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

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Abstract

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 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. 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 vs. tolerance could have spread faster if we were not extrapolating our emotional reactions to incest disproportionately depending on whether we study animals or plants.

Introduction

What would evolutionary theory look like had Darwin been a slime mould? Despite popular culture insisting that aliens' morphology resemble that of humans (give or take some variation in limb number or the size of the head or eyes), 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.

Buss [1], though definitely not hypothesizing about aliens, essentially makes this point in the first chapter of his book *The evolution of individuality*. He divides species that form the tree of multicellular 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. Buss uses the term *preformation* to describe species that differentiate their germline from the soma very early during an individual's ontogeny. *Somatic embryogenesis* is the other extreme that features no distinct germ line: here one cell lineage is capable of performing somatic functions as well as giving rise to gametes (for a review on how plants manage their stem cells see [2]). Between these extremes lies the intermediate solution of epigenesis, which in Buss' terminology (which differs from many modern uses [3-5]) describes cases where a distinct germline is formed only once the adult morphology is reached (e.g. annelids).

Buss [1] then provides a table listing the occurrence of each of these developmental modes in multicellular taxa, providing us with a strong reminder species such as *Drosophila* — 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, with 'preformational development' dictating the rules for how somatic performance rewards successful genotypes. While modelling such a process an undoubtedly good starting point when trying to understand *Drosophila* or humans, it is a choice that is, across taxa, relatively rarely chosen by nature herself. Counting across taxa, somatic embryogenesis is by far more common than the other two, with plants, fungi and most protists following this developmental mode — which also occurs in no fewer than nine animal phyla (Table 1 in [1]).

Obviously, we wouldn't even know about the cases deviating from 'human-like' life histories if all of us restrictively studied what is most familiar to us. That there is accumulating scientific knowledge about biodiversity's wondrous alternative forms is a testament to our ability to be excited about discovering rules of life that deviate from our own. However, the fact remains that 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 the research question is also phrased differently for endotherms and ectothermic vertebrates [6]. Assuming that the degree to which a scientific paper strives to address a general question can be measured as the number of lines in the introductory section before the species is mentioned, papers on reptiles, amphibians or fish have to spend more than double the effort of mammal or bird papers on this metric [6].

Still, 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 [7]. 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.

But does it matter for our understanding of evolution?

The above exercise, documenting the relatively ignored research status of much of life compared to our favourites, can be repeated for evolutionary questions [8], though one should not necessarily expect a linear scale of research effort increasing with decreasing phylogenetic distance to humans. More complex patterns are possible. For example, while there is a study [9] showing that parental care research in 6 sampled journals (*Animal Behaviour, Behavioral Ecology, Behavioral Ecology and Sociobiology, Ethology, Hormones and Behavior, and Physiology & Behavior*) is disproportionately based on avian research, this does not necessarily show a scarcity of care studies in, say, primates. These may simply be more often published in journals entirely devoted to primatology, with potential harmful consequences for free flow of knowledge and ideas across subfields.

Another pattern is our preference for specific model species. While I above rather provocatively reminded readers that *Drosophila* are very human-like in many fundamental aspects of their life histories — and indeed numerous traits are shared among all insects and all vertebrates — 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. Zuk et al. [10] 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.

Sex, sexual reproduction, and sexual conflict are indeed 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 (with the latter being treated as interesting phenomena to study, but nevertheless described as curious oddities rather than systems firmly integrated in the central theory). Human evolution and sexual selection are both conspicuously absent from Darwin’s *Origin of species* [11]. He returns to these topics in his later book titled ‘*The descent of man, and selection in relation to sex*’ [12]. This curious mix of two rather unrelated topics may simply reflect the fact that two very major topics were left out from his most significant work, and have little to do with human sexual behaviours particularly inspiring this combined work. 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.

But 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 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 noninsect animal species [13]; curiously, the only examples of hermaphroditism in he massively specious *Insecta* are restricted to *Iceryini* scale insects [14], with rather fanciful routes to ‘borderline hermaphroditism’ such as, in the androdioecious *I. purchasi*, a daughter having tissue that contains extra sperm of her father from the time that the sperm penetrated the oocyte [15].

Cases like *I. purchasi* are clearly unique (at least until future research perhaps uncovers analogous cases), and no-one can blame an author who, when working on a textbook of reproductive strategies, omits to mention that one should not take it for granted that an individual produces its own testes or ovaries, as it might instead rely on one of its own parents' cells to create one type of gamete within its body. Our descriptions of basic theory — for example, making all textbook readers think of separate sexes as the norm when first describing the theory of sexual selection — are full of such tacit assumptions, and some of them are less justifiable than others. One could start raising eyebrows when the alternative, for example, bog-standard hermaphroditism (as opposed to 'truly weird' cases like *I. purchasi*), is really quite common. 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 [16-17]. Quoting Schärer [17]: "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 [18]. 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. [19] were conducting their study of red-winged blackbirds *Agelaius phoeniceus*. The purpose of this study was to examine male sterilization as a way to control a population of birds perceived as pests. As one male can be socially mated with multiple females in this bird species, then perhaps making key males infertile could reduce population growth better than focusing efforts on females (variants of this idea live on in modern insect pest control [20]). Bray's data showed that the nests of manipulated males suffered surprisingly little fertility reduction, with the risk of infertility increasing with isolation from other males. This made him conclude that out 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, especially as there was earlier anecdotal evidence available that females (and not just males) might be promiscuous [21-22].

Ever since, the question of *why* females mate multiply has attracted great both by theoreticians and by empiricists [23-24]. Potential answers range from avoiding infertility [25] to the acquisition of better or more compatible genes [26], receiving parental care from multiple males [27] to 'convenience polyandry' where it is simply cheaper to stop resisting male mating efforts than to try to remain monandrous [28-30]. 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 [24,31]).

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 defining the scope of what can be explained without evoking more complex phenomena [32]. 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 [33]. 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 monandry 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 [32]. 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 [32]).

So what can being a human actually teach us?

Above, I have not highlighted a single example where a human study would have prompted an idea that then expands to uncovering general principles about life. It is not difficult to come up with examples, however. The discovery of sperm, for example, occurred when Antoni von Leeuwenhoek turned his microscope from pond life to bodily fluids [34], including his own sperm [35]. He then proceeded to find these little 'animalcules' in the semen of many animals, also determining that they were made in the testes [36]. While not all gametes are formed this way (and sex can also occur without gametes [37-38]), this was obviously a pathbreaking discovery during a time when the mainstream theory among natural philosophers was quite different: the embryo was seen to be entirely the product of a female, with the egg merely 'woken up' by the sperm. What followed was a battle of the 'ovists' and the 'spermists' [39], eventually leading to the consensus of inheritance via chromosomes (and mitochondria) as we know today. In this case humans do happen to share a trait, sperm production, with all anisogamous life (correct if we consider pollen equivalent to sperm).

Amusingly, Leeuwenhoek himself took great care to mention that proper coitus with his wife had led to the production of the investigated sample, which gives implicit insight to the moral standards of the time. Should there have been scientific or non-scientific reasons that had made all microscopy of human sperm 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?

The discussion of the role of human studies as inspiration for uncovering general rules of life becomes much more interesting, when one turns to the four ways of asking 'why' as defined by Tinbergen [40]. Much of evolutionary biology is about understanding how a particular trait of a particular organism has come about, and Tinbergen realized that this can be answered in four distinct ways without any answer pre-emptying the need to study the other three versions (Table 1). Although not put this way by Tinbergen, one could expand his message to say that the word 'why' itself should ideally come in four different versions. This would avoid many misunderstandings as each sentece was forced to make it clear which of the possible questions we intend to be asking. But human language, preceding the development of evolutionary theory, hasn't provided us with sufficiently nuanced grammar to do this.

A little digression is in place: one should tread carefully to avoid parochialism when talking about language. Features of the writer's own mother tongue will never represent all of 'human language'. Although I am fairly sure that no natural language forces its speakers to differentiate between Tinbergen's different versions of *why* when asking a question about characteristics of living beings, one should not extrapolate from one's own linguistic skill set to general properties any more than one should conclude from one species that sex and reproduction always involve sperm. I invite the reader to think of a useful grammatical features that appears useful but remains absent in all the languages one knows, and then proceed to check if linguists have discovered this feature in their samples of world languages. For example, many sentences could be made more precise if one was automatically forced to distinguish between '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 [41]; it just so happens that none of the indoeuropean or fenno-ugric languages that the author of this MS knows make this distinction. The parallel to taxonomic chauvinism should be obvious.

That Tinbergen needed to point out that the question 'why' can refer to very different ways to understand what is going on can be seen to make a point about scientific understanding itself: science 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 (depending on the research field this also comes with a more or less good ability to predict what happens next around us or, say, in an experiment that replicates previous findings). 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).

Robert Trivers has perhaps been most open about the fact that scientific ideas very often come to him through a process of self-inspection. In his own words [42]: "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?" This, of course, assumes some reliability of the self-inspection programme. Intriguingly, 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, including the idea that natural selection itself might equip us with such mental blinds [43].

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: we begin to look for ideas and potential explanations based on a thought process that resembles the phrase 'putting oneself in someone else's shoes'. Much of teaching in behavioural evolutionary ecology is about making students analyze situations where individuals (and sometimes lower-level entities within individuals) are in conflict with other entities, perhaps with their interests somewhat (but not perfectly) aligned. The fact that much of human social life prepares us for exactly this kind of mental simulation has definite upsides. It is usually quite easy to describe the most complicated research program in behavioural ecology to an interested layperson, as all that is required is to prompt a thought process that involves imagining a dilemma (with trade-offs and perhaps multiple players with divergent interests) and asking, hoping for honest self-inspection, 'what would you do?' Although our mind prefers shortcuts and heuristics over painstaking calculations of all relevant probabilities [44], our ability to intuit scenarios involving likely personal gain, and weigh 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 question and research programs 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' while proper answers, then, require much more focused logical and empirical efforts [45-47] where self-inspecting and/or emotional answers are set aside.

…but what if the shoe doesn't 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 make it harder to get at the correct evaluation of fitness options. Whenever our motivations are socially undesirable, we may be particularly prone to lie about them in our explanations. Second, turning to contexts that do not qualify as self-deception, human introspection still cannot be trusted to give an correct evolutionary answer to the ultimate reasons behind each of our behaviours. 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 [48-49]? Finally, the idea of evolution itself feels non-intuitive, if not downright repulsive, to many.

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 the evolutionary implications of uncertain paternity as well as some economics of parental care — 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 next and perhaps also foregoing foraging during that time) — then it becomes quite intuitive why paternal care in fish may involve some filial cannibalism (not beneficial to the ones who get eaten, but may be the best solution for the male's chances of raising much of the brood to independence [50]) and, more importantly, why 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 [51]. The next consequence is that the trade-off between caring and mating may disappear for the male, which selects for more male care [52]. 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 antrhopomorphizing language (to an extent; see [53-54] 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 find themselves in. If the rules of the game change from set A to set 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. (Mathematical modellers often rejoice when they find something counterintuitive; probably because this allows them to feel the model achieved something 'more' than merely confirming our first intuition.) Finding out whether the hypothesized causation is strong enough to leave a trace in the phylogenetic pattern then necessitates much more work; [55-61] provide recent examples on a very diverse set of questions. Being forced to examine whether our initial predictions hold water when looking at the circumstances of many species, differing in the relevant parts of their ecology, is definitely part of what makes evolutionary and behavioural ecology so exciting.

…or we can't even find the feet?

Judging if we are generally 'good' or 'bad' at putting ourselves in others' shoes is a statement akin to a glass that is half-empty or half-full. Above, I provided the enthusiastic perspective. The corresponding bad news is that extrapolating from one species simply might not work when the game becomes too dissimilar to our own, similar to our intuition breaking down when we move from human-scaled physics to the nanoscale or, alternatively, 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, at least if one wants to avoid the cheeky solution of listing traits such as 'publishing in Proc. R. Soc. B'. Nevertheless, human sociality comes with characteristics that appear to result in unusually much cooperation [63-64] — and much more *nuanced* cooperation, with complex assessment how much to invest in the current interaction [65-66] — especially in non-kin contexts [67-69]. It is beyond the scope of this essay to review the extensive debates surrounding cooperation theory and the various explanations for prosocial behavior; suffice it 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: [70], non-humans: [71], in general: [72-74]), while others clearly favour the interpretation that inclusive fitness effects (roughly synonymous with kin-selected interactions) provides clear and sufficient explanations [75-79].

The debate can, in some years at least, be described as heated [71, 77, 81-82]. This is curious in the sense that 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 quite 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 [83-85]. Given that nature does not really care about the words surrounding the equations (evolution simply happens, and the mathematics at hand might already describe it quite well), an astute student of social behaviour has all the justification for feeling perplexed. 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?

The existence of the debate reminds us of the fact that 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, or even think about a scientific way to evaluate its validity — it simply comes from my own experiences as a teacher — 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 (with unusual here referring to an interspecific comparison). Whether the human level of prosociality is innate, or frequently enough drilled during upbringing to become part of our psyche, is an interesting debate in its own right [86-88]. But regardless of the trait's precise ontology, the outcome is that by the time a biology student enters university, there is usually 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 much more strongly than the other. Most university lecturers of biology have heard a student express the idea that a trait could evolve to make some members of a population die, so that overpopulation is avoided. I have not come across an equivalently illogical idea, phrased in terms of kin selection, that arises with equal regularity in students' brains. Once the necessary training then takes place, 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'". Obviously, this is not true as the more advanced debates show the matter to be more subtle [85, 89], 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 of traits where the human experience matches the fitness structures in us as well as many other species, while yet other species might be quite distinct from this. Here we might take a trait (inbreeding avoidance) for too 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 judgment [90]. 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 e.g. by dispersing far enough [91-93]. Since Fisher's work in 1941 [94], 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. 95-97] — 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 [95, 98]. 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 [99]. A mixed mating system should be *a priori* unstable, because inbreeding depression is strongest when outcrossing is the norm, leading to positive feedback [98-99]: little selfing means that a rare selfing individual has offspring with severely compromised fitness due to homozygosity, while a 'routinely' selfing population experiences purging that keeps recessive deleterious alleles at bay. Given this insight, it is striking that a review of the topic that had an animal focus was still ignoring the population genetic insights (while paying attention to an alternative, outbreeding depression) more than 50 years after Fisher's results and more than ten after Lande's [100].

Maybe time lags do not matter in hindsight, given that we these days seem to understand the complexity of the question [96-97, 101-102]. Taxonomic myopia, i.e. animal researchers not following and citing the plant literature and perhaps vice versa, is no doubt part of the explanation, but 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 with little hope of testing it scientifically, 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 [90] 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 [103]. 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.

Conclusions? 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 [104], 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, an mere unusual but not categorically different outcome of more general principles of life-history theory with respect to 'slow' and 'fast' life histories [105-106].

All in all, we cannot change the fact that Darwin was a human being, 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 the rules of life experienced by a parasite with a complex life cycle, or indeed *I. purchasi* with its unusual germ line arrangement. 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'?)

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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 [107], 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 current state	(Physiological) mechanism, *causation*	Function, adaptive value, *survival value*
Focus on history	Ontogeny	Phylogenetic history, *evolution*

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