

Title: Ageing and the Goal of Evolution

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Abstract: There is a certain metaphor that has enjoyed tremendous longevity in the evolution of ageing literature. According to this metaphor, nature has a certain *goal* or *purpose*, the perpetuation of the species, or, alternatively, the reproductive success of the individual. In relation to this goal, the individual organism has a *function, job, or task*, namely, to breed and, in some species, to raise its brood to maturity. On this picture, those who cannot, or can no longer, reproduce are somehow invisible to, or even dispensable to, the evolutionary process. Here, I argue that the metaphor should be discarded, not on the grounds that it is a metaphor, but on the grounds that this particular metaphor distorts our understanding of the evolution of ageing. One reason the metaphor is problematic is that it frames senescence and death as nature's *verdict* on the value of older individuals. Instead, we should explore a different metaphor: the lengthy post-reproductive period in humans and some other animals is not an accident of culture, but designed by nature for the purpose of supporting and guiding younger generations. On this alternate picture, different stages of life have their own evolutionary rationale, their distinctive design features.

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1. A picture and some questions.

There is a certain picture – I will not yet call it a “metaphor,” since that remains to be shown – that has enjoyed significant longevity in the evolution of ageing literature. According to this picture, we should think of nature as having a *goal* or *purpose*, as something like the perpetuation of the species, or the reproductive success of the individual. Additionally, each one of us has a certain *function*, *task*, or *job* to perform in relation to this goal, namely, to breed and to raise our brood to maturity.

Consider the following examples, which have been drawn from over a century of theoretical reflection on ageing and evolution. The first is from August Weismann, from his 1881 lecture, “The Duration of Life.” This lecture is generally considered to be one of the first serious contributions to the evolution of ageing:

The connection between activity and shortness of life...is explicable because the increased rate at which the vital processes take place permit the more rapid achievement of the aim and purpose of life, viz. the attainment of maturity and the reproduction of the species. When I speak of the aim and purpose of life, I am only using figures of speech, and I do not mean to imply that nature is in any way working consciously. (Weismann 1889, 8)

The basic picture here is that nature has a certain goal – keeping the species alive – and the individual has a function in relation to that goal. In this passage, he explicitly recognizes that these expressions (“aim,” “purpose”), when applied to nature, should not be taken literally; they are figures of speech. Nonetheless, he relies on them throughout the text.

We will continue following Weismann’s trail of thought. If the goal of nature is the perpetuation of the species, what is the job of the individual? He continues:

It is of no importance to the species whether the individual lives longer or shorter, but it is of importance that the individual should be enabled to do its work towards the maintenance of the species. This work is reproduction, or the formation of a sufficient number of new individuals to compensate the species for those which die. As soon as the individual has performed its share in this work of compensation, it ceases to be of any value to the species, it has fulfilled its duty and may die... We should therefore expect to find that, as a rule, life does not greatly outlast the period of reproduction except in those species which tend their young; and as a matter of fact we find that this is the case. (Ibid., 10)

What is striking about this passage is that the idea that nature has a goal, and the function of the individual is to breed, an idea which he admits is figurative, appears to perform a vital explanatory role in making sense of senescence – the deterioration of cells with age – and death: once one fulfills the goal of life by reproducing (and in our case, raising our brood to maturity), one is dispensable to the species, and perhaps even a hindrance to it. This is why nature permits senescence and death.

Let's set aside Weismann, whose arguments have, at any rate, largely been seen as discredited due to their reliance on group-selectionist thinking, which fell out of fashion in the 1960s for various reasons, some scientific and some sociological.¹ Now jump forward about 75 years, to a book written in 1956 by the scientist and physician Alex Comfort. Here is how Comfort (1956) explains ageing:

The limited life of the gonad is in a special category only because, in terms of evolutionary teleology, the gonad is the significant part of the organism. (31)

What is evolutionary teleology? "Teleology," of course, just means the study of purpose. So, what this passage means is that, from the point of view of evolution's purpose – what evolution is really after, if you will – the gonad, the organ that produces sperm or egg, is the significant organ. Notice that he does not say it is "a" significant organ. He says it is "the" significant organ. He continues:

Ageing of the whole organism after a prolonged post-reproductive period is a process which is realized only by human interference, at least so far as most species are concerned, and not 'envisaged' by evolutionary teleology. (31-2)

For Comfort, the fact that human beings enjoy a long "post-reproductive period" was not something that nature anticipated (foresaw, expected). Nature anticipated that we would be a bit more like salmon, which all die shortly after spawning. Of course, people are unlike salmon in that our offspring depend on us for a long time after birth, so we need to survive long enough for them to be self-sufficient. It is only an accident of human culture and medicine, with its relative freedom from predation, starvation, and disease, that we live for a long time even *after* our children are on their own.

Peter Medawar uses similar imagery. This passage is from his landmark 1946 paper, "Old Age and Natural Death:"

...the changes which an animal may undergo after it has ceased to reproduce are never directly relevant, and are in most cases quite irrelevant, to the course of its evolution. A genetic catastrophe that befell a mouse on the day it weaned its last litter would from the evolutionary point of view be null and void. This state of affairs is tacitly acknowledged in the celebrated half-truth that 'parasites live only to reproduce': the whole truth is what parasites do *after* they reproduce is not on the agenda of evolution. (Medawar 1957, 34)

Like Comfort, Medawar colorfully views evolution as having a certain *agenda*. An agenda is something more specific than a goal; it is a goal with an accompanying plan of action: if such-and-such steps are carried out in such-and-such sequence, then the goal will be realized. An academic conference, for example, has a certain agenda: there will be presentations, question-and-answer periods, meals, conversation over drinks, and once

¹ See Sober and Wilson (1998).

those things have happened, the goal of the conference will have been fulfilled. What the participants do after they leave the conference is not on that agenda. Similarly, Medawar says, what individuals do after they have finished weaning their last offspring is not on evolution's agenda, either.

It is easy to think that the fact that Weismann, Comfort, and Medawar use such colorful imagery to describe ageing has no parallel in contemporary scientific literature. In other words, one might think that these quotations, if they illustrate anything, illustrate how scientists, through the 1950s, were more comfortable than we are today using anthropomorphic imagery to give voice to their scientific theories. That would be an error. Below are two examples of the same imagery drawn from contemporary scientific sources.

The first example is taken from a review article written in 2002 by three prominent ageing researchers. It appeared in the *Journal of Gerontology Series A*:

Molecular disorder occurs and accumulates within cells and their products because the energy required for maintenance and repair processes to maintain functional integrity for an indefinite time is *unnecessary* after reproductive success. Survival beyond the reproductive years and, in some cases, raising progeny to independence, *is not favored by evolution* because limited resources are better spent on strategies that enhance reproductive success to sexual maturity rather than longevity...*Thus, aging is a product of evolutionary neglect, not evolutionary intent.* (Olshansky et al. 2002, B294, my emphases)

Neglect, intent, favor, disfavor: these are attributes of goal-directed creatures. In this passage, then, evolution is likened to a goal-directed being. Ageing is explained by the fact that "survival beyond the reproductive years" is not useful for evolution's goal.

The second example comes from an article written by the biologists Shalev and Belsky, in 2016, from the journal *Medical Hypotheses*:

Also important to consider are *evolutionary theories of aging*, including the Mutation Accumulation Theory, the Antagonistic Pleiotropy Theory, the Disposable Soma Theory, and the recent Reproductive-Cell Cycle Theory. These, like the aforementioned perspectives, highlight trade-offs between growth and *the ultimate goal of evolution, reproductive success*, at the expense of longevity later in life. (41, latter emphasis mine)

In this passage, reproductive success is not merely one of evolution's goals; it is evolution's *ultimate* goal. Incidentally, one should recall that the very label for one of the most prominent evolutionary theories of ageing – Thomas Kirkwood's "disposable soma" theory – borrows imagery that is more appropriate to the realm of artifacts than biology. Electronics like televisions or microwaves are manufactured so cheaply today that, once they have served their purpose, they are disposable. They can be thrown out rather than

repaired. The concept of a *disposable soma* carries, inside of it, the idea of outliving one's purpose.

To summarize, there is a certain picture that has enjoyed significant longevity in the evolution of ageing literature: nature has a goal, to perpetuate the species, and the individual has a role or a function in relation to that goal, namely, to breed and, in some species, to raise its brood to self-sufficiency. Furthermore, anyone who cannot, or can no longer, contribute to that role has no value, or perhaps reduced value, from evolution's point of view, *and this is part of an ultimate explanation of senescence and death.*

I have extracted a certain picture from the evolution of ageing literature. In the remainder of this paper, I will pose three basic questions about it. *First*, is this picture a metaphor? In other words, might it be literally true that nature has a goal? *Second*, assuming that it is a metaphor, what is the underlying truth of nature the metaphor is trying to capture? In other words, what is that non-metaphorical, factual, proposition that the metaphor is, perhaps awkwardly, pointing to? *Third*, should we keep the metaphor? Is it helpful? Is it harmful? Is it doing more harm than good? I will argue that we should dispense with the metaphor, for two reasons: it distorts our understanding of the evolutionary process and, quite possibly, reinforces ageist attitudes. To clarify, the argument here is *not*: “the metaphor is ageist, so we should get rid of it.” The argument is: “the metaphor misleads about science, which is a good enough reason to get rid of it; if it's ageist, then even more reason to.”

The problem I raise here evokes a number of important and related questions that far exceed the scope of this paper, not to mention my expertise. One problem is how to think about the relationship between aging and philosophical conceptions of health more generally (see Sholl's [t.c.] contribution to this topical collection). Another question concerns the formal definitions and models that evolutionary thinkers have used to come to grips with aging. Giaimo (t.c.) provides a rigorous overview of the topic. A third concerns manner in which ageing should be operationalized for science. In this connection, Green and Hillersdal (t.c.) discuss the search for specific *biomarkers* of ageing, and Nathan (t.c.) explores the fissure between chronological time and biological time. My goal here is somewhat orthogonal to these lines of questioning: it is to expose a certain image or metaphor that runs, as a subcurrent, through the evolutionary literature, and to interrogate its continued usefulness.

2. Functions and goals in nature.

The first question is whether this picture – that nature has a goal, and that the individual has a function in relation to this goal – is or is not a metaphor. *On the one hand*, it might seem obvious that it *is* a metaphor and, more specifically, an anthropomorphic depiction of the evolutionary process. We are repeatedly reminded that evolution is not a purposive, conscious, intentional, deliberate, goal-directed process, but that it is blind and

purposeless.² *On the other hand*, we have enjoyed decades of philosophical reflection on teleological concepts such as goal, purpose, and function in biology; many of these philosophers have sought to give such concepts a literal meaning and application.³ It does not *seem like* a metaphor to say that the function of the heart is to pump blood or a goal of the paramecium is to move up a food gradient. So, it is worth seeing whether the idea that nature has a goal can be understood literally using the tools of contemporary philosophical theorizing about teleology. Put simply, what are we doing when we attribute functions, goals, and purposes, to entities in the non-human, even non-sentient, world?

The first thing to notice is that there are actually two quite distinct teleological concepts that appear to play into the imagery surrounding ageing: *goals* and *functions*. There are two different “levels” of teleology moving together here. First, nature is depicted as having goals. Second, individual organisms are depicted as having functions, namely, the function of promoting those goals. Until the 1970s, philosophers of science who reflected on the problem of teleology in nature made a sharp distinction between these two teleological concepts, goals and functions, though, for better or worse, the distinction has started to fade into oblivion.⁴ So it is worth taking a moment to bring to mind the traditional distinction between the two.

One very preliminary way of understanding the difference between functions and goals is by noting a conceptual distinction: *goals belong to wholes, and functions belong to parts*. At least in biology, a function is the kind of thing that belongs to a “contained” system, and a goal a “containing” system. A mouse, for example, might be goal-directed with respect to obtaining a scrap of food, but a mouse does not have the *function* of obtaining food. The mouse, considered as a whole, does not have a function at all. Its *parts* have functions (for example, its feet have the function of locomotion).

The fact that goals belong to wholes and functions belong to parts, helps explain why, as a rule, we do not attribute functions to *organisms*: we generally see organisms as self-contained systems. There is at least one obvious exception to this rule: ecologists are often willing to give functions to whole organisms and even populations of organisms. They say things like, “the function of the mountain lion is to regulate the deer population.” But to the extent that they do so, it is because they are seeing the mountain lion as a part of a larger system, namely, the ecosystem. So, this example doesn’t violate our basic rule: goals belong to wholes; functions to parts. (This is, in fact, how I understand the picture of teleology in the evolution of ageing literature: in relation to nature’s *goal* of promoting the species or maximizing the fitness of individuals, each individual has the *function* of breeding. That individuals may have their own “goals” is not pertinent to this metaphor.)

² Dawkins (1986).

³ E.g., Millikan (1984); Neander (1991); see Garson (2016) for an overview.

⁴ But see McShea (2012), Trestman (2012), Piccinini (2015, Chapter 6), and Maley and Piccinini (2018), who have sought to recover it.

When we hold this difference between goals and functions in mind, it becomes very tempting to imagine a logical connection between them: *functions are simply contributions to goals* (e.g., the mouse's foot has the function of locomotion because that is how it contributes to the mouse's goal). In the 1960s, and even in the 1970s, this was a prominent idea. Ernest Nagel (1961, 1977) argued that functions are just contributions to goals. William Wimsatt (1972) and Christopher Boorse (1976) also held this view. If one succumbs to this temptation, then functions become relatively uninteresting, philosophically speaking. That is because, once one knows what an organism's goal is, one knows immediately what the functions of its parts are (or, more precisely, one knows immediately what one would have to do to figure out what the functions of its parts are): a function of a part is just a contribution to a goal. The philosophically exciting task would be to figure out what goals are.

What, then, is a goal? One attractive and commonsensical idea is that goals are simply intentions, whether conscious or unconscious ones (e.g. Woodfield 1976). To have the goal of running a half-marathon is simply to have the intention to do so. On this view, when we attribute goals to ants, paramecia, or thermostats, we're engaged in an anthropomorphic extension of the way that we think about human intentional actions. I accept something like this view about what goals are, for reasons to be considered below. From about the 1930s through the 1970s, however, philosophers of science who wrestled with the problem of goal-directedness took a very different approach. They wanted to articulate a notion of goals and goal-directedness that would apply, quite literally and unproblematically, to ants and thermostats as much as to intentional human action. The idea was that once we understood goal-directedness in this sweeping, naturalistic, sense, we would see how human intentional action is just one special case of it.

Among these latter philosophers – those who wanted to give a broad, naturalistic, construal of goals and goal-directedness – a standard view was that, *what it is* for an organism to be goal-directed is for it to behave, or tend to behave, in the right sort of way. In particular, the organism should exhibit “plasticity and persistence” with respect to a certain state of affairs (though different theorists defined those terms somewhat differently).⁵ Imagine a bird attempting to eat a worm. The bird exhibits “persistence” in that, if the position of the worm changes, the bird will also change its position appropriately. It also shows “plasticity” in that it can reach the same “end,” the same “goal-state,” from many different starting points. Homeostatic systems, such as the system that regulates the water content of the blood, can also be described as “goal-directed” in that they tend to exhibit plasticity and persistence with respect to that state. If the water content of the blood dips significantly below, or rises above, 90%, diverse physiological mechanisms will kick in and the system will tend to return to 90%.

One might feel satisfied that this naturalistic account, or something in its neighborhood, is true for organisms. But is this account of goal-directedness applicable to nature, evolution, or natural selection, as such? In other words, does natural selection, quite literally, have the goal (in the sense of “plasticity and persistence”) of perpetuating the

⁵ The canonical texts are Sommerhoff (1950), Braithwaite (1953), and Nagel (1961).

species, or maximizing the average fitness of the population, or maximizing the individual's reproductive success (or what have you) and, by virtue of that fact, the individual the function of breeding and raising its brood to maturity?

There are two reasons that we probably cannot think of natural selection as a goal-directed process in any literal sense. I'll put the point in a nutshell and then elaborate. First, historical attempts to develop a naturalistic account of goals and goal-directedness did not meet with success. Instead, somewhat stubborn conceptual problems have hindered their development. Second, even if those problems could be resolved, traditional theories of goal-directedness are, at best, applicable to organisms, some systems within organisms (such as systems responsible for dopamine homeostasis), and perhaps some machines such as heat-seeking missiles or thermostats. It would be hard to see how natural selection, or for that matter evolution more broadly, would be the kind of thing that is "eligible" to have a goal. I will develop each point in turn.

As noted above, theorists like Braithwaite, Sommerhoff, and Nagel attempted to define the notion of goal-directedness using the "plasticity and persistence" criterion. But, as Scheffler (1959) and others pointed out, those definitions face at least two problems. First, while this criterion does seem to characterize many cases of goal-directedness, it is far from sufficient: there are plenty of things that exhibit plasticity and persistence but do not have goals. A marble rolling to the bottom of a bowl shows plasticity and persistence but does not have any goals. So does a taut rubber band returning to its relaxed state. Nor is the criterion necessary. Surely, we can imagine a mouse that has the goal of getting some food, but because of a neurological deficit, it does not show any plasticity or persistence in doing so. For example, if a brain-injured mouse can only do *one thing* and one thing alone to obtain food – such as claw helplessly toward it with its left arm – it would not, by definition, exhibit plasticity and persistence with respect to that goal. Does that mean it doesn't have the goal of getting some food?

Scheffler pointed out other problems as well, such as the problem of "goal failure" and of "multiple goals." The problem of "goal failure" is that the plasticity and persistence criterion doesn't clearly allow one to have a goal but *fail* to attain it. The problem of "multiple goals" is that most of the standard analyses entail that if an organism is goal-directed with respect to X, and X always leads to Y, then the organism is goal-directed with respect to Y, too. For example, if a rabbit is goal-directed with respect to eating a pellet, and doing so always leads to defecation, then it is goal-directed with respect to defecation, too. But the rabbit doesn't have the goal of defecating simply in virtue of the fact that it has the goal of eating a pellet. To my knowledge, these problems with "plasticity and persistence" formulations remain unresolved.

McShea (2012; 2016) has argued that, despite their conceptual problems, these definitions of goal-directedness in terms of "plasticity and persistence" *do* capture something vitally important about goal-directed systems. He thinks that, as an empirical matter, most goal-directed systems actually exemplify these features. But McShea does

not present this viewpoint as part of a *philosophical definition* of goal-directedness. In fact, he does not attempt to define the term at all.⁶

I agree with McShea that these features of plasticity and persistence *do* capture something notable about goal-directedness. At the very least, plasticity and persistence are *robust empirical indicators* of the presence of goal-directedness. They should not, however, be part of a philosophical definition of goal-directedness (whether we conceive the task of a philosophical definition to be one of conceptual analysis, theoretical definition, or conceptual engineering). That is because, in my view, the most interesting feature of goal-directedness is *goal-failure*. In other words, to me, the most interesting question about goal-directed systems is not, “how is it possible that this system is able to exhibit plasticity and persistence with respect to a goal?” but, “by virtue of *what* does a system possess a goal despite its failure – even repeated, systematic failure – to achieve that goal?” Millikan (1989, 299) put the point quite aptly when she wrote that philosophical accounts of purpose or function “run afoul exactly when they confront the most central issue of all, namely, the problem of what failure of purpose and defectiveness are.”

A second, perhaps lesser, problem is this: even if one thinks that these problems can be surmounted, and that there is a plausible theory of goal-directedness along these lines (plasticity and persistence), it is hard to see how such theories would apply to natural selection as such, or evolution more broadly. First, natural selection is not a “biologically real system,” like an organism, a sub-system of an organism, a thermostat, or even a population of wolves. (That said, I’m not entirely sure what ontological category natural selection itself falls under: a force? a process? an abstract synopsis of a multitude of low-level processes?) Moreover, it is not clear to me what, precisely, natural selection would exhibit “plasticity and persistence” *toward*. Figuratively put, what is natural selection trying to do? Recently, McShea (2012) has argued that to the extent that we’re willing to use goal-directedness to think about evolution, we should think of *evolving lineages* as goal-directed, not evolution or natural selection itself. In his view, it’s really the *lineage* that exhibits a certain amount of plasticity and persistence with respect to attaining and maintaining, say, a certain phenotype. Still, I think his view struggles to overcome the traditional objections.

If we are to reject naturalistic attempts to understand goals and goal-directedness, what are we to replace them with? How *should* we understand goals? As Woodfield (1976) urged, the notion of goal-directedness is probably best understood by reference to intentions, that is, the (conscious or unconscious) intentions of sentient creatures. What makes a mouse goal directed is, simply put, that it has the intention of obtaining some food. To the extent that we are willing to characterize artifacts (like thermostats) as inherently goal-directed, it is because we are treating them as if they had intentions. Note that my discussion here does not take into account recent work on the question of *how far*

⁶ McShea (pers. comm.) Also see McShea (2016, 93).

into the natural world we can literally attribute psychological predicates such as preferences and intentions.⁷

My own view on goals, then, is much closer to Woodfield's than Nagel's: when we treat a non-sentient being as having a goal, we are adopting the "intentional stance;" we are agreeing to treat the thing *as if* it possesses beliefs and desires, even if it's not, in fact, capable of such cognitively sophisticated states (Dennett 1987, 259). This is also true when we think about nature, itself, as having goals, purposes, or "free-floating rationales." Put differently, we are using what Godfrey-Smith (2009) and Okasha (2018) call "agential thinking:" we are thinking of the thing as if it is a conscious agent, even though we know it's not a conscious agent. And interestingly enough, sometimes that stance does allow one to predict an entity's behavior quite effectively. The problem is that it can also be harmful because it can lead us to imagine that the entity has properties it does not actually have, as we will shortly see.

3. The declining force of natural selection with age.

In the last section, we concluded that the statement, "nature has a goal, and in relation to that goal, the individual has the function of reproducing," is a metaphor. It treats evolution, natural selection, or nature itself as if it were an agent with beliefs and desires of its own, even though nature isn't really such an agent. But that raises a new question. What exactly *is* the underlying truth of nature that the metaphor points to? Given the longevity of the metaphor, presumably there *is* a literal, non-metaphorical proposition that the metaphor, quite improperly, gestures toward, and that explains its enduring allure. So, what is that proposition?

One preliminary way of expressing this proposition comes from the biologist Michael Rose, writing in 1991:

Since Weismann gave up his early invocation of group selection, all evolutionary theorists who have published on the causes of aging have agreed that the ultimate cause is the declining force of natural selection with age. This is the essential evolutionary theory of aging (16).

The force of natural selection declines with age. That is what Rose takes to be the core axiom of an evolutionary theory of ageing. On the surface, the declining force of natural selection with age points to a *phenomenon*: the rate at which natural selection eliminates a harmful mutation from a population depends upon the average age at which those harms first appear (or, in Hamilton's (1966, 12) words, "an effect of a given form always has a larger consequence [in terms of fitness], or at least one as large, when it occurs earlier.") To give a simplistic illustration, suppose there were a gene that causes its bearer to die at the age of 20, a second gene that causes its bearer to die at the age of 40, and a third that causes its bearer to die at 60. The first gene would be eliminated from the

⁷ For a recent exploration of this question, see Figdor (2018).

population more rapidly than the second, and the second more rapidly than the third. Of course, this holds “all things equal,” for example, the DNA underlying each of these genes mutates at the same rate (no “mutation hotspots”), no heterozygote superiority, and so on.

So far, however, we have merely pointed to a phenomenon that occurs in nature. The question we must confront is: why is this so? Why would genes with late-acting harms be eliminated more slowly than genes with early-acting harms? Why would natural selection stand back, as it were, and allow diseases such as dementia, arthritis, or glaucoma to ravage our older populations so mercilessly?

This is where metaphors become dangerous. For the metaphor that evolution has a goal suggests, or insinuates, the quite mistaken idea that this phenomenon, this “declining force of natural selection with age,” represents *nature’s verdict on the value, or the utility, of older individuals*. It is because older individuals have already contributed to evolution’s goal that natural selection, as it were, has no use for them anymore, and can’t be bothered with those diseases that differentially impact older people. This metaphor significantly distorts the truth, as I’ll shortly show.⁸

This picture – that the declining force of natural selection with age represents nature’s verdict on the value of the aged – is certainly suggested by Medawar when he says that what an organism does after it raises its brood is not “on the agenda” of evolution. It is the picture that Comfort points to when he says that post-reproductive life was not “‘envisaged’ by evolutionary teleology.” This is also the picture that Olshansky, Hayflick, and Carnes evoke when they say that ageing is “a product of evolutionary neglect, not evolutionary intent.” A recent educational article published in *Nature* also alludes to this picture when it informs us that, “selection *ignores* the performance of individuals late in life. As a consequence, selection is unable to favor beneficial effects, or to counteract deleterious effects, when these effects are expressed at advanced ages. For example, if a beneficial or deleterious mutation occurs only after reproduction has ceased, then it will not affect fitness (reproductive success) and can therefore not be efficiently selected for or against.” (Fabian and Flatt 2011, emphasis mine).

Incidentally, it seems to me that this final passage, from the educational article in *Nature*, suggests, to the incautious reader, a tempting though false idea. The idea is that, once a person is beyond reproductive age, then, by definition, they cannot affect the evolutionary process. After all, the way that one affects the evolutionary process is through breeding and raising one’s brood; thus, if one cannot breed, or one’s brood has reached maturity, one has no bearing on the evolutionary process, like a detached cog

⁸ For those who are impatient, and eager to know exactly why this is a mistake, it’s this: the canonical – though not universally accepted – explanation of the “declining force of natural selection with age” is that, at least until recently, so few people actually survived until old age because of the hazards of the natural environment. Put crudely, it’s not that older people have no evolutionary value to the population; it’s just that, until not so long ago, there were not that many older people around.

whirling away aimlessly. So the “declining force of natural selection with age” is just a consequence of the way that evolution works, one that any clear-minded and educated person would grasp.

But we know this to be false. We know that there are other ways that natural selection can act on a trait, even if that trait doesn’t affect one’s number of viable offspring. That is the whole point of kin selection and the related notion of inclusive fitness. In kin selection, natural selection acts on a trait not because it helps *me* have viable offspring, but because it helps my *relatives* have viable offspring. The honeybee’s stinger isn’t there because it helps the bee have viable offspring; it’s there because it helps her sister have viable offspring.

Closer to ageing, consider the so-called “grandmother hypothesis,” which could perhaps be read as a version of kin selection, and for which Kristen Hawkes has been advocating for some time (e.g., Hawkes et al. 1998). Consider those societies, like some of the societies she studied in Tanzania, in which the grandparents, particularly the grandmother, play a vital role in promoting the welfare of the grandchildren. (Recently there have been two large studies, using data from Quebec and from Finland, that showed the same effect. In these societies, there is a significant fitness difference between mothers whose own mothers participate in child rearing and those who do not.⁹) Hawkes and her colleagues believe that menopause was actually shaped by natural selection to encourage women to make the transition from producing and supporting *offspring* to supporting *grand-offspring*. Nor is this pattern limited to humans; bottle-nose dolphins and pilot whales also fend for their grand-offspring (Lee 2003, 9637). The point here, for us, is that it is simply false to say that once an individual has stopped reproducing, then they are no longer “on evolution’s agenda.” In this view, *that* human beings and some other creatures should enjoy a long phase of “post-reproductive” existence is not an accident of culture: it is by nature’s design.

Intriguingly enough, both Hamilton and Medawar noted, in passing, the possibility of something like a grandparent effect. Hamilton (1966, 37) writes: “In fact, the 15 or so years of comparatively healthy life of the post-reproductive woman is so long in itself and so conspicuously better than the performance of the male that it inevitably suggests a special value of the old woman as mother or grandmother during a long ancestral period, a value which was for some reason comparatively little shared by the old male.” Medawar (1957, 45), in a tantalizing footnote, acknowledges that, “Grandparents, though no longer fertile, may yet promote (or impede) the welfare of their grandchildren, and so influence the mode of propagation of their genes. A gene for grandmotherly indulgence should therefore prevail over one for callous indifference...” It is unfortunate that Medawar chose not to work through the implications of his footnote more systematically, as it might have softened his insistence that what we do after reproducing is “never directly relevant, and in most cases quite irrelevant,” to the course of evolution.

⁹ Chapman et al (2018); Engelhardt et al. (2018).

There is another mechanism to consider, in addition to kin selection; this is group selection.¹⁰ Group selection is the idea that natural selection can act on a trait *not* because it affects my individual fitness or even my inclusive fitness but the fitness of my group, where the fitness of my group is usually thought of as its total reproductive output relative to other groups (though there are other ways of conceiving of what a group's fitness is). As noted above, in the 1960s this idea became taboo, but it has been making a gradual comeback in the last 40 years or so, thanks largely to David Sloan Wilson, Elliott Sober, and Charles Goodnight; more recently, Martin Nowak, Corina Tarnita and E. O. Wilson have been vigorously promoting group selection.¹¹

If we take group selection seriously, then one hypothesis we should consider is that if older individuals are making positive impacts on the group, for example, through providing *information, resources, or guidance*, then they *are* “on evolution's agenda.” Selection would act against genes that have late-stage harmful effects. (To the extent that group selection plays into ageing literature today, it is usually to support the existence of a so-called “programmed death gene;” this is a modern-day incarnation of Weismann's idea that death is, as it were, by nature's design to prevent overcrowding.¹² But in theory, one could argue the other way, namely, that group selection could *prolong* the post-reproductive period of life rather than shorten it.)

Surely, however, there is a declining force of natural selection with age, as age-related diseases attest to. What explains this phenomenon? The standard explanation in the literature – though not entirely uncontested – is that most people, at least until recently, simply did not live to be very old. At least until recently, the odds of living to be, say, 70, given all the dangers of our environments – famine, predation, disease, cliffs, infections, snakebites, wars, drownings, etc. – were pretty slim. It is not that 70-year-olds were useless to evolution's purposes; it is just that there were so few of them around. The declining force of natural selection is simply a reflection of this. This explanation was gestured at by Medawar, and set out quite explicitly by Hamilton (1966). In fact, Hamilton thought that the declining force of natural selection with age would be seen even if reproductive ability *increased* with age (23-4).¹³

¹⁰ There are complex debates about the relation between kin selection and group selection, which I'll leave to one side; see Sober and Wilson (1998); Okasha (2006).

¹¹ Sober and Wilson (1998); Goodnight and Stevens (1997); Nowak et al. (2010).

¹² E.g., Mitterdorff (2004).

¹³ Baudisch (2005) gives a particularly clear overview of Hamilton's views, though she does not entirely agree with his assessment. In a recent paper, she and her colleagues argue that the explanation for the declining force of selection with age is not so much that most people don't survive to old age because of external accidents, but because of the age-structure of the population: they argue that even in a population without mortality, so long as older people make up a disproportionately small segment of the population and younger people a disproportionately large one, then the force of selection would still decline with age (Wensink et al. 2017). I leave it to the mathematically-inclined reader to pursue these contrasting theories.

Putting the point simply, and perhaps a bit crudely: the reason for the prevalence of age-related disease is not that people are evolutionarily useless once they're done breeding (and raising their brood), but that most people, at least until recently, didn't live to be very old. A problem with the metaphor of the goal of evolution is that it comes dangerously close to framing this somewhat interesting statistical phenomenon as nature's *verdict* on the value of the older generation. Instead, we ought to consider the prospect that a long post-reproductive phase in humans and some other animals is intended by nature for the purpose of supporting and guiding younger generations.

4. An Assessment.

The only question that remains is whether the metaphor – nature's goal is to perpetuate the species; the function of the individual, vis-à-vis that goal, is to breed and raise its brood – is worth keeping, or whether we should get rid of it. Note that there is no suggestion here of getting rid of the metaphor *simply because it is a metaphor*. I assume that metaphors in science can be helpful, harmful, or harmless. Some think that the notion of genetic information is a metaphor (Sarkar 1996), but that, alone, wouldn't suggest we eliminate it. Rather, the relevant questions to ask about metaphors in science are questions like: are they illuminating? Do they help us discover new things? Do they have negative social impacts?

I think we should get rid of the metaphor and its associates, not only because it distorts the nature of ageing, but because it potentially plays into ageist attitudes. (On the problem of ageism, see Jecker's [t.c.] and Gullette's [t.c.] important contributions to this topical collection.) The metaphor can mislead laypersons about the reason for the declining force of natural selection with age. It makes it easy to infer one of two things: first, that if an organism is unable, or chooses not to, breed, that organism becomes somehow *invisible* to the evolutionary process; second, if an organism is unable (etc.) to breed, it is somehow *dispensable* to that process. Both are untrue; it is hard to see how they would not inculcate ageist attitudes. At least in humans, members of the older generation contribute substantially to shaping the course of evolution, by providing information, guidance, and resources that impact the survival prospects and reproductive choices of younger generations. The metaphor inappropriately suggests that the prevalence of age-related disease, senescence, and death, is something like nature's judgment on the value of the aged. Given that we are apt to use metaphors, if we wish to have a more constructive and illuminating metaphor, we might try out something like this: various stages of life have their own evolutionary rationale, their own design features, their own special *mandate*.¹⁴

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¹⁴ Blasimme (t.c.) in this collection, also takes steps in this direction by describing the “functional plasticity” of the ageing organism, and contrasting it with the reigning conception of aging as an “unmodifiable trajectory of decline.”

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