kahneman, D., Knetsch, J. L., & Thaler, R. H. (2008). The endowment effect: Evidence of losses valued more than gains. *Handbook of Experimental Economics Results*, 1, 939–948.
- Kahneman, D., Slovic, P., & Tversky, A. (1982). *Judgment under uncertainty: Heuristics and biases*. Cambridge and New York: Cambridge University Press.
- Kahneman, D., & Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica*, 47, 263–292.
- Kannegiesser, P., Santos, L. R., Hood, B. M., & Call, J. (2011). The limits of endowment effects in great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*). *Journal of Comparative Psychology*, 125(4), 436.
- Klass, G., & Zeiler, K. (2013). Against endowment theory: Experimental economics and legal scholarship. *UCLA Law Review*, 61, 2–64.
- Knetsch, J. L. (1989). The endowment effect and evidence of nonreversible indifference curves. *The American Economic Review*, 79, 1277–1284.
- Knetsch, J. L., & Sinden, J. A. (1984). Willingness to pay and compensation demanded: Experimental evidence of an unexpected disparity in measures of value. *Quarterly Journal of Economics*, 99, 507–521.
- Koszegi, B., & Rabin, M. (2006). A model of reference-dependent preferences. *Quarterly Journal of Economics*, 121, 1133–1165.
- Kummer, H. (1991). Evolutionary transformations of possessive behavior. *Journal of Social Behavior and Personality: Special Issue on To Have Possessions: A Handbook on Ownership and Property*, 6(6), 75–83.
- Lakshminarayanan, V., Chen, M. K., & Santos, L. R. (2008). Endowment effect in capuchin monkeys (*Cebus apella*). *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 363, 3837–3844.
- Maddux, W. W., Yang, H., Falk, C., Adam, H., Adair, W., Endo, Y., ... Heine, S. J. (2010). For whom is parting with possessions more painful? Cultural differences in the endowment effect. *Psychological Science*, 21(12), 1910–1917.
- McCaffery, E. J. (1994). Cognitive theory and tax. *UCLA Law Review*, 41, 1861–1947.
- McDermott, R., Fowler, J. H., & Smirnov, O. (2008). On the evolutionary origin of prospect theory preferences. *The Journal of Politics*, 70(2), 335–350.
- Morewedge, C. K., & Giblin, C. E. (2015). Explanations of the endowment effect: An integrative review. *Trends in Cognitive Sciences*, 19(6), 339–348.
- Morewedge, C. K., Shu, L. L., Gilbert, D. T., & Wilson, T. D. (2009). Bad riddance or good rubbish? Ownership and not loss aversion causes the endowment effect. *Journal of Experimental Social Psychology*, 45(4), 947–951.
- Plott, C. R., & Zeiler, K. (2007). Asymmetries in exchange behavior incorrectly interpreted as evidence of endowment effect theory and prospect theory? *American Economic Review*, 97, 1449–1466.
- Pollick, A. S., & de Waal, F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences*, 104(19), 8184–8189.
- Sapolsky, R. M. (2017). *Behave: The Biology of Humans at Our Best and Worst*. Penguin Press.
- Sayman, S., & Öncüler, A. (2005). Effects of study design characteristics on the WTA-WTP disparity: A meta analytical framework. *Journal of Economic Psychology*, 26, 289–312.
- Sigg, H., & Falett, J. (1985). Experiments on respect of possession and property in hamadryas baboons (*Papio hamadryas*). *Animal Behaviour*, 33(3), 978–984.
- Slovic, P., Fischhoff, B., & Lichtenstein, S. (1982). Facts versus Fears: Understanding perceived risk. In D. Kahneman, P. Slovic, & A. Tversky (Eds.), *Judgment Under Uncertainty: Heuristics and Biases* (pp. 463–490).
- Stutt, A. D., & Willmer, P. (1998). Territorial defence in speckled wood butterflies: Do the hottest males always win? *Animal Behaviour*, 55(5), 1341–1347.
- Sunstein, C. (2000). *Behavioral law and economics*. Cambridge: Cambridge University Press.
- Tunçel, T., & Hammitt, J. (2014). A new meta-analysis on the WTP/WTA disparity. *Journal of Environmental Economics and Management*, 68, 175–187.
- Wang, X. T. (2011). Evolutionary psychology of decision making at risk. In X. T. Wang, & Y. J. Su (Eds.), *Thus Spake Evolutionary Psychologists* (pp. 198–208). Beijing: Peking University Press.
- Wrangham, R. W., Mc Grew, de Waal, & Heltne, P. (1994). *Chimpanzee cultures*. Published by Harvard University Press in cooperation with the Chicago Academy of Sciences.
- Zeiler, K. (2018). What explains observed reluctance to trade? In J. C. In Teitelbaum, & K. Zeiler (Eds.), *A comprehensive literature review* (pp. 347–430). Research Handbook on Behavioral Law and Economics.