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Correcting some common misrepresentations of evolution in textbooks and the media

Kevin Padian

Abstract

Topics related to evolution tend to generate a disproportionate amount of misunderstanding in traditional textbooks, other educational materials, and the media. This is not necessarily the fault of textbook and popular writers: many of these concepts are confusingly discussed in the scientific literature. However, faults can be corrected, and doing so makes it easier to explain related concepts. Three general areas are treated here: ideas and language about evolution, historical and philosophical aspects of evolution, and natural selection and related concepts. The aim of this paper is to produce a template for a more logical, historically and scientifically correct treatment of evolutionary terms and concepts.

Keywords: Evolution, Evolution education, History of biology, Natural selection, Charles Darwin

Textbook and popular writers have a difficult task. Their job is to present science to students and other members of the public who, increasingly, come from disparate cultural and economic backgrounds, live in states that have conflicting guidelines for what should be presented in science texts, and are being subjected to deteriorating state support and increasing political factionalism. With less money to spend on instructional materials, competition is tougher than ever.

It is nearly impossible for a scientist to keep up with the literature in evolutionary biology, or virtually any other scientific field. There are more journals, more online sources, more columns, stories, blogs, postings, and videos than ever before. How can professional writers (most of whom do not have advanced or even basic degrees in science), let alone biologists, keep up with this explosion of literature and judge its relevance?

The answer is, they cannot, and in practice, they do not. Teachers who compare closely the treatments of subjects in competing textbooks will notice that they promise the moon, advertising the individual and unique effectiveness of their pedagogical approach. Be that as it may, the science content is peculiarly uniform among publishing houses, although specific examples and details of concepts 'may vary' (to quote traditional textbook jargon). And sometimes that content is wrong, and it has been for many years. Writers are in a difficult position because, if new research seems to contradict traditional information, it is hard for them to tell whether this new finding is really legitimate or will be overturned in a matter of months. And they have been burned in the past (just look up 'Protoavis'). But textbook writers are also reluctant to change their presentations, even when they are long outdated, because they worry about being 'too different' from other textbook programs and confusing some teachers who expect certain content and cannot always keep up with new developments in the field. An example is how long it is taking textbooks to get rid of the Linnean classification system and teach phylogenetic systematics (cladistics).

Because the treatment of scientific subjects is so uniform among textbooks, specific errors and misrepresentations are common to most publishing houses. These have been picked up by other media, and many of them are of longstanding. In the following suggestions I try to point out why certain conventions in science texts and popular publications are either incorrect or technically correct but could be presented better, and to suggest alternative treatments. I hope it will become clear that much of the engendered confusion is due to us scientists, who have not been as precise with their diction as we should be. Even though we often agree among each other that we know what we mean, this does not help textbook writers, reporters, teachers, or students.

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The list of topics that follows is wide-ranging but necessarily incomplete; I have tried to divide them generally into 'The ideas and language of evolution', 'Historical and philosophical aspects of evolution', and 'Natural selection and related concepts'. For related articles see Padian (1997, 1999, 2007, 2008a, b, c, 2009), and many issues of William J. Bennetta's *The Textbook Letter* (see http://www.textbookleague.org/missn.htm). The goal of this paper is to stimulate awareness and discussion among scientists, educators, textbook writers, and journalists who have to interpret evolution to students and the general public. Although there is a lot of room for interpretation and debate of language and concepts, the hope is that a forthright discussion of ambiguities and infelicities should eventually improve the presentation of evolution to the public.

The ideas and language of evolution

Distinguish evolution as fact, pattern, and process

The word 'evolution' has several meanings. So do lots of useful words. Let us take 'business'. What's my business? I'm an architect. Where's my business? On Fourth Street. How much do I make? None of your business. Three different senses of the same word. And so it is with evolution. Evolution is a fact: science understands that life has evolved through time, and there is no reasonable doubt about this anywhere in the scientific community. It is a theory: it comprises a great many patterns, processes, observations, and hypotheses - all testable. Evolution has patterns, such as the patterns of diversity through time. It has processes, such as natural selection, sexual selection, species selection, drift, and more. Evolution is a big subject with a lot of dimensions. As long as you are clear about which dimension of evolution you mean, there's no conflict for readers.

Defining evolution

Following the paragraph above, how does one choose a definition of evolution to use? Because science has no catechisms, there is not a single, standard definition of evolution. But some are more and less useful. A popular one, especially among scientists who work on population biology, is 'a change in gene frequency in a population'. This means, for example, that an allele with a frequency of 0.75 in one generation can change to 0.73 in the next, and this is evolution. Well, sort of. In the next generation, the frequency can change back to 0.75. So what has evolved? It is like defining a football game as the process of hiking the ball. This simple (or simplistic) definition gets to one level of the processes of evolution (yet it misses many processes from speciation to what causes changes in gene frequencies in populations). Other definitions, such as 'the history of life', get to the patterns of evolution, but do not describe their causes. So both kinds of definitions are inadequate on their own.

Darwin's definition, which he used in *On the Origin of Species*, was 'descent with modification'. Although it may seem at first glance simplistic or vague, it embodies both the patterns of evolution (descent) and its processes (modification). It is as useful on a short timescale as on a long one; it suggests minor evolutionary modifications as well as major ones. In the last paragraph of Chapter 6 of the *Origin*, Darwin used this simple definition to settle a century of debate about what controls the morphology of form in the first place (Figure 1). Geoffroy St.-Hilaire and others had stressed 'unity of type', the features that characterize major groups of animals (mollusks, arthropods, vertebrates) and separate them from others. Baron Georges Cuvier had emphasized 'conditions of existence', circumstances that made it advantageous for herbivorous animals to have cropping teeth, complex guts, and hooves for fleet escape. Darwin brushed away this conflict in a single paragraph by showing that common descent could explain the common body plans of related organisms, and that natural selection could explain their adaptive differences as they were modified to fit the conditions of existence.

Avoid the term 'modern'

About half the American populace has trouble of some kind with understanding evolution. It only introduces further confusion to use a word that has connotations of progressivism. Progressivism is the idea that, through history, things get better and better; or in this case, that

Former view	***Darwin's view***
Unity of Type (Geoffroy)	**Common Descent**
Conditions of Existence (Cuvier)	**Adaptation through Selection**

Evolution is "descent with modification"

Figure 1 Before Darwin (1859), similarities and differences in morphology, the 'queen of the sciences' in the early Enlightenment years, were explained in pre-evolutionary terms. Geoffroy St.-Hilaire stressed the 'Unity of Type' found in similar animals such as mollusks and vertebrates; Cuvier stressed the 'Conditions of Existence' by which otherwise similar animals differed by virtue of ecological specializations. Darwin's simple definition of evolution as 'descent with modification' proposed that most similarities can be traced to common descent, whereas most differences in broadly similar (related) animals result from divergent adaptation.

evolution always works to improve organisms, so it makes evolution a march of progress through history up to the superior forms of today (humans often, if tacitly, being the apotheosis). The word 'modern' carries the connotation of 'improvement' over what came before. Whereas we accept that in the struggle for existence better adapted forms should prevail over others, the ecological landscape changes constantly as well, so a given strategy is not foolproof for all ages. Just as 'modern' art is not necessarily better than any other kind of art, 'modern' (that is, living) organisms are not either (Figure 2). (Would a 'modern' cow be well-adapted for the Jurassic Period?) Instead say 'living', 'extant', or 'present-day'. The term 'modern' adds a value judgment for many readers that should not be there.

Avoid the words 'primitive' and 'advanced' (See 'modern')

These words also carry value judgments. Remember that what we might call a 'primitive' characteristic of some tetrapod wanna-bes from the Devonian was not only perfectly useful to them at that point; it may have given them a considerable advantage over what their fellow wanna-bes had at the time. It does not make sense for us to judge Devonian critters by the standards of what organisms have evolved in the ensuing 350 million years.

Evolutionary biologists, when they examine changes in characters through lineages of organisms (clades), do this with reference to a phylogeny (Figure 3) based on a great many evolutionary features, and on which the characters of interest are mapped. The character state that appears first in a lineage is usually called 'basal' instead of 'primitive', and the various permutations of that basal character that appear later in the tree are called 'derived' instead of 'advanced'. (This is explained, along with the concept of the *evogram*, at http://evolution.berkeley.edu/evolibrary/article/evograms_02.)

Think of it as you would human cultures. We no longer talk of some rituals and practices as 'primitive' and others as 'advanced'. It makes things clearer for readers to avoid the same terms in biology.

'Many scientists believe' is a phrase with three fundamental difficulties

This phraseology, and others like it ('Some scientists think'), is not as prevalent as it used to be in K-12 texts, but its permutations persist. It poses a triple threat to science education (Figure 4). First, 'many': science is not decided by vote, so it does not matter how many scientists accept an idea. It is about the quality of the evidence. Second, 'scientists': in one sense, certainly, scientists are doing this work, not milkmen or stockbrokers. And presumably scientists are better trained than milkmen or stockbrokers to analyze scientific evidence. Again, it is the quality of the evidence. But even so, science is a very heterogeneous business. A physicist is likely to have little expertise in the complexity of paleontological problems, and this is reciprocally true for paleontologists and string theory.

Third, 'believe': saying that scientists 'believe' their results suggests, falsely, that their acceptance is not based on evidence, but is based somehow on faith. Yet again, it is about the quality of the evidence: scientists accept their results as the best explanation of the problem that we have at present, but we recognize that our findings are subject to re-evaluation as new evidence comes to

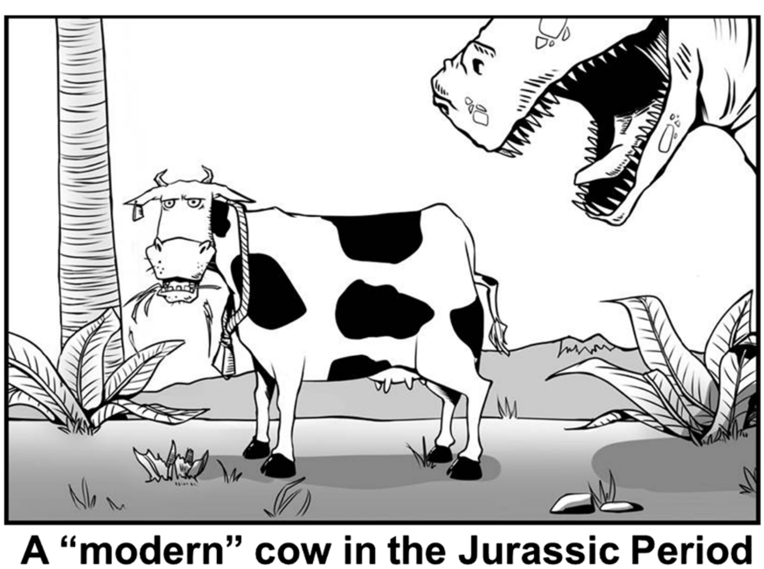


Figure 2 **The problem with using the term 'modern' is that it implies superior adaptability, whereas the evidence of evolution implies that organisms are fit for their present circumstances and not necessarily all possible past and future ones.**

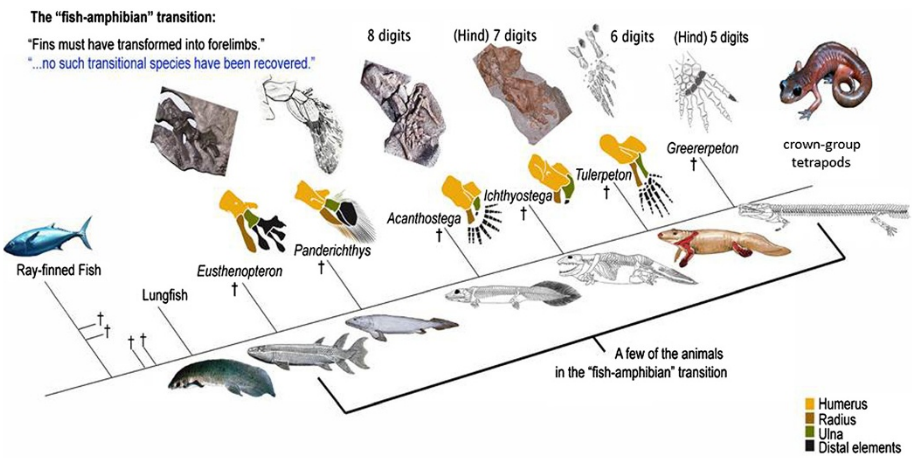


Figure 3 Evogram of the transition of tetrapods from water to land in the Devonian, by Brian Swartz. The quotation at upper left is from the creationist textbook *Of Pandas and People* (Davis et al. 1989). An evogram provides a variety of information, including a phylogeny based on numerous characters, pictures and reconstructions of actual living and fossil specimens, and illustrations of homological transitions of features such as limb bones and digit numbers. Note that the 'fish-amphibian' transition is given in quotation marks: true fishes (rayfins like the trout) did not evolve into amphibians (frogs and salamanders and their relatives). Rather, this evogram depicts the evolution of the first tetrapods from basal sarcopterygians in the Devonian.

light. This is a problem because scientists themselves often use the word 'believe' when discussing their results! It is just sloppy diction: they would not say that their conclusions are a matter of faith, rather than of evidence.

Instead of saying 'many scientists believe' or 'some scientists think', it is more productive to talk about the evidence. What evidence (if any) supports a certain hypothesis, and what evidence (if any) seems to contradict it? And two more things: first, discuss what else we would have to know before we can advance the question further; and second, be clear about how we would know if a hypothesis were wrong. This, more than anything else, shows students what the process of science is all about. It takes a little more work on the part of the writer, but it is worth it in raising student interest and understanding. (An indispensable reference for explaining how science actually works is at http://undsci.berkeley.edu/article/howscienceworks_01.)

Problems with "Many scientists believe ..."

"Many": Science is not put to a vote

"Scientists": Who else is doing the work?

"Believe": Is science a matter of faith?

Science is about evidence, not opinions

Figure 4 The phrase 'Many scientists believe …', long a staple of textbook writers, is seriously misleading for at least three reasons and should be expunged from science writing.

For example, many texts and the vast majority of news reporters like to repeat the idea that an asteroid crashed into the Earth some 65 million years ago and destroyed the dinosaurs and a lot of other organisms. This is a complex idea, and parts of it could be wrong or right without destroying the general concept that a large asteroid impact could have created substantial environmental havoc. Scientists from many disciplines have worked on this problem for decades. No one has all pieces of the puzzle, and their individual trainings influence what they think is important and even what they understand. But none of this is a question of belief or faith.

It is accurate to say that many people accept or think that an asteroid killed the dinosaurs, and this includes a lot of scientists. But most scientists who actually work on the dinosaurs of that time period do not agree that an asteroid killed them. That by itself should be important, but it is not as important as the evidence: when various lineages of vertebrates are traced across the Cretaceous-Tertiary boundary, it turns out that some mammal lineages were affected and some were not, most vertebrates such as crocodiles, lizards, and amphibians were not severely affected, and that all but three kinds of dinosaur had disappeared during the preceding six million years - presumably not in anticipation of the great crash. So the evidence is what scientists rely on - or should. And this is true for those who report on the issues.

Do not personalize a scientific debate

A scientific controversy is usually not mainly about the people involved (unless they make it personal), but about how independent lines of evidence converge on the same conclusion or conflict. To punch up the history of evolution, textbook writers often contrast the views of Lamarck and Darwin on how the giraffe got such a long neck. They do not say that Lamarck wrote 50 years before Darwin, that they never met or corresponded, or that neither man devoted more than a paragraph to the subject among the thousands of pages that each published (Figure 5). Lamarck's views were complex and would be strange to us today, because like many early Enlightenment savants he devised a grand 'system' that purported to explain everything from the motion of rivers and oceans to blood circulation (see Gould's *Structure of Evolutionary Theory*). Lamarck's ideas were obscure even in his own day, and it is questionable to devote space to them in current textbooks.

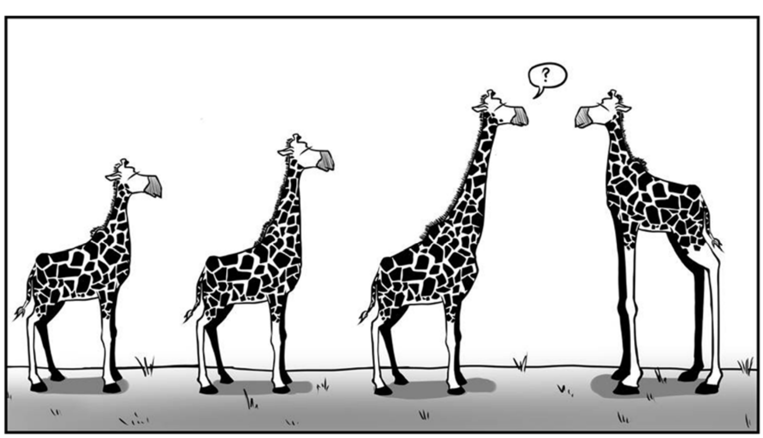
Often, however, the personal aspect intervenes as scientists in a certain field will tend to favor one hypothesis over another, simply because they have been educated to understand (and therefore trust) some lines of evidence over others. The story is still usually not about individual scientists, but about standards of evidence in different fields.

For example, until about a decade ago paleontologists and molecular biologists differed on the subject of the closest relatives of whales. Geneticists had found some very unusual and diagnostic molecular sequences called SINEs in both whales and hippopotamus (Shedlock et al. 2000). They inferred that these animals were each other's closest relatives, and that made sense, some molecular biologists said, because both groups are large, aquatic, and hairless. Paleontologists dismissed this because the earliest known whales were first found in the early Eocene, some 50 million years ago; whereas the first hippos are not known until about 15 million years ago. Where could you hide the missing hippos for 35 million years? Moreover, the first known hippos were not large, aquatic, and hairless, but small, terrestrial, and probably not hairless.

The reconciliation came with the paleontological discovery that hippos seem to have evolved from a more basal group of mammals called anthracotheres, which are found as far back as the Eocene, and could be closely related to whales (Figure 6; Thewissen et al. 2009). These anthracotheres were not aquatic or especially large, and they did not resemble whales at all. But they did share a common ancestor with whales. It was not that the paleontologists suddenly accepted the evidence of the molecular biologists, who had made naïve statements about the presumed common ancestral features and habits of whales and hippos. It was more that paleontologists found evidence from their own field that made sense to them, and allowed a re-evaluation of the question. Now we have agreement on both sides.

This is not a perfect system, but it is how science often works. Note that this example was not about individual scientists arguing with each other, but about the kinds of evidence that scientists in certain fields are trained to understand and preferentially accept. (For more information, visit http://evolution.berkeley.edu/evolibrary/article/evograms_03 and cited references.)

Students and other audiences will benefit more from having the evidence explained to them than from asking them to choose sides based on profiles of opposing scientists. (Textbooks often ask students to make judgments about the social implications of scientific questions such as climate change after receiving only minimal information.) In so doing, they will experience more accurately



Evolution of the giraffe (homage to Gary Larson)

Figure 5 Hypotheses for the evolution of the giraffe neck fascinated early writers on evolution and continue to do so today. However, despite impressions given in some K-12 textbooks, Lamarck and Darwin never had an argument about it. This figure honors a classic 'Far Side' cartoon by Gary Larson that would be prohibitively expensive to reproduce here.

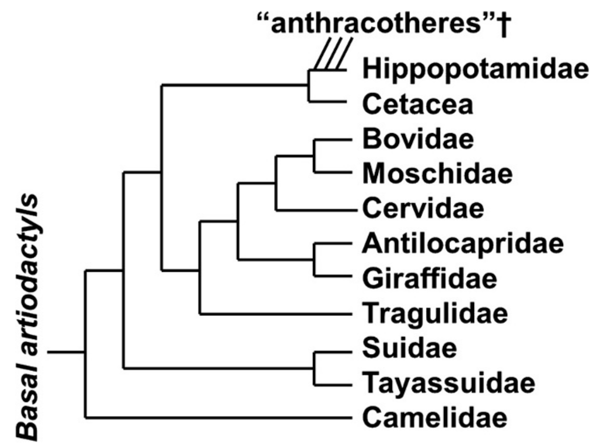


Figure 6 A phylogeny of artiodactyls, based on various current sources. Whales and hippos are each other's closest living relatives, but they diverged more than 50 million years ago, and the earliest members of their lineages looked very different than their living representatives.

how the scientific enterprise works, which is by analyses and arguments that fit the evidence together and provide more or less inclusive explanations of that evidence (see http://undsci.berkeley.edu/article/howscienceworks_01). And, whereas it does little service to profile scientists who are on different sides of an issue, and personalize and polarize their arguments for students to choose between, it is perfectly useful to profile individual scientists who have pioneered concepts in a field, as well as including other people who have worked with them, to show how science is a cooperative enterprise. After all, most present-day scientific problems are advanced not by lone individuals but by teams of people from many institutions who take years to propose hypotheses, make research plans, and carry out interdisciplinary research.

Historical and philosophical aspects of evolution

'Evolution' has meant different things at different periods of history

Darwin used the root word only once in the *Origin of Species* (the last word of the book is 'evolved'), because in his day 'evolution' denoted the gradual, predetermined unfolding of organismal development (a fiddlehead fern, for example, or the shell of a snail). He wanted to avoid the 'predetermined' aspect, and this is why he preferred the term 'transmutation' when discussing changes in species through time. But, after the publication of his book, 'evolution' increasingly came to mean what it does today. (See Bowler 2009 for good background on this and related topics.)

It was possible in pre-Darwinian times to accept some or most lines of evidence for what we would now encompass as 'evolution'. For example, the sequence of fossilized life through time in the geologic record was established by the earliest stratigraphers, such as William Smith, the civil engineer who published his geological map of England in 1801. Smith was no 'evolutionist' in our sense of the word. But he saw that fossils and rocks succeeded each other through the rock column, what was called the progression of life through time. (Of course, in those days no one really knew how much time was involved.) This was pretty much undeniable for any scientist by the 1820s.

However, the progression of life through time could be explained in various ways. A creditable view in the 18th and early 19th centuries was that there could have been a series of events of creation, following large-scale global or regional extinctions. But where in Scripture was this view validated? Besides, long before the 19th century, natural philosophers had stopped looking to Scripture for answers about science. Alternatively, it could be proposed that species were transformed into other species through succeeding geological strata. But what would have been the mechanism of this change? That mechanism, in the end, was what Darwin hoped to provide in the *Origin of Species* in the form of natural selection. But he had to overcome a lot of skepticism that such an explanation was even possible. Moreover, he was providing a strictly material explanation of this transformation. In this he was departing from many of his contemporaries, including Richard Owen and Charles Lyell, who were uncomfortable with an explanation of evolutionary change that did not include some role of a Higher Power, however mechanistic (Bowler 2009).

In the Victorian Era, one could accept evolution (the 'unfolding' of organisms through time, like the predetermined 'unfolding' of a leaf or fiddlehead fern) but not transmutation (a direct change of one kind of organism into another). This seems strange to us today, but if we want to understand Victorian and pre-Victorian sensibilities to scientific explanation, we have to wrap our heads around it. (See the description of Richard Owen's views below.)

'Gradual' did not always mean gradual

The avatars of the Modern Synthesis of Evolution saw evolution as 'gradual' in Darwin's terms, which they read as a series of slow and insensibly small changes. Darwin was more pluralistic. In his diary he described the huge earthquake at Concepcion, Chile, the effects of which he witnessed from the *Beagle*, suddenly uplifting the sea cliffs by meters, as a 'gradual' change. This makes no sense to us until we realize that the root of 'gradual' is in the Latin *gradus* or 'step', so 'gradual' implies a step-like change. For Darwin the steps were small, but they were not insensibly so (Padian 2008a, 2009). It is tempting to suggest that Darwin would have seen little difference between the evolutionary tempos of classic Mayrian 'gradualism' and 'punctuated equilibria' (Figure 7).

It is very important to explain to students that small steps (as in punctuated equilibria) and insensible changes (as in classical gradualism) are more like each other than are small steps and very large steps. The latter mechanism - sudden, great morphological changes - has never been seriously considered in evolutionary theory, and the notion that 'large steps' create macroevolutionary changes (for example, that a bird could have hatched from a lizard egg) is a caricature. There should not be a need to mention Richard Goldschmidt's (1940) much-maligned, scientifically naïve 'hopeful monster', because hardly anyone has ever considered it seriously as a mechanism of major evolutionary change, or has uncovered any evidence for it. That said, Goldschmidt's book is a brilliant survey of ecophenotypic variation by a first-rate laboratory geneticist and field biologist, and it should be read closely rather than dismissed.

Use care in characterizing the religious beliefs of historical figures

Like most men of the Enlightenment (including most of American's founding fathers), Darwin (for much of his life) was a Deist: he thought there was something bigger than human consciousness, but he did not personify it (as theists do), and gradually he lost all feeling that we would call religious (as opposed to spiritual: Desmond and Moore 1992, Moore 1994). His colleague Thomas Henry Huxley coined the word 'agnostic', and Darwin grew more comfortable with that term as he grew older (Padian 2009). Darwin's views on religion changed through life, from fairly conventional beliefs through doubt in Providence to the absence of all interest in the subject.

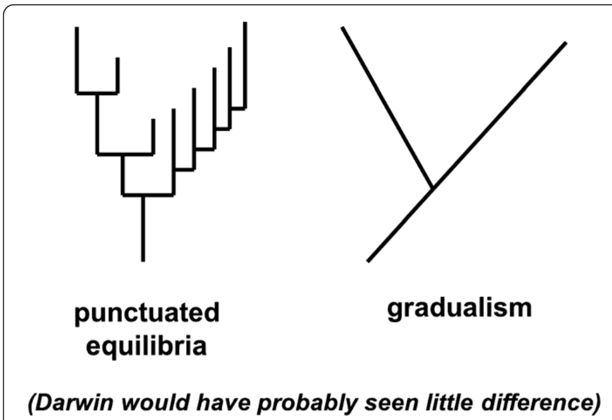


Figure 7 Because Darwin used the term 'gradual' to mean small steps in a much larger progression over time, as in the sudden elevation of the Chilean coast following an earthquake, he probably would regard the dichotomy between 'punctuated equilibria' and classic Neo-Darwinian gradualism as mainly a question of scale.

Other historical figures, respected scientists who rejected Darwin's views, or the ideas of evolution advanced in their times, were not necessarily creationists, and not usually in the strict sense of biblical literalism that we understand it today. Cuvier, for example, was not a biblical creationist, as he is often portrayed. He was a Lutheran by birth, but he seemed to have little interest in religion, and it did not enter his scientific work. He was not a catastrophist in the conventional sense of the term, either. His studies of abrupt transitions in the rock types and fossils of the hills around the Paris Basin were observational: he reported what he saw. He knew that these transitions reflected regional environmental events, but one reason why he maintained his respected status for so long in a turbulent France was that he avoided making rash pronouncements. Cuvier did not think that these transitions were the result of divinely mandated catastrophes; and although he did not fully understand the mechanisms behind them, he hypothesized that the animals that succeeded those of earlier strata may have migrated in from elsewhere as the environments changed. He was not positing the transformation of species, but neither was he suggesting a series of divine creations of each new fauna (Rudwick 1997; Taquet 2006).

In the same way, it would be wrong to call Richard Owen, Darwin's greatest nemesis, a creationist, or even an anti-evolutionist. Owen was likely a deist, though he assuaged the theistic views of much of his Victorian audience. He knew the fossil record well and accepted the progression of life through time. He even thought that species could arise continually through a common ancestral form, modified somehow by development and the influence of the environment; but he was shadowy on these points (Padian 1997, 2007).

Avoid pitting science against religion, even though sometimes there are real conflicts

There has always been some kind of religious opposition to any and all ideas about evolution (and other scientific concepts). Nevertheless, there has been no serious scientific opposition to evolution since the Victorian Era. Yes, scientists do disagree and debate about various evolutionary mechanisms and patterns, and their relative importance, although they do not dispute that all living things have evolved from common ancestors. But just because all is not solved does not mean that evolutionary biology is in a state of turmoil. We like to say that 'science is open-minded, not empty-headed': trying to advance solutions to problems, based on what we already have found and want to know next, is why scientists get up in the morning. Scientific propositions are supposed to be testable, and 'Science' does not equal 'Truth', a word that should not be used in science.

Oddly, perhaps, the very openness of science is what attracts scorn from religious fundamentalists, who build their lives on what they accept as immutable truths of faith. The principal act of faith of a scientist is accepting that the natural world is knowable, and that we can use our (however imperfect) faculties and judgment to learn about natural phenomena and trust our results, wherever our investigations lead. After that, the rules of scientific inquiry are not about faith, but about posing and testing hypotheses. But science has its limits, and the supernatural is one of them. In short, science does not deal with the supernatural. Religion has its limits too, and one of them is in making statements about the natural world. There is only conflict between science and religion if people want it; or rather, there is conflict when people want it. That conflict comes from either side saying more than it reasonably can about its domain. But the non-theistic axiom of science (see below) means that it does not favor or disfavor any particular religious or other supernatural beliefs. In return, its statements about the natural world should not be contradicted on the basis of any sectarian religious beliefs. So, regardless of what some interpretations of old writings about Scripture-professed, scientific evidence affirms that the Earth cannot be 6,000 years old. That is in direct conflict with some religious views. Contemporary evolutionary biologists hold varying religious views; contrast, for example, Gould (2002a), Miller (2007), Coyne (2009), and Asher (2012). But when they operate as scientists, they do not place religious views above empirical evidence.

In textbooks, it is appropriate to discuss why evolution or any scientific idea or hypothesis was or is controversial as science (cold fusion is an example). But it is not appropriate to pretend that well-established scientific concepts are controversial. It is also not appropriate to note that some scientific concepts were controversial in the past, without noting the present state of understanding of those concepts (a great many important scientific ideas are controversial when they are first proposed). Cultural and religious controversy about science has no place in science texts, and pedagogical activities that encourage children to have debates about evolution or global warming - in an educational system where they can have only the most rudimentary exposure to these subjects - merely amplify the prejudices of the students' families.

Is there room to discuss cultural and social controversies over scientific ideas in textbooks? Perhaps, although the focus of a science textbook should be squarely on the science. But textbook authors who choose to discuss cultural and social controversies should be careful to ensure that they are not misrepresenting the science as controversial or offensive to the beliefs of their readers, and thus undercutting the legitimacy of the science.

Avoid giving the impression that evolution is atheistic, or that evolutionists must be atheists

All science is non-theistic, by which is meant that it does not entail or require any concept of a god or other supernatural being or force. In fact, science is completely independent of any ideas about gods or other supernatural beliefs. But science is not anti-theistic: it does not deny such beings or forces, any more than it accepts them (or leprechauns or unicorns), because these things are not within the purview of science. There are many meanings of 'atheism' (literally, 'without god'). We too often lump together various permutations of non-belief, and in so doing we allow religious fundamentalists (anti-anti-theists, so to speak) to treat scientists and others, who simply operate without reference to any particular deity, as if they were anti-religion (Figure 8; Onfray 2011).

Individual scientists, like accountants, plumbers, and postal employees, can be atheistic or deeply religious in any number of ways. But science places no strictures on their beliefs except to ask them to be checked at the door when it is time to test the hypotheses. This has been the case since the Enlightenment coalesced.

Furthermore, the scientific study of nature, or naturalism, has two main approaches, but only one is scientific; the other is philosophical. Philosophical naturalism says that observable nature is all there is; methodological naturalism says that there may or may not be more than the observable phenomena of nature, but science is only concerned with what can be observed.

Natural selection and related concepts

Do not personify natural selection

Natural selection is not an entity like Cher, Lady Gaga, or the Statue of Liberty, and it is not a force like wind. It is more correctly characterized as a description of a mechanism of differential survival of individuals in a lineage, rather than the cause itself. In his later years, Darwin regretted using the term in a causal sense, rather than sticking with the more forthright 'struggle for existence'. Natural selection, personified as a force that acts on organisms, becomes little more than a rhetorical equivalent of a Deity when placed in sentences such as 'Natural selection would favor the acquisition of such-and-such a feature'. Substitute 'God' or 'elves' for 'natural selection' and the emptiness of this rhetoric becomes clear, even though, with evidence, the statement about what was favored could be supported (Figure 9). The problem is in writing as if you were ascribing the 'favoring' of a trait to an actual, personified third party, rather than explaining the circumstances by which it was favored. Language like this is really not much different than that used by the advocates of 'Intelligent Design'. Yet Darwin used it many times himself in *The Origin of Species*.

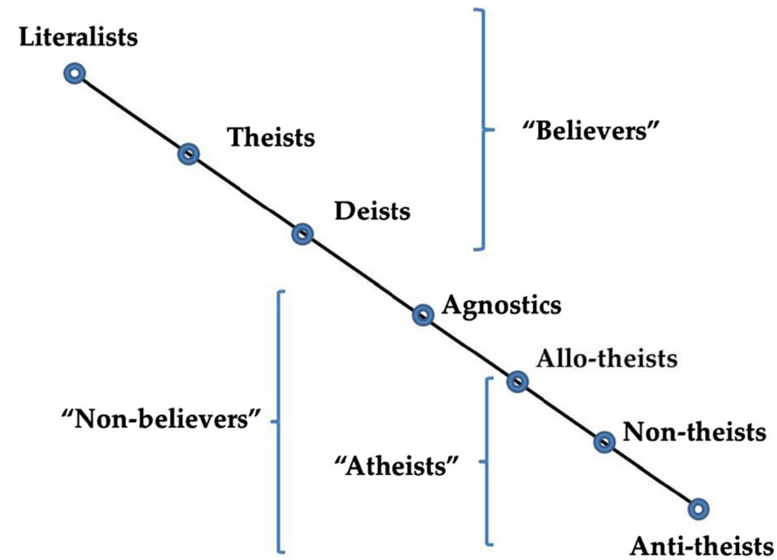


Figure 8 A taxonomy of religious belief and non-belief. Believers include various kinds of theists (those who personify their gods) and deists (who do not). Non-believers include agnostics (who think it is impossible to decide whether a god exists), what I call 'allo-theists' (who believe in gods, only not the ones that others think you should believe in, such as Christians who regard Muslims as infidels and vice versa), non-theists (who unlike agnostics do not think the question of the existence of God is relevant to them), and anti-theists (who are convinced there is no god or gods, and are opposed to religions in general).

How better to phrase this? Darwin's own formulation was to explain that the traits in any given lineage at any given time showed considerable variation. Some of these variations worked better than others at the time, for whatever circumstantial reasons. Their bearers were more likely to survive to leave offspring with these same variations. In the struggle for existence, they were better able to persist. We would call that entire process natural selection. This is more accurate than saying 'natural selection favored this particular trait'.

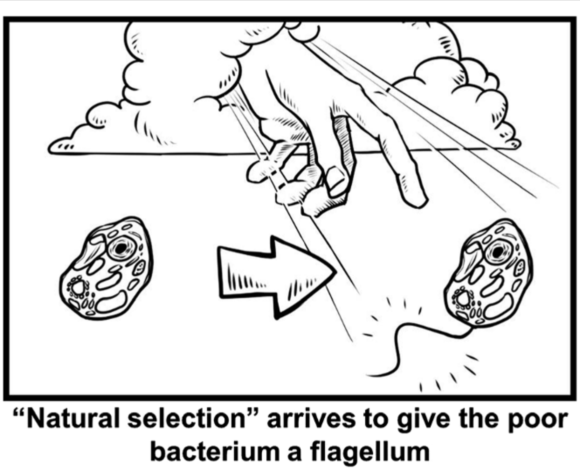


Figure 9 The problem with personifying natural selection is that it always seems to come to have an identity of its own. In this way it is little different from the narrative actions committed by gods or even leprechauns.

An extension of this kind of personification is when an author says, 'Natural selection would have favored the acquisition of such-and such a trait'. Nobody knows in advance what 'natural selection would favor', because virtually everything we know about the effects of natural selection is in hindsight. This phraseology suggests a naïve faith in the optimality of evolutionary processes, and some omniscience on the part of the author, in continuing to personify natural selection as if it were a conscious being. Of course, scientists do not really think these things (do we?); we just write as if we do. Natural selection is a description of a process, not an actor; we recognize it as a *post hoc* outcome of the struggle for existence.

Natural selection is not 'creative'

Remembering the previous point, it is more accurate to say that in the struggle for existence, some individuals are weeded out before they can reproduce. This process is not creative, any more than a lawnmower is creative with your backyard grass. Recombination of features through sexual reproduction might - *might* - be analogized as 'creative', except that the recombination is entirely random. (In contrast, the pigment splashes on a Jackson Pollock painting only look random; they are actually highly creative.) And really: why push it? The term is anthropomorphic. Leave creativity to the artists.

Avoid 'evolved for'

Teachers knowledgeable about evolution have a very hard time with this expression. It is almost obvious as soon as you say it. We all know that structures do not 'evolve for' some function. But this sloppy diction gives the uninitiated the impression that there is a direction to evolution that is manifestly teleological. Yes, there are evolutionary trends of many kinds; but organisms do not want to get to one point on an evolutionary continuum and look backward with the idea that life has been a long struggle to get to that point, as if consciously.

For example, feathers did not evolve 'for' flight. They were already performing several functions for the dinosaurs that had them before one lineage happened to use them aerodynamically. Among the earlier functions were insulation, color patterns (display or camouflage or species recognition), and even brooding on nests (Padian 2008c). The evolution of features in a group of organisms can be like the man who got up on his horse and rode off in all directions. There was not a goal in sight, so it is better to avoid language that suggests it.

Evolution is not universally a question of 'pressure'

There is no doubt that individuals in nature face enormous selective pressure throughout their lives - the result of competition, predation, insufficient resources, and environmental stress. However, when we think about new adaptations that seem to have contributed so much to the success of varied groups of organisms, we get a different picture. Most of the critical 'inventions' in evolutionary history do not seem to have happened because there was intense pressure for something like that to happen. At least, we cannot find much evidence for this, except perhaps in cases such as the evolution of dense fur by mammals as ice ages encroached. (We presume that natural variations in the length and thickness of fur were favored in the struggle for existence.) Rather, these 'inventions' evolved because organisms found an opportunity to exploit a new way of doing things. For example, we do not think that birds evolved flight because they were forced to do so. However flight evolved, it was an opportunity to turn the structure and functions of forelimbs and feathers to new purposes.

One way to explain this is through economics. Given that analogies are only teaching tools; they do not represent a real material connection. Nevertheless, students understand it when you explain that microwave technology was developed during World War II as a way to try to detect aircraft activity; and now we have ovens that use this technology in virtually every home and office. There was not an economic 'pressure' to develop microwave ovens; it was an opportunity that manifested itself, based on an incentive to solve a completely different problem. In evolution we call this exaptation, and it is one of the most important concepts in the field, even though it was only identified in 1982 by Stephen Jay Gould and Elisabeth Vrba.

'Fitness' is not about how many offspring you leave

Darwin (1859) used the word 'fitness' to describe how well-suited an organism is for its environment. If a horse were more fit, it could better outrun its predators (or at least outrun the horse next to it, who became someone's breakfast). On the face of it, this concept does not seem to be related to leaving offspring, so let us see how the concept of 'fitness' became for so many evolutionary biologists 'how many offspring you leave'.

In the early days of the Modern Synthesis of Evolution, nearly 1 century ago, mathematical biologists were struggling with ways to quantify the ability of some individuals to survive better than others. Darwin called this 'fitness'. But how were these modelers to quantify an adaptive advantage? The advantage needed to be hereditary, but there were no obvious genes for 'adaptive advantage', even though coefficients of selection for given alleles were used even in the earliest literature of the Modern Synthesis (Provine 2001).

Consider the larger picture. Those individuals that were better adapted, Darwin and Wallace said, would be more likely to survive and reproduce, passing their traits to the next generation. The mathematicians took a shortcut, redefining 'fitness' to represent the number of offspring that an individual left. That became the 'mean fitness' or '*w*' of a population.

But here is the problem. What is important is not that individuals who are better adapted will leave more offspring. (They do not always.) It is that they are more likely to survive to reproductive age and leave offspring. What's more, their offspring will be better adapted to environmental conditions than other offspring. What is the difference between these ideas? Plenty. Consider that in any population there could be genes for higher and lower fecundity (the production of offspring). In other words, how many offspring you produce is independent of how well adapted they will be to their surroundings.

The corruption of the Darwinian term 'fitness' can be shown mathematically. Consider two lineages, A and B. B has 1.2 times the fecundity of A, but in hard times B has only 0.60 the survivability of A, which is a better competitor. In times of relaxed selection, B will outreproduce A by 20% per generation. But if selection pressure is strong, that increased fecundity will be diminished by a 60% survival rate, so compared to lineage A, lineage B will have a survival rate of 1.2×0.6, or 72% of that of lineage A. It is not about the number of offspring you produce; it's about their survivability (Figure 10).

This would have been obvious to Darwin and Wallace, who were (like all other literate people of their time) well steeped in Malthus's (1803, among many editions) *Essay on Population*. The poor, Malthus wrote, are profligate with their offspring, irrespective of their means of

		Fecundity	Survivability	Product
Soft selection				
	A	1.0	1.0	1.0
	B	1.2	1.0	1.2
Hard selection				
	A	1.0	1.0	1.0
	B	1.2	0.6	0.72

Figure 10 Why fecundity (the Neo-Darwinian index of 'fitness') alone does not assure better representation in the next generation. It depends on survivability, that is to say, adaptive 'fitness', which is what Darwin was talking about. The underlined numbers convey the differential in success under hard and soft selection. See text for explanation.

support or future prospects. But it does not make them more successful.

By this reasoning, the number of offspring you leave cannot be regarded as a proxy for your adaptive 'fitness', because those offspring could be competitively inferior. If the 'struggle for existence' is particularly difficult, few of them (if any) will survive, so fecundity alone is not a virtue. (In fact, it could be a disadvantage if many offspring have to compete for the same limited resources.) When Darwin speaks in the *Origin* about leaving more offspring, he is presuming that these offspring carry inherited traits that are better adapted for the environment; and the reason their parents are leaving more offspring is that more of them are surviving to reproductive age than the individuals who were less well adapted.

What, then, is fitness? The population biologists appropriated the term long ago, so we are stuck with regarding it as related to reproductive success (essentially, fecundity) rather than individual adaptiveness, as Darwin used it - unless it is implicit that the success carries with it better genes, not simply more offspring. It is therefore a question of the quality of the offspring, a reflection of their inherited characteristics. Individuals with features better adapted to their surroundings will pass on those features to their offspring, who are likely to be better adapted than others who lack them. But the reason that they have better adapted offspring is that they have passed on more advantageous features to the next generation.

Now we can see our way through a classic evolutionary paradox, notably pointed out by the evolutionary geneticist C.H. Waddington (1967). In the diction of the Modern Synthesis, he noted, 'survival of the fittest' becomes a tautology. The ones who leave the most offspring are the most fit; and how do we know they are the most fit? Because they leave the most offspring. Creationists seized on this circular reasoning to embarrass evolutionists, and the definition of the Modern Synthesis provided no way out of it.

But there is a way out. The missing logical step, as Waddington said, is the one that the population modelers omitted (see above): the most fit (that is, prolific) individuals - those who leave the most offspring in the next generation - are assumed to be the ones whose traits are best adapted to their environments. That is a testable hypothesis. We can test whether the traits that we think are most advantageous were really preferentially inherited by the next generation. If not, the hypothesis of natural selection is not sustained in a particular case. Without testing whether presumably better adapted individuals are the ones with greater reproductive success, natural selection is an assumption rather than a scientific hypothesis.

Sexual selection is not a kind of natural selection

Darwin faced a problem when he was writing his great treatment on natural selection that eventually was distilled to *On the Origin of Species*. He could explain, he thought, why features that improved the ability of an organism to survive and carry out its functions would be favored and passed along in future generations. But he knew it would be harder to explain why some features (such as the famous peacock's tail) persisted and were often strongly conspicuous, even though they seemed to have no purpose in helping an organism to survive. He observed that in nearly all cases, these features were useful in the struggle for mates, rather than in the struggle for existence. And for this reason he separated this phenomenon, which he called sexual selection, from the process of natural selection.

Although some authors state that sexual selection is 'a kind of' natural selection, this view is incorrect (Padian and Horner 2011a, 2011b). Darwin not only explicitly separated the two concepts; he acknowledged that they were quite often in conflict (what if the peacock's long tail makes it easier for a predator to catch it?). He even wrote a book about it: *The Descent of Man, or Selection in Relation to Sex* (1871). He clearly felt that sexual selection was as important in the evolution of humans as natural selection was. And, although he acknowledged that the roles of some morphological structures of animals are difficult to determine, he was adamant about how to recognize when they had a role in sexual selection (Figure 11). This brings us to the next point.

Sexual selection requires sexual dimorphism

Despite extensive confusion in the recent literature, Darwin was clear about what sexual selection is, and what the role of sexual dimorphism (conspicuous differences between males and females) is in it (Padian and Horner 2011a, 2011b). He stated in the plainest language in the *Origin of Species* (pp. 79–80):

The Hierarchy of Species Recognition and Sexual Selection

Species recognition: the ability of individuals to recognize conspecifics for all relevant social purposes (cooperation, competition for resources, group behavior including colony formation, defense, etc.), and the processes by which they do so

Mate recognition: the ability of individuals to recognize what other individuals in their species are potential mates (e.g., in estrus), or even for zygotes of opposite genders to recognize each other chemically, and the processes by which they do so

Mate choice: the processes by which individuals, presented with potential mates, decide actively on acceptance and rejection

Mate competition: the process of competition for mates by members of the opposite sex

Sexual selection: the process of selection for traits possessed by one sex but not the other, or used by one sex and not the other, that increase access to mates by attracting them or by repelling rivals for mates

Figure 11 Darwin regarded sexual selection, a concept he originated and defined precisely, as something very different than natural selection. In this hierarchy of terms related to social recognition in lineages, it can be seen that sexual selection is only a small and very specialized syndrome within a larger context of choosing and competing for mates.

'Thus it is, I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms; and have transmitted these advantages to their male offspring'.

Because Darwin invented sexual selection, and because he based it on observations that have never been falsified,

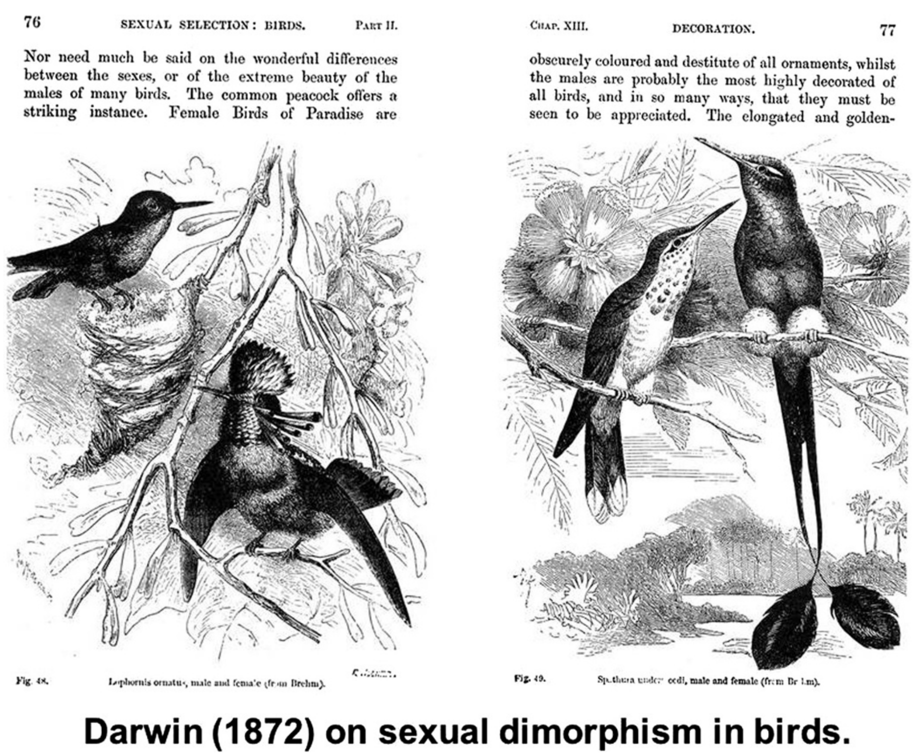


Figure 12 Darwin stressed that sexual dimorphism was the linchpin of sexual selection; indeed, this was the only way he could explain the evolution of bizarre features in one sex - because they were used either to attract mates or repel rivals.

his definition cannot be wrong. It has three components: (1) it explains why sexual dimorphism exists, and its central role in sexual selection; (2) the dimorphic structures or behaviors are used by one gender to attract mates or repel rivals for mates; and (3) these structures and behaviors help the bearer gain access to mates (not necessarily leave more offspring, but to leave offspring more competitive in mating; Figure 12). Darwin needed to define this concept as he did because he knew that opponents would complain that natural selection (which was a description of how the adaptive, Darwinian 'fitness' of individuals should increase through generations) could not account for bizarre structures that were used to enhance mating success, but could be a liability to one's survival, as we have seen in the previous point. Sexual selection was invented precisely to explain unusual dimorphic structures used in mating, and therefore dimorphism is essential to it.

Again, as with natural selection, sexual selection is not simply a matter of producing more offspring. It is about leaving more offspring in the next generation who have the features that are desired by potential mates, or competitive in attracting them. This advantage should eventually allow the numbers game to take care of itself in future generations; it is not simply a matter of fecundity.

Conclusion

The objective of this paper has been to identify and explore some persistent misconceptions in evolutionary biology that are broadly found not only in textbooks and popular science publications, but in scientific journals and books. I have no illusion that other scientists will be in unanimous agreement with all the points I raise here. I challenge all of us, however, to consider the points and improve upon them, so that in turn we can help journalists, textbook writers, and others to interpret our science for the public.

Competing interests

The author declares that he has no competing interests.

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