

Natural Selection: Descent with Modification

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Tim Lewens

University of Cambridge

Department of History and Philosophy of Science

Email: tml1000@cam.ac.uk

“The single best idea that anyone has ever had”

Near the beginning of his book *Darwin's Dangerous Idea*, Daniel Dennett tells us that “If I were to give an award for the single best idea anyone has ever had, I’d give it to Darwin, ahead of Newton and Einstein and everyone else” (1995: 21). Of course, the idea Dennett had in mind was natural selection. But what, exactly, is that idea?

Should we even think of it as a “single” idea? I suggest we should think of natural selection as a family of related modes of explanation, which have changed gradually over the years as the theories in which they are embedded have been reformulated in order to address different problems. In other words, our understanding of natural selection itself has been subject to a process of “descent with modification.”

This chapter uses some of these transformations in our thinking to reflect on conceptual puzzles about what natural selection is, and how it works. In particular, I focus on a series of contentious questions. Does natural selection entail “gradualism”?

In other words, is Jerry Fodor right when he asserts that “Darwinism can work only if...there is some organic parameter the small, incremental variation of which produces correspondingly small, incremental variations of fitness” (2001: 89)? Is sexual selection a different process to natural selection, or just a type of natural selection? In what sense does natural selection involve a “struggle for existence”? Can natural selection work with any form of inheritance, or must inheritance be “particulate”? How does our verdict on these questions affect the prospects of efforts to apply natural selection to cultural change, rather than to organic change? And what, finally, does all of this tell us about how natural selection explains the phenomena that were of central interest to Darwin—namely the emergence and perfection of structures and habits that adapt organisms so well to their conditions of life?

Darwin’s Question

In the introduction to the *Origin of Species*, Darwin (1859) pointed out how much strong evidence there is in favour of “transformism.” This is the view, espoused by others before him such as the then-anonymous author of the 1844 work *Vestiges of the Natural History Creation*, that the species we see around us are modified descendants of earlier ancestors they hold in common. Transformism can be supported, for example, by pointing to facts about the anatomical similarities of distinct species, their distribution around the globe, and so forth. But this sort of transformism faces a significant problem. How on earth, Darwin asks, have “the innumerable species inhabiting this world...been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration” (1859: 3)? By itself the hypothesis of common ancestry contains nothing that might

explain, to use just one of Darwin's examples, "the structure...of the woodpecker, with its feet, tail, beak, and tongue so admirably adapted to catch insects under the bark of trees" (1859: 3).

Darwin considers a mystical response on behalf of the transformist: "The author of the 'Vestiges of Creation' would, I presume, say that, after a certain unknown number of generations, some bird had given birth to a woodpecker," and that it had been produced "perfect as we know them" (1859: 3-4). Needless to say, Darwin immediately responds that "this assumption seems to me to be no explanation, for it leaves the case of the coadaptations of organic beings to each other and to their physical conditions of life, untouched and unexplained" (1859: 4) Darwin observes, in other words, that transformism is incomplete unless it offers some explanation for the emergence of organic structures that are brilliantly adapted to each other, and to the life of the organisms that bear them. Darwin designs natural selection in such a way that it can serve as an answer to what we might call *Darwin's question*:

How have all those exquisite adaptations of one part of the organic organisation to another part, and to the conditions of life, and of one distinct being to another being, been perfected? (1859: 60)

In this chapter I will argue that by focusing on the pragmatic origins of natural selection as a response to the question of adaptation—and by focusing on exactly how Darwin himself understands that question—we can understand why Darwin tends to describe natural selection as he does, and why his descriptions often depart from more recent accounts of what natural selection is. In some cases these differences are superficial, and in other cases they are profound.

Darwin's Answer

Darwin does not usually define natural selection in any short, pithy way, nor does he give a set of conditions that are necessary and sufficient for natural selection to act. Instead, he tends to give far longer descriptions that illustrate, in a schematic form, how complex adaptations can come to exist. The organic world, he says, is characterised by struggle. In his *Notebooks* he writes of “the dreadful but quiet war of organic beings” (Barrett et al 1987: E114), a competition so intense that “a grain of sand turns the balance” between life and death (E115c). This struggle has profound consequences, as he later explains in the *Origin*:

Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection.

(1859: 61)

For Darwin, “this principle” names a wide set of processes whereby valuable variants are generated, maintained and refined in a population of organisms.

In contrast to this, modern treatments of evolution are often at pains to give far more compact definitions of natural selection. We might be told, for example, that natural selection occurs whenever organisms—or indeed entities of any kind—vary in their “fitness”—roughly speaking, when they vary in their abilities to leave offspring—and whenever these abilities are passed from parents to their babies (e.g. Lewontin 1970). This very general account allows us to ask whether selection might act at several different levels of natural organisation—perhaps at the level of the group, or the species, perhaps at the level of the cell or the gene—and it also allows us to ask whether selection might act on entities outside the organic realm—computer viruses, tools, scientific theories. Call this the “inherited variation in fitness” definition.

We can appreciate one limitation of this definition by imagining a population which obeys all these conditions for the action of natural selection, and which also has very few members. Maybe it is divided into slow and fast runners, babies grow to run at the same speed as their parents, and running speed assists in catching prey. Consistent with this, it might also turn out, let us suppose, that the fastest running predators in this population all happen to die young from infections. These infections are just as likely to affect slow and fast individuals: the fast ones just happen to be unlucky. The result is that the slower individuals dominate. Here, modern biologists will say that “drift” is at work, in addition to selection.

So one drawback of our equation of natural selection with “inherited variation in fitness” is that, taken by itself, it does not help us to distinguish natural selection from drift. Modern theorists often move on to define to define selection in a way that allows us to ask which evolutionary “forces” are at work on a population, and which allows us to give a quantified description of how strong those forces are (Sober 1984).

In this mode, we need to find a way of understanding what “selection” is that distinguishes it sharply from other “forces” including drift, mutation and migration. A standard way of doing this is to propose that natural selection is a force that tends to make the fitter variant in a population increase in frequency, and whose strength depends on the fitness differences between the variants in the population. Drift, on the other hand, is then understood as a force whose strength is in an inverse relationship with population size. In small populations it can overwhelm selection. The broad issue of whether evolution should be understood in terms of interacting “forces” has been the subject of lively debate in recent years, with defences from Sober 1984, Stephens 2004, Reisman and Forber 2005 and Sober and Shapiro 2007, and dissent from Walsh et al 2002, Matthen and Ariew 2002 and Lewens 2010a, among several others.

In contrast to these modern theorists, Darwin did not approach evolution in a way that demanded a quantified decomposition of different evolutionary “forces,” hence he was not driven to define evolutionary processes in a way that would permit sharp differentiation between selection, drift, mutation, and migration. His strong conceptual linkage between natural selection and the explanation of adaptation meant that he sometimes omitted to distinguish between what we would now think of as mutation, on the one hand, and selection, on the other. Instead, because a constant supply of novel variation is essential if complex adaptations are to be produced at all, he often understood the introduction of variation itself as part of the overall process of selection.

More generally, Darwin thought that a diverse variety of circumstances would tend to augment, or undermine, the production of complex adaptations, and he tended to think of these as factors “favourable” or “unfavourable” to the action of selection.

The sorts of factors he mentioned include traumatic environmental shifts that can (he thought) act on reproductive organs to stimulate the production of a wide range of “profitable variations” (1859: 82); increases in population size that increase the chances of beneficial variations arising merely because the population is larger; and the geographical isolation of populations, which can allow new varieties to become established and improved in an environment that is comparatively shielded from competitive immigrants (1859: 101-109).

We should not exaggerate how significant these differences are. Darwin understood, even if he did not approach the topic in a mathematically disciplined way, that factors such as the size of a population and the rate at which variation appears within it can affect the production of complex adaptations. Similarly, even though they might isolate selection as just one evolutionary force among many, more recent theorists have often argued that the question of whether a population is able to produce complex adaptations will depend on many other factors, in addition to the question of whether the population is affected by selection in their own rigorously defined sense. For example, Sewall Wright (1932) is well known for his suggestion that drift can in fact facilitate the production of complex adaptation, roughly speaking because of the way it frees an evolving lineage from the demands of immediate gradual improvement, allowing it to colonise unexplored, and potentially profitable, areas of design space. (For a sceptical assessment of Wright’s ideas see, among others, Coyne et al. 1997.)

To take another example, Richard Lewontin (1978) has argued that the production of complex adaptations will be favoured if the developmental organisation of individual organisms is “quasi-independent.” Suppose an organism’s developmental processes are so tightly enmeshed and integrated that mutations affecting, for

example, the structure of the eye end up having further knock-on effects on the heart, the ears, the brain, the kidneys and so forth. And suppose the same is true for all traits: a mutation that alters one ends up altering all the others. Lewontin's idea is that under these circumstances, even when a mutation arises which improves the functioning of the eye, the chances are that its overall effects on the fitness of the organism will be negative, because it will most likely damage the functioning of many of those other systems the mutation affects. The end result is that iterated sequences of adaptive improvement will be vanishingly unlikely to arise. Hence Lewontin's notion that developmental processes themselves need to be fairly isolated from each other if complex fitness-enhancing organs like eyes are to be built over time. On this view, natural selection is an important element of the explanation for the emergence of complex adaptations, but it is not the full explanation for how these structures come to be.

To summarise the results of this section, we can say that Darwin and more modern theorists disagree in their definition of natural selection. Darwin tends to favour a conception of selection that is explanatorily expansive, in that it encompasses many processes that contribute to adaptation. The price paid is that selection, as he understands it, is resistant to quantification and comparison with alternative evolutionary "forces." Modern theorists make the opposite choices, defining natural selection in a way that is more narrowly focused on just one aspect of the evolutionary process, but more amenable to quantification because of that. Nonetheless, all agree on the more general and pragmatic point that if we want to understand the production of complex adaptations, we cannot focus solely on the processes that cause the fittest variants to dominate in a population.

Gradualism

By considering the explanatory task that Darwin intends natural selection to discharge, we can also understand why he describes natural selection in a way that makes it an essentially gradual process. Darwin tells us, for example, that, “As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modification; it can only act by very short and slow steps” (1859: 471). This might seem like another contrast with modern understandings of natural selection. If we think of natural selection as a process that acts to favour fitter variants in a population, then selection can be at work regardless of whether the fitter variants have sprung forth as fully formed functional macromutations, or whether they are instead tiny modifications of what has gone before. Indeed, if we think—as modern population geneticists tend to—of selection as a force whose strength increases in proportion with fitness differences in the population (see Sober and Shapiro 2007), then selection will be more powerful in a population of eyeless organisms when a fully formed eye comes into existence all in one go, than in a population where a novel variant is only a slight improvement on the eyeless variants that characterise the bulk of the population.

Of course, the reason that Darwin insists that selection must work on successive, slight variations is that it is only in this way that his whole explanatory schema can do the work it needs to. If he could regularly appeal to large “saltations,” or “macromutations,” then his own theory would offer no better an explanation of how adaptations come to be—how, that is, the woodpecker comes to be so good at catching insects—than the mystical version of transformism that he sneers at in the *Origin*’s introduction (see Ariew 2003).

This also helps to explain the otherwise puzzling, and seemingly varied, ways in which Darwin discusses the relationship between natural selection and “use-inheritance.” Darwin thought it was an empirically established fact that habits acquired during the life of an adult organism would, if practised enough, develop as instincts in the adult’s offspring. In the *Expression of Emotions*, Darwin (1872) seems to suggest that use inheritance is an alternative explanation—and a better explanation—than natural selection for many of our forms of emotional expression. Indeed, natural selection hardly features at all in Darwin’s explanation for the nature of our facial expressions and their associated physiological dispositions (Lewens 2007). However, in the *Origin*, Darwin suggests that natural selection and use and disuse might often be complementary, hazarding that the diminished and poorly functioning eyes of moles probably owe their reduced state “to gradual reduction from disuse, but aided perhaps by natural selection” (1859: 137). These differing relationships asserted between use inheritance and natural selection can be understood once we see that if practised habit in the life of an adult is able to account for the origination of a complex functional trait, then it is use inheritance, rather than natural selection, which explains adaptation. Here, habit passed on to offspring effectively constitutes a saltationist mode of explanation, albeit one that Darwin thinks is well supported by evidence, and hence a legitimate way of accounting for emotional reactions. If disuse works in a gradual way to reduce the eye of a creature that lives in darkness, even though this reduction does nothing to assist the organism in the struggle for life, then again use-inheritance explains a phenomenon that natural selection does not address. (It is striking, and surprising, that Darwin thinks “it is difficult to imagine that eyes, though useless, could be injurious to animals living in darkness,” but it is because of this that he attributes their loss “wholly to disuse,” and

not at all to selection [1859: 137].) But use-inheritance can also be the mechanism whereby Darwin's "successive, slight, favourable variations" can be introduced into a population: here, use-inheritance works as a form of inheritance underpinning the natural selection of complex functional traits. Darwin believes that natural selection aids the effect of disuse in cases where the reduction of a structure—perhaps because a reduced structure will be less likely to attract damaging infections—is of benefit in the struggle for existence (1859: 137).

Sexual Selection

Our pragmatic focus on "Darwin's Question" also helps us understand why Darwin is so often at pains to distinguish natural selection from sexual selection. For modern theorists, this distinction can often seem unimportant: what matters is whether organisms vary in their inherited abilities to have offspring, regardless of whether these abilities are conferred by the organisms' resilience to disease, their relative superiority compared with other members of their population in evading predators or competing over food, or their relative attractiveness to the opposite sex. These modern theorists will not deny that many traits are best explained as adaptations to the capricious preferences of potential mates—in that sense, they think of sexual selection as an important process—but they also tend to think, since natural selection is always about differences in fitness, that "sexual selection" names just one of the many ways in which selection pressures might act on populations.

For Darwin, on the other hand, natural selection is formulated in order to explain how structures come into existence that are of benefit to individual organisms. He tells us that "Natural selection works solely by and for the good of each being" (1859:

489), and that it acts on variations that are “useful to each being’s welfare” (1859: 127). It is no surprise, then, that when Darwin turns to consider a process that “depends, not on a struggle for existence, but on a struggle between the males for possession of the females” (1859: 88), and which can result in traits that are highly injurious to an animal’s prospects for survival, but instead contribute to perceived attractiveness—think of the over-sized and encumbering antlers of the Irish Elk—he does not think of that process as natural selection at all.

This is what explains Darwin’s insistence that if the structures that enable an oceanic crustacean to hold on to its mate in a buffeting sea should turn out to be “absolutely required...in order to propagate their kind,” then they should be attributed to natural selection. If, on the other hand, these structures simply give a relative advantage, compared with other males, with respect to the speed or ease with which mates can be secured, then “sexual selection must have come into action, for the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males.” (1877: 244) Again, we see a difference between Darwin’s conception of natural selection and the modern view. For Darwin, natural selection concerns that which is “absolutely required,” sexual selection that which gives “a relative advantage.” For the modern theorist natural selection is always about differences in fitness, hence it is always about relative advantage.

Fitness

I have suggested that, for Darwin, natural selection is understood as a process that favours variation that aids individual organisms in the struggle for existence. Sexual

selection, on the other hand, works to promote those traits that assist in the struggle for mates. As we will now see, modern theorists think of natural selection in a more generalised manner that encompasses not only Darwin's natural and sexual selection, but further processes that Darwin would not have recognised as selection at all. That is because of the intimate link in modern theories between natural selection and fitness, and because of the greatly expanded manner in which fitness is now understood.

This point is easiest to appreciate if we look at a curious case initially explored by the population geneticist John Gillespie (1974), and discussed by Elliott Sober (2001), Denis Walsh (2010), and myself (Lewens 2010a), among several others. Sober (2001) explains the case in simplified terms like this. Imagine that reproduction is asexual, and that offspring resemble parents perfectly. Now suppose a finite population contains individuals with one of two reproductive strategies. Type A individuals always have two offspring. Type B individuals either have one offspring or three, with equal probability. So both types have exactly the same expected number of offspring, namely two. But in spite of this, type A—which has narrower variance in offspring number—will reliably increase its frequency in the population.

To see why this will happen, imagine that in generation one there are just 2 As and 2 Bs in our population. In the second generation there will be 4 As. What about the Bs? Each one has a 50% chance of having just 1 offspring, and a 50% chance of having 3. So there is a 25% chance there will be just 2 Bs, a 50% chance there will be 4, and a 25% chance there will be 6. The point that is crucial to this example is that the number of Bs also makes a difference to the overall population size, hence to the frequency of A. The overall population size (As plus Bs) can be 6, 8, or 10. So the expected frequency of A is calculated by a weighted average of $4/6$, $4/8$ and $4/10$. A

calculation will reveal that the expected frequency of A in generation two is 0.52. In other words, we should expect A to increase in frequency.

Gillespie (1974) thinks of this as a case where there is selection for lower variance. That is justified by the fact that lower variance reliably increases its frequency in the population, hence lower variance is thought of as fitter than higher variance. And if lower variance is fitter, it must be being favoured by selection. But it is a considerable stretch to argue that type A's reproductive strategy offers some kind of advantage in the struggle for existence, or the struggle for mates. Using the A strategy does not confer any sort of advantage to individual "welfare," and Darwin would surely not have thought of the A strategy as being favoured by natural selection at all.

This one example illustrates how, in modern population genetic treatments of evolution, natural selection is understood in a way that is far more general than it was for Darwin. In modern treatments, natural selection and fitness differences are synonymous: if a trait has higher fitness than another, that is equivalent to saying that the former is favoured by selection over the latter. Moreover, population geneticists tend to understand fitness itself in an expansive way, such that a trait has higher fitness than an alternative under a very broad variety of circumstances where it can be reliably expected to increase its frequency over that alternative (see, e.g., Frank and Slatkin 1990). We can now see that this expansion in how natural selection is understood means that natural selection no longer has such a tight conceptual linkage with adaptation—in the specific sense of structures that are of benefit to individual survival and individual welfare—that prompted Darwin's theorising in the first place. As evolutionary theory turns its attention to understanding the factors that explain the reliable increase in frequency in traits in a population, rather than the structures that

improve an individual organism's welfare, the notion of natural selection is reformulated and made more general.

Struggle

We have seen repeatedly in this chapter how Darwin tends to think of natural selection as promoting those variations that assist in the struggle for existence.

Darwin puts great stress on the importance of extreme struggle when he explains the workings of natural selection. Some modern textbook treatments begin by quoting Darwin on selection and struggle, before moving on to give their own definitions of natural selection in terms of "inherited variation in fitness," in a way that seems to suggest the "inherited variation in fitness" condition is merely a short summary of Darwin's own explanation for the workings of selection (e.g., Ridley 2003: 72-4). But they fail to notice that a population might show inherited variation in fitness in spite of the fact that there is no struggle for existence going on at all.

This is a point that has been noted by many commentators, from Fisher (1930) to Lewontin (1970) to Sober (1984). When Darwin talks about the struggle for existence, he stresses that it inevitably results from a situation in which "more individuals are born than can possibly survive" (1859: 63). He leans heavily on Malthus's earlier argument (1798), which aimed to establish that populations will always grow so as to outstrip the food that is available to them. But a population that is so blessed with food and other resources that all of the individuals born into it end up surviving might still undergo selection in the modern "inherited variation in fitness" sense, just so long as the individuals in the population differ with respect to

how many babies they have. Is this a profound difference between Darwin's theorising and modern theorising, or just a superficial one?

The difference seems to me to be quite profound. Darwin is careful to remind us that he uses the notion of struggle "in a large and metaphorical sense" (1859: 62). But he does not say this in order to shrug off the ideas that resources are scarce, and that organisms of all kinds consequently find themselves in situations where all but the best adapted will perish. Instead, he simply means to remind his readers that he is not asserting that organisms literally do battle with each other, hence plants can "struggle" for water just as dogs can struggle over a bone. Darwin's picture of natural selection is "the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms" (1859: 63). Why is this Malthusian doctrine so important to him?

Part of the answer to this question lies in a surprising place. Modern commentators sometimes suggest that Darwin's idea of natural selection has persisted into modern biology more or less unchanged, but they qualify this with the assertion that we now know far more about the mechanisms of inheritance than Darwin ever suspected. Poor Darwin was hampered by his ignorance of genetics. Dennett's summary of the conceptual history of evolutionary theory is a good example of this approach:

In all his brilliant musings, Darwin never hit upon the central concept, without which the theory of evolution is hopeless: the concept of a gene. Darwin had no proper unit of heredity, and so his account of the process of natural selection was plagued with entirely reasonable doubts about whether it would work. Darwin supposed that offspring would always exhibit a sort of blend or

average of their parents' features. Wouldn't such "blending inheritance" always simply average out all differences, turning everything into a uniform gray? (Dennett 1995: 22)

Darwin did indeed note that blending might undermine the action of selection. He acknowledged this worry in the first edition of the *Origin*, but he thought that exceptionally strong struggle would counteract the erosion that blending would otherwise occasion: "The process [of selection] will often be greatly retarded by free intercrossing. Many will exclaim that these several causes are amply sufficient wholly to stop the action of natural selection. I do not believe so" (1859: 108).

As usual, Darwin makes his case by using an analogy between what talented breeders can do on the farm, and what nature can achieve in the wild. He did indeed suppose that the traits of offspring were often just an average of their parents' traits. But he supposed this to be just as true of baby lambs in a barn as it would be of baby wolves in a forest. Even so, animal breeders had been able to improve wool and meat in sheep. This suggested to Darwin that it must be possible for improvements to occur even with blending: the important thing was that breeders made sure that the best animals only mated with each other. If struggle in the wild were exceptionally intense, then nature could achieve something similar to the demanding breeder. Only the best specimens would then be able to mate—hence they would only mate with each other—because intense competitive struggle would ensure that all the other inferior specimens perished. That is why, when Darwin reminds us in his 1868 book *The Variation of Plants and Animals under Domestication* of his argument in the *Origin*, the strength of competition is so boldly underlined:

It was there shown that all organic beings, without exception, tend to increase at so high a ratio, that no district, no station, not even the whole surface of the land or the whole ocean, would hold the progeny of a single pair after a certain number of generations. The inevitable result is an ever-recurrent Struggle for Existence...[The] severe and often-recurrent struggle for existence will determine that those variations, however slight, which are favourable shall be preserved or selected, and those which are unfavourable shall be destroyed.

(1868: 5-6)

Our interpretation of Darwin's own understanding of natural selection needs to make sense of his repetitive insistence on the severity of struggle. We can do so by noting that severe struggle ensures not merely differential rates of survival and reproduction, it ensures that all but the very best adapted forms die. This allows Darwin to argue for the exceptionally discerning eye of nature, which determines who will be allowed to mate, and who will not. That, in turn, allows him to make a case for thinking that natural selection will be no less efficacious—indeed, it will be far more efficacious—than famed animal and plant breeders, in spite of the fact that (as he thought) all laboured against a backdrop of blending inheritance.

Particles

Dennett's comments about Darwin's failure to understand the mechanism of inheritance are not especially unusual. Peter Godfrey-Smith, too, has recently written that "One of the weaker points in Darwin's work was his understanding of reproduction and inheritance..." (2014: 9). Dennett, remember, suggests that Darwin

was confused by his insistence that inheritance would have a “blending” character. Similarly, Godfrey-Smith informs us that R. A. Fisher “argued in 1930 that inheritance *had* to operate in a ‘particulate’ manner, with discrete and stable genes, in order for sustained Darwinian evolution to be possible” (2014: 97).

It would be easy to infer from all of this that there has been an important transition from Darwin’s image of selection as a process that works against a background of blending inheritance, to a more modern understanding that it would be impossible for selection to work in such a way, and that selection instead requires particulate inheritance. Occasionally modern commentators even suggest that Darwin himself may have dimly appreciated the importance of particulate inheritance for the efficacy of selection: the thought goes that nearly ten years after the *Origin* was first published, Darwin formulated a theory of inheritance based on the transmission of particles from parents to offspring, and that he did so in order to save natural selection from the problems posed by blending (e.g., Charlesworth and Charlesworth 2009).

The historical picture sketched in the preceding paragraph is misleading. We have already seen that Darwin was not much troubled by blending. He thought that because the struggle for existence was exceptionally powerful, blending would not overwhelm the tendency of selection to discern and retain beneficial variations. Moreover, the theory of inheritance that Darwin published in 1868 was mentioned only once in the fifth and sixth editions of the *Origin* (Peckham 1959). Surely if Darwin had formulated that theory in order to deal with problems posed by blending, he would have mentioned it incessantly in those later editions. It seems that Darwin himself thought that his hypothesis of inheritance—which did indeed explain parent-offspring resemblance in terms of the transmission of particles—was wholly irrelevant to the case he wanted to make for the efficacy of natural selection.

Darwin called his theory of inheritance the hypothesis of “pangenesis.” He thought that all the cells in the body: “throw off minute granules which are dispersed throughout the whole system... They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms a new being” (Darwin 1868). Much later, R. A. Fisher would write that it was “universally admitted” that “Darwin accepted the fusion or blending theory of inheritance” (1930: 1). This may seem like an odd pronouncement, for we have just seen that Darwin explicitly thought that offspring acquired a set of particles from their parents, passed on at conception. He thought these particles matured during the growth of the new organism in such a way as to explain trans-generational resemblance. But Darwin also thought that the traits of offspring would often—although not always—be an average of their parents’ traits.

Darwin seems, then, to have held a particulate theory regarding the mechanism of inheritance, while simultaneously holding a blending theory about the relationship between the characteristics of parents and offspring. Understood like this, blending and particulate views of inheritance are obviously compatible: they address phenomena at different levels. Fisher famously wrote of them in a way that suggests one must choose between the two. He argued that “one of the main difficulties felt by Darwin is resolved by the particulate theory” (1930:12). But Darwin himself espoused a particulate theory. So what is going on here?

Fisher did not make a mistake, or somehow overlook Darwin’s theory of pangenesis (Lewens 2015a). When Fisher described “the great contrast between the blending and the particulate theories of inheritance” (1930: 4), his exploration of the consequences of the two systems addressed *phenomenal* patterns of inheritance. Fisher entertained no theory of the *mechanism* that might underlie a blending system.

He showed us how quickly variance will disappear in a system whereby offspring trait values are always intermediate between the values of the parents, regardless of what the underlying processes that explain such a pattern might look like. He then contrasted this purely phenomenal model with a different phenomenal model, whereby offspring trait values follow what he called “the modern scheme of Mendelian or factorial inheritance” (1930: 7). Evidently a population characterised by the simple blending model will behave differently to a population that follows a Mendelian scheme. In a simple blending model, for example, the offspring of a given pair of parents are always identical, and reversion to the character of a grandparent is impossible. In the Mendelian case, the traits of siblings can differ, and characters can disappear for a generation before reappearing again. And so, Fisher argued that “the mechanism of particulate inheritance” results in “no inherent tendency for the variability to diminish” (1930: 9).

It is important to recognise that Fisher did not argue that selection could not *possibly* work with this blending pattern. Instead, he pointed to the demanding conditions that would need to be in place for selection to work with blending:

The important consequence of the blending is that, if not safeguarded by intense marital correlation, the heritable variance is approximately halved in every generation...If variability persists, as Darwin rightly inferred, causes of new variability must continually be at work. Almost every individual of each generation must be a mutant... (1930: 5)

In other words, if inheritance follows a blending pattern, then for selection to be efficacious it must also be the case that like organisms mate with like (“intense

marital correlation”), or that new variations are constantly arising, or both. We have already seen that Darwin thought a condition very much like the first was satisfied. He thought that the struggle for existence was frequently so intense that only the very best adapted individuals would survive, hence they would end up mating with each other. He also thought something close to the second condition was satisfied, too. He thought that “sports”—that is, rare variations, of large magnitude—were of little significance for evolutionary change when compared with what he called “individual differences.” These were the “many slight differences” which Darwin thought regularly appeared in populations (Vorzimmer 1963). In short, Fisher argued that improbably strong conditions would need to be in place for natural selection to work with blending inheritance. Darwin was untroubled by blending because he felt these strong conditions were satisfied (Lewens 2010b).

Cultural Selection

We have just seen some significant differences between Darwin’s detailed conception of selection and more modern conceptions that build on Fisher’s population genetics. But our discussion of the relationship between selection and inheritance is instructive for other reasons. We have seen that Fisher allowed that it was possible—just highly unlikely in practice—that selection could work with a “blending” pattern of inheritance. This concession is important when we think about applying evolutionary thinking in non-standard domains. Theorists of cultural evolution, for example, often propose that techniques, ideas, and so forth evolve by natural selection (see Richerson and Boyd 2005 and Mesoudi 2011 for overviews, and Lewens 2015b for philosophical evaluation). There are many different ways of making pots, one

generation's pottery techniques often resemble the techniques of earlier generations, and techniques are adopted or rejected according to how well they match the demands of users and manufacturers. So something like our "inherited variation in fitness" conditions are satisfied. Even so, one might worry that techniques are not transmitted in a manner analogous to the genetic transmission of organic traits: one person's pot-making technique might be an inferred mish-mash of the techniques of many teachers—a blend, that is—with the result that techniques are not at all "particulate" in their mode of transmission. If cultural transmission is nothing much like genetic transmission, we might then wonder whether it makes sense to think that culture evolves by a process of natural selection.

We now see that the mere fact that techniques may follow a "blending" pattern of inheritance does not suffice to show that techniques cannot evolve by natural selection. The evolutionary theorists of culture Richerson and Boyd (2005: 88-90) point out, for example, that even though biologists follow Fisher in thinking that organic mutation rates are too low to sustain organic evolution with blending, we might yet wonder whether cultural entities such as techniques enjoy much higher rates of mutation. They also suggest that features of how we influence each other socially—such as our apparent tendency to conform with the majority views that we encounter, and our practices of actively policing social norms—might help to maintain group-level variation that selection can act on, even when single individuals rarely copy each other in ways that parallel faithful genetic inheritance. Natural selection might work in the cultural domain, but in a manner that is quite different to its operation on genetic variation.

Fisher did not show that natural selection requires that inheritance be particulate, or gene-like: instead, he showed that the character of inheritance affects what else

needs to be the case for natural selection to be effective. What is more, Fisher's appreciation of the significance of inheritance required him to develop a mathematically sophisticated way of figuring out how patterns of parent-offspring resemblance would be reflected in the makeup of populations over time. It did not depend on any detailed understanding of the molecular basis of genetic transmission. The historical development of evolutionary theory consequently offers encouragement to those who want to develop an illuminating evolutionary theory of cultural change even in the absence of a detailed understanding of the precise processes by which cultural transmission works.

Origins

Darwin introduced the concept of natural selection in order to explain the phenomenon of adaptation. It is essential for this task that natural selection does not merely explain why beneficial adaptive traits, once they arise as variants, become widely distributed in a population. Darwin also took it that natural selection could explain why these adaptive traits come to exist in the first place. In Peter Godfrey-Smith's (2009, 2014) language, natural selection is supposed to answer demands for *origin* explanations, as well as demands for *distribution* explanations. If natural selection cannot discharge this first role, it is unclear how natural selection is supposed to be an improvement either over the mystical version of transformism that Darwin rejects at the beginning of the *Origin*, or over the "special creationist" view that says a beneficent creator has fashioned adaptations.

We have seen that modern accounts of natural selection tend to characterise it as a force that can increase trait frequencies. How, then, does natural selection also explain

the origination of beneficial adaptations? The answer must be that by increasing trait frequencies, selection makes the emergence of further adaptations more likely.

Several writers, including Neander (1995), myself (Lewens 2004), and Godfrey-Smith (2014) have sketched how this can happen.

First, suppose that genomic bases X, Y and Z produce eyes of increasing functionality. Second, suppose—and this is not at all trivial—that it is more likely that Z will be produced by mutation from Y, than it is that Z will be produced by mutation from X. Now, imagine that Y appears by chance mutation in a population of organisms that all have X. Natural selection will favour Y, and it will tend to increase the number of organisms with Y in the population. Selection has now made it more likely that Z will appear, by increasing the number of organisms with Y. Selection has explained the origination of a more functional eye.

The problem with this story is that it presupposes that selection acts in one specific way. In general, modern theorists tend to think that selection increases the *frequency* of one trait over another. But if the chances of Z appearing are to be increased by selection, then it seems necessary that selection specifically increases the *absolute* number of organisms with Y. Selection need not act in this way, even though it sometimes might do, because Y might increase its frequency over X even when the absolute numbers of both are declining (Lewens 2004, 2015a; Godfrey-Smith 2009, 2014).

Godfrey-Smith has recently suggested that it is under conditions of scarce resources that selection ends up increasing absolute numbers of the favoured variant. This suggestion seems to give a further boost to Darwin's own insistence on Malthusian struggle as a key component of any explanation for the origination of complex adaptations. Godfrey-Smith writes that, "the fact of scarce resources—when

it is a fact—ties relative reproductive success and absolute reproductive success together” (2014: 42). Unfortunately this linkage can break, for if resources are in exceptionally short supply the result might be that all of the different types in a population end up decreasing in absolute numbers, with some decreasing less quickly than others, and increasing their frequency as a result. When this is the case we will find that selection ends up lowering the absolute numbers of the favoured variant, precisely because resources are so scarce.

A better way to think about the relationship between selection and the origin of adaptive traits requires us to distinguish two ways of understanding what it means to say that selection increases the chances of adaptation (Lewens 2004, 2015a). Let us return to our example of eyes. Suppose, again, that resources are exceptionally scarce. Because of this, the absolute numbers of Y variants are decreasing, but less quickly than the absolute numbers of X variants. This means that in each generation the chances of a Z variant appearing in the population get lower. In that sense, selection makes adaptation less likely. Even so, Y is increasing in frequency: in that sense, it is favoured by selection. Crucially, the population would have been even less likely to have produced Z variants if X, rather than Y, had been increasing in frequency. So even when resources are scarce, and even when the chances of a Z variant are constantly diminishing, we can say that selection explains the origination of adaptation, in the sense that the chances of Z arising are higher if Y increases its frequency than they would have been if X had increased its frequency.

This brings us back to Darwin. Nature, he said, works in a similar manner to a skilled breeder. But nature is far more discerning in its choices, and far more devoted in performance of its duties, than any human:

It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, wherever and whenever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. (1859: 84)

We have now seen one way of making sense of this. A population is more likely to produce novel beneficial variations when that population is primarily composed of fitter, rather than less fit, variants. Natural selection helps to ensure that populations are continually transformed in ways that make them apt to produce valuable new traits. In that sense, natural selection does indeed preserve and add up what is good, in a way that gives an answer to Darwin's question. Natural selection can, it turns out, explain "that perfection of structure which most justly excites our admiration" (1859: 3).

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