

## PROCEEDINGS B

rsob.royalsocietypublishing.org

## Review



**Cite this article:** Kokko H. 2017 Give one species the task to come up with a theory that spans them all: what good can come out of that? *Proc. R. Soc. B* **284**: 20171652. <http://dx.doi.org/10.1098/rsob.2017.1652>

Received: 18 September 2017

Accepted: 16 October 2017

**Subject Category:**

Evolution

**Subject Areas:**

evolution, behaviour

**Keywords:**

biological diversity, humans, progress in science, taxonomic bias, behavioural ecology, evolutionary ecology

**Author for correspondence:**

Hanna Kokko

e-mail: [hanna.kokko@ieu.uzh.ch](mailto:hanna.kokko@ieu.uzh.ch)

One contribution to a special feature 'Humans as a model for understanding biological fundamentals'.

# Give one species the task to come up with a theory that spans them all: what good can come out of that?

Hanna Kokko

Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

HK, 0000-0002-5772-4881

Does the progress in understanding evolutionary theory depend on the species that is doing the investigation? This question is difficult to answer scientifically, as we are dealing with an  $n = 1$  scenario: every individual who has ever written about evolution is a human being. I will discuss, first, whether we get the correct answer to questions if we begin with ourselves and expand outwards, and second, whether we might fail to ask all the interesting questions unless we combat our tendencies to favour taxa that are close to us. As a whole, the human tendency to understand general biological phenomena via 'putting oneself in another organism's shoes' has upsides and downsides. As an upside, our intuitive ability to rethink strategies if the situation changes can lead to ready generation of adaptive hypotheses. Downsides occur if we trust this intuition too much, and particular danger zones exist for traits where humans are an unusual species. I argue that the levels of selection debate might have proceeded differently if human cooperation patterns were not so unique, as this brings about unique challenges in biology teaching; and that theoretical insights regarding inbreeding avoidance versus tolerance could have spread faster if we were not extrapolating our emotional reactions to incest disproportionately depending on whether we study animals or plants. I also discuss patterns such as taxonomic chauvinism, i.e. less attention being paid to species that differ more from human-like life histories. Textbooks on evolution reinforce such biases insofar as they present, as a default case, systems that resemble ours in terms of life cycles and other features (e.g. gonochorism). Additionally, societal norms may have led to incorrect null hypotheses such as females not mating multiply.

## 1. Introduction

You can study zebras all your life, and throw all other hoofed animals into the bargain, but what do you then know about zebras or hoofed animals? Next to nothing compared to what you know about yourself. So if you are interested in social theory based on natural selection, isn't it often better to start with yourself and then argue outwards? [1, p. 15]

Not all of us are as willing as Robert Trivers [1] to admit that scientific ideas very often come to us through a process of self-inspection. But how much self-inspection is healthy, in the sense of helping us to propel science forward? This depends on the reliability of the self-inspection programme in two distinct ways. In the first part of this essay, I will reflect on our ability to answer evolutionary questions correctly when we begin with some level of baseline knowledge, which in itself is part intuition, part scientific results that have already accumulated. This pot of knowledge suffers from an unavoidable imbalance: the intuition comes from being human, while the facts may have equally well accumulated from observing pigeons [2]. Thereafter, I will ask whether being a human—a fact we cannot change—might also hamper our ability to pick interesting questions to study in the first place.

While we cannot help being humans, we can choose our study objects relatively freely. Facts can be established via the study of pigeons, *Drosophila* or *Escherichia coli*, or via observing or experimenting on human subjects. Have human studies been helpful at all for understanding life in general? The simple answer is yes: as an example of a case where attention to our own biology has led to general insight, the discovery of sperm occurred when Antoni von Leeuwenhoek turned his microscope from pond life to bodily fluids [3], including his own sperm [4]. He then proceeded to find these little ‘animalcules’ in the semen of many animals, also determining that they were made in the testes [5]. In this case, humans do happen to share a trait, sperm production, with all anisogamous life (correct if we consider pollen equivalent to sperm). Should microscopy of human sperm have been impossible at the time, it probably would not have taken long for this prolific researcher to find his samples from other animals. So: is the study of humans important?

## 2. The first problem: interpreting causalities as a human being

The discussion of the role of human studies as inspiration for uncovering general rules of life becomes much more interesting when one shifts away from finding facts (sperm exist) to the interpretation of causalities. This is the domain of the Trivers quote. It is intriguing that Trivers himself has also emphasized how routinely we lie—not only to each other, but also to ourselves—about our true motivations behind our actions, and has proceeded to investigate whether natural selection itself might equip us with such mental blinds [6]. To what extent should we then follow his advice to take one species (ourselves) as a vantage point from where to then argue outwards?

Trivers’ phrase ‘knowing about zebras’ refers to an understanding of *why* something occurs in the zebra world. As pointed out by Tinbergen [7], when a *why* question addresses how a particular trait of a particular organism has come about, one can envisage four different answers to the same question. Each of them can be correct, without any answer pre-empting the need to study the other three versions (table 1). This is a point about scientific understanding itself: it is never a complete description of what happens in nature. Rather, scientific progress is about making us, humans, able to simulate a process in the conscious part of our brains so that we find the explanation satisfying. This human-centric view of understanding is particularly important when we consider the one ‘why’ that refers to *function*, also called adaptive value (or in Tinbergen’s parlance, survival value): this is the why that equates ‘why is this trait there’ with ‘what is it for; how might it aid reproductive success?’ This is the one *why* for which the human experience becomes particularly pertinent, especially so if we are specifically interested in the subset of traits classifiable as behaviours (like Tinbergen was).

### (a) How to put oneself in another organism’s shoes. . .

There is a truly intriguing consequence of the fact that we acquire a sense of understanding when we ‘get’ the purpose of a behaviour, in a way that Trivers and Tinbergen alluded to. Our thought processes begin to resemble the phrase ‘putting oneself in someone else’s shoes’. Behavioural evolutionary ecology in particular teaches students to analyse situations where

**Table 1.** Tinbergen’s ‘four why’ scheme. (Tinbergen’s original names for the categories have experienced some modernization in the literature, with e.g. survival value being replaced by a more general task of understanding the relationship between a trait and fitness, as adaptation is not only about maximizing survival. I give Tinbergen’s original category names in italics. As pointed out by Bateson and Laland [8], some (insignificant) confusion may also follow from the fact that the four ‘why’ also tend to be split into two ‘why’ and two ‘how’ questions.)

	the ‘how’ questions (proximate)	the ‘why’ questions (ultimate)
focus on	(physiological)	function, adaptive
current	mechanism,	value, <i>survival</i>
state	<i>causation</i>	<i>value</i>
focus on	ontogeny	phylogenetic history,
history		<i>evolution</i>

individuals, and sometimes lower-level entities within them, are in conflict with other entities, with interests somewhat (but not perfectly) aligned. The fact that much of human social life prepares us for exactly this kind of mental simulation has upsides. It is usually quite easy to describe the most complicated research programme in behavioural ecology to an interested layperson. All that is required is to imagine a dilemma with trade-offs, perhaps with multiple players with divergent interests, and hope for honest self-inspection: ‘what would you do?’ Although our mind prefers shortcuts and heuristics over painstaking calculations of all relevant probabilities [9], our ability to intuit scenarios involving personal gain, weighing the relevant pros and cons, is decidedly better than, say, our ability to truly grasp quantum physics or cosmological timescales.

The upside of the relative ease of stepping into others’ shoes obviously extends beyond outreach: sophisticated questions and research programmes can be generated with relative ease. Questions such as ‘why do male birds often continue to feed at the nest even though some offspring are probably fathered by someone else?’ arose naturally after female multiple mating habits became known; the subtext is obviously ‘if I was in this situation, I’d be tempted to leave and/or punish the female’. Proper answers, then, require much more focused logical and empirical efforts [10–12] where self-inspecting and/or emotional answers are set aside.

### (b) . . . But what if the shoe does not fit. . .

There are obvious downsides for using human intuition and experience to guide research. Firstly, if Trivers is correct that self-deception is common and could conceivably be an evolved adaptation, it will be hard to evaluate fitness options correctly. When our motivations are socially undesirable, we may be particularly prone to lie about them. Secondly, in contexts that do not qualify as self-deception, human introspection still cannot be trusted to give a correct evolutionary answer to the ultimate reasons behind a behaviour. One problem is that none of us experience all possible life histories in our personal life trajectory. If we cannot truly grasp the challenges experienced by more senior or junior members of our own species, or those of a different gender, sexual orientation or socioeconomic status, what hope do we have to figure out a totally different

problem, say, why a bird parent can be very suspicious of unusual eggs in its nest but, should a cuckoo chick manage to hatch, the chick typically will be fed to fledging [13,14]?

Still, my own opinion is that most students of evolution, at least if exposed to sufficient natural history, preferably in the field, manage to overcome this particular set of hurdles quite well. For example, once one has understood some parental care economics—that it can be very costly to the parent, but sometimes giving care to 10 offspring is no more expensive than giving care to 200 (this occurs, e.g. when offspring do not need to be fed, and caring instead requires defending the nest and perhaps also foregoing foraging)—then it becomes quite intuitive why paternal care in fishes may involve filial cannibalism. While not beneficial to the ones who get eaten, it may maximize the male's chances of raising many of the young [15]. Under these conditions, females can evolve preferences for males who already care for other females' young: this dilutes the risk that her own eggs are cannibalized [16]. The next consequence is that the trade-off between caring and mating may disappear for the male, which selects for more male care [17]. To anthropomorphize, it is logically clear that sexual jealousy should be a foreign concept to females under the above-stated rules.

While scientists avoid using such anthropomorphizing language (to an extent; see [18,19] for critical views), it would be dishonest to deny that such thoughts are essential for the ease with which we grasp the many dilemmas that individuals of other species face. If the rules of the game change from A to B, the expected behaviours or life-history traits change too, and unless a mathematical model forces us to reconsider, we accept the implicit 'what would I do if . . .' as a powerful hypothesis generation tool. Finding out whether the hypothesized causation is strong enough to leave a trace in the phylogenetic pattern then necessitates much more work. Being forced to examine whether our initial predictions hold water when looking at the circumstances of many species is definitely part of what makes evolutionary and behavioural ecology so exciting.

### (c) . . . Or we cannot even find the feet?

Does extrapolating from our species always work? It might not, when the game becomes too dissimilar to our own, just like our intuition breaks down when we move from human-scaled physics to the nanoscale or the cosmological realm. I suspect that making good first guesses on the function of an observed behaviour might be greatly hampered in two scenarios: (i) we might be dealing with a trait for which humans differ substantially from non-human animals in general (in which case, we might expect general trouble getting closer to the true explanation), or (ii) we differ from *some* non-human animals but not all (here the trouble is a likely failure to realize that one set of rules does not apply to all). I will present some thoughts on these two scenarios.

Does case (i) exist? It is difficult to come up with human traits that have no analogue in non-human animals at all. Nevertheless, human sociality comes with characteristics that appear to result in unusually much cooperation [20,21]—and much more *nuanced* cooperation, with complex assessment of how much to invest in the current interaction [22–24]—especially in non-kin contexts [25,26]. It is beyond the scope of this essay to review the extensive debates surrounding the various explanations for prosocial behaviour; suffice to say that there are schools of thought favouring the interpretation

that selection for cooperation can be based on multiple levels of selection, such that group-level fitness remains an important driver of evolutionary processes (humans: [27], non-humans: [28], in general: [29–31]), while others clearly favour the interpretation that inclusive fitness effects (roughly synonymous with kin-selected interactions) provides clear and sufficient explanations [32–36].

The debate can, in some years at least, be described as heated [29,35,37–40]. This is curious, because a heated debate should *a priori* be an unlikely outcome when models built to investigate a process provide all possible tools for agreement. There is some consensus that many *mathematical* formulations of the relevant evolutionary process can be equivalently built to reflect the inclusive fitness point of view or, instead, phrased in terms of two (or more) levels of selection acting simultaneously [41–43]. But if kin and group selection are simply two angles from which to view the same set of equations, how can one possibly be a 'bad' and the other one a 'good' explanation?

With the possible exception of quantum physicists, we do not consider having really understood something if the 'mathematics say so'; we try to create a mental representation of what is going on. Although I cannot possibly prove the following claim, I consider it an interesting conjecture to think about how living in human societies makes us unusually strongly aware of the group-level consequences of our actions. Whether innate, or frequently enough drilled during upbringing to become part of our psyche, the outcome is clear. By the time a biology student enters university, there is a belief in place that evolution in general produces traits because they benefit entire species. Irrespective of the correctness of any real science that examines group or kin-level benefits, it appears to be far easier for students to spontaneously come up with *incorrect* explanations that involve group selection than to come up with *incorrect* kin-based arguments.

What follows, then, is that teachers need to point out the flaws in one set of ideas (e.g. 'individuals die to avoid overpopulation') much more strongly than the other. After the necessary training, students then graduate with the lesson not only learnt but also *generalized*, at which point it takes the form 'as soon as someone evokes group-level thinking, we've entered "bad logic territory"'. The more advanced debates show the matter to be more subtle [43,44], but a typical BSc degree is over before such nuances can be addressed. It is interesting to speculate if the scientific debates themselves were more balanced if the initial asymmetry in the types of spontaneous argumentation did not exist—and if humans were not so astonishingly willing to cooperate beyond simple family structures.

Turning to case (ii), inbreeding avoidance and tolerance appear to be examples where the human experience matches the fitness structures in us as well as many other species, but not all. Here, we might take a trait (inbreeding avoidance) for granted because we think it is the obvious expectation. Self-inspection tends to reveal strong disgust when imagining incestuous matings, and incest-involving thought experiments have even been used to discuss general properties of human moral judgement [45]. So why is the matter complex? Inbreeding depression can cause strong selection to go for outbreeding opportunities, whether or not the organism actually recognizes kin (in the absence of this ability, inbreeding can be avoided, for example, by dispersing far enough [46–48]). Since Fisher's work in 1941 [49], however, it has

been known that inbreeding also has an ‘upside’: it gives identical-by-descent alleles additional opportunities to transmit to future generations. By now, a sizeable literature has accumulated how exactly the balance of these factors plays out—the answers depend on how matings redistribute given inbreeding tolerance or avoidance (e.g. [50–52])—but what is worth commenting on is why it took so long.

For a long time, Fisher’s line of reasoning appeared to be appreciated by plant biologists but not by animal ecologists [50,53]. In plants, the study of mixed mating systems flourished after Lande and Schemske pointed out the theoretical expectation of either selfing or outcrossing, but not a mix, as soon as inbreeding depression is allowed to evolve depending on how much selfing is occurring [54]. But a review of the topic that had an animal focus was still ignoring these population genetic insights (while paying attention to an alternative, outbreeding depression) more than 50 years after Fisher’s results and more than 10 after Lande’s [55].

Maybe time lags do not matter in hindsight, given that we these days seem to understand that the benefits and costs of inbreeding have to be computed for each social setting and that rules of thumb may mislead [51,52,56,57]. Taxonomic myopia, i.e. animal researchers not following and citing the plant literature and perhaps vice versa, is no doubt part of the explanation. Going beyond that, it is tempting to speculate why it happened to be the study of plants, rather than animals, where the population genetic message had an easier time getting across. Although this is an  $n = 1$  comparison, it might well be that researchers tended to ignore one side of the equation in animals *because* we so routinely self-inspect when developing evolutionary arguments. If we extrapolate from our own behaviours and feelings [45] to what an animal should do, this could well make it hard for us to think of any genetic ‘upside’, as we do not happen to be social spiders that routinely inbreed [58]. Given an equivalent botanical task, we might identify less strongly with an individual plant and get to the more impersonal task of counting alleles more quickly.

### 3. The second problem: which questions to ask?

What would evolutionary theory look like had Darwin been a slime mould? Popular culture insists that aliens’ morphology resemble that of humans, give or take some variation in limb number or the size of the head or eyes. Yet, it is not inconceivable that intelligent life could be based on life forms in which individual morphology—or even the concept of individuality itself—is not as fixed as in our own species. Should societies of such creatures become interested in understanding evolution, one wonders if their most popular study species would be chosen based on different criteria from the ones we encounter in our evolutionary textbooks.

Does it matter which life forms we allow to inform our understanding of life? Consider a linguistic analogy. Tinbergen had to point out that the simple word ‘why’ can mean different things, and arguably, much scientific confusion would be avoided if natural languages were less ambiguous. Although I do not know of a language that would have different ‘whys’ for different causalities, I should also not extrapolate from my own linguistic skill set to general properties any more than to conclude, from human studies, that sex and reproduction always involve sperm. Think of a grammatical feature

that appears useful yet remains absent in all the languages you know. It might nevertheless exist somewhere. For example, imagine the improved precision if one was automatically forced to distinguish between the ‘we’ that implies that the addressee of the sentence is included (what we see in front of us is a perfect example of...) and the exclusive version (we come in peace). Aboriginal languages of Australia have these two versions of the word ‘we’, and so do numerous languages on all other continents *except* Europe [59].

Linguistics would not be able to ask many of its current questions if only a handful of languages were ever studied. In evolutionary biology, we similarly might never even realize which questions are begging to be answered, if only a subset of organisms are allowed to inform us of what is possible. This is a point clearly made by Buss in the first chapter of his book *The evolution of individuality* [60]. He divides species that form the tree of multi-cellular life into three developmental categories, depending on the degree to which the germline and the soma are kept distinct during the ontogeny of the organism: species with *preformation* differentiate their germline from the soma very early during an individual’s ontogeny, while *somatic embryogenesis* is the other extreme that features no distinct germ line. Between these extremes lies the intermediate solution of epigenesis, which in Buss’ terminology describes cases where a distinct germline is formed only once the adult morphology is reached (not to be confused with epigenetics [61], though both can lead to identical phrases such as ‘epigenetic development’).

Buss [60] then reminds us that species such as *Drosophila*—one that we happened to study during the time when the modern synthesis was being developed—canonized an idea of evolution occurring in discrete, genetically uniform individuals forming successive generations. This assumes preformational development, a good starting point when trying to understand *Drosophila* or humans—but it remains a choice that, across taxa, is relatively rarely chosen by nature herself. Plants, fungi and most protists follow somatic embryogenesis instead, and it also occurs in no fewer than nine animal phyla [60].

#### (a) Taxonomic chauvinism

Obviously, we would not even know about the cases deviating from ‘human-like’ life histories if all of us restrictively studied what is most familiar to us. All the accumulated knowledge about biodiversity’s wondrous alternative forms shows our ability to be excited about discovering rules of life that deviate from our own. Even so, there is a tendency to disproportionately focus on species that in some sense (usually phylogenetically) resemble our own. Termed taxonomic chauvinism, this pattern leaves clear traces in the literature: not only do birds and mammals dominate the literature on vertebrates in ecological and evolutionary journals, but research on them also seems to require less effort when it comes to the need to explain the rationale behind each study question. This has been ingeniously studied by measuring how many lines of text the introductory section of a publication contains before revealing the species in question [62]. Papers on reptiles, amphibians or fishes spend more than double the effort of mammal or bird papers on this metric. The finding is striking, given that the first lines of a scientific paper are typically spent describing a general ecological or evolutionary question before ‘zooming in’ to describe why the species of choice is useful for addressing

it. The results [62] are therefore consistent with an interpretation that papers on certain species (those intrinsically more interesting to us) achieve reader interest with less thorough scientific justification.

Still, even reptiles appear more ‘loved’ than, say, invertebrates, when considering e.g. active efforts to conserve them: a global database of reintroduction projects shows that a null expectation of equal conservation effort across taxa would predict 8.3 times as many invertebrate reintroduction projects than actually happen, while the corresponding ‘fair’ number for reptiles would be only 0.85 of what actually takes place [63]. For mammals, the ratio is 0.2. Put another way, a randomly chosen mammal species is almost 42 times as likely to attract reintroduction effort than an insect or a mollusc.

Taxonomic chauvinism [62–65] is a mild malaise if it only slows down the rate of discovery across some parts of the tree of life, but it might also distort the building of an entire theoretical framework, with consequences on whether it occurs to us to ask grand questions about life. Sex, sexual reproduction and sexual conflict are topics that provide us with perhaps the clearest examples of how studies seem to be taking one kind of system as a ‘default state’ from which deviations occur. Textbook descriptions of the basic theory of sexual selection, for example, make the readers think of separate sexes as the norm. If we strictly follow Trivers’ guidance to expand our knowledge outwards, we probably end up precisely in this state. Had we started with some other organism first, taking e.g. a broadcast spawner as the primary mental image when talking about an event of sexual reproduction, the realization that there are true questions to be asked might have come sooner: why did anything ever develop internal fertilization [66]?

Obviously, Trivers is not the only one to blame here—he might be merely more vocal about his self-inspection habits than most of us dare to be. Darwin’s books form an interesting case, as the *Origin* [2] remains largely silent both on human evolution and on sexual selection, and he then addresses these topics in his later book titled ‘*The descent of man, and selection in relation to sex*’ [67]. The first taxa specifically mentioned in the sexual selection part of the book are ‘insects’, ‘mammals’, ‘marsupials’, ‘certain fishes’, ‘frogs’, ‘bees’ and *Culicidae* and *Tabanidae* flies; Darwin does not refer at all to the fact that a few pages ago, the book was all about humans.

If we take our taxonomical chauvinism detective work seriously, we might want to tell Darwin that his initial list of examples all make us think about a female and a male in a gonochoristic (separate-sexed) animal that come physically together to mate. Even today, most researchers probably underestimate how common even mild deviations from this pattern are. Hermaphroditism, for example, is estimated to occur in approximately one-third of non-insect animal species [68]. Here, what is the ‘norm’ and what ‘surprises’ us appears to be defined, more or less, by similarity to what humans do, so much that two recent special issues on the diversity of sexual reproduction in nature both had to comment, in their respective editorials, on the fact that what is categorized as ‘weird’ seems to be ‘what we tend not to do’ rather than anything more objective [69,70]. Quoting Schärer [70, p. 101]: ‘A deeper understanding of the evolution of anisogamy and its consequences for sexual reproduction now urgently requires that we dare to leave our gonochoristic islands and learn to swim in the vast sea of sexual diversity’.

At least, however, when authors use gonochorism as a tacit assumption when discussing a model of sexual selection or when introducing students to the topic in a textbook, no crime is being committed in the sense that we still are discussing the default case first, given the ratio of gonochoristic and hermaphroditic organisms is biased towards the former in *Animalia*—though a reminder is here in place too: if we remember to include unicellular life, then the question ‘whether the male and female function occur in the same body or not’ gets replaced with whether males exist at all, as sex often involves *mating types* instead of males and females, and often also occurs facultatively, such that life cycles can also follow each other asexually [71,72].

### (b) Societal norms and multiple mating

Stronger evidence that a human-centric view truly can distort out thoughts can be found in cases where the null hypothesis that comes to mind naturally is actually false. One clear example is that of multiple mating. Today’s biology students are taught to expect polyandry to be common in natural populations, but this was not the case in the 1970s, when Bray *et al.* [73] were conducting their study of red-winged blackbirds *Agelaius phoeniceus*. Bray’s data showed that the nests of sterilized males suffered surprisingly little fertility reduction, with the risk of infertility increasing with isolation from other males. This made him conclude that out of the various possible explanations considered—sperm retention with or without new females arriving on the territory, or polyandry—the one involving multiple mating appears most likely.

Ever since, the question of *why* females mate multiply has attracted great interest both by theoreticians and by empiricists [74,75]. Potential answers range from avoiding infertility [76] to the acquisition of better or more compatible genes [77], receiving parental care from multiple males [78] to ‘convenience polyandry’ where it is simply cheaper to stop resisting male mating efforts than to try to remain monandrous [79–81]. Interpreting the situation in its historical context, societal norms that were strong during Darwin’s lifetime (and to quite a great extent operate even today) may have caused the initial assumption that females should *a priori* not be interested in mating with more than one male (for discussions, see [75,82]).

A more correct—in the sense of being simpler, i.e. more parsimonious—null assumption would be that females do not treat one male any different from another male. This is not meant to imply that pair bonds should not exist; null models are not judged by how correct they are, instead they help define the scope of what can be explained without evoking more complex phenomena [83]. The redefined viewpoint dictates that when we see pair bonds, especially if also genetically monogamous, we have detected an interesting pattern worthy of further explanatory efforts [84]. If we instead consider monadry (or pair bonds) a default case that does not warrant further consideration, we have not provided a wrong explanation but no explanation at all: taking them for granted makes us miss the opportunity to investigate them as exciting phenomena.

The same logic can be applied to variation in insect mating systems: here, monadry and polyandry both exist, but the former requires a more complicated set of behavioural rules (accept males according to certain criteria until mated once, thereafter accept no males) than polyandry, which at least in principle can operate with the same acceptance

threshold applied for each male that a female encounters throughout her life [83]. Changing the viewpoint from ‘why do they mate multiply?’ to ‘why not mate at every mate encounter?’ can thereafter help to understand, for example, why some females remain completely mateless: this becomes an expected response even if females follow an optimal strategy; sometimes death simply occurs unusually early while the encounter with a suitable mate (exceeding the acceptance threshold) happened to be delayed, purely stochastically [83].

### (c) But what can we do about it?

An oft-heard recommendation in science is to think about the best possible research question first, and choose the best study species accordingly, rather than vice versa. While the advice is in itself good, one possible negative consequence is a disproportionate focus on so-called model species. Above, I rather provocatively reminded readers that *Drosophila* are very human-like in many fundamental aspects of their life histories, as numerous traits are shared among all insects and all vertebrates; life is much broader than that. But this should not prevent us from recognizing that within-taxon patterns, too, can become biased if we trust any one model species to represent the way things work in nature. In other words, just like the *Drosophila*–human axis fails to represent all life, *Drosophila* itself should not be assumed to represent all insect life. Zuk *et al.* [85] provide this argument in a sexual conflict context: the more we study this topic in a diverse set of entomological systems, broadening our view from *Drosophila* only, the less we end up emphasizing direct male harm to females as a factor driving sexual selection.

Research effort that increases linearly with decreasing phylogenetic distance to humans is not the only possible form of chauvinism; unnecessary taxonomic focus in citing patterns is another [64]. For example, if a study [86] shows that parental care research in six sampled journals is disproportionately based on avian research, this does not necessarily mean that there are few care studies in, say, primates. These may simply be more often published in journals entirely devoted to primatology, with potential harmful consequences for the free flow of knowledge and ideas across subfields.

## References

- Trivers RL. 2015 *Wild life: adventures of an evolutionary biologist*. New Brunswick, NJ: Biosocial Research.
- Darwin C. 1959 *On the origin of species by means of natural selection*. London, UK: Murray.
- Leeuwenhoek DA. 1674 Microscopical observations from Mr. Leeuwenhoek, about blood, milk, bones, the brain, spittle, cuticula, sweat, fatt, teares; communicated in two letters to the publisher. *Phil. Trans.* **9**, 121–131. (doi:10.1098/rstl.1674.0030)
- Leeuwenhoek DA. 1677 Observaciones D. Anthonii Lewenhoek, De Natis E Semine Genitali Animalculis. *Phil. Trans.* **12**, 1040–1046. (doi:10.1098/rstl.1677.0068)
- Snyder LJ. 2015 *Eye of the beholder: Johannes Vermeer, Antoni van Leeuwenhoek, and the reinvention of seeing*. New York, NY: WW Norton & Company, Inc.
- Trivers RL. 2011 *Deceit and self-deception: fooling yourself the better to fool others*. London, UK: Allen Lane.
- Tinbergen N. 1963 On aims and methods of ethology. *Zeitschr. Tierpsychol.* **20**, 410–433. (doi:10.1111/j.1439-0310.1963.tb01161.x)
- Bateson P, Laland KN. 2013 Tinbergen’s four questions: an appreciation and an update. *Trends Ecol. Evol.* **28**, 712–718. (doi:10.1016/j.tree.2013.09.013)
- Kahneman D. 2011 *Thinking, fast and slow*. Farrar, MI: Straus and Giroux.
- Houston AI, McNamara JM. 2002 A self-consistent approach to paternity and parental effort. *Phil. Trans. R. Soc. Lond. B* **357**, 351–362. (doi:10.1098/rstb.2001.0925)
- Kamel SJ, Grosberg K. 2012 Exclusive male care despite extreme female promiscuity and low paternity in a marine snail. *Ecol. Lett.* **15**, 1167–1173. (doi:10.1111/j.1461-0248.2012.01841.x)
- Griffin AS, Alonzo SH, Cornwallis CK. 2013 Why do cuckolded males provide parental care? *PLoS Biol.* **11**, e1001520. (doi:10.1371/journal.pbio.1001520)
- Davies NB. 2000 *Cuckoos, cowbirds and other cheats*. New York, NY: Academic Press.
- Grim T. 2006 The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evol. Ecol. Res.* **8**, 785–802.
- Klug H, Bonsall MB. 2007 When to care for, abandon, or eat your offspring: the evolution of parental care and filial cannibalism. *Am. Nat.* **170**, 886–901. (doi:10.1086/522936)

## 4. Conclusion? Ask an alien

Unfortunately, most of my conjectures above are quite hard to prove (or disprove), but I hope this does not make them less interesting to reflect on. I have not provided an exhaustive list of features of human life that are tricky to categorize in terms of ‘uniqueness’. For example, consider the demographic transition [87], where increasing wealth and decreasing death rates lead to such low birth rates that entire populations can fall below the replacement level. This could to be something truly unique and inexplicable in evolutionary terms—why should increasing material wealth ever lead to lower Darwinian fitness?—or something less drastic, a mere unusual but not categorically different outcome of more general principles of life-history theory with respect to ‘slow’ and ‘fast’ life histories [88,89].

All in all, we cannot change the fact that Trivers, Tinbergen and Darwin were all human beings, as are all his readers. This keeps many of my claims in the  $n = 1$  realm. We share the same cognitive biases, give or take certain cultural differences and personal experiences. Differences among ‘us’ may look significant until one remembers how greatly they differ from, say, the rules of life experienced by a parasite with a complex life cycle. We have to keep teaching students, generation after generation, that what is important to you (or your pet dog) might not be representative of all life. The good news is that both diversity appreciation and critical thinking can be learnt, after which there is definite joy in figuring out exactly why (and when) the dilemmas encountered by a slime mould differ from those of a human individual. During writing this opinion piece, I also finally realized what I would ask an alien, should I ever encounter one: can I possibly see your most recent textbook on evolution? (and, as an aside, how does your way of communicating treat the concept of ‘we’?)

**Data accessibility.** This article has no additional data.

**Competing interests.** I declare I have no competing interests.

**Funding.** I thank the Swiss National Science Foundation and the Academy of Finland for funding.

**Acknowledgements.** I thank Sarah Brosnan and Erik Postma for their invitation to produce this opinion piece, and them as well as two reviewers and the Kokkonuts journal club for kind and constructive comments.

16. Forsgren E, Karlsson A, Kvarnemo C. 1996 Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behav. Ecol. Sociobiol.* **39**, 91–96. (doi:10.1007/s002650050270)
17. Kokko H, Jennions MD. 2012 Sex differences in parental care. In *The evolution of parental care* (eds NJ Royle, PT Smiseth, M Kölliker), pp. 101–116. Oxford, UK: Oxford University Press.
18. Karsson GK, Madjidian JA. 2011 Active males, reactive females: stereotypic sex roles in sexual conflict research? *Anim. Behav.* **81**, 901–907. (doi:10.1016/j.anbehav.2011.01.033)
19. Dougherty LR, Burdfield-Steel ER, Shuker D. 2013 Sexual stereotypes: the case of sexual cannibalism. *Anim. Behav.* **85**, 313–322. (doi:10.1016/j.anbehav.2012.12.008)
20. Melis AP, Semmann D. 2010 How is human cooperation different? *Phil. Trans. R. Soc. B* **365**, 2663–2674. (doi:10.1098/rstb.2010.0157)
21. Silk JB, House BR. 2011 Evolutionary foundations of human prosocial sentiments. *Proc. Natl Acad. Sci. USA* **108**, 10 910–10 917. (doi:10.1073/pnas.1100305108)
22. Efferson C, Lalive R, Fehr E. 2008 The coevolution of cultural groups and ingroup favoritism. *Science* **321**, 1844–1849. (doi:10.1126/science.1155805)
23. Jaeggi AV, Burkart JM, van Schaik CP. 2010 On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality. *Phil. Trans. R. Soc. B* **365**, 2723–2735. (doi:10.1098/rstb.2010.0118)
24. Fehr E, Gächter S. 2002 Altruistic punishment in humans. *Nature* **415**, 137–140. (doi:10.1038/415137a)
25. Boyd R, Richerson PJ. 2009 Culture and the evolution of human cooperation. *Phil. Trans. R. Soc. B* **364**, 3281–3288. (doi:10.1098/rstb.2009.0134)
26. Powers ST, van Schaik CP, Lehmann L. 2016 How institutions shaped the last major evolutionary transition to large-scale human societies. *Phil. Trans. R. Soc. B* **371**, 20150098. (doi:10.1098/rstb.2015.0098)
27. Bowles S. 2006 Group competition, reproductive leveling, and the evolution of human altruism. *Science* **314**, 1569–1572. (doi:10.1126/science.1134829)
28. Eldakar OT, Wilson DS, Dlugos MJ, Pepper JW. 2010 The role of multilevel selection in the evolution of sexual conflict in the water strider *Aquarius remigis*. *Evolution* **64**, 3183–3189. (doi:10.1111/j.1558-5646.2010.01087.x)
29. Nowak MA, Tarnita CE, Wilson EO. 2010 The evolution of eusociality. *Nature* **466**, 1057–1062. (doi:10.1038/nature09205)
30. Akcay C, Van Cleve J. 2012 Behavioral responses in structured populations pave the way to group optimality. *Am. Nat.* **179**, 257–269. (doi:10.1086/663691)
31. Simon B, Nielsen A. 2012 Numerical solutions and animations of group selection dynamics. *Evol. Ecol. Res.* **14**, 757–768.
32. Bourke AFG. 2011 The validity and value of inclusive fitness theory. *Proc. R. Soc. B* **278**, 3313–3320. (doi:10.1098/rspb.2011.1465)
33. Herrera EA. 2013 Ecological and genetic distribution of eusociality: the case for kin selection. *Behav. Ecol.* **24**, 331–333. (doi:10.1093/beheco/ars166)
34. Hatchwell BJ, Gullett PR, Adams MJ. 2014 Helping in cooperatively breeding long-tailed tits: a test of Hamilton's rule. *Phil. Trans. R. Soc. B* **369**, 20130565. (doi:10.1098/rstb.2013.0565)
35. Liao X, Rong S, Queller DC. 2015 Relatedness, conflict, and the evolution of eusociality. *PLoS Biol.* **13**, e1002098. (doi:10.1371/journal.pbio.1002098)
36. Bourke AFG. 2015 Sex investment ratios in eusocial Hymenoptera support inclusive fitness theory. *J. Evol. Biol.* **28**, 2106–2111. (doi:10.1111/jeb.12710)
37. Abbot P *et al.* 2011 Inclusive fitness theory and eusociality. *Nature* **471**, E1–E4. (doi:10.1038/nature09831)
38. Rousset F, Lion S. 2011 Much ado about nothing: Nowak *et al.*'s charge against inclusive fitness theory. *J. Evol. Biol.* **24**, 1386–1392. (doi:10.1111/j.1420-9101.2011.02251.x)
39. Nowak MA, Allen B. 2015 Inclusive fitness theorizing invokes phenomena that are not relevant for the evolution of eusociality. *PLoS Biol.* **13**, e1002134. (doi:10.1371/journal.pbio.1002134)
40. Queller DC, Rong S, Liao X. 2015 Some agreement on kin selection and eusociality? *PLoS Biol.* **13**, e1002133. (doi:10.1371/journal.pbio.1002133)
41. Marshall JAR. 2011 Group selection and kin selection: formally equivalent approaches. *Trends Ecol. Evol.* **26**, 325–332. (doi:10.1016/j.tree.2011.04.008)
42. Kramer J, Meunier J. 2016 Kin and multilevel selection in social evolution: a never-ending controversy? *F1000Res.* **5**, 776. (doi:10.12688/f1000research.8018.1)
43. Lehtonen J. 2016 Multilevel selection in kin selection language. *Trends Ecol. Evol.* **31**, 752–762. (doi:10.1016/j.tree.2016.07.006)
44. Birch J, Okasha S. 2015 Kin selection and its critics. *BioScience* **65**, 22–32. (doi:10.1093/biosci/biu196)
45. Haidt J. 1995 The emotional dog and its rational tail: a social intuitionist approach to moral judgment. *Psych. Rev.* **108**, 814–834. (doi:10.1037/0033-295X.108.4.814)
46. Motro U. 1991 Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. *Am. Nat.* **137**, 108–115. (doi:10.1086/285148)
47. Gandon S. 1999 Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* **200**, 345–364. (doi:10.1006/jtbi.1999.0994)
48. Perrin N, Mazalov V. 1999 Dispersal and inbreeding avoidance. *Am. Nat.* **154**, 282–292. (doi:10.1086/303236)
49. Fisher RA. 1941 Average excess and average effect of a gene substitution. *Ann. Eugen.* **11**, 53–63. (doi:10.1111/j.1469-1809.1941.tb02272.x)
50. Kokko H, Ots I. 2006 When not to avoid inbreeding. *Evolution* **60**, 467–475. (doi:10.1111/j.0014-3820.2006.tb01128.x)
51. Duthie AB, Reid JM. 2016 Evolution of inbreeding avoidance and inbreeding preference through mate choice among interacting relatives. *Am. Nat.* **188**, 651–667. (doi:10.1086/688919)
52. Duthie AB, Bocedi G, Reid JM. 2016 When does female multiple mating evolve to adjust inbreeding? Effects of inbreeding depression, direct costs, mating constraints, and polyandry as a threshold trait. *Evolution* **70**, 1927–1943. (doi:10.1111/evo.13005)
53. Lehtonen J, Kokko H. 2012 Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. *Phil. Trans. R. Soc. B* **367**, 211–221. (doi:10.1098/rstb.2011.0177)
54. Lande R, Schemske DW. 1985 The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* **39**, 24–40. (doi:10.1111/j.1558-5646.1985.tb04077.x)
55. Pusey A, Wolf M. 1996 Inbreeding avoidance in animals. *Trends Ecol. Evol.* **11**, 201–206. (doi:10.1016/0169-5347(96)10028-8)
56. Kamran-Disfani A, Agrawal AF. 2014 Selfing, adaptation and background selection in finite populations. *J. Evol. Biol.* **27**, 1360–1371. (doi:10.1111/jeb.12343)
57. Jacob G, Prévot AC, Baudry E. 2016 Feral pigeons (*Columba livia*) prefer genetically similar mates despite inbreeding depression. *PLoS ONE* **11**, e0162451. (doi:10.1371/journal.pone.0162451)
58. Ruch J, Heinrich L, Bilde T, Schneider JM. 2009 The evolution of social inbreeding mating systems in spiders: limited male mating dispersal and lack of pre-copulatory inbreeding avoidance in a subsocial predecessor. *Biol. J. Linn. Soc.* **98**, 851–858. (doi:10.1111/j.1095-8312.2009.01322.x)
59. Cysouw M. 2013 Inclusive/exclusive distinction in independent pronouns. In *The world atlas of language structures online* (eds MS Dryer, H Haspelmath), pp. 419–443. Leipzig, Germany: Max Planck Institute for Evolutionary Anthropology.
60. Buss LW. 1987 *The evolution of individuality*. New Jersey, NJ: Princeton University Press.
61. Bonduriansky R, Day T. 2009 Nongenetic inheritance and its evolutionary implications. *Annu. Rev. Ecol. Syst.* **40**, 103–125. (doi:10.1146/annurev.ecolsys.39.110707.173441)
62. Bonnet X, Shine R, Lourdaïs O. 2002 Taxonomic chauvinism. *Trends Ecol. Evol.* **17**, 1–3. (doi:10.1016/S0169-5347(01)02381-3)
63. Seddon PJ, Soorae PS, Launay F. 2005 Taxonomic bias in reintroduction projects. *Anim. Conserv.* **8**, 51–58. (doi:10.1017/S1367943004001799)
64. Rosenthal MF, Gertler M, Hamilton AD, Prasad S, Andrade MCB. 2017 Taxonomic bias in animal behaviour publications. *Anim. Behav.* **127**, 83–89. (doi:10.1016/j.anbehav.2017.02.017)
65. Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F. 2017 Taxonomic bias in biodiversity data and societal preferences. *Sci. Rep.* **7**, 9132. (doi:10.1038/s41598-017-09084-6)

66. Henshaw JM, Marshall DJ, Jennions MD, Kokko H. 2014 Local gamete competition explains sex allocation and fertilization strategies in the sea. *Am. Nat.* **184**, E32–E49. (doi:10.1086/676641)
67. Darwin C. 1871 *The descent of Man, and selection in relation to sex*. London, UK: Murray.
68. Jarne P, Auld JR. 2006 Animals mix it up too: the distribution of self-fertilization among hermaphroditic animals. *Evolution* **60**, 1816–1824. (doi:10.1111/j.0014-3820.2006.tb00525.x)
69. Aanen D, Beekman M, Kokko H. 2016 Weird sex: the underappreciated diversity of sexual reproduction. *Phil. Trans. R. Soc. B* **371**, 20160262. (doi:10.1098/rstb.2016.0262)
70. Schärer L. 2017 The varied ways of being male and female. *Mol. Reprod. Dev.* **84**, 94–104. (doi:10.1002/mrd.22775)
71. Lehtonen J, Kokko H, Parker GA. 2016 What do isogamous organisms teach us about sex and the two sexes?. *Phil. Trans. R. Soc. B* **371**, 20150532. (doi:10.1098/rstb.2015.0532)
72. Burke NW, Bonduriansky R. 2017 Sexual conflict, facultative asexuality, and the true paradox of sex. *Trends Ecol. Evol.* **32**, 646–652. (doi:10.1016/j.tree.2017.06.002)
73. Bray OE, Kennelly JJ, Guarino JL. 1975 Fertility of eggs produced on territories of vasectomized red-winged blackbirds. *Wilson Bull.* **87**, 187–195.
74. Jennions MD, Petrie M. 2000 Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* **75**, 21–64. (doi:10.1017/S0006323199005423)
75. Parker GA, Birkhead TR. 2013 Polyandry: the history of a revolution. *Phil. Trans. R. Soc. B* **368**, 20120335. (doi:10.1098/rstb.2012.0335)
76. Reding L. 2015 Increased hatching success as a direct benefit of polyandry in birds. *Evolution* **69**, 264–270. (doi:10.1111/evo.12553)
77. Arbuthnott D, Crespi BJ, Schwander T. 2015 Female stick insects mate multiply to find compatible mates. *Am. Nat.* **186**, 519–530. (doi:10.1086/682675)
78. Harada Y, Iwasa Y. 1996 Female mate preference to receive maximum paternal care: a two-step game. *Am. Nat.* **147**, 996–1027. (doi:10.1086/285890)
79. Rowe L. 1992 Convenience polyandry in a water strider: foraging conflicts and female control of copulation frequency and guarding duration. *Anim. Behav.* **44**, 189–202. (doi:10.1016/0003-3472(92)90025-5)
80. Lee PLM, Hays GC. 2004 Polyandry in a marine turtle: females make the best of a bad job. *Proc. Natl Acad. Sci. USA* **101**, 6530–6535. (doi:10.1073/pnas.0307982101)
81. Trontti K, Thurin N, Sundström L, Aron S. 2007 Mating for convenience or genetic diversity? Mating patterns in the polygynous ant *Plagiolepis pygmaea*. *Behav. Ecol.* **18**, 298–303. (doi:10.1093/beheco/arl083)
82. Dewsbury DA. 2005 The Darwin-Bateman paradigm in a historical context. *Integr. Comp. Biol.* **45**, 831–837. (doi:10.1093/icb/45.5.831)
83. Kokko H, Mappes J. 2013 Multiple mating by females is a natural outcome of a null model of mate encounters. *Entomol. Exp. Appl.* **146**, 26–37. (doi:10.1111/j.1570-7458.2012.01296.x)
84. Whiteman EA, Côté IM. 2004 Monogamy in marine fishes. *Biol. Rev.* **79**, 351–375. (doi:10.1017/S1464793103006304)
85. Zuk M, Garcia-Gonzalez F, Herberstein ME, Simmons LW. 2014 Model systems, taxonomic bias, and sexual selection: beyond *Drosophila*. *Annu. Rev. Entomol.* **59**, 321–328. (doi:10.1146/annurev-ento-011613-162014)
86. Stahlschmidt ZR. 2011 Taxonomic chauvinism revisited: insight from parental care research. *PLoS ONE* **6**, e24192. (doi:10.1371/journal.pone.0024192)
87. Colleran H, Jasienska G, Nenko I, Galbarczyk A, Mace R. 2015 Fertility decline and the changing dynamics of wealth, status and inequality. *Proc. R. Soc. B* **282**, 20150287. (doi:10.1098/rspb.2015.0287)
88. Lawson DW, Mace R. 2011 Parental investment and the optimization of human family size. *Phil. Trans. R. Soc. B* **366**, 333–343. (doi:10.1098/rstb.2010.0297)
89. Mace R. 2014 When not to have another baby: an evolutionary approach to low fertility. *Demogr. Res.* **30**, 37. (doi:10.4054/DemRes.2014.30.37)