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

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Humans as a model for understanding biological fundamentals

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How special are humans? This question drives scholarly output across both the sciences and the humanities. Whereas some disciplines, and the humanities in particular, aim at gaining a better understanding of humans *per se*, most biologists ultimately aim to understand life in general. This raises the question of whether and when humans are acceptable, or even desirable, models of biological fundamentals. Especially for basic biological processes, non-human species are generally accepted as a relevant model to study topics for which studying humans is impractical, impossible, or ethically inadvisable, but the reverse is controversial: are humans 'too unique' to be informative with respect to biological fundamentals relevant to other species? Or are there areas where we share key components, or for which our very uniqueness serves to allow novel explorations? In this special feature, authors from disciplines including biology, psychology, anthropology, neuroscience and philosophy tackle this question. Their overall conclusion is a qualified yes: humans do tell us about biological fundamentals, in some contexts. We hope this special feature will spur a discussion that will lead to a more careful delineation of the similarities and the differences between humans and other species, and how these impact the study of biological fundamentals.

1. Introduction

A key tenant of biology is that there are biological fundamentals that are applicable broadly across living things. Therefore, although the research programmes of most biologists necessarily focus on a few species at most, they generally do so in the belief that their findings are applicable to a wider range of taxa, and that they thereby provide insight into biological fundamentals. This is true whether one is exploring a widely shared phenomenon (i.e. male competition for mates in species with maternal care) or the intriguing exception (i.e. female competition in species like seahorses, where the males provide offspring care). Indeed, explaining how one's work relates to fundamental questions in biology is essential for most biologists. Aside from a deep-seated belief that these fundamentals exist, and can help explain general phenomena, there is a more practical consideration; virtually every paper published in a generalist, especially top-tier, journal, as well as grants written to almost any funding agency, will require a section that explicitly details how the work informs our broader understanding of general biological principles.

Particularly those biologists studying non-human animals often go one step further, and not only argue that their results can teach us about biological fundamentals, but they also either explicitly or implicitly explain why their findings are important for understanding our own species. Indeed, it is beyond doubt that non-human animals can act as powerful models for answering questions that are impossible or unethical to address in humans directly. However, whereas studying other species can thus help us develop an understanding of and therapies applicable to our own species, biological research on humans typically

focuses solely on gaining a better understanding of *human* behaviour, evolutionary history, genetics, anomalies, etc. Despite humans being animals, results obtained in humans are generally considered to be valid primarily or only for humans, and it is often argued that humans' uniqueness renders us irrelevant to our understanding of other species, or indeed, for biological fundamentals.

We believe this asymmetry to be a critical oversight, and that by failing to recognize the value of research on humans across species boundaries, we miss out on a great opportunity to further improve our understanding of the key principles of biology. But are we alone, or is this a concern that is shared by biologists across a range of research areas? In this special feature, we provide a diverse set of perspectives on whether and, if so, how we can use humans as a model for the study of fundamental biological principles. Our set of authors includes biologists, psychologists, anthropologists, neuroscientists and philosophers, who cover both topics that are typically seen as primarily related to humans (e.g. sport), others that are primarily considered in relation to non-humans (e.g. trade-offs), and yet others that span the divide (e.g. personality, cooperation, sociality, cognition). As a result, we have a diversity of perspectives and a variety of answers to our key questions. This provides a nuanced consideration of this topic that we hope will drive the field to think more carefully about humans' place in biology.

In this introductory paper, we begin by outlining our reasons for editing this special feature on the value of humans for the study of biological fundamentals, and why we believe this to be a particularly timely moment to discuss this topic. We then go on to list the key reasons we see for why many consider non-human animals to be good models for humans, but the opposite is considered less self-evident. Following this, we discuss our reasons for explicitly including humans in our discussions of biological fundamentals. In our ultimate section, we summarize the views of the authors in this special feature, then conclude with some thoughts on future directions. It is our hope that if you have come across our paper separately from this special feature, you will use this as a starting point to dig deeper into each of the readings it comprises.

2. Why this special feature?

In order to understand what brought us to propose this special feature, we ask you to first pardon a brief digression into our personal interest in this question. In particular, how did we come to view humans' presumed uniqueness as an asset rather than a burden, seeing humans not only as a part of biology, but also as a treasure trove of data? Why do we believe that our specialization makes us an ideal subject for understanding fundamental questions in biology, and moreover, why did we feel that this was an issue worth addressing now?

We both are scientists who got our start exclusively studying non-human species and who have come into studying humans more recently, attracted to what they have to offer as a model species. We strongly feel that there are some general biological questions that are best answered by studying humans, either by themselves or in conjunction with comparative research programmes encompassing multiple species, and that our work on humans is relevant for informing our work with other species. We also feel that this is broadly applicable across areas of study. Indeed, although we both trained as evolutionary biologists, we also represent rather different areas of study. One of us (S.F.B.) studies decision-making behaviour, and in particular, how individuals make decisions in the context of cooperation. The other (E.P.) studies the causes and consequences of individual variation, with a special interest in the quantitative genetics of life-history traits. We do not attend the same meetings, and rarely even publish in the same journals, not to mention are housed in different university departments. However, we both have found that we routinely have two different conversations, one with our 'human' colleagues, and one with our 'non-human' colleagues. While we find that our 'human' colleagues tend to be quite receptive to our research, and want to know how our work might inform their understanding of human behaviour, our 'non-human' colleagues are not always terribly interested in our human work.

Aside from our personal interest, this is at this moment in time a key issue for *Proceedings B*. It has always been a flagship journal for studying biological fundamentals, but, similar to our personal experiences interacting with our colleagues, of late there has been a difference of opinion about the degree to which human research is reflective of biological fundamentals and, therefore, the degree to which human research belongs in the journal. Trivially this relates to the question of what counts as a biological fundamental (i.e. is studying dictatorial leaders in modern human societies relevant to understanding dominance and leadership in other species?). At a more fundamental level, this relates to the question of whether humans are so far removed from biology that we can no longer learn anything that is 'fundamental' to all species from studies of humans. To explore these issues further, and to highlight our feeling that *Proceedings B* provides a great service by being one of the few journals that includes both human and non-human research, we have proposed this special feature.

3. Why the disconnect?

Although Darwin famously left humans out of 'On the origin of species', he did hint at the relevance of his ideas to our own species [1], and he explicitly included them in his later writings [2,3]. The original exclusion was likely due to Victorian religious and cultural sensibilities, and Darwin's later inclusion of humans shows that at least some biologists recognized these similarities. Indeed, in the early twentieth century, psychologists often considered both humans and other species in their work (e.g. Robert Yerkes's work on intelligence). When, then, did this change, and why? Although we cannot answer that question in full here, we have a few thoughts on the matter.

First, and most practically, in many cases the people who study humans do not interact with those studying other animals. For example, researchers studying human behaviour are typically in anthropology, psychology, economics, political science or philosophy departments, while non-human animal behaviour is mostly studied in ecology, biology, evolution, behaviour or, increasingly, neuroscience departments. Indeed, the 'exception that proves the rule' may be primatologists, who are often housed in psychology or anthropology

departments, presumably because of these species' phylogenetic closeness to humans. Perhaps not surprisingly, our subjective experience is that scientists who study non-human primates may be among the most likely to explicitly compare their results to human outcomes, or to use human models to guide their research (see, for example, Weiss' contribution to this issue; [4]). In addition to this physical separation, researchers studying human behaviour often attend different meetings and read different journals than those working on behaviour in non-human species. Although we are not the first to note this separation (see, for example, [5,6]), we feel it plays a key role in exacerbating the tension over whether humans can help us understand biological fundamentals.

Second, there are historical reasons for this disconnect. This separation was not always as strong as it is now; the emergence of sociobiology [7] resulted in a flourishing in the evolutionary study of human behaviour in the 1970s. However, this was rapidly followed by a major backlash. Given that we both missed the excitement, we refer readers to one of the many first-hand accounts of this controversy (for a recent example, see [8]). Irrespective of how and why it came about, it resulted in a purging of sociobiology and, by association, of biological perspectives on human behaviour in general. Even if there has been a modest resurgence of late (as evidenced by the contributions in this special feature), the effects of this uproar are still felt today; social scientists remain wary of biological perspectives on human behaviour and its possible implications, and many biologists continue to avoid any association with the taint of sociobiology.

Third, humans are often seen as being wildly distinct from other animals: in several ways we appear more different from our closest evolutionary relatives than are other equally-closely related groups of species. In addition, we possess characteristics, like language [9,10] and extreme prosocial behaviour [11,12], that, while they have roots that we can see in other species, have also been argued to fundamentally set us apart. Nevertheless, being human ourselves, we are biased towards seeing ourselves as distinct and special. Much as history books are written by the victors, biology texts are written by the humans, and we are very good at emphasizing the distinctions and minimizing the underlying similarities. The implicit assumption that we are somehow outside of biology, however, not only blinds us to cases in which other species might be better models for a given question than are humans, but also means that we fail to see how research on ourselves has the potential to cross species-boundaries, informing us about the animal kingdom at large. Hence, although humans are certainly, to use an unfortunately ever-present redundancy, 'more unique' in many ways than other species, we are no less interesting for understanding fundamentals than an egg-laying mammal or an air-breathing fish. Seeing humans as 'too unique' to be of general relevance hinders our ability to see continuity across species and uncover biological principles that work with *all* animals, not just *non-human* animals.

Finally, humans are not only considered to be 'too unique', but at least subconsciously we still tend to be influenced by the old idea of the *scala naturae*, placing humans firmly above all other life forms (but below angels and God). Whenever we find a 'lower' species that does something previously only seen in 'higher' species, it is front-page news and we are surprised and impressed (for example, coordinated hunts between groupers and moray eel; [13]), but when a 'higher' species uses a similar mechanism to a 'lower' one, this tends to receive far less attention. Indeed, this latter point is no doubt in part because when discussing humans, there is the ubiquitous, typically untested, assumption that humans' outcomes are the result of higher-order cognition. In contrast, showing a similar phenomenon in other species would require extensive testing and controls to demonstrate that they are not relying on a lower level cognitive mechanism.

4. Why consider humans?

Above we have argued that we should not *a priori* ignore humans when it comes to the study of biological fundamentals, but can we go beyond that? Are there some biological fundamentals for which humans are in fact a particularly *good* model species? For both practical and theoretical reasons, we answer this question with a resounding 'yes'.

First, for humans we have access to historic and contemporary datasets that are unmatched in any other species in terms of both quality and quantity. For instance, we have copious quantities of genetic and genomic data, as well as individual-based longitudinal data that cover everything from education to friendships to careers to medical issues. Although people are notoriously poor at self-reporting [14], this is further aided by the fact that no other animal can articulate their conscious thoughts and feelings. It is this data-richness that provides us with a unique ability to see how genes, environment and culture interact over the lifespan to generate and maintain variation within and among individuals, populations and species, both in space and time. Related to this, because research on humans is so broad (e.g. genetics and genomics, behaviour, cognition, neuroscience, endocrinology, development, life history, infection dynamics, culture, environmental interactions, evolutionary genetics and morphology), there is an opportunity for a degree of interaction that is unattainable in other species. As a result, we can link across ideas and disciplines in a way that is possible only in humans.

Second, our extreme specialization for cognition and cumulative culture allows us to rely on cognition and problem-solving [15], more so than strength and physical power, when it comes to re-shaping our environment to suit our needs, and to occupy what may be the broadest range of environments of any other single species. However, although this means that humans (and hominins before us) can occupy an unusually broad range of niches as compared to most species, none of these features are unprecedented; niche construction is common across species [16], and other species also make dramatic changes to their environments. Moreover, if we are to understand underlying biological principles, we must be able to explain *all* species, including extreme ones.

Third, while we may be particularly aware of the intricacies of the many environmental and cultural factors that make us who we are, it is precisely this level of insight that provides us with the ability to dissect and account for those intricacies. Indeed, as we are probably the species that has experienced the most dramatic changes in our environment (see also previous paragraph), humans present an excellent model to study the evolutionary, ecological and demographic consequences of environmental change.

Finally, a range of experimental and analytical techniques that were refined in humans can readily be applied to non-human species. For example, the emerging line of work using techniques from experimental economics has proven particularly helpful in understanding behaviour in other species [17–22]. Indeed, we would never have dreamed of the degree to which other species cooperate if we would not have had our own species as a starting point. Similarly, technology developed for the large-scale sequencing of whole human genomes, as well as methods to analyse them, is increasingly applied to answer fundamental evolutionary questions in a wide range of species [23–25].

5. But do others agree?

In this special feature, we bring together researchers from either side of the divide who share our interest in the value of humans as a model for understanding other species and biology in general. Within their areas of study, these authors consider the ways in which models developed for humans are being applied to better understand non-human behaviour in the broadest sense, or how they could be in the future. While not all of them may agree with us, or with one another, by exploring this issue they provide a balanced overview that we hope kick starts a lively and constructive discussion which will ultimately lead to a greater consensus that positively impacts our understanding of biology across all species. Below we will briefly introduce all contributions and how they fit within the overarching theme of this special feature, with the hope that this tasting platter will leave the reader hungry for more.

Above we suggested that humans provide a treasure trove of data that is of a quality and resolution that is rarely attainable for other species, and that attempts to analyse these data have led to a range of generally applicable methodological and analytical advancements. Indeed, Briga *et al.* [26] show how research tools first developed to gain a deeper understanding of the dynamics of human populations (demography) and the importance of genes versus environment (i.e. nature versus nurture) in shaping individual variation (quantitative genetics) have now successfully been applied to a wide range of non-human species and questions. Similarly, research aimed at understanding human cooperation using game theory has been applied successfully to the study of cooperation in other species [27].

Furthermore, and arguably even more excitingly, researchers have gone beyond the adoption of analytical tools: originally developed by psychologists, the human model of personality has now successfully been applied to non-human species, and extensive work indicates that it is a good model of the behaviour of other species than our own [4]. Similarly, research initially aimed at understanding traits often believed to be uniquely human, including some aspects of cooperation [27], menopause and a prolonged post-reproductive lifespan [26], and culture [28], has now revealed similar characteristics in other species. These contributions provide empirical examples of how a human model has demonstrably enabled a deeper understanding of the biology of other species and thereby illustrate how research on humans has fundamentally altered our perception of what makes us human, and what is not unique to us. Together, these have helped to identify and understand biological fundamentals. As a matter of fact, Weiss [4] argues that the reason that studies of personality in non-human species have come so far is because the human model was both simple and rigorously tested before it was applied to other species, leading to a relatively well-described model with good explanatory power.

While this convincingly shows how methods and concepts developed to gain a better understanding of human biology can be applied to other species, it does not answer the arguably more controversial question of whether human data can provide insights into the biology of other species. Several of the authors in this special answer also this question with a resounding 'yes': for example, Kasumovic & Blake [29] make the case that when it comes to the study of human contest behaviour, the adoption of tools developed in psychology has the potential to significantly advance our understanding of contest behaviour and dynamics, not only in humans, but also in species that are not amenable to these methods. Others were positive, but with caveats. For example, Bshary & Raihani [27] highlight the general insights that may be offered by studying human cooperation, but carefully discriminate between the unique possibilities allowed by humans' advanced cognitive tool box, and in particular language and language-enabled culture, and the likely substantial similarity in other mechanisms underlying cooperation (e.g. endocrine mechanisms). Similarly, Burkart *et al.* [30] consider prosocial behaviour and its relationship to cooperative breeding, concluding that while there are unique aspects to human cooperation, they are strongly underpinned by shared endocrine mechanisms across the animal kingdom and, at least among primates, some shared psychological mechanisms as well. In his synthesis of all contributions to this special feature, it is the latter perspective that Sterelny [14] agrees most closely with. His conclusion is that, in many ways, humans can make an excellent model system: while there are some areas, such as cognition, where humans may be too advanced compared to other species to be of relevance, in terms of our physiology and perception, we 'really are just another mammal'. Indeed, he argues that our knowledge of biological fundamentals may be best served by exploiting our differences (e.g. see Wilson *et al.* [31]) and to gain data that are impossible obtain in other species.

In addition to the review and opinion papers arguing for or against the applicability of results obtained in humans to other species, we are fortunate to have two empirical contributions that directly address this question at hand: Wilson *et al.* [32] expose football [soccer] players to a battery of tests to quantify the relative importance of athleticism and skill in shaping performance. Both studies argue strongly for the importance of interdisciplinary research, and they make a case for the relevance of their findings not only for understanding humans, but also other animals. Vale *et al.* [28] even go one step further: by performing the same test in both human children and chimpanzees, they are able to directly test whether results obtained in one species are applicable to the other.

Earlier we stated that our aim was to provide a balanced overview of the pros and cons of humans as a model for the study of biological fundamentals. However, as we have invited researchers to contribute to this special feature that work on both human and non-human systems, or that at least have an interest in how the two may complement each other, it could reasonably be argued that we have put

together a group of authors that is not representative of biologists in general. To gain a more representative picture of the prevailing opinion on the value of research on humans and its ability to address general biological questions, Briga *et al*. [26] therefore chose to poll the evolutionary biology community. Although they received encouragingly positive responses, a significant proportion of the respondents nevertheless expressed some scepticism, raising the problems posed by the inability to perform experimental manipulations, and our unique and arguably unnatural environment.

This raises an intriguing problem: do those aspects that make humans such a good model system, such as our ability to ask them questions or to provide them a relatively complex task, at the same time limit their general relevance as a model species (see e.g. Kasumovic & Blake [29])? Or, as both Wilson *et al*. [31] and Bshary & Raihani [27] argue, even if humans are unique in terms of their mating system and degree of cooperation, respectively, should we strive towards understanding all variation, including the extremes? Moreover, as Bshary and Raihani write, even if some aspects vary, these should not distract us from the underlying similarities.

There is one other key issue that must be considered, which is the degree to which the very fact of our being human may influence our ability to assess this question. While there may be problems with human data, Kokko [33] argues that it is especially the fact that we are human ourselves that may pose a problem. While she acknowledges that 'putting oneself in another organism's shoes' can act as a useful hypothesis generator, she at the same time warns against taxonomic chauvinism and suggests that looking at the natural world through a human lens may hinder scientific progress, especially for traits for which humans are outliers. Interestingly, at the same time Arbilly & Lotem [34] argue explicitly against *a priori* separating human from non-human animals. In their contribution, they argue for the utility of what they call 'scientific anthropomorphism', or using what we know about human behaviour as the foundation of initial hypotheses regarding apparently similar behaviours in other species. When faced with a novel behaviour, they write, this is a very effective way to generate empirically testable hypotheses. Finally, Mason & Shan [35] address another component of this issue, which is that for some behaviours that are key to humans, definitions are inherently value-laden. They address this with the concept of sociality, for which they argue that discussions should be based on frequency and direction independent of valence to avoid the human bias.

6. What next?

Here we have highlighted an asymmetry in the degree of interaction and the flow of information between research on humans and other species. We believe this exacerbates the perceived differences and downplays the similarities between humans and the rest of the living world, and it limits our understanding of the biological fundamentals that shape them. By understanding the degree to which species are using the same mechanisms and are reaching the same endpoints, that is by understanding both the similarities and differences, we learn about the key principles in biology that underlie these behaviours.

We believe this requires us to re-think our role in biology and see humans as a useful and informative part of biology. While, as the papers in this special feature amply demonstrate, it is not the case that all findings in humans are important for understanding biological fundamentals, many are, and changing our perspective on how we see humans will help to highlight these areas of synergy and improve our science. With the caveat that we invited authors who we anticipated would be open to at least considering the question, the enthusiasm with which they contributed to this special feature suggests we may slowly be moving towards a re-assessment of humans' role in biology. This push must go beyond this special feature, however, and both the writers and the readers of these words must incorporate them into their thinking. As is demonstrated so effectively by all contributors, progress comes with open-mindedness to both the strengths and the limitations of both our own and others' approaches.

In practice, this means paying attention to a different literature, attending new meetings, or simply walking down the hall or across campus to talk to that colleague you had been meaning to meet for so long. We think that this will lead to better science, and that the rewards of doing so will be worth the costs that come with exploring a new literature or field. Indeed, many universities or foundations offer support for faculty who wish to diversify their interests, which may assist with at least the financial costs. We have both done this and, while it is scary to jump into a field about which we know nothing, it is also fun and rewarding.

Overall, we are very pleased that the contributors to this special feature have done such a thoughtful job reflecting on these questions. We have immensely enjoyed this opportunity to ask others their thoughts on what humans can tell us about biological fundamentals, and we hope that you enjoy reading this just as much. Our deepest hope, however, is that it marks the beginning of a conversation that leads to an increased inclusion of humans into the work of biologists (and the reverse) with the goal of a truly integrated biology that is able to unearth fundamentals relevant to *all* species, not just most species.

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