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Phylogenetic Economics: Animal Models and the Study of Choice

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Abstract

While the investigation of non-human economic decision-making is increasingly popular, it is not clear exactly what role it can play in settling debates in economics. This paper argues that—contrary to recent claims otherwise—data on animal decision-making do not help in (dis-)confirming economic theories of choice. Rather, such data help in spelling out the representationally proper domains of models of choice. To play this role, though, these data must be placed into phylogenetic comparative analyses: correlations with specific environmental features need to be assessed, and these correlations need to be corrected for the presence of phylogenetic signals.

1. Introduction

An increasingly popular interdisciplinary area of research concerns the question of how non-human animals (“animals”) make economic decisions. While there is no question that this is an inherently interesting and important area of research (Santos and Rosati 2015; Kalenscher and van Wingerden 2011), the study of animal decision-making is also said to be of use in economics (for humans). So, Kalenscher and van Wingerden (2011, 8) note that “comparative research [can] uncover inconsistencies in choice behavior between humans and animals that allow for an improved, more comprehensive description of choice behavior and possibly force us to re-think the basis of economic theory in the light of the evolutionary roots of choice.” Other authors, too, argue for the appeal to data on animal economic decision-making in the investigation of economic questions (Santos and Chen 2009; Brosnan et al. 2008; Glimcher et al. 2005). It is this economic-focused use of data on animal decision-making that is the focus of this paper.

However, it turns out that establishing exactly what role such data can play in debates in contemporary economics is not as straightforward as it first may appear. In particular, this paper shows that this role does *not* concern the corroboration of economic theories of choice—as might have been expected, and as is suggested by some of the above authors (including Kalenscher and van Wingerden 2011). Rather, it

concerns the delineation of the proper domains of application of different economic models of choice. The paper goes on to show that, in order to play this role, data on animal economic decision-making need to be embedded in detailed phylogenetic comparative analyses.

To make this clearer, the paper begins, in section 2, by laying out the nature of the (for present purposes) key contemporary economic debates concerning decision-making. Section 3 presents some of the major data on animal economic decision-making. Section 4 details the structure of evolutionary biological phylogenetic comparative analyses, and uses this structure to develop a compelling methodology for linking the data on animal economic decisions from section 3 to the debate described in section 2. Section 5 concludes.

2. Economics and decision-making

While it is uncontroversial that one of the major areas of inquiry in economics is human decision-making, it is not uncontroversial *how* this study is to be conducted. Two such controversies are particularly important to mention here.

First, there is the question of whether economics should study *all* kinds of human decision-making (see, e.g., Robbins 1932; Fumagalli 2016b), or just a *subset* of this—e.g., and most famously, merely choices resulting from a desire for wealth (and only in so far as these choices stem from this desire or its opposite, the desires for leisure and consumption) (Mill [1836] 1967). While there may well be reasons to sometimes treat the economic study of choice as having a narrow domain, in this context, it is the former, broader perspective that is relevant.

On the one hand, this is inherently compelling; after all, much contemporary work in economics, either explicitly or implicitly, does take on this broader perspective (Fumagalli 2016b). On the other hand, reading economics narrowly would greatly complicate appealing to data from animals in economics—but in a way that is perpendicular to the issues at stake here. In particular, we would need to identify an evidentially relevant alternative trait to (e.g.) a desire for wealth in animals (such as a motivation to acquire status, mates, or offspring), and then use this trait to bridge the human and non-human cases. This, though, concerns an entirely separate suite of considerations, and can be left for another occasion. Instead, the present paper adopts a broad view of economics, according to which economics studies how agents—whether human or not—allocate scarce resources among competing ends (Robbins 1932). Whether the arguments of the paper carry over to a narrower reading of economics will not be further considered.¹ That said, the fact that the paper adopts this broad view should not be taken to imply that it assumes that a *particular* economic model of choice applies to some group of animals. On the contrary, as will be made clearer below, determining whether or not a given model is a useful way to approach the behavior of some animal is a key part of the proposal defended in this paper.

Somewhat related points hold for the second major area of controversy concerning the economic study of choice: whether economics studies the decisions that humans do or would make in various circumstances (including hypothetical ones), or whether

¹ Indeed, the paper can accept an even weaker starting point. As also noted in section 3, the paper is really only asking: if we accept that animals make economic decisions, how can this be used to inform economics? Answering this question is interesting even if one has doubts about the antecedent.

it studies the decisions that it would be *rational* for humans to make in these circumstances. In what follows, it will be the first, descriptive and non-rational, reading that will be central.

On the one hand, this is again inherently plausible. While rationality is undoubtedly central to much work in economics (see, e.g., Robbins 1932; Hausman 2012), it should not be seen as being central to all such work. Much of economics tries to determine how agents actually make economic decisions (see, e.g., Kahneman and Thaler 1991; Thaler 2000, 1980; Glimcher et al. 2005; Rabin 1998; Hutchinson and Gigerenzer 2005, 105, 110–11, 119; Fehr and Camerer 2007; Camerer 2007). For example, Thaler (2000, 137) writes: “[T]o attempt richer characterizations of economic agents via a better understanding of human cognition [. . .] will be a major area of effort over the next two decades.”

On the other hand, even if economics is seen as providing a sort of “logic of choice” (Jeffrey 1983; Savage 1954; Robbins 1932), then this would indeed complicate efforts to appeal to data from animals in economics. For example, we would need to find a way of bridging the is/ought gap.² However, these complications would again be *in addition* to the issues raised in this paper: even if a particular way of bridging this gap is accepted, it would still need to be shown how the data from animals can be related to the human case. That is, even if we can show that what *humans ought to do* is related to what *they in fact do*, it is not obvious how this relates to what *animals do*. The goal in what follows is to determine how we can relate the psychology and behavior of animals to humans. If and how to use this relation to ascertain appropriate standards of rationality can be left for another occasion.³

Given this view of economics as the descriptive study of all kinds of (human) decision-making, a major area of dispute and investigation concerns the fact that there is a multitude of accounts of decision-making that have been developed, each of which has some empirical support. Some of the major candidates include the following (many further such theories could be mentioned, and each of the above theories comes in several different versions as well; for good overviews, see, e.g., Heap et al. 1992; Resnik 1987; Bradley 2017; Angner 2016):⁴

Expected utility theory (EUT): Agents are assumed to maximize the expected utility they obtain upon completing action A_i in state S_i , weighted by the probability of S_i : $\max[EU(A_k) = \sum_{i=1}^n P(S_i) u(A_k \& S_i)]$, with $P(x)$ being a probability function ranging over S and $u(x)$ a (set of positive affine transformations of a) real-valued utility function ranging over $(A \times S)$ (see, e.g., Jeffrey 1983; Savage 1954; Hausman 2012; Resnik 1987).

Prospect theory (PT): Agents are assumed to maximize their expected prospects—i.e., the change in the status quo—upon completing action A_i in

² For example, some authors have appealed to a version of an “ought implies can” principle to argue that certain standards of rationality are not biologically plausible (see, e.g., Gigerenzer 2008; Santos and Rosati 2015).

³ See also Okasha (2018) for a discussion of how rationality and agency assumptions relate to work in evolutionary biology.

⁴ What follows is restricted to relatively high-level accounts of economic decision-making. However, all that follows can be extended to cases of low-level decision-making; see, e.g., Busemeyer and Townsend (1993).

state S_i , weighted by the decision weight of S_i (which is partially similar to the probability of S_i , but diverges towards the extrema of the probability function): $\max[\text{EP}(A_k) = \sum_{i=1}^n \pi(S_i) v_c(A_k \& S_i)]$, with $\pi(x)$ being a decision weight function ranging over S and $v_c(x)$ a value function ranging over $(A \times S)$ that is concave in gains and convex in losses (see, e.g., Barberis 2013; Köszegi and Rabin 2006; Tversky and Kahneman 1992; Kahneman et al. 1982; Kahneman and Tversky 1979).

Regret theory (RT): Agents are assumed to minimize the expected regret—i.e., the utility they counterfactually could have gotten, if they had chosen differently—upon completing action A_i in state S_i , weighted by the probability of S_i : $\text{ER}(A_k, A_l) = \sum_{i=1}^n P(S_i) Q[u(A_k \& S_i) - u(A_l \& S_i)]$, with $P(x)$ being a probability function ranging over S and $Q(x)$ a regret function ranging over $(A \times S)$ that is symmetric, convex for positive values of $Q(x)$, and concave for regrets (among other features) (Bleichrodt and Wakker 2015; Loomes and Sugden 1982, 1987).

Theory of simple heuristics (SH): Agents are assumed to rely on many rules that are domain-specific, easy to apply, and satisficing, such as “Take the Best,” where agents make decisions by focusing on just one, predictively highly relevant, decision attribute, or “Take the First,” where agents make decisions by considering only the first feasible option that comes to mind (among many other such rules) (Gigerenzer and Selten 2001; Todd 2001; Gigerenzer 2007; Lieder and Griffiths 2020).

There has been much discussion of many aspects of these theories. For present purposes, though, the issue at center stage is the fact that all of these accounts have some empirical evidence that speaks in their favor. While a full review of this evidence goes beyond the confines of this paper (and is not necessary here either), some key data points include the following.

- EUT has generally been found to be an accurate account in many situations where people have time to learn about the payoffs and adjust their behavior accordingly (see, e.g., Binmore 2007; Glimcher et al. 2005). In such cases, people tend to act in ways that are captured well by a model that assumes they probabilistically evaluate the outcome space, and then look for the optimal value in this space.
- As shown by the behavioral economic revolution, there are also many cases in which people diverge from the predictions of EUT and instead act in ways that are well predicted by PT (Kahneman and Tversky 1979; Kahneman et al. 1982; Kahneman and Thaler 1991; Barberis 2013). Some of the well-known findings here concern the documentation of framing effects (where choices framed as losses are treated differently from choices framed as gains) and endowment effects (where the evaluation of an item an agent has in their possession differs from that of the same item when not in possession).
- In a related body of work, neuroscientific and behavioral data indicate that sometimes people anticipate the regret/rejoicing they feel from different actions, and then act accordingly (Zeelenberg 1999; Coricelli et al. 2007). There

are also considerable empirical data showing that people often act intransitively (Bleichrodt and Wakker 2015; Kalenscher et al. 2010; Tsai and Bockenholt 2006; Sophor and Gigliotti 1993; Loomes et al. 1991), which is predicted by RT, given that it conceptualizes decision-making as dependent on what the contrast class is against which a given action is evaluated (Loomes and Sugden 1987, 1982; Loomes et al. 1991).

- SH draws support from classic cognitive scientific data (Gigerenzer and Selten 2001; Gigerenzer et al. 2000; Kruglanski and Gigerenzer 2011; Lieder and Griffiths 2020), including the fact that in various decision-making tasks, people often forgo using all of the available information and are instead drawn particularly to decision options that they are familiar with (Henrich and McElreath 2007; Goldstein and Gigerenzer 2002), or that they often use a lexicographic hierarchy of simple cues and stop assessing options once a cue is found that discriminates among them (Dhimi 2003; Broder 2000).

When considering these data, it is important to note that the issue here is not one of accommodation, but prediction. All of the above models can *accommodate* all the data; however, they do not all *predict* all of it (Hitchcock and Sober 2004).⁵ While there is nothing in EUT that *rules out* the possibility of endowment effects, intransitive choices, or familiarity-based decision-making, there is also nothing in the theory that should lead us to *expect* such findings. The same goes for the other theories and findings. Put differently, any of the above theories can be *retrospectively* fitted to all of the above data, but different such data are differentially well predicted by the different theories *ex ante*.⁶ It is in this sense that the different accounts are empirically well supported in different contexts.

This leads to the major point that needs to be emphasized concerning the dispute about economic decision-making. The continued empirical success of all these different decision models suggests that it is a serious possibility that they need to *all* be taken seriously. Of course, it is possible that new data will turn up that clearly show one of them to be superior to the rest, or that a new account is developed that is an improvement over all of the above. However, given that the above accounts have had

⁵ For example, the fact that people make what seem to be intransitive decisions is consistent with EUT, since people may individuate the option space more finely than the experimenter, or quite simply changed their utilities across the different choices (Fumagalli 2020). Similar remarks can be made for the other findings noted above.

⁶ This is a non-historical, structural sense of prediction: see also Hitchcock and Sober (2004); Worrall (1989). Note also that this is not a case where standard statistical model selection tools are helpful to assess the different models (see, e.g., Burnham and Anderson 2002; Hitchcock and Sober 2004; Rochefort-Maranda 2016; Forster and Sober 1994). Since these are not nested models with clearly demarcated numbers of parameters, comparing them with AIC, likelihood ratios, or even Bayesian methods is not easily (or at all) possible. For example, PT is not an expanded version of EUT: the two have similar parameter *numbers*—it is just that what these parameters represent is different. (It may be thought that the decision weight is a function of probabilities. While this is indeed often how this notion is presented, this is not the most straightforward way to understand this psychologically. In particular, it is reasonable to treat the decision weight as a psychological primitive.) In the case of SH, it is not even clear what the parameter number is: the exact nature and number of the simple heuristics people use is not known, making it hard to assess this in model selectionist frameworks. In turn, this means that other ways to evaluate these models are needed.

empirical successes for several decades, it is looking ever more plausible that neither of these options will come to pass. Instead, we may need to accept that all of these accounts are here to stay. Put differently, it increasingly looks like Rabin and Thaler (2001, 230) were wrong when they said, some 20 years ago: “it is time for economists to recognize that expected utility is an ex-hypothesis, so that we can concentrate our energies on the important task of developing better descriptive models of choice under uncertainty.” On the contrary: unlike Monty Python’s ex-parrot, EUT is still very much alive. However—and this is the key point here—the same is true of PT, RT, and SH.

How can this be? One way is as follows. EUT, PT, RT, and SH need to be recognized as *models* (despite their name!) (Morrison and Morgan 1999; Morgan 2012; Weisberg 2013; Morrison 2015). These different accounts all get at *some aspect* of human economic decision-making, and thus have some predictive successes. In turn, this is due to the fact that human economic decision-making is a multifaceted trait: we sometimes do something like maximizing EUT, sometimes something like maximizing EP, sometimes something like minimizing regrets, and sometimes we rely on something like SH.⁷ Because of this, the last two decades of work in neuroeconomics, behavioral economics, and cognitive science show support for all of EUT, PT, RT, and SH: they all get something right about how we make decisions—though none of them get all of it right.

This kind of absence of “one right account” of the phenomenon is characteristic of model-based methodologies in many contemporary sciences (see also Fumagalli 2016a). So, for example, in evolutionary biology, the question is not whether a phenotypic selection-based model, or a population genetic model, or a molecular genetic model, or an evo-devo model (etc.) is *the* right model of the evolutionary dynamics of some population. Each of these models foregrounds different aspects of these dynamics—natural selection, laws of genetic segregation and assortment, development, etc.—and as such, they can *all* be good models (Potochnik 2017). They are simply different elements of our tool kit with which we can investigate the underlying biological reality, depending on which aspect of that reality we are looking to explore further (Morrison and Morgan 1999; Morgan 2012; Weisberg 2013; Morrison 2015). The same is true here: EUT, PT, RT, and SH (among others) all get at different aspects of the complex psychological reality underlying economic decision-making. They foreground different aspects of this reality—the calculation of expected utilities, weighted prospects, etc.—and they should all be seen to be part of the contemporary economic toolkit (Hochstein 2022). This has two important implications.

On the one hand, pragmatic considerations such as analytical convenience or data availability are an important determinant of the choice of models (Potochnik 2017; Levins 1966; Orzack and Sober 1993; Weisberg 2006; Morrison 2015; Samuelson 2002; Massimi 2018; Parker 2020). The present case is no exception (Binmore 2007). On the

⁷ This could be because we actually calculate expected utilities in some cases, weighted prospects in others, and so on. Or it could be that we are always calculating—perhaps using a set of simple heuristics as instruments—the same quantity (“expected happiness”), but this quantity sometimes looks a lot like expected utilities, at other times like weighted prospects or regrets, and sometimes just like the heuristic instruments (see also Glimcher et al. 2005, 252). For example, we could be heuristically instrumenting $\max[\text{EH}(A_k)] = \sum_{i=1}^n [d_i P(S_i) + (1 - d_i) \pi(S_i)] [d_2 u(A_k \& S_i) + d_3 v_C(A_k \& S_i) + d_4 \sum_{j=1}^n Q[u(A_k \& S_i) - u(A_j \& S_i)]]$, with $d_i \in [0, 1]$, $(d_2 + d_3 + d_4) = 1$, and differing across decision situations. Distinguishing these two options is not important here, though (pace Schulz 2020, chap. 4).

other hand, though, this does not mean that pragmatic considerations should be assumed to be all that is going on here. The fact that EUT, PT, RT, and SH are recognized to be models does not mean that we should take an “anything goes” purely instrumentalist attitude here (Friedman 1953; Gul and Pesendorfer 2008; Hausman 2008). In particular, there is also an important set of representational questions to be asked. These questions concern the situations in which a given model foregrounds the right causal factors. That is, we want to know the proper domains of each of the models: which of the available models of choice are useful when, and why is this the case? Why do we make PT-like decisions *here*, and EUT-like decisions *there*? How can we characterize “here” and “there?” While the choice of a model partially depends on pragmatic factors and our interest, it also depends on the world: foregrounding cause C_1 will not be empirically compelling if C_1 is not a significant cause in the case at hand.

This is again similar to other model-based inquiries: while replicator-dynamics-based, population genetic, and evo-devo models all have their place in evolutionary biology, which is partly determined by pragmatic factors, this does not exhaust the debate there. These different models foreground different causal factors, and so it is also interesting to ask which empirical situations are well modeled with what (Potochnik 2015, 2010, 2017). Which evolutionary scenarios feature few genetic and developmental constraints—making purely selection-based models adequate—and which feature prominent genetic or developmental processes that should be foregrounded—making other models representationally superior? The same is true in economics: the question of which situations feature mostly EUT-like decision-making, which mostly SH-like decision-making, etc., is an important, and so far unanswered, question.

Note that this question cross-cuts the familiar instrumentalism/realism debate surrounding economic models of choice (see, e.g., Friedman 1953; Gul and Pesendorfer 2008; Angner 2018; Hausman 2008). The question here is not whether we should see economic models as being psychologically neutral, purely behaviorist predictive devices, or as psychologically realistic descriptions of our neurocognitive architecture (though this is an interesting question, too: Fumagalli 2016a). Rather, the question here is how to best model the neuro-psychological mechanisms underlying economic decision-making, while acknowledging that none of the above models can be expected to be fully accurate, and yet still making room for these models to be differentially empirically compelling in different contexts.⁸

Note also that answering this question is not straightforward, especially in economics, where there are many experimental constraints. For example, it is hard to experimentally test the idea that EUT-like decision-making is particularly common in cases where the stakes are high and time constraints low: for ethical reasons, it is hard to induce truly high-stakes decision situations in a lab. More than that: even if it were determined that a given model is a good fit to situations A, B, and C, it is not obvious

⁸ In this sense, the model pluralism defended here can be weaker than the radical pluralism defended, e.g., by Giere (1999, 2004). That is, there may well be one highly complex true account of economic decision-making that incorporates, as special cases, the above types of more specific models. It remains the case that the above models are accurate in their own domains, and that the modeling of economic decision-making does not require the specification of the one true account (indeed, the latter may be positively unhelpful, given its complexity). See also note 7.

how to step back and assess what these situations have in common (other than that they fit the parameters of the model in question). What do the many cases where EUT-like decision-making is observed have in common?

It is therefore in this context that the (for present purposes) key contemporary dispute surrounding economic decision-making is located. Once it is recognized that all of EUT, PT, RT, and SH (etc.) are in-principle adequate models, and that the choice between them is context-dependent and not to be made once and for all, it becomes clear that, from a representational perspective, the main issue to be settled is to understand their individual causal domains better. It is one thing to know *that* there are many different ways to model economic decision-making in different circumstances. It is another thing to know *which* situations are empirically particularly well-modeled with EUT, which with PT, and so on. Determining this is an important task, and one that does justice to both the model-based nature of EUT, PT, RT, and SH *and* the non-purely instrumentalist nature of economics.

3. Animal economic decision-making

Over the last few years, researchers have used variants of the kinds of choice situations typically used in economic experiments to investigate the ways in which a wide variety of animals make decisions. For example, animals have been given choices between safer and riskier options, between investing in value streams with different reward patterns, and between different goods when they had control over them and when not (good overviews are here: Santos and Rosati 2015; Kalenscher and van Wingerden 2011; Brosnan et al. 2008). While there is much that can be said about this work, for present purposes, the major point to note is that a key overall upshot of it is the finding that many of the same kinds of results familiar from human studies can also be found in animals. (Some more details about some of these studies will be noted in the next section.)⁹

So, a number of different animals, including macaques, rats, and pigeons, have been shown to adjust their behavior in ways that is well predicted by assuming they are assessing the expected value of the relevant actions' consequences (Kagel et al. 1995; Santos and Chen 2009; Glimcher et al. 2005). For example, Glimcher et al. (2005, 230) summarize some cognitive neuroscientific studies of decision-making in macaques by noting that "something very close to an economic choice variable was indeed being carried by the firing rates of these neurons [in the LIP area of macaque brains]. [...] Together, these results suggested an interesting possibility, that the topographic map in area LIP encodes something like the relative expected value, or perhaps even the relative expected utility, of each possible eye movement

⁹ Note that the point in what follows is not that we can metaphorically apply economic models of choice to these animals. As noted in section 2, the present paper adopts a broad view of the domain of economics, according to which the animals can *actually* make economic decisions. Of course, we often transfer models in a metaphorical way, too: e.g., we can treat some firms as "predators," and some as "prey," and then model mergers and acquisitions using the Lotka-Volterra equations—though we are of course not saying that they are actually predator and prey in a biological sense. Here, though, we are trying to model the *actual* behavior of animals in a representationally accurate manner (in line with the discussion of the previous section).

under the conditions we had been studying.” However, this is not all that has been shown concerning non-human economic decision-making.

It is also the case that that a highly varied group of animals comprising (among others) chimpanzees, gorillas, orangutans, Capuchin monkeys, rats, honeybees, and starlings has been shown to be subject to framing effects (Chen et al. 2006; Brosnan et al. 2008; Kacelnik and Bateson 1996; MacDonald et al. 1991; Marsh and Kacelnik 2002; Shafir et al. 2008). A significantly smaller group of these animals—a fact that will become very important below—has even been shown to display an endowment effect; these animals include chimps, gorillas, orangutans, and capuchin monkeys (Lakshminarayanan et al. 2008; Brosnan et al. 2007; Drayton et al. 2013; Flemming et al. 2012).

Even this does not exhaust the findings in this context, though. Other studies have found evidence of RT-like decision-making—including intransitive decision-making—in macaques, chimpanzees, bonobos, grey jays, and honeybees (Waite 2001; Shafir 1994; Rosati and Hare 2013; Lee et al. 2005; see also Hayden et al. 2009; Abe and Lee 2011). On top of this, much work in behavioral ecology and cognitive ethology is based on the fact that many animals act in ways that suggest reliance on simple heuristics, such as choosing what is familiar instead of engaging in exhaustive search of the option space, or picking the first option that hits a minimal threshold in a fixed hierarchy of cues (Goulson 2000; Karsai and Penzes 2000; Shettleworth 2009; Gibson 1996; Kacelnik 2012).

Now, there is no question that the details of the above studies (and others like them) deserve to be closely scrutinized. Did the studies control for all the necessary confounders? Are the conclusions drawn by the studies’ authors warranted, or are other conclusions more reasonable? However, these questions can be sidestepped here. In the present context, what is relevant is just the conditional: *if* these studies hold up, how can they be used in the economic investigation of decision-making (as laid out in the previous section)? This question retains its interest, even if some of the above studies turn out to be problematic for one reason or another.

In order to see how to answer this question, it is best to begin by considering the full passage from Kalenscher and van Wingerden (2011) that was partially quoted in the introduction:

In the worst case, results obtained in animals will corroborate those obtained from humans, strengthening the existing theory. Preferably, though, comparative research will uncover inconsistencies in choice behavior between humans and animals that allow for an improved, more comprehensive description of choice behavior and possibly force us to re-think the basis of economic theory in the light of the evolutionary roots of choice.

(Kalenscher and van Wingerden 2011, 8)

What is important about this quote is that it expresses a thought that deserves to be looked at in more detail. This is the idea that the data on animal economic decision-making can be disambiguating of the empirical work in economics, in that it can lead to the corroboration or disconfirmation of existing economic theories. This is not a *prima facie* implausible thought: theoretical disputes in various contexts have been usefully illuminated in precisely these ways. For example, there has been a long-

standing dispute over whether dinosaurs were warm- or cold-blooded, with data pointing in different directions. Here, data suggesting a high metabolic rate can be seen to corroborate the former theory (Wiemann et al. 2022). It is not unthinkable—and in fact quite reasonable—to presume something similar is true in economics.

However, as made clearer in the previous section, this is not in fact the best way of reading the dispute in economics. Data on animal economic decision-making cannot “corroborate [the results] obtained from humans,” thus “strengthening the existing theory”—as Kalenscher and van Wingerden (2011) suggest—simply because there is no *one* existing theory in economics. Indeed, as also noted in the previous section, this is the wrong way to think about the dispute in economics to begin with. EUT, PT, RT, SH (and others like them) are *models* of choice. They can all be adequate; the question is which of them is best used when.

Given this, it becomes important to ask how the data on animal decision-making can be used to address *this* dispute. Making this clearer is the aim of the next section.

4. A methodology for interspecies economics

To see how to advance the economic study of choice (as detailed in section 2) using data on animal economic decision-making, a brief detour into evolutionary biological reasoning is needed. In evolutionary biology, comparative analyses are used in the investigation of the factors that shaped the evolution of a trait. They work by determining correlations between a focal trait and other traits and aspects of the organisms’ environments (Harvey and Pagel 1991; Harvey et al. 1995a,b; Felsenstein 1985; Fisher and Owens 2004). If we know that trait A and feature of environment B tend to co-evolve (across a set of species), then this provides us with a narrowed hypothesis space as to what determines this evolution. For example, it may be that A is a selective response to B, or that B is a causal consequence of A, or that A and B are developmentally, genetically, or epigenetically linked in some way. While distinguishing among these possible explanations requires further studies, a phylogenetic comparative analysis provides the constraints within which these further studies are situated (Schulz 2013). These studies make precise the extent to which backgrounding the consideration of B is plausible when investigating the evolution of A.

There is an important wrinkle to the use of comparative methods that needs to be noted, though: the presence of a phylogenetic signal. In general, the correlation between A and B is mediated by phylogenetic inheritance (and may in fact be entirely due to the latter). So, both A and B may be (partially or fully) inherited from a common ancestor, so that the correlation between them may be (partly or fully) due to this inheritance. If so, the phylogenetically meaningful evolutionary correlation between A and B will be less than a standard regression analysis would suggest (Fisher and Owens 2004). This is a well-known issue in phylogenetic comparative analyses, and various methods exist that correct for it (Fisher Owens 2004; Freckleton et al. 2002; Harvey and Pagel 1991; Harvey et al. 1995a,b; Felsenstein 1985). The details of these methods are not greatly important here, but it is important to note that this is an issue to which phylogenetic comparative analyses need to pay attention.

All of these points are important here, as they make for the other half of the formulation of a compelling methodology for linking the data on animal economic decision-making to human economics. Recall that the first half of this formulation

consisted in showing that the relevant theoretical and empirical conflict surrounding the contemporary economic study of choice concerns the question of which models of decision-making foreground the right causal factors in which circumstances. Putting this insight about the nature of the dialectic in economics together with the structure of phylogenetic comparative analyses just laid out yields the core idea behind the methodology defended in this paper: data on animal economic decision-making can be used to do a phylogenetic comparative analysis of specific forms of economic decision-making, thus helping to determine the latter's appropriate domains of application.¹⁰

This works in two related, mutually reinforcing, ways. On the one hand, by seeing which models are predictively useful in which groups of organisms, we can triangulate on the environmental circumstances that make up the domain of application of these models. If we learn that EUT decision-making is found in organisms O_1 to O_n , we can look for choice contexts C_1 to C_m that these organisms have in common. We can then use this insight to narrow the domain of application of EUT by focusing on C_1 to C_m . On the other hand, and in addition, we can consider different environmental circumstances directly, especially if we have ancillary reasons to think that some such are particularly important. For example, from studies in humans, we may *suspect* that EUT decision-making is found in circumstances C_1 to C_m . We can then use phylogenetic comparative analyses to test this suspicion by seeing whether being in circumstances C_1 to C_m phylogenetically correlates with EUT in organisms O_1 to O_n . Looking at non-human animals thus broadens the data we can access to check on our suspicions about domains of application of models of choice, compared to just looking at humans.¹¹

In short: data on animal economic decision-making are important precisely because they allow us to find correlations between different ways of making economic decisions and different environmental circumstances. In turn, this can then help determine which ways of making decisions are usefully foregrounded in which circumstances. It is important to emphasize from the get-go, though, that the upshot of this method is just *evidence*. It is possible that different organisms make decisions differently in different circumstances (e.g., humans may make EUT decisions in different circumstances compared to other organisms). Still, all organisms are related. This makes phylogenetic correlations important to consider—here and in evolutionary biology more generally. I return to this issue below, but for now, it is useful to consider an example to make these points clearer.

Consider the endowment effect. As pointed out in the previous section, this effect, while found in some animals, is quite limited in its phylogenetic instantiation. In particular, it seems to be a primate-specific trait: humans show it in a wide variety of circumstances, other great apes (chimps, orangutans, gorillas) do so in a more limited manner, and capuchin monkeys in a very narrow range of cases only. Beyond this, though, the effect has not been clearly established (Brosnan et al. 2007, 2012;

¹⁰ Brosnan and Wilson (2023) also advertise a form of “comparative economics,” but they do not spell this out as is done here.

¹¹ Similarly, if we only have data on one species (humans, say), then determining whether brain size evolved as a response to increased demands for mental state attribution is very difficult. If we have data on more than one species, though, we can correlate brain size and demands for mental state attribution across different species, and thus have a better sense of whether foregrounding demands for mental state attribution is empirically compelling when investigating the evolution of brain size.

Lakshminarayanan et al. 2008; Drayton et al. 2013; Flemming et al. 2012; Kanngiesser et al. 2011). Of course, this could be due to the fact that, outside these primates, suitable experimental studies have not been done (e.g., because they are difficult to do). However, it is at least a reasonable empirical presumption that the endowment effect is primate-specific (and uniquely widespread in the human case).

This matters, as it suggests that parts of the domain of PT (which, as noted in section 2, yields the endowment effect as one of its key predictions) is tied to features of primate living. A key—though, as noted momentarily, not the only—set of candidates for these features are the rich, dynamically changing psychological textures underlying primate social environments. The endowment effect seems to express the idea that when exchanging items (of biological value—Jaeger et al. 2020), I appreciate that you may be tempted to keep your part and take mine. That's a rich psychological thought and famously a classic aspect of primate social living (Humphrey 1986; Whiten and Byrne 1997).

There are two caveats concerning this conclusion that need to be noted, though. First, so far, it is not clear *exactly* which aspects of primate lifestyles correlate with the PT-like, endowment effect-yielding economic decision-making. There are many aspects to these lifestyles, and not all of them need to be correlates with the endowment effect. Furthermore, it is also not clear—as is true for phylogenetic comparative analyses in general—whether PT-like, endowment-effect-yielding decision-making is an evolutionary consequence of primate lifestyles, or whether the opposite is true (or whether both are due to a third evolutionary, genetic, or developmental factor). For this, further studies will need to be done that can help isolate the specific features of primate ecologies that PT-like, endowment-effect-yielding decision-making correlates with. I return to this point momentarily; for now, it is just important to note that the above conclusion about the domain of PT-like decision-making as having something to do with primate lifestyles needs to be recognized as relatively abstract, and as something in need of further investigation.

The second caveat concerning this conclusion that needs to be noted here concerns the need to correct this conclusion for phylogenetic inertia. Given that chimps, gorillas, orangutans, and humans are very closely related—with capuchins a little further off, but not drastically so—there is every reason to think that some of the correlation in PT-like, endowment-effect-yielding decision-making and primate ecologies is due to the fact that the decision-making mechanisms and ecologies of these species have been (partly) inherited from a common ancestor. Again, the exact details need to await a closer scrutiny of the exact features of primate ecologies that are correlated with the endowment effect. Here, it just needs to be noted that the corrected correlation is likely to be weaker than it may at first appear—and thus, that it yields a less clear signal about the domain of application of PT-like, endowment-effect-yielding decision-making.

These points are usefully contrasted with the situation concerning EUT-like decision-making. As noted in the previous section, a wide variety of animals have been shown to act in ways that are well predicted by a model based on expected utility maximization: other than humans, macaques, rats, and birds have been shown—sometimes using neurophysiological measures—to make decisions by evaluating which outcomes yield the highest expected rewards (Kagel et al. 1995; Santos and Chen 2009; Glimcher et al. 2005). In turn, this suggests that responding to primate sociality is *not*

the main domain of EUT, but rather something common to a wider variety of organisms. In the present context, this is an important point to note, as it marks for effective and illuminating contrast to the previous case.

On the one hand, finding the specific set of environmental features that EUT-like decision-making is correlated with—i.e., determining the exact domain of application of EUT—is harder than when it comes to PT-like decision-making and primate ecology. While the latter lacks some precision, there are at least a number of clear possibilities to consider (Sterelny 2003; Tomasello 2022). When it comes to EUT-like decision-making, though, this is more difficult: finding meaningful environmental circumstances in common among the ecologies of humans, rats, and some birds (among others) is not straightforward. In turn, this makes it harder to do specific phylogenetic comparative analyses here: it is not easy to find candidate environmental circumstances that EUT-like decision-making may be correlated with.

On the other hand, though, since these organisms are so different and since their average degree of relatedness is relatively low, there is at least less reason to think that any phylogenetic corrections will be major here. Whatever exact set of environmental features turns out to be well correlated with EUT-like decision-making, this correlation is unlikely to be much skewed by phylogenetic inheritance. In this way, it becomes clear that there is a tradeoff when engaging in phylogenetic comparative analyses of economic decision-making: analyses involving more distant—i.e., relatively less closely related—animals are less subject to the need for phylogenetic corrections, but these analyses are made harder by the fact that it is harder to determine the *exact* domain of application of this way of making economic decisions.

Stepping back from these particular cases yields two more general points concerning the phylogenetic comparative approach towards the economic study of decision-making (as laid out in section 2). First, as has been noted throughout this section, so far, the work needed to put the approach into practice is only in its infancy. There are few concrete conclusions to provide here yet, as the relevant specific correlations have not been investigated yet. This is something that it will take the combined effort of primatologists, economists, anthropologists, comparative psychologists, and philosophers to achieve.

Second—and this is the key upshot of this paper—it is now at least clearer that *this* is the right methodology for linking data on animal economic decision-making to contemporary economics. To link the data on animal economic decision-making to the human case, we need to do two things. First, we need to correlate these data with specific other traits and environments: which ways of making decisions link up with which situations? In turn, this requires investigating what these traits and environments might be. Depending on the details of the case, this can be more or less difficult, but is a key element of the approach. Second, we need to strip these correlations of their phylogenetic signal, in line with standard comparative methods. In turn, this requires assembling systematic data sets on sufficiently large classes of species, and then applying the appropriate methods.

In this way, the right methodology here is, in some ways, the opposite of Kalenschner and van Wingerden's claim. The goal of this analysis is not to “uncover inconsistencies in choice behavior between humans and animals” that can “force us to re-think the basis of economic theory in the light of the evolutionary roots of choice.” Rather, the goal is to find *correlations* between different ways of making

economic decisions and other traits and environments, whether these are shared or not shared. (In line with the discussion of section 2, it is not clear what it even means to “re-think the basis of economic theory in the light of the evolutionary roots of choice.”) Put differently: phylogenetic comparative studies can extend the economic methodological tool kit to clarify the domains of application of the different models.

It is important to emphasize this last point: the proposal laid out here is meant to supplement, not supplant, other methodological approaches—including other evolutionary tools, such as formal evolutionary (game theoretic) models (see, e.g., Cooper 1987; Okasha 2011, 2018; Okasha and Binmore 2012; Güth and Kliemt 1998; Samuelson 2002; Huck et al. 2005). As noted earlier, the phylogenetic approach just provides *evidence*. Other studies are needed to strengthen this evidence. Turning this around, the comparative analysis can *advance* the discussion here—but it cannot *resolve* it.

That said, the phylogenetic approach has some specific advantages. On the one hand, it can make suggestions as to what to look for in our other studies. As made clear earlier, it can suggest specific environmental circumstances to further test when assessing the domains of application of different models of choice. On the other hand, the phylogenetic approach does not need to commit to a specific evolutionary modeling framework (e.g., concerning the payoffs of different ways of making economic decisions, or the nature of evolutionary dynamics) and opens up a whole new source of data and experiments. However, other tools—including other evolutionary approaches—are very useful as well and have their own strengths, such as being able to easily consider different modeling assumptions, or making predictions about the kind of environments that foster certain kinds of decision-making.

For example, there are models suggesting that RT-like, alternative option-dependent decision-making is adaptive in autocorrelated environments (Fawcett et al. 2014): if two successive states of the environments are more likely to be similar to each than ones further apart in time, it can be adaptive to treat seemingly irrelevant alternatives as “insurances” that can be relied on in times of need. In turn, this can yield intransitive decision-making across time. However, the nature of the modeling assumptions (such as the degree of autocorrelation, the nature of the options and payoffs, etc.) matters greatly here, with different such assumptions leading to different outcomes (Fawcett et al. 2014). In turn, this makes it useful to compare these insights with the results of phylogenetic comparative analyses: we can test whether autocorrelated environments phylogenetically correlate with RT-like decision-making, and perhaps also use the results of the latter analyses to triangulate on the kinds of autocorrelation needed for RT-like decision-making to be adaptive. In this way, the phylogenetic approach can be seen to be a fruitful expansion of traditional economic methodology.

5. Conclusion

An increasingly popular interdisciplinary area of research concerns the question of how animals make economic decisions. What is less clear is what role this research can play in economics. This paper has argued that—contrary to some recent claims otherwise—data on animal economic decision-making do not help in corroborating or falsifying existing economic theories of choice. In turn, this is due to the fact that,

first, such corroboration and falsification is not looked for. The real question is not which of the different approaches towards choice—EUT, PT, RT, and SH—is the right one; rather, it is what the representationally proper domains are of the different models of choice.

Once it is clear that this is the question we are trying to answer, the role of data on animal economic decision-making becomes clearer. This role can now be shown to consist in enabling the establishment of correlations between the different ways of making economic decisions and different features of the environment. In order to establish these correlations, though, the data on animal economic decision-making need to be placed in a phylogenetic comparative analysis: they need to be correlated with specific features of the environment, and these correlations need to be corrected for the possible presence of distorting phylogenetic signals. While the precise upshot of such a phylogenetic approach towards economics is not yet clear, it is hoped that the paper has at least made clearer why this is the right approach to take.

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