

Research



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Author for correspondence:

Kim Sterelny

e-mail: kim.sterelny@anu.edu.au

One contribution to a special feature: Humans as a model for understanding biological fundamentals. Edited by Sarah Brosnan & Erik Postma.

Humans as model organisms

Kim Sterelny

Philosophy, Australian National University, Canberra, Australian Capital Territory 0200, Australia

KS, 0000-0003-3159-6698

Like every other species, our species is the result of descent with modification under the influence of natural selection; a tip in an increasingly large and deep series of nested clades, as we trace its ancestry back to increasingly remote antecedents. As a consequence of shared history, our species has much in common with many others; as a consequence of its production by the general mechanisms of evolution, our species carries information about the mechanisms that shaped other species as well. For reasons unconnected to biological theory, we have far more information about humans than we do about other species. So in principle and in practice, humans should be usable as model organisms, and no one denies the truth of this for mundane physical traits, though harnessing human data for more general questions proves to be quite challenging. However, it is also true that human cognitive and behavioural characteristics, and human social groups, are apparently radically unlike those of other animals. Humans are exceptional products of evolution and perhaps that makes them an unsuitable model system for those interested in the evolution of cooperation, complex cognition, group formation, family structure, communication, cultural learning and the like. In all these respects, we are complex and extreme cases, perhaps shaped by mechanisms (like cultural evolution or group selection) that play little role in other lineages. Most of the papers in this special issue respond by rejecting or downplaying exceptionalism. I argue that it can be an advantage: understanding the human exception reveals constraints that have restricted evolutionary options in many lineages.

1. Introductory remarks

To the best of biological knowledge, the history of every living organism converges to a common ancestor. All have evolved by descent with modification, with natural selection playing an important role in the emergence of their biological organization. This common genealogical history has resulted in genetic and cellular mechanisms that are shared across the whole tree of life. At a somewhat finer grain, modern humans exemplify a broad range of morphological, physiological, neurocognitive and behavioural traits shared with the other primates, the other mammals, the other amniotes and so forth, though as the origins of these nested clades go further back in time, the extent of divergence is greater, and the similarities become fewer, coarser or both. Thus the geno-phenotype of our species, like those of other species, implicitly carries information about the general biological mechanisms that explain their existence, stability and function. Given that, why would our species *not* be an appropriate choice as a model system?

Of course, there are practical problems, including ethical considerations, that block some potentially informative experimental manipulation. We cannot, for example, test Chomsky's hypothesis about the innateness of grammar by exposing a cohort of children only to an artificial language with linear order but no recursively specified embedded structures [1,2]. Likewise, human lifespans are too long for experimental evolution projects. But, equally, there are practical advantages. For any biological question with potential medical implications, funding is available, allowing researchers to explore questions about disease and disease resistance, fertility and fertility decline, aging, the mechanical

bases of sex ratios and sex determination. It is true that the basic mechanisms of human bodies differ somewhat from those of other mammals and primates. For example, while menopause is not uniquely human, women lead an unusually long, active and competent post-menopausal life [3]. For another, we are adapted to eat cooked food, and this has important consequences for teeth, jaws and gut [4]. But nonetheless, human teeth and human digestive systems depend on the same mechanical and chemical systems found in other animals. Moreover (as Michael Briga and his colleagues note) there is often quite detailed information on population history, making demographic and life history questions relatively empirically tractable [5].

So there are uncontroversial cases in which humans make natural model systems: cases where there are relevant similarities between humans and other species, and where (often for reasons unconnected to biological theory) we have unusual access to relevant information, or at least to the resources we need to get that information. As with any other case, the choice of humans as model organisms must be strategic. But there is no special, in-principle problem in pursuing any of Tinbergen's four questions using humans.

This defence of the in-principle relevance of humans to general biological phenomena amounts to a rejection of human exceptionalism—a view rarely defended explicitly in the life sciences, but quite often found in the social sciences (see for example [6]). Exceptionalism is the idea that though humans are the product of descent with modification, the outcome is a species so radically unlike others that cross-species comparisons are often uninformative, even misleading, in both directions. Indeed, humans may be so different that the mechanism of evolutionary change is different (e.g. because cultural transmission is very important in hominin evolution, and of minor importance in other lineages [7]). Of course, no defender of human exceptionalism argues that humans are too exceptional to be informative about other species with respect to every trait. For example, our physiology clearly resembles that of other great apes. That said, in practice medical experiments are performed on chimpanzees to inform us about human physiological response, rather than vice versa. Rather, the exceptionalist idea questions the relevance of work on humans to questions about the general phenomena of cognition, social learning, social and technical behaviour, patterns in social life. These are cases in which humans are at the very least extreme outliers of more general phenomena: communication, large-scale cooperation and the production of public goods, social learning and teaching, and adaptive plasticity mediated by learning.

Of course, other species cooperate, reciprocate, communicate, learn from one another, adapt behaviourally to environmental changes. But, the argument goes, in all of these aspects of cognition and social behaviour, in their extent and their character, humans are radically unlike other primates, other animals. We are both extreme and complex cases. So, for example, if one wanted to understand the circumstances in which honest communication evolves between agents with partially overlapping and partially divergent interests, would one study humans? It is true that we have a lot of case material on human communication. Many humanities departments do little else but document, discuss and add to the documentary corpus of human communication. Moreover, there has been much theoretical reflection on such communication in linguistics, sociology,

psychology, philosophy, anthropology and many other disciplines. But no one could claim that there is anything like a consensus on its nature. There continues, for example, to be deep theoretical divides on what a symbol is, and what cognitive capacities are needed to produce and understand symbols. While there is a vast amount of data, the data are packed in an enormous array of mostly incommensurable disciplinary frameworks. So the human examples are problematically obscure in themselves; they are embedded in a social environment demonstrably unlike that of other animals, and perhaps they are so unlike other cases as not to be informative about them.

To what extent, and with respect to what phenomena (if any) are such claims about human exceptionalism warranted? This question comes up explicitly and implicitly through this whole special issue. If humans are indeed radical outliers with respect to (for example) social cognition and theory of mind, does it follow that there is little to learn about social cognition in other animals from the human case? I shall suggest that humans can be useful models, even in those domains in which exceptionalism is plausible. However, in those domains in which humans are not radical outliers I shall also suggest that, judging from a couple of the papers in this special issue, extracting information of general relevance from rich human data is not without problems. In pursuing these questions, I will occasionally make sceptical remarks about other papers in this issue. That being so, the reader should know that I have had the last and only word: these authors have had no opportunity to see and respond to those remarks.

2. Exceptionalism

As noted above, many of the papers in this issue link the use of humans as model organisms to rejecting exceptionalism: they assert that humans are just another unique species. Thus one paper, in defending a general definition of social behaviour, remarks that 'Beyond the implicit bias that humans are special, rather than a representative of the vertebrate or mammalian or primate clade, there is no more reason to examine human exceptionalism than that of squids, lobsters, lizards, or bobcats' [8, p. 18]. No one with a serious interest in these issues doubts that humans are the product of evolution with natural selection. Nonetheless, human social life and human cognition may be in important respects different in kind from the lives and minds of other living animals, and those differences may be the result of unique mechanisms. For example, Rob Boyd has recently argued that humans are objectively extraordinary in their distribution, numbers and ecological impact in ways that require special explanation, and have been since the late Pleistocene [7]. Likewise, it has been argued that human cooperation depends on cultural group selection, and that cultural group selection is powerful only in rather special conditions. Those conditions are satisfied by human groups (and perhaps extinct hominins), but not otherwise [7,9–11]. If that were right, one might wonder whether we could learn anything about animal cooperation from studying human cooperation. Even successful models of uniquely human traits like large-scale cooperation and language will not tell us much about the general mechanisms that explain the evolution of cooperation and communication.

Perhaps in response to such worries, at the end of their paper, Bshary & Raihani are inclined to simply reject exceptionalism [12]. Their point of view depends on the distinction between evolutionary and proximate questions, for they accept that some of the proximate mechanisms supporting human cooperation are not in play in other animals. However, they argue that theoretical and empirical work on humans can reveal evolutionary mechanisms, sources of costs and benefits, that play a general role in the evolution of social interaction. For example, they think there is evidence in cleaner fish of reputation and third-party punishment, mechanisms at the centre of work on human cooperation [9]. However, their way of connecting the very rich literature on human cooperation to the more general issue depends on a very sharp proximate/ultimate distinction. Perhaps too sharp [13], if the proximate mechanisms operating in the human case make evolutionary mechanisms relevant that are otherwise not important. That seems likely. Cooperation is apt to evolve under positive assortment; it evolves only if cooperators are more likely to interact with other cooperators, and the uncooperative with others like them. Culturally mediated proximate mechanisms in play in human social life support modes of positive assortment not otherwise found.

Somewhat similar considerations apply to Wilson *et al.*'s incisive review of recent ideas on sexual selection and their application to human evolution [14]. Many features of human life are supposedly shaped by sexual selection. These include morals and moralizing, storytelling, music, language, and handaxe making. Yet the somewhat unusual reproductive dynamics of human populations make it less easy to use human data to probe sexual selection theory. For one thing, in many contexts fathers invest heavily in their children, as do mothers by default, and so both sexes are selected for choosiness. Moreover, there is great variation in reproductive strategy within and across society. The exceptional features of human proximate mechanisms—for example, the variation of family structures within groups—shape the operation of sexual selection. Mating systems usually reflect foraging ecology: females chase the resources they need, and this controls their distribution over the landscape; male strategy responds to that distribution. In some ways, human mating systems do show the effects of such resource constraints: polygyny is more common in environments in which a woman can generate most of the resources she needs for herself or her children, and in which males can monopolize a dense resource like a herd of domestic animals [14, p. 12]. In such societies (mostly very recent ones), there are massive differences between the lifetime reproductive success of the most successful males compared with the most successful females [14, p. 14]. Even so, human foraging patterns are plastic and variable, especially as they began to engineer the supply of resources, and probably have been so over deep time. So it is not surprising that we have some traits that are associated with monogamous, pair-bonded mating patterns and others associated with other mating systems. For example, the two sexes are readily visually discriminable, which would be unusual were we strictly monogamous primates. Wilson *et al.* suggest we see this variation as an opportunity rather than a problem: it gives theorists the ability to test predictions about the relationships between mating systems and other social and individual characteristics. That is true, but made

more complex by the variability of reproductive strategy within societies: Wilson *et al.* point out that even within supposedly polygynous societies, most men only have one wife. Even in those societies, reproductive skew is not as striking as one might suppose. Indeed, perhaps their most important conclusion, based on data that include herders and horticulturalist [14, p. 15], is that sexual selection has probably only been of modest importance in human evolution. The intensity of selection is not very high. Even in their hands, though, it is notable that the flow of information is largely from nonhuman models to human phenomena, rather than vice versa.

I think there is an alternative way of linking work on *prima facie* exceptional human characteristics with more general phenomena, one that does not downplay the extent of difference. Work on human evolution may reveal the subtle and unobvious constraints that have limited the evolutionary options of almost all lineages, even those closely related to humans. If cooperation, communication or episodic memory and mental time travel are evolutionary fuels for success in a wide range of environments, what prevented their evolution in other lineages? Consider, for example, social learning. It is very common across a very wide range of animal taxa (reviewed in [15]); mostly from cues, but with a few cases that involve active teaching [16]. However, in cumulative social learning, an initial innovation is refined by spreading through the community, being improved, with that improvement itself being adopted as a basis for potential further improvement. Outside the hominins, such learning is very rare, perhaps with an example from New Caledonian crows [17], and a few others [18]. There is a considerable debate within the cultural evolution community on the cognitive prerequisites of cumulative cultural learning. It was initially argued that cumulative cultural learning required high-fidelity learning, in particular imitation, and that imitation was itself cognitively demanding [19]. Fairly recently there has been push-back against that position, claiming both that imitation is not especially cognitively demanding and that cumulative cultural learning does not in any case depend on single-episode high-fidelity link-to-link learning. Redundancy combined with fairly simple heuristics guiding model choice suffices for high-fidelity transmission at the community level [7,10,11,20,21]. There is recent evidence that great apes are fairly discriminating and fairly capable social learners [22], some reported in this issue [23], even though it is not their default social learning strategy. That is exemplified by evidence suggesting that when chimps choose to learn socially, their choice of model is influenced by information about how successfully that model deploys the target skill (though admittedly the experimental set-up does not seem a paradigm of ecological validity; see [23]). These considerations suggest that the fundamental constraint on nonhuman social learning is social rather than cognitive. There is not enough social tolerance (let alone active cooperation) for potential social learners to have easy access to enough models for the redundancy effects modelled by Henrich & Henrich to compensate for noisy one-on-one transmission [21].

Consider as well the plasticity of human social relationships. As far as I am aware, no study has tried to compare the ecological and technical diversity of chimpanzee communities (or those of any other ape) with their social diversity. But my impression from surveying the literature is that chimps (and perhaps other great apes) show a good deal of

ecological and technical plasticity, responding to their different environments with appropriate adjustments to their extractive foraging, including varying the extent of their hunting efforts. But their social organization is everywhere the same. Males are always philopatric; their social world is dominance structured, with some male coalitions; groups always have tense interactions with neighbours, with only adolescent females being able to move between groups. There is some variation in communicative behaviour, with gesture varying cross-culturally. But for a chimp sociologist, it would not be too much of an exaggeration to say 'see one chimpanzee society, and you have seen them all' (for a more general survey, see [24]). The same seems to be true of other great apes: orangutans do not seem to be solitary in some places, but living in multi-male, multi-female groups in others, though there is certainly some variation in their social behaviour [25]. By contrast, human foragers show a wide variety of family and social organizations, even when their habitats are (relatively) similar. Contrast the elaborate kinship and marriage systems of Aboriginal Australians [26], and their very strict restrictions on marriageability, with the extremely relaxed customs of the Hadza [27], and the almost as relaxed customs of the San [28].

If this impression of restricted social diversity contrasting with greater ecological and technical diversity is correct, what might the explanation be? One possibility is that the social world of (say) chimpanzee society is at a Nash equilibrium. No single chimp can improve his/her situation by a unilateral change in a pattern of social interaction. Perhaps all the chimps in two neighbouring groups would be better off if they made peace and were able to safely forage in border zones. But no single individual can make peace. In general, the pay-offs to social behaviour (and hence to changes in social behaviour) depend on others' responses. That is much less true of forging behaviour. Only in exceptional circumstances can a single individual change the pattern of social interaction in a group.¹ Another possibility is that great apes (and many other animals) simply lack the emotional plasticity to support social plasticity; to support different patterns of social organization. But hominins (though perhaps only relatively recent hominins) somehow transformed enough natural variation in personality and in patterns of social interaction to make possible the varied forms of forager social life. We do not have an explanation of the origins of human social plasticity, but once we do, it promises to explain why primate social patterns are so generally rigid within a species (though varied in the clade as a whole).

3. Humans as cognitive models: anthropomorphism and Morgan's canon

Claims about human exceptionalism are most plausible when made about human cognitive traits. Individually and collectively, our capacities to understand our physical and social environment seem radically and qualitatively different from those of other animals. As a consequence, using human cognition as a tool to understand the cognitive lives of other animals seems fraught, raising familiar themes of anthropocentrism and Morgan's canon. The worries about over-interpreting animal behaviour are exacerbated by evidence from cognitive psychology that humans are apt to interpret the world around them in agentive terms, even when the

phenomenon in question has simple physical causes. This research tradition began with a famous experiment in which subjects watched simple geometric shapes moving on a screen, and interpreted those movements as agentive interactions: one shape was chasing the other; the other was trying to escape [30]. This research tradition suggests that we have a cognitive bias which inclines us to see agency where there is no agency at all, and human-like agency when there is at most much more limited forms of agency. This bias presumably is particularly acute when we see, not shapes on a video screen or an avalanche thundering down a mountain slope, but animals interacting, with recognizable expressions, and acting in ways which have clear functionality. The more we see physical and functional similarities between humans and these animals, the more powerful the temptation to interpret them as having human-like agency.

Appeals to Morgan's canon are supposed to play a hygienic role here, constraining the temptation to over-interpret animal behaviour: 'In no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale' [31, p. 53]. That said, the exact warrant for Morgan's canon is far from clear. It is often sold as a parsimony principle: explanations that depend only on lower mechanisms are simpler than those that depend on higher capacities. But as Kirsten Andrews has emphasized [32], it is far from clear just what these claims of simplicity amount to, and why, say, a simpler hypothesis about the cognitive mechanism underlying a particular form of behaviour (e.g. an animal's apparent ability to take into account the field of view of another) is more likely to be true. We know, after all, that animals like cetaceans, apes and elephants have large, complex and energetically expensive brains, and that these lineages share a good deal of our evolutionary history [33,34]. I think the regulative validity of Morgan's canon comes not from simplicity but from two other sources. One is the known bias noted above. It is a corrective to a known temptation to error. A second is a preference for a hypothesis that depends on a mechanism for whose existence and capacity we have independent evidence, over a hypothesis that invokes a mechanism whose existence has not been independently established. Associationist explanations that depend on an agent's capacity to, say, associate an act with its consequences, positive and negative, are credible not because they are simple, but because across a huge range of taxa and forms of behaviour we have robust evidence that animals are capable of such learning [35]. Likewise, if, for example, false-belief experiments did provide independent evidence that chimps possess a concept of belief and that they use that concept to guide their expectations of other agents' behaviour, then there is no violation of an appropriately formulated Morgan's canon in explaining tactical deception as the manipulation of belief: in such a case, we would have independent evidence that chimps have that capacity.

I noted above our cognitive bias in favour of agentive explanations. Kokko suggests that, appropriately tamed and appropriately trained, this cognitive bias can be made productive [36]. In her view, the combination of a good feel for the natural history of the animals which are targets of investigation, together with our imaginative capacity to project ourselves into their place and in particular into the dilemmas they face, is often fruitful. When we have a feel for their ecology, we are good intuitive economists, with a good understanding of the various trade-offs animals face through

their life history challenges. But Kokko's rehabilitation is very modest, limited in three ways. (i) It is at best a source of hypotheses; as philosophers of science used to say, this projective strategy is a feature of the context of discovery, not the context of justification. (ii) It is a source of hypotheses about the selective structure of the animal's environment; about the benefits and risks of its various options. It is not a source of hypotheses about the cognitive mechanisms through which animals evaluate their circumstances and make their choices. (iii) Our talents as intuitive economists have bounds; as animals face dilemmas with no analogue in human life, imaginative projection is less fruitful. Kokko suggests that this might explain the fact that biology has been slow to recognize the adaptive benefits of incest.

Even if the bias can sometimes be made useful, the deep difference between human cognition and that of other animals clearly complicates some of the projects canvassed in this issue. Consider, for example, Mason & Shan's proposal to define social behaviour in a way that is independent of valency. As they define social behaviour, a behaviour is social if and only if the presence of conspecifics affects its probability of occurrence [8]. On this deliberately minimalist view, my urinating counts as a social behaviour because (I confess) I am less likely to do it while others are around. This apparently clean and spare definition is threatened by the fact that at least for humans, there is an important distinction between actually being alone, and an agent confidently realizing they are alone, without superstitious anxiety about being observed. There is impressive though still controversial evidence that putting pictures of eyes above an honesty box increases the rate of contribution [37]. Honesty box contributions are social by Mason & Shan's definition, as the rate of contribution varies between the solitary and the social condition. But their approach will not count as social the difference between contributions to the unadorned and the eyes-present honesty box; they are two strangely different versions of a solitary condition. Likewise, their definition is stretched if there are behaviours which are learned socially, but once learned, their expression is not tuned to the presence of an audience. Wearing culturally typical and gender-appropriate clothes might be such a case. Few of us go naked when by ourselves (though some dress very differently in public than when alone). Clambering into my habitual jeans, sweater and hoodie may well not count as social behaviour by their definition.

Anthropomorphism is most obviously relevant when considering the cognitive foundations of actions that are similar, physically or functionally, to those of humans. Piping plovers' injury-feigning distraction displays are functionally deceptive, and its easy to slip into supposing that they are cognitively deceptive; likewise a young chimp's attempts to use his hand to muffle copulation cries. Functionally similar behaviour may of course depend on cognitively similar mechanisms; equally, of course, they may be very different. Ideally the use of humans as model organisms should help us tell whether, for example, a particular form of functionally deceptive behaviour in nonhuman animals depends on such mechanisms as the capacity to track attention, the capacity to represent the differences between what the agent of deception perceives and remembers, and what the target of deception perceives and remembers, and whether the agent can represent and use the connection between a cue and what the target will infer from that cue. This is the idea

behind the project of 'scientific anthropomorphism'. We use the informational and experimental advantages of working with humans to identify the mosaic of components on which sophisticated forms of cognition depend, and then use experimental and observational data to identify (or not) the presence of those components in other agents. Thus Arbilly & Lotem say: 'Our approach is to use humans as a model. The advantage of the human model is that it forces us to consider complex cognitive abilities that are normally not attributed to animals, explain them using simple biological principles, and then, to carefully examine their possible application to animals' [38, p. 5].

Suppose for example that human deception relies on: theory of mind, representing the fact that agents act on their beliefs, possibly false, about their environment; representing gaze tracking and the influence of differences perceptual of standpoints on belief; remembering over time the differing samples of information other agents have; and representing the connection between a perceptual cue and a belief (for example that another agent will both recognize the producer of a copulation cry and recognize it as a copulation cry). We might then use experimental and observational information to (for example) assess whether chimps do in general recognize agents from their voices, or whether they can remember in the afternoon what another saw in the morning. In some respects, Burkart *et al.*'s paper on cooperative breeding converges with this strategy: they point out that cooperative breeding in humans is a synthesis of three cooperative strategies, two of which are usually found in separate lineages: biparental care, care from older to younger siblings and alloparental care from plural breeding [39]. So they see human cooperative breeding as a mosaic of associated elements, in both its behavioural organization (where the help comes from, and what are the costs and benefits for the helpers and the helped) and in its proximate underpinnings (these include both hormonal mechanisms for much elevated social tolerance and hormonal mechanisms that drive positive prosociality).

In principle, this is a good idea; the problem is with its implementation. To the best of my knowledge there are no complex human cognitive capacities for which there is a consensus decomposition into interacting simpler capacities. Not language; not theory of mind; not causal reasoning; probably not planning and conditional reasoning; not episodic memory and mental time travel. There continues to be intense debate on the extent to which human cognitive organization is modular (contrast [40,41]), and on the extent to which computational models of cognitive processes are productive and explanatory (contrast [42,43]). Arbilly & Lotem [38] attempt to escape from this problem in part by considering psychological phenomena that are not, *prima facie*, psychologically complex (like hunger), and in part by giving rather deflationary accounts of the supposedly complex cognitive phenomenon in question.

However, this strategy has two problems. First, the deflationary accounts of human cognitive competence are sometimes not very plausible. For example, they follow Clayton & Dickison [44] by describing the results of corvid caching behaviour as showing 'episodic-like' memories, because the corvids are shown to keep some track of the time between caching and retrieval. Their analysis follows Clayton & Dickison in treating episodic memory as who-what-where-when memory [44]. But semantic memory

includes both knowledge of general phenomena (that a cached worm decays quickly) and of particular events. I remember that World War I was triggered by the assassination of the Archduke Ferdinand by Gavrilo Princip on 28 June 1914. That is a who–what–where–when memory, but it is a paradigm case of semantic memory. The distinction between semantic and episodic memory is *not* the distinction between memory for the particular and the general. Rather, it is a distinction between a form of memory that abstracts away from the source of the information remembered, and a form of first-person memory, where the source of the information is part of the information retained in memory. The distinction is hard to make precise, and that is one reason why the nature of episodic memory, and appropriate empirical, behavioural tests for it, remain problematic. Second, to the extent that the project does succeed in showing that target cognitive competences depend on early evolving, phylogenetically widespread associationist mechanisms, it is no longer clear that the investigatory dogleg through the human examples adds to the explanatory project. So, for example, in discussing decision-making, planning and language, Arbilly & Lotem [38] point out that the behavioural demands on animals are often complex, and call for controlled activity, timed to the right time and place, and with little margin of error. Given this, it is certainly appropriate for behavioural ecologists to identify contexts in which we would expect selection for planning, for the control of complex motor sequences and for representing categories functionally rather than sensorily. But why route that investigation through questions about language or human capacities more generally?

4. An upside: humans, data and mundane traits?

In some respects, humans really are just another unique species of mammal. For example, no one thinks anthropocentrism is a problem with physical comparisons. In pursuing proximate and ultimate questions about the development of physical abilities, and on whether there are (for example) general indexes of physical skill that will be manifest in different contexts, it makes a lot of sense to choose humans as experimental animals. Investigators have access to a large sample size, and can often be confident that their subjects both understand what is asked of them and are well motivated to perform to the best of their abilities. Moreover, the research community has access to rich information about human populations and about the changes in human populations over time (though with declining reliability as it extends into the past), so we can explore a large variety of life history and demographic questions through large amounts of generally reliable and sometimes historically deep data; for example about persistent differences in male and female life expectancy, or about the sensitivity of female reproduction to context.

One informational difference between studies of humans and of other animals is that experimenters can talk to their human subjects. A number of the papers in the special issue mention this advantage: experimenters can find out not just how subjects act, but also their views on why they made the choices they did. The most systematic exploration of this difference was that of Kasumovic *et al.*, in arguing for the advantages of humans as a lever to improve contest

theory [45]. Animal contests are a classic domain of the application of costly signalling theory. There is some overlap of interests between the contestants, as actual fights are expensive, especially to the loser, and so in many circumstances an agent who is likely to lose should concede, to the advantage of both. But the very fact that contestants sometimes back off creates the temptation to bluff. Thus, in contests, each agent faces a difficult informational challenge in assessing the true capacity of their opponent; one that they manage through some variable mix of cues and signals, though as Kasumovic *et al.* point out, it is very difficult to know just how accurate these assessments are. In addition, A's decision on whether to fight or concede depends not just on their assessment of B's power; it depends on A's assessment of A's own capacities, and self-assessment is far from informationally trivial. Moreover, there is suggestive evidence of an interaction between self-assessment and capacity: contest losers are more likely to lose again next time, and winners are more likely to win again next time. To improve contest theory, it is important to incorporate the impact of self-assessment, experience and their effects on decisions to withdraw or not, on actual contests. Kasumovic *et al.* suggest that human studies are a good vehicle for deepening contest theory in this way for two reasons. One is that we can effectively simulate contests through video games. There is evidence that video games recruit the same psychological and motivational mechanisms as physical contests, and that success and failure have similar psychological and motivational effects. Yet video games are not just cheap; they lend themselves to experimental manipulation of the conditions that determine success or failure. The experimenters could, for example, probe the effects of success with differential success distributed across a population of players equalized in skill.

The second reason is that we can ask agents about the clues they use to assess themselves and others. Moreover, we can ask humans what they would do in a range of possible but not actual circumstances: 'Measuring contest outcomes in non-human animals is costly. Manipulating perceptions of fighting ability—for example, by affecting an animal's ability to signal—can also be ethically problematic. Because humans can suspend disbelief and think hypothetically, utilizing humans in contest theory research can circumvent the ethical and methodological issues of measuring contest decision-making in non-human animals' [45, p. 9]. This line of thought raises a problem: humans do not always have insight into the bases of their own action. For example, Kasumovic *et al.* show that one cue humans use in assessing potential threat is the ratio between face width and face height. Not many of us could report on that. They are aware of this problem and suggest a solution: psychologists have various experimental techniques that circumvent the need for conscious awareness and explicit report: examples are eye tracking and priming. However, these methods have a limit. Cognitive science distinguishes between system one cognitive processing and system two cognitive processing. System one processes are fast, automatic, parallel, not much subject to introspective monitoring. System two processes are slow, top-down, serial, subject to introspective monitoring and report [46]. The reliability-checking methods Kasumovic *et al.* have in mind tap into system one processes. But hypothetical thinking and the consideration of counterfactual scenarios is a standard instance of a system two process.

Nothing guarantees that what an agent thinks they will do in such a scenario is what they will do in it.

A number of papers in the issue exemplify other versions of this idea: there is information to be had about humans that would be difficult or impossible to collect about other animals. Moreover, these are cases in which the challenges of anthropocentrism and exceptionalism are less compelling. In this connection, Weiss's contribution is an interesting intermediate case [47]. Weiss argues that a standard social psychology model of human personality types, characterized along five dimensions of difference, is both a good model of human individual difference, and extends quite well to intraspecific differences among nonhuman primates. The dimension are: extraversion, agreeableness, conscientiousness, openness to new experience and neuroticism. The model has traction in the human case, he argues, as there is quite strong between-subject agreement about where known individuals fall in this space. Moreover, the personality maps seem to be fairly stable over time, and there is some reason (based on twin studies and the like) to think that personality type has a genetic component. On Weiss's view, this research on human personality types latches onto something real. Moreover, he suggests it can be extrapolated to other primates because (i) there is quite good evidence of inter-rating reliability; (ii) there is evidence of stability across time (not complete stability—in both humans and primates there is some, fairly predictable, change over time); (iii) there is modest evidence of heritability; (iv) finally and importantly, there is some evidence of validity. The differing personality types of agents have reasonably consistent effects on life outcomes. So Weiss argues that a model of personality developed for humans extends fairly naturally to nonhuman primates.

Weiss suggests that the theory is successful because it is simple, straightforward, and under challenge the theory was developed empirically into more robust forms [47, pp. 21–22]. That is a plausible explanation of why it is a decent model of human personality. It is no explanation of its extension to other primates. For that to be valid, we must conjecture that personality type depends on ancient features of the cognitive system, features not profoundly transformed through hominin evolution. That seems very plausible for three of the standard dimensions: extraversion, agreeableness and openness to experience (i.e. neophilia versus neophobia). But what of conscientiousness and neuroticism? What would conscientiousness even mean in the ruggedly individualist and living-in-the-now world of nonhuman primates?

So there is still something of a question about the export of the full-blown human personality structure to primates. There is no such problem with the two papers focusing on physical skills, though there is, as I shall note, still a challenge in getting the human data to speak to more general models. One of those takes up the difficult problem of explaining the existence and stability of inter-agent variation in traits

that seem importantly relevant to fitness. Wilson *et al.* use soccer to probe the basis of physical excellence, and variation in physical excellence [48]. Their conclusions are initially surprising: balance, for example, turns out to be very important. But the upshot of the paper for behavioural ecology seems mostly to be a cautionary tale: soccer skill depends on a complex mix of ingredients, and the same will be true of physical agency in the world. In real ecological situations, successful action depends on smoothly integrating a range of physical skills, which interact in complex ways to explain success or failure. This is surely right: no doubt cheetah hunting success depends not just on speed but on balance, agility, timing, strength. The problem is that the traits that are easiest to measure (like maximum running speed) are just one ingredient in physical capacity, and probably not a very reliable index of overall capacity. The conclusion is very plausible, but it is hard to see what, say, a behavioural ecologist working on cheetah behaviour and variation in behaviour is to do. They do not have access to agents as tractable as soccer players. Should we conclude that the problem of intraspecific variation is for now *too hard*? For the variation we can measure is not the variation that will determine success and failure in natural environments?

5. Final words

The upshot: there is potential to leverage the study of humans. Sometimes that is for mundane reasons. Most obviously, in our basic physiology we really are just another mammal, and for medical purposes, we have invested heavily in researching our own physiology. Our perceptual systems, likewise, are unlikely to be very different from our relatives, and here being able to talk to your subjects really matters. For example, many experiments on vision rely on perceptual effects that subjects must report: on illusions; colour and colour changes; the limits of discrimination. It would be extraordinarily difficult to mimic these experiments on nonhuman animals. The more intriguing possibility, one that I have recommended, is to exploit our atypicality rather than downplay it. To explain, for example, the species-specific rigidity of primate mating systems by explaining why family organization is so plastic in our lineage. Differences and their explanation are informative.

Data accessibility. This article has no additional data.

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Endnote

¹For a striking exception, see [29].

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