

Combating the Assumption of Evolutionary Progress: Lessons from the Decay and Loss of Traits

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Abstract Contrary to popular belief, evolution is not necessarily progressive. Indeed, traits are often lost or substantially reduced in the process of evolution. In this article, we present several case studies that can be used in the classroom to illustrate both the ubiquity and diversity of cases of trait loss. Our recently acquired knowledge of genetic and developmental processes can provide insight into how traits are gained and lost through evolution. Several practical applications also emerge from studies of trait loss and degeneration, and we focus on those with medical relevance. Examining trait loss also provides perspective on the crucial differences between Darwinian evolution and social Darwinism. We encourage educators to devote greater attention to trait loss in secondary biology and undergraduate

evolution courses, and discuss how such information may be best incorporated into evolution curricula.

Keywords Appendix · Cavefish · Relaxed selection · Trait loss · Whale evolution

Introduction: Overcoming a Biased History

A common misconception is that evolution implies a progressive and linear climb from ancient “simple” organisms at the bottom to more recent “complex” ones further up, with humans usually at the apex. This is an old view—much older than evolution itself. It follows from a venerable and pervasive tradition in Western thought that places all living entities in the universe on a “great chain of being” stretching from lowest to highest, worst to best. When evolutionary ideas began to influence scholarly views of nature in the late eighteenth to early nineteenth centuries, the new ideas blended perfectly with that older paradigm: this chain of being, this *scala naturae*, was temporal! Life gradually unfolds upward to perfection (Lovejoy 1936; Mayr 1982)! In the words of one proponent, “In the prodigiously varied sequence of the animals below man, I see Nature in labor advancing fumblingly towards that excellent being who crowns her work.” (Jean-Baptiste Robinet 1768, cited in Lovejoy 1936). It was an elegant view, preserving the intelligibility and hierarchy inherent in the universe and adding to it a concept of developmental progress that could explain the variability and change we see in nature. A century later, this progressivism fit superficially with Darwin’s idea of natural selection tending toward the “improvement” of organisms in relation to their environments. Darwin himself occasionally used progressivist language, but

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was less emphatic than most of his contemporaries. In this as in other aspects of his thought, he seemed in a process of rising above his cultural environment. For instance, he wrote in the *Origin of Species* (1859, 345) that:

The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, insofar, higher in the scale of nature; and this may account for that vague yet ill-defined sentiment, felt by many palaeontologists, that organisation on the whole has progressed.

Darwin also wrote a note to warn himself against sloppy progressivist language he found in some contemporary writing, “Never use the word [sic] higher and lower” (Darwin et al. 1903, §70 n2).

Darwin ultimately rejected the great chain of being, and modern biologists have largely followed suit (Gould 1989; Ruse 1996). Darwin's own idea of natural selection undermines any idea of an empirically detectable goal or *telos* to the evolutionary play as a whole. In addressing whether evolution progresses in this way, evolutionary biologist George C. Williams (1966: 34) wrote:

Many biologists have stated that it does, and many more have tacitly assumed this position. I would maintain, however, that there is nothing in the basic structure of the theory of natural selection that would suggest the idea of any kind of cumulative progress.

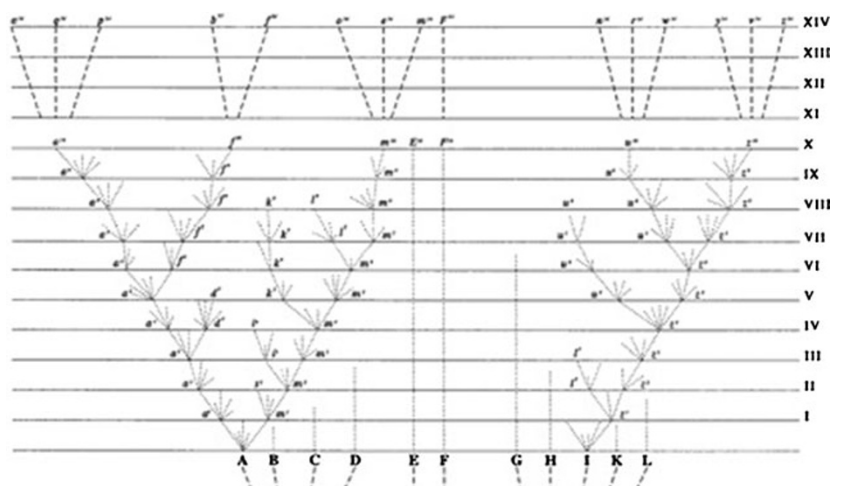
Philosopher of biology Michael Ruse sums things up succinctly: “Progress is impossible in the world of Darwinism, simply because everything is relativized in the sense that success is the only thing that counts.” (Ruse 1995: 178). Selective forces that guide evolution relate only to features of particular organisms in interaction with the environments they face from generation to generation. The cumulative effect of short-term evolutionary mechanisms over long timescales has produced

all of life's diversity. This point has become so well established within evolutionary biology that in our experience little or no debate on this point remains in the field.

Darwin emphasized the diversity of life, and how this diversity could arise from natural selection. In what Darwin called “the divergence of character,” which is akin to what most modern biologists call “character displacement” (Pfenning and Pfenning 2010), natural selection arising from competition between closely related species, or between individuals within the same species leads to ever greater diversification. The one figure in *The Origin* (Fig. 1) is more than just the representation of the branched nature of biological diversity; it is also a demonstration of this principle of “the divergence of character” (Gould 2002; Pfenning and Pfenning 2010). Whether or not it arises from character displacement, the branching of life highlighted by Darwin and subsequent evolutionary biologists contradicts the notion of universal progression. The evolution of life takes many directions, not all of which are toward more complexity or progress as we know it. Certainly, there are local hotspots of various sorts, including pinnacles of neural complexity, but increasing complexity is not an inherent trend in the whole of evolution.

Nevertheless, old ideas not only die hard, but they can also leave behind subtle warps of attitude and language. Even notable evolutionary biologists in the twentieth century gave way to occasional progressivist language (e.g., Huxley 1953; Stebbins 1966; Ayala 1974). Our failure as biologists and educators to eradicate this misconception has allowed it to linger in the public perception of evolution. Several cultural phenomena undoubtedly contributed, including the historical prominence of the great chain of being idea, the tendency to progress of some cultural changes such as science and technology, and our understandable preoccupation with our own unprecedented species. Unless we are taught otherwise, we may tend to look at evolution as a whole through the lens of

Fig. 1 Figure illustrating the pattern of divergence of life, from Darwin's *Origin of Species*. The “bushy” character of a phylogenetic tree is even more appreciated by evolutionary biologists today. This is not a “great chain of being” moving to greater complexity or perfection, but rather many branching chains spreading outward in diversity. And, even more relevant here, what is true of whole organisms is also true of their individual traits: movement in many directions, rather than a unified progression



our own idiosyncratic history, having descended from organisms that are in real senses undeniably simpler and less intelligent than ourselves.

One of the legacies of our interest in progress is that we concentrate overwhelmingly on the appearance and spread of new functional traits when providing students with examples of evolution. This tendency does not reflect the true scope and trend of evolution, however. Many studies show the loss of a previously functional trait to be at least as common as the evolution of a novel functional trait (e.g., Wiens 2001; Porter and Crandall 2003). We suggest that trait losses will usually far outnumber gains of most common and ancient traits, such as eyes, wings and other limbs, and sex. Consider the many independent losses of traits related to feeding and locomotion in endoparasitic lineages, for instance, the lost traits often having evolved only once in a common ancestor. For another example, although the four limbs of tetrapods probably evolved only once, there have been dozens of independent losses, including as many as 25 in the lizards and snakes alone (Wiens et al. 2006). This skew for common and ancient traits is not surprising—as with most organized structures, to demolish a thing is much simpler than to build it. A random mutation affecting a trait is more likely to detract from its functionality than to maintain or enhance it. Several known mutations are available that drastically reduce or obliterate development of major structural traits, for instance. Even in birds, where no wingless or limbless forms are known, there are *wingless* and *limbless* mutants (discovered in chickens) that show a failure of limb development (Bejder and Hall 2002).

Sheer commonality is one major reason why we should incorporate instances of trait loss into our teaching of evolution. There are at least three additional reasons. One is that trait loss helps undermine the concept of general evolutionary progress. The degradation of a trait violates any misguided expectations that evolution should always be building everything up, making everything work better, and moving all traits toward perfection. Instances of trait loss allow us, as educators, to distinguish the mechanisms of evolution, which are general and operate on all traits, from the evolution of novelty or an increase in functional integration, which are relevant to some traits but not others, at some times but not others. Another educational benefit is that such traits provide excellent arguments for evolution in contrast to the rosier assumptions inherent in creationist thinking. Darwin realized this, beginning his section on this subject in *The Origin of Species* on “Rudimentary, atrophied, or aborted organs” with the observation that “Organs or parts in this strange condition, bearing the stamp of inutility, are extremely common in nature.” He then pointed to these structures as traces of the evolutionary process, having descended from functional precursors in

the organisms’ ancestors. Finally, a study of the mechanisms of trait loss can bring certain general principles of evolution into sharp relief, and can even inspire novel insights into trait evolution, despite the fact that the mechanisms of trait loss are the same ones that are involved in other sorts of evolution. We can learn much about an object by observing not only when it works and persists, but also when it fails and disintegrates.

In what follows, we highlight a few cases of trait loss and reduction that are especially appropriate for inclusion in evolution curricula. Some examples are particularly memorable because the changes are so drastic, even sensational—losses of limbs, eyes, or the ability to sexually reproduce! Sometimes trait loss can occur very rapidly, such that it can be observed via historical records or even in real time. It can also proceed in large increments, providing probably the most blatant exceptions to the general rule that evolution proceeds by small steps. Other cases are notable for the insights they provide into evolutionary mechanisms, including unexpected ways in which natural selection can operate. Moreover, during the past decade, research has revealed parts of the genetic basis for trait reduction or loss in a variety of organisms. In a few systems, our understanding of trait evolution now extends from genetic changes, through developmental patterns, to selective regimes in different habitats.

Being Careful with Words

What is trait loss? Because a trait is any feature of an organism, one could consider it so broadly that just about any evolutionary change in phenotype could be considered the loss or reduction of some trait. For instance, consider a lineage of sexually dimorphic animals where males have horns and females do not (Emlen et al. 2005; Moczek et al. 2006). If females were to acquire horns, this could also be considered a loss of sexual dimorphism. Likewise, any color change could be considered a reduction in the previous color. We suggest that cases of trait evolution are best considered trait loss when *the loss or significant reduction in a trait follows a loss or significant reduction of its function*. So, whether the gain of female horns is best taught as a gain of horns or a loss of sexual dimorphism would depend on whether the horns in females has mainly to do with a function for female horns, or the loss of the function related to sexual dimorphism. Likewise, to teach that an organism has lost a color is effective if the color changed because a former function declined in importance. We prefer this perspective because it captures the spirit of what non-scientists care about when they talk about trait loss in colloquial terms: some feature of an organism that used to do something doesn’t need to do it anymore, and the trait is disappearing.

Trait loss may or may not involve a phenomenon known as “reverse evolution” (e.g., Porter and Crandall 2003; Teotónio and Rose 2001). Reverse evolution or evolutionary reversal, occurs when change proceeds first in one direction and then in the opposite direction, such that a new phenotype is identical or at least similar to a past one. In some cases, trait losses are reversals. For instance, dark forms of the peppered moth *Biston betularia* increased during the nineteenth century, and then decreased during the latter part of the twentieth century, resulting in a reversal to the lighter phenotype via a loss of melanin that no longer functioned in camouflage (Grant and Wiseman 2002; Cook 2003). Many instances of trait loss are not reversals, however, meaning that a trait has been lost without reverting to some earlier stage in phenotypic evolution. When cavefish lose their eyes, for instance, they are presumably not reverting to an earlier evolutionary state, because with negligible exceptions, their ancestors had eyes as long ago as they were fish. The concepts of trait loss and reversal should therefore be kept distinct.

A related issue arises with the use of the terms “regression” or “regressive evolution.” These concepts have a distinguished history, having been used by Darwin and, more recently, by eminent biologists such as Theodosius Dobzhansky (1970), roughly as synonyms for trait loss. This term should be avoided, however, because it misleads in at least two ways that follow from its having the sense of “backwards evolution.” If the backwardness means simply in time, then regression is incorrect in cases where trait loss is not a reversal, as described above; the loss of cavefish eyes is not regression in a temporal sense. Another interpretation of regression is as the opposite of progression. This, in fact, is how many classic evolutionary biologists used the term. This use is misguided for the same reason that the concept of progressive evolution is misguided. If we cease to think of evolution as progressive in general (as we should), then we should also cease to single out apparent exceptions as regressive.

Case Studies of Trait Loss

Just as the examples supporting evolution in general have grown tremendously in both number and variety since Darwin’s time, so have the cases supporting trait loss. Here, we cover five well-studied cases of trait loss that either illustrate an important principle or would be likely to catch the attention of students.

The Silence of the Crickets

On a quiet night, walk outside. If the temperature is high enough, you will likely hear crickets chirping. Males of

most cricket species produce these chirps in order to attract and secure mates. Sound production arises when a male rubs its forewings together in a process known as stridulation. Curiously, in a Hawaiian population of the Polynesian field cricket, *Teleogryllus oceanicus*, such sounds have been greatly diminished. Why have the crickets gone silent?

Native to Australia, the Polynesian field cricket migrated eastward to oceanic islands, reaching Hawaii sometime before 1877. In Hawaii, a parasitoid fly, *Ormia ochracea*, is attracted to the male song. Thus, males who sing run a much greater risk of parasitism. Parasitism from the fly, which is not found in the native range of the cricket, has altered the singing behavior of males where the fly is present. In an extreme case, a morphological mutation causes males to lack the structures on the forewing that are needed for song; thus, males with this mutation are silent. This mutation, called *flatwing* is likely adaptive. On the Hawaiian island of Kauai, the frequency of *flatwing* increased from near zero to 91% between the late 1990s and 2004 (16–20 generations) (Zuk et al. 2006).

Results from a preliminary genetic analysis (Tinghitella 2008) are consistent with *flatwing* being a mutation at a single X-linked gene. The genetic basis of this trait is of interest as a sex-linked allele that is expressed in the heterogametic sex (the one with two different types of sex chromosomes) would be conducive to a rapid increase in frequency, as opposed to a trait that had a polygenic basis.

Given that the flatwing males don’t sing, how do they find and attract mates? The flatwing males act as satellite males: they wait for other males to sing, approach those males, and then attempt to mate with females attracted to the singing male (Zuk et al. 2006; Tinghitella and Zuk 2009). Mating preference tests by Tinghitella and Zuk (2009) revealed that females are significantly less likely to mount flatwing males. This preference varies across populations; however, females from populations with flatwing reject flatwing males less than do females from populations without flatwing males. There is no significant heterogeneity for female preference among the different populations that have male song. Tinghitella et al. (2009) showed that male satellite behavior preceded the origin of the flatwing mutation and evolved independently of it.

Singing males face a very high risk of parasitism, but the satellite males that take advantage of the singing males do not face this risk. Obviously, this strategy cannot persist if there are no singing males, so the advantage of the flatwing males who are forced to be satellites will be lost if the percentage of singing males drops too low. This situation sets up the prospect for frequency-dependent selection maintaining an equilibrium, wherein both types of males are maintained at more or less constant frequencies. The exact frequencies of the two types of males will depend on the magnitude of the parasitism pressure and the nature of

the mating disadvantage to satellite males when singing males are rare.

In the Polynesian field crickets of Hawaii, the changed environment due to the presence of the parasitoid led to natural selection directly favoring the loss of song, a trait under sexual selection. This loss occurred by a morphological mutation affecting wing structure instead of a behavioral suppression of the song. Loss of traits that originally evolved due to sexual selection is a common phenomenon (Wiens 2001). For instance, phylogenetic analysis of 47 genera of fruit-eating birds known as tanagers reveals that evolutionary changes from colorful males to drab males are about five times more frequent than changes from drab to colorful. In at least some of these cases, the loss of the sexually selected trait correlated with changes in environmental conditions. A common environmental change resulting in the loss of sexual displays is a new parasite or predator that would be attracted to the display, as the parasitoid wasp is to the song of the Polynesian field cricket. Another circumstance in which a sexually selected trait might be lost is if the transmission of the signal is hindered. For example, some African rift lakes have become polluted such that their waters are murky. If the visibility is so poor that female cichlid fish can no longer see the male color displays, this will reduce or relax selection maintaining the bright male colors and they may fade, even leading to mating confusion among species (Seehausen et al. 1997).

Better Living Without Sex?

From an evolutionary perspective, the mating systems of plants are rather changeable, as plants that engage in sexual reproduction often have close relatives that are asexual. Moreover, even within species, some populations may be fully sexual while others are completely or mostly asexual (Eckert 2002). The causes of such variation include both physical and biotic features of the environment, which are often unknown. Interestingly, in species that vary with respect to sexuality, asexual reproduction is often found at the periphery of the species range (Eckert 2002). At the edge, population sizes are usually lower and the match between the plant's adaptations and the environments are usually less good than in the main portion of the species' range (e.g. Eckert et al. 2008).

Swamp loosestrife *Decodon verticillatus* is one example of variation in mating systems. This perennial, aquatic plant is found in wetlands in eastern North America. Sexual reproduction occurs in this species via insect-pollinated flowers, and asexual reproduction occurs via adventitious rooting of branch tips. Throughout most of its range, most populations of *D. verticillatus* reproduce sexually. Across the northern part of the range of this species, from northwestern Massachusetts through southern New Hampshire

and up along the Maine coast, most populations are asexual, and the loss of the capacity to reproduce sexually (sexual sterility) appears to have arisen several times. The asexual populations have much lower genetic and morphological variability than the sexual ones, though it is not clear whether the loss of sex led to the lower genetic variability or vice versa (Dorken and Eckert 2001).

What evolutionary hypotheses account for the loss of sex in these northern populations of *D. verticillatus*? We can distinguish three general hypotheses: mutations that cause the loss of sex are (1) neutral and neither increase nor decrease fitness, (2) advantageous because they enhance asexual reproduction either by freeing up resources or by some other means, or (3) are deleterious but become fixed due to what is known as the mutational meltdown (Eckert 2002). In the mutational meltdown, deleterious mutations accumulate because the population size is low and thus subject to strong genetic drift (Lynch 2007). Populations at the periphery of species ranges would be most likely to encounter a mutational meltdown scenario because they are more subject to population bottlenecks and the associated strong genetic drift. The lower variability of the asexual populations (Dorken and Eckert 2001) is consistent with, but not proof of, the mutational meltdown.

One way to test these competing hypotheses would be to compare how well the sexual and asexual populations do in asexual "vegetative" growth and reproduction in the same setting (a "common garden experiment"). If the loss of sex is due to mutational meltdown, vegetative growth should be lower in the asexual population. The neutral mutation hypothesis would predict that the populations would have equivalent vegetative growth rates, and the advantageous mutation hypothesis would predict that the asexual populations would actually have higher vegetative growth. With such a common garden experiment, Dorken and colleagues (2004) showed that sterile genotypes have a fitness advantage in asexual populations, thus supporting the hypothesis that the loss of sex is actually advantageous at least under some circumstances. Exactly what this advantage is, and the ecological circumstances that led to this plant losing the ability to reproduce sexually, are subjects for future inquiry.

No Eyes Are Better than Two

An estimated 100,000 species of animals live in caves. Since before Darwin's time, biologists and naturalists have been fascinated with the unusual convergent adaptations to life in caves as well as the loss of previously adaptive traits, such as eyes and skin pigments that no longer provide an advantage in the absence of light (Culver et al. 1995). The adaptation to darkness, including the loss of these traits, is called troglomorphy.

The Mexican “blind cavefish” (a form of the tetra *Astyanax mexicanus*) is emerging as a model system for the study of cave organisms and the evolution of troglomorphy (reviewed in Espinasa and Espinasa 2008; Jeffrey 2009). Unlike most cave-dwelling animals, *A. mexicanus* is fully fertile with surface populations and can be bred in the lab; thus, the features of this species associated with cave life are easily amenable to genetic analysis. Moreover, this species can be found in about 30 caves in Mexico, raising the prospects for multiple incidents of independent evolution. Molecular phylogenetic studies (Jeffrey 2009) indicate that the caves were settled at least three (and possibly four) independent times and that eyes were lost independently several more times, demonstrating parallel and convergent evolution.

Simple genetic analysis can reveal information about the nature of the evolution of eye reduction. For instance, eyes in the hybrids in F1 crosses between some different cave populations are substantially larger than those of the parents (Wilkens and Strecker 2003). This finding is evidence that some of the genetic changes that have led to eye reduction differ across the cave populations and act in a mostly recessive manner. Why would that be the case? Consider the simple situation wherein the two populations evolved reduced eye size and that the reduction was due to different recessive alleles (a and b) at different genetic loci (*A* and *B*, respectively). The two populations would have genotypes aaBB and AAbb. Hybrids between the populations would be AaBb, and thus would have wild-type-sized eyes. Even in more complex situations where more than two loci are involved and the dominance relationships are not complete, hybrids would still have larger eyes than the parental populations if different genetic changes were responsible for the eye reduction in the two populations and the eye-reducing mutations are mostly recessive. In contrast, if the same genetic changes had occurred in the different populations or had the eye-reducing alleles been dominant, then the F1 hybrids between cave populations would have eyes roughly the same size of those of their parents.

More sophisticated studies of the genetic architecture of eye size differences rely on quantitative trait locus (QTL) analysis. In this commonly-used technique, a series of crosses between two extreme forms (in this case, the surface populations and the cave populations) generate a sample of organisms that vary both in genotype and in the trait of interest (see Conner and Hartl 2005 for a review). Some of the genes of these individuals derive from the surface population, the rest of their genome derives from the cave population, and different individuals vary in the sources of their genetic material. A series of genetic markers, usually DNA-based, then determine whether a particular individual has cave or surface genetic material at a given location in the genome. If individuals that have surface population DNA at

a given location in the genome tend to have larger eyes than individuals that have cave population DNA there, then this region is likely a gene or is near a gene that influences the eye size difference between the two forms. Such QTL analysis has revealed several regions of the genome that influence eye size differences between cave and surface forms (Jeffrey 2009; Protas et al. 2008). Among these is a region near the *sonic hedgehog* (*shh*) gene.

What evolutionary forces have led to the degeneration and loss of eyes in this cavefish? Darwin (1859) speculated about the evolutionary reasons for eye loss and degeneration in caves. He noted, “As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss solely to disuse.” At least for *A. mexicanus*, Darwin’s explanation appears incorrect. Similar to the case for loss of sex in *Decodon verticillatus* (see above), loss of eyes appears to be advantageous: evidence suggests that eyes are costly because their development reduces the resources available for at least one other sensory system (Jeffrey 2009). Specifically, eye precursors and taste receptors share some developmental underpinnings such that scaling back the eyes allows for greater development of taste receptors (Yamamoto et al. 2009). Cave and surface *A. mexicanus* differ in the expression levels of several genes, including the gene *sonic hedgehog* (*shh*) whose expression is higher and differently situated in cavefish than in surface fish. Interestingly, *shh* is involved in the eye/taste bud differentiation: overexpression of *shh* decreases eye formation but increases taste receptors and other aspects of the olfaction system and the jaw. Inhibition of *shh* leads to the opposite: decreased development of taste buds and jaws, but increased eye formation. Moreover, QTL analysis shows that the QTLs found in crosses between surface and cave populations are all in the same direction (the surface allele increases eye size and the cave allele decreases it) (Jeffrey 2009; Protas et al. 2008). This pattern is strong support for the action of natural selection operating on the trait (Orr 1998). These clues point to a possible evolutionary mechanism: natural selection operated to increase taste receptors and jaw size through changing the expression of *shh* (and likely other genes). The increased *shh* expression had the pleiotropic consequence of leading to decreased eye development. *Indirect selection* is the term that refers to this phenomenon of a change in one trait occurring through selection on a correlated trait. Indirect selection may play a role in the loss of many traits in nature (Lahti et al. 2009).

In the extreme dark, vision has little utility; thus, eyes would not be of much selective value. In both dark and the light environments, the ability to taste and strong jaws are beneficial. In the light, there is a tradeoff between the developmental precursors of eyes on the one hand, and taste

buds and jaws on the other; thus, the optimum in light environments is to compromise and funnel resources to both. In the dark, however, resources spent on eyes are wasted; thus, genetic changes that lead to fewer resources devoted to eyes are selectively advantageous.

When Legs Get in the Way

Whales and snakes provide among the most fascinating and recognizable cases of trait loss. The fact that these legless animals (among others) descended from typical tetrapods with four limbs provides an excellent angle for evolutionary education. Unlike the previous three situations, whose examples and evidence are primarily extant organisms and can be studied by field evolutionary ecology and laboratory experimentation, limb loss in vertebrates occurred many millions of years ago, and phylogenetic and paleontological studies have played a much larger part in our understanding of these events. Here, we briefly highlight the evolution of hindlimbs and locomotion in the whale lineage.

The cetaceans, an order comprised of the whales, dolphins, and porpoises, descended from land-walking four-limbed ancestors about 50 Mya (million years ago) (Xiong et al. 2009). Only recently have many of the details of their evolution come to light (see Fig. 2), through fruitful deposits of fossil material, such as several sites in Pakistan (Gingerich et al. 2001, 2009). Overall, the picture is one of an increasingly aquatic existence over a period of about 12–15 Mya, accompanied by “mosaic evolution” of several different kinds of traits. While some traits such as echolocation, blubber, and the tail fluke newly evolved, other traits such as hindlimbs and fur were reduced or lost. Limb loss in whales was probably fostered by natural selection for swimming efficiency, because a vertical undulation (the locomotive strategy of cetaceans) is optimized with a hydrodynamic form, and legs would only get in the way (Thewissen 1998). Other traits remained but changed form: nostrils shifted backwards and upwards, and forelimbs turned into flippers. And, of course, body size greatly increased. All of these changes related to or were facilitated by life in the water (Bejder and Hall 2002). This scenario illustrates the important fact that trait loss does not represent or require a fundamentally different kind of evolution than we see in traits that are growing or changing in other ways. We advocate an increased focus on trait loss not because it involves unprecedented mechanisms, but because it is often overlooked in evolutionary education whereas, as the whale situation shows, it is just as much a part of major evolutionary transitions as other sorts of trait changes are.

The developmental mechanisms that underlie trait loss provide potent case studies of the way in which evolution and development interact. In only the most extreme cases does an entire developmental sequence relating to a trait disappear, as in the loss of teeth in cypriniform fish, for instance (Stock et

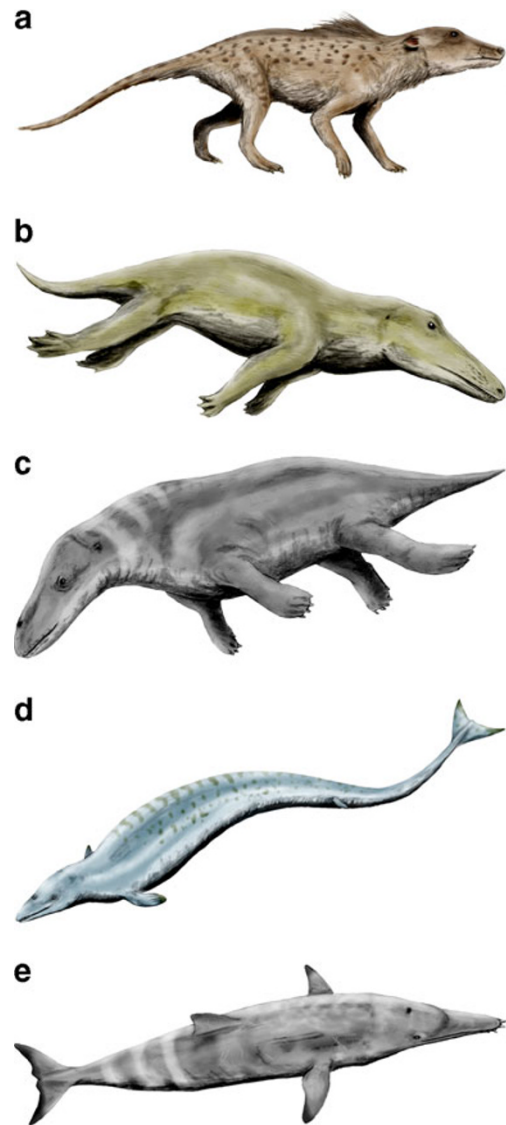


Fig. 2 A gradual evolution of whale traits. **a** *Pakicetus*, the terrestrial “Pakistan whale” lived about 50 Mya. Features of the inner ear place this animal at the base of whale evolution. **b** The amphibious *Ambulocetus* flourished a few million years after *Pakicetus* and displayed many more typical cetacean characteristics, but like all fossils found from this period so far, still had fully developed hindlimbs. **c** *Rodhocetus* likewise had full hind limbs, but a more weakly anchored pelvis, and the sacral vertebrae that are fused in other mammals were loose. **d** By 38 Mya several species of fully marine whales such as *Basilosaurus* grew to a very large size, up to 17 m. Its pelvis was no longer connected to the vertebral column, and the tiny remaining hindlimbs were probably used primarily as mating claspers. **e** The diminutive hind limb parts of later whales such as the North American *Squalodon* (33–14 Mya) probably showed no external evidence, as in all extant cetaceans. Notice that whales had entered the water long before we find evidence of lost or even reduced limbs. This sequence does not necessarily represent a chain of direct ancestors and descendents. It does, however, exemplify the successive evolutionary changes that some branches of the whale lineage underwent between the Eocene and the Miocene periods, leading to extant whales. (Artist renditions by Nobu Tamura, used with permission. Images not to scale)

al. 2006). In perhaps most cases, early development of the trait proceeds but is eventually halted. In embryos of modern cetaceans, limbs do begin to develop, but they later disintegrate. For instance, developmental evidence from dolphins demonstrates that limb buds develop normally in the first few weeks, but then shrink in later embryonic development (Sedmera et al. 1997; see Fig. 3). Comparative embryology was one of the earliest sources of evidence for evolution, and still today results like this can be used to solidify students' understanding of evolution, and in particular the “tinkering” nature of evolution—the fact that current traits do not start from scratch but from precursors. The case of whale limb buds can now be added to other well-known cases, such as our pharyngeal gill arches, where the traces of ancestral trait loss remain in the embryos of modern organisms.

The Mysterious Appendix

When people think of a vestigial trait, the human appendix often comes to mind. Indeed, the word appendix also refers to parts of a book or article that are set apart from the main text, and could be skipped without major loss of understanding of the work. Ironically, the mammalian appendix may not be vestigial organ, but actually serve a function.

The appendix has been viewed as an expendable organ because it can be removed (appendectomy) without causing any apparent loss of function. Appendectomies are performed because appendices can become inflamed (a condition known as appendicitis). If left untreated, this inflammation can lead to death. Although it can occur at any age, appendicitis is most common in older children, teenagers, and young adults. A 1990 epidemiological study estimated the lifetime risk of

acquiring appendicitis at 8.6% for males and 6.7% for females in the United States (Addiss et al. 1990). As we will discuss below, the incidence of appendicitis has dropped since 1990, but a sizeable fraction of people still develop inflamed appendices. Interestingly, the lifetime risk for having an appendectomy is much higher than the risk of appendicitis, especially in females (Addiss et al. 1990).

Appendicitis increased in frequency during the nineteenth and early twentieth centuries, peaking during the late 1920s (Kang et al. 2003). Starting around 1930, its incidence has declined in the United States, the UK, and other industrial countries. This downward trend has continued at least through the 1990s, and is not explained by changes in medical practices, such as diagnoses (Kang et al. 2003). Among the first to note the decline in appendicitis was Kenneth Castleton, who was struck by the dramatic decline in the death rate from appendicitis in post-war America. He noted that the annual appendicitis-related death rate had fallen from 8.1 per 100,000 in 1941 to 1.3 per 100,000 in 1956 (Castleton et al. 1959). Castleton questioned whether the six-fold decrease could be explained solely by the use of antibiotics and other improvements in medical care or if the actual incidence of acute appendicitis. Surveying a wide range of hospitals, Castleton and colleagues found that the actual incidence had fallen by roughly two-fold, both in urban and in rural hospitals.

Castleton, like many before and after him, was at a loss to explain such a decline, and suggested nutritional factors and the use of antibiotics might be behind it. Of course, as Kang et al. (2003) point out, the decline in appendicitis incidence had begun before antibiotics were used by a large segment of the population. Kang et al. (2003) also present some of the historical reasons given for both the rise and fall of appendicitis rates. In summary, physicians have frequently tied appendicitis to diet, though often without much supporting evidence. Some evidence does support that tomatoes and some leafy vegetables may protect against inflammation of the appendix, but the data supporting this conclusion are correlational (people who eat those vegetables and tomatoes have lower rates of appendicitis), but not causal (Kang et al. 2003). Even now, we don't have a good understanding of either why appendicitis rose in frequency in the nineteenth century or why it fell through most of the twentieth.

So why do we have appendices in the first place? One intriguing hypothesis presented by Bollinger et al. (2007) is that the appendix evolved as a storehouse for biofilms of commensal bacteria. Following Scott (1980), they argue that appendix-like structures are relatively rare and scattered throughout the phylogeny of mammals, present in rabbits, opossums, and wombats in addition to humans and closely related primates. Such a pattern is suggestive of a structure that evolved for a specific function. Bollinger et al. also argue that the structure of the human appendix is well suited

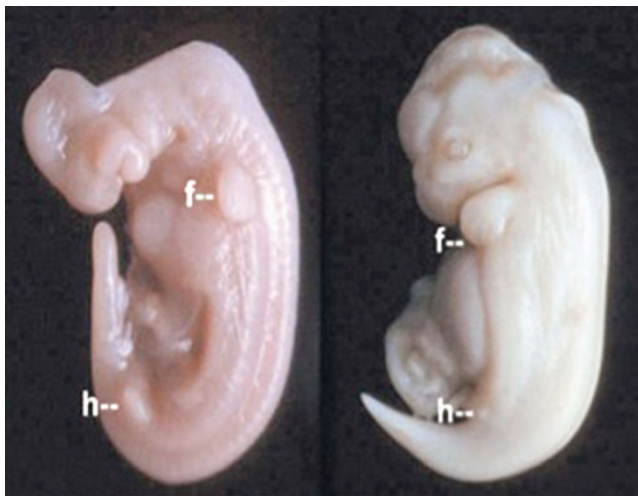


Fig. 3 Development of lost traits: the hindlimbs of cetaceans. The embryo of the spotted dolphin *Stenella attenuata* at 24 days (left) has a well-developed early hindlimb bud (*h*), which has regressed by 48 days (right), while the forelimb bud progresses—note the primordial digits (*f*) (from Sedm)

for the formation of biofilms of bacteria, as well as protection of said biofilms.

So, why does the appendix present problems for a relatively small, but not insignificant minority of people? A likely explanation is that the appendicitis was not a major health problem for most of the evolutionary history of our species, but that changes in the environment (diet? changes in parasite load?) have made it so. Thus, according to that explanation as well as the dietary explanations given for its rise and subsequent fall in frequency, appendicitis is a condition of mismatch between the environments in which we evolved and those in which we dwell.

While intriguing and supported by some data, the biofilm hypothesis has not been fully confirmed. Moreover, other hypotheses also exist. One alternative is that the appendix does not serve a function, but that further reductions in its size would enhance the likelihood of appendicitis because smaller appendices were more likely to be infected (Nesse 1994). If this hypothesis were true, it would be an example of the limitations of evolution: no appendix would be ideal, but we can't get there from here. Unfortunately, we currently lack the data to test this hypothesis.

Recommendations and Conclusions

Even among those secondary and university students who accept evolution, misunderstandings of evolution abound (Alters and Nelson 2002; Cavallo and McCall 2008; Moore R 2009). Many students harbor Lamarckian and progressive views, for example (Alters and Nelson 2002). Unfortunately, we educators may perpetuate such misunderstandings, for example, if we describe only instances of evolution and selection that are progressive. On the other hand, teachers in both secondary schools and colleges and universities can directly challenge progressivist assumptions and enhance students' appreciation for and understanding of evolution by using examples of trait loss as well as gain, therefore representing more accurately the observed diversity of evolutionary outcomes. In this final section, we offer three specific practical recommendations for educators with regard to trait loss.

First, we think such examples would be most useful if they were integrated into the overall evolutionary curriculum rather than relegated to special topics. For instance, these examples can be used to illustrate the nature of natural selection and its lack of an overall goal. In some environments, individuals with more complex structures or greater functionality will have a selective advantage, whereas in other environments, those with less complex structures will have the advantage. The cricket example (“[The Silence of the Crickets](#)” section) can be used to illustrate that evolution can be a compromise between opposing selection pressures:

in this case, natural selection from predation and sexual selection. The cavefish example (“[No Eyes Are Better than Two](#)” section) demonstrates tradeoffs: resources can be directed to eyes or to jaws and taste buds, and devoting more resources to one requires devoting fewer resources to the other. Incorporating trait loss seamlessly into evolutionary courses will emphasize that it is not a peculiar evolutionary phenomenon, but is simply business as usual in nature.

Second, as with studies of evolution in general, studies of trait loss through evolution have the potential to be applied to numerous situations of practical importance, in such areas as medicine, agriculture, and conservation biology. Educators are increasingly seeing the benefits of using practical examples when teaching evolutionary biology (Bull and Wichman 2001; Hood and Jenkins 2008). Many of the most salient examples in applied evolution involve trait loss, and we echo the opinions of others that such examples can make evolutionary biology interesting to those students who require relevance in order to listen or move beyond their intellectual comfort zone (Zeigler 2008).

Pathogen evolution is a prime example of how trait loss can be discussed in the context of a medically relevant evolutionary adaptation. As pathogens adapt to their human hosts, they often lose certain traits while gaining others. Consider the adaptation of the bacterium *Pseudomonas aeruginosa* to humans. Infection by this bacterium is responsible for cystic fibrosis (CF). Smith et al. (2006) followed the evolutionary course of *P. aeruginosa* adaptation in a CF patient, taking DNA sequences from two isolates of the bacterium, one 6 months after infection and the other after 96 months. The sequences revealed a clear sign of positive selection operating on the bacterium as it adapted to the host, namely a greater rate of change of non-synonymous substitutions (those DNA changes that alter the amino acid sequence) than of synonymous substitutions (those that do not alter the amino acid sequence). What is most interesting in Smith et al.'s (2006) study from the trait loss perspective is the observed decrease in virulence factors (loss of serotype-specific antigenicity, loss of secreted protease activity, reduced biofilm production) in the 96-month isolate. Smith et al. (2006) also showed that genes for virulence factors are particular targets of selection. They claim that the likely reason that these virulence factors are under negative selection is that they lead to immune evasion (the immune system targets the virulence factors). A related application is the evolution of antibiotic resistance in pathogens. If selection on antibiotic resistance is relaxed, will the resistance be lost or will it persist? If it is lost, how quickly will it be lost? A key determinant here is the cost of resistance. Andersson (2006) suggests that in many cases resistance will persist, especially if compensatory mutations have arisen in the pathogen, reducing or eliminating the cost of resistance. Similar applied questions pertain to the loss of resistance of insect pests to pesticides: after usage is discontinued, will the

insects retain or lose their resistance? Population genetic theory makes certain predictions about this process. Loss of resistance is likely when the cost of being recessive is not recessive; that is, the heterozygotes for the resistance allele pay a fitness cost relative to the homozygotes for the susceptible allele (Carrière and Tabashnik 2001). Other genetic conditions favoring the loss of resistance include a low frequency of resistance alleles in populations and the presence of large non-dosed reservoir populations that are connected by gene flow to with populations sprayed with pesticides (Carrière and Tabashnik 2001).

Third and finally, an appreciation for trait loss and an abandonment of progressivism in evolution rightfully undermines the unfortunate conflation of Darwinian evolutionary biology with social Darwinism. We encourage educators to make this point when it becomes relevant. It was William Jennings Bryan's opposition to social Darwinism that led him to oppose evolutionary biology (Larson 1997), and many still attack evolutionary biology by pointing to social Darwinism consequences that they perceive as emanating from principles of evolutionary biology. For instance, much of the attack on evolution made in Ben Stein's film *Expelled* is based on the assumption that biological evolution leads to social Darwinism and fascism (e.g., Zimmerman 2010). Social Darwinism involves notions such as inherent progress in evolution and inherently favored classes or groups of humans as a basis for moral norms and social attitudes and action. This inherent directionality and progress was also part of the pre-Darwinian notion of the Great Chain of Being, without which social Darwinist attitudes have no grounding. Moreover, as we have highlighted earlier, there is no inherent directionality in biological evolution: complexity can decline and traits can decay or become lost within a lineage when such changes provide a selective advantage in a given local environment at a particular time. Discussions of trait loss can demonstrate to students, and to the general public, this crucial aspect to biological evolution and how it undermines social Darwinism. With regard to understanding the role of progress in evolution, the implications for getting evolution wrong are much graver than simply getting it wrong.

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References

- Addiss DG, Shaffer N, Fowler BS, Tauxe RV. The epidemiology of appendicitis and appendectomy in the United States. *Am J Epidemiol.* 1990;132:910–25.
- Alters BJ, Nelson CE. Perspective: teaching evolution in higher education. *Evolution.* 2002;56:1891–901.
- Andersson DI. The biological cost of mutational antibiotic resistance: any practical conclusions? *Curr Opin Microbiol.* 2006;9:461–5.
- Ayala FJ. The biological concept of progress. In: Ayala FJ, Dobzhansky T, editors. *Studies in the Philosophy of Biology.* London: Macmillan; 1974. p. 339–54.
- Bejder L, Hall BK. Limbs in whales and limblessness in other vertebrates: mechanisms of evolutionary and developmental transformation and loss. *Evol Dev.* 2002;4:445–58.
- Bollinger RR, Barbas AS, Bush EL, Lin SS, Parker W. Biofilms in the large bowel suggest an apparent function of the human vermiform appendix. *J Theor Biol.* 2007;249:826–31.
- Bull JJ, Wichman HA. Applied evolution. *Annu Rev Ecol Syst.* 2001;32:183–217.
- Carrière Y, Tabashnik BE. Reversing insect adaptation to transgenic insecticidal plants. *Proc Biol Sci.* 2001;22:1475–80.
- Castleton KR, Puestow CB, Sauer D. Is appendicitis decreasing in frequency? *Arch Surg.* 1959;8:794–801.
- Cavallo AML, McCall D. Seeing may not be believing: examining students' understandings and beliefs in evolution. *Am Biol Teach.* 2008;70:522–30.
- Conner JK, Hartl DL. *A primer of ecological genetics.* Sunderland: Sinauer Associates; 2005.
- Cook LM. The rise and fall of the *carbonaria* form of the peppered moth. *Q Rev Biol.* 2003;78:399–417.
- Culver DC, Kane TC, Fong DW. *Adaptation and natural selection in caves: the evolution of Gammarus minus.* Cambridge: Harvard University Press; 1995. p. 1995.
- Darwin CR. *The origin of species.* London: John Murray; 1859.
- Darwin C, Darwin F, Seward AC. *More letters of Charles Darwin.* New York: D. Appleton & Co; 1903.
- Dobzhansky T. *Genetics of the evolutionary process.* New York: Columbia University Press; 1970.
- Dorken ME, Eckert CG. Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *J Ecol.* 2001;89:339–50.
- Dorken ME, Neville KJ, Eckert CG. Evolutionary vestigialization of sex in a clonal plant: selection versus neutral mutation in geographically peripheral populations. *Proc R Soc Lond B.* 2004;271:2375–80.
- Eckert CG. The loss of sex in clonal plants. *Evol Ecol.* 2002;15:501–20.
- Eckert CG, Samis KE, Loughheed SC. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol Ecol.* 2008;17:1170–88.
- Emlen DJ, Hunt J, Simmons LW. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. *Am Nat.* 2005;166:542–68.
- Espinasa M, Espinasa L. Losing sight of regressive evolution. *Evol: Educ Outreach.* 2008;1:509–16.
- Gingerich PD, Haq M, Zalmout IS, Khan IH, Malkani MS. Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science.* 2001;293:2239–42.
- Gingerich PD, Haq M, Koenigswald WV, Sanders WJ, Smith BH, Zalmout IS. New protocetid whale from the middle Eocene of Pakistan: birth on land, precocial development, and sexual dimorphism. *PLoS One.* 2009;4(e4366):1–20.
- Gould SJ. *Wonderful Life.* New York: W. W. Norton; 1989.
- Gould SJ. *The structure of evolutionary theory.* Cambridge: Belnap; 2002.
- Grant BS, Wiseman L. Recent history of melanism in American peppered moths. *J Hered.* 2002;93:86–90.
- Hood E, Jenkins KP. Evolutionary medicine: a powerful tool for improving human health. *Evol: Educ Outreach.* 2008;1:114–20.

- Huxley J. *Evolution in Action*. New York: Harper and Bros; 1953.
- Jeffery WR. Regressive evolution in *Astyantax* cavefish. *Annu Rev Genet.* 2009;43:25–47.
- Kang JY, Hoare J, Majeed A, Williamson RCN, Maxwell JD. Decline in admission rates for acute appendicitis in England. *Br J Surg.* 2003;90:1586–92.
- Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP, Blumstein DT, Coss RG, Donohue K, Foster SA. Relaxed selection in the wild. *Trends Ecol Evol.* 2009;24:487–96.
- Larson EJ. *Summer for the Gods: the scopes' trial and America's continuing debate over science and religion*. Cambridge: Harvard University Press; 1997.
- Lovejoy AO. *The Great Chain of Being*. Cambridge: Harvard University Press; 1936.
- Lynch M. *The origins of genome architecture*. Sunderland: Sinauer Associates; 2007.
- Mayr E. *The growth of biological thought: diversity, evolution, and inheritance*. Cambridge: Belknap; 1982.
- Moczek AP, Cruickshank TE, Shelby A. When ontogeny reveals what phylogeny hides: gain and loss of horns during development and evolution of horned beetles. *Evolution.* 2006;60:2329–41.
- Moore R, Decker HD, Cotner S. No prospect of an end: chronology of the evolution-creationism controversy Santa Barbara, CA: ABC-CLO; 2009.
- Nesse R, Williams GC. *Why we get sick: The New Science of Darwinian Medicine*. New York: Times Books; 1994.
- Orr HA. Testing natural selection vs. genetic drift in phenotypic evolution using quantitative trait loci. *Genetics.* 1998;149:2099–104.
- Pfenning DW, Pfenning KS. Character displacement and the origins of diversity. *Am Nat.* 2010;176:s26–44.
- Porter ML, Crandall KA. Lost along the way: the significance of evolution in reverse. *Trends Ecol Evol.* 2003;18:541–7.
- Protas M, Tabansky L, Conrad M, Gross JB, Vidal O, Tabin CJ, Borowsky R. Multi-trait evolution in a cave fish, *Astyanax mexicanus*. *Evol Dev.* 2008;10:196–209.
- Ruse M. *Evolutionary naturalism: selected essays*. London: Routledge; 1995.
- Ruse M. *Monad to man: the concept of progress in evolutionary biology*. Cambridge: Harvard University Press; 1996.
- Scott GB. The primate caecum and the vermiform appendix: a comparative study. *J Anat.* 1980;131:545–63.
- Sedmera D, Misek I, Klima M. On the development of cetacean extremities. I. Hind limb rudimentation in the spotted dolphin (*Stenella attenuata*). *Eur J Morphol.* 1997;35:25–30.
- Seehausen O, van Alphen JJM, Witte F. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science.* 1997;277:1808–11.
- Smith EE, et al. Genetic adaptation by *Pseudomonas aeruginosa* to the airways of cystic fibrosis patients. *Proc Natl Acad Sci U S A.* 2006;103:8487–92.
- Stebbins GL. *Processes of organic evolution*. Englewood Cliffs: Prentice Hall; 1966.
- Stock DW, Jackman WR, Trapani J. Developmental genetic mechanisms of evolutionary tooth loss in cypriniform fishes. *Development.* 2006;133:3127–37.
- Teotónio H, Rose MR. Perspective: reverse evolution. *Evolution.* 2001;55:653–60.
- Thewissen JGM, editor. *The emergence of whales: evolutionary patterns in the origin of Cetacea*. New York: Plenum Press; 1998.
- Tinghitella RM. Rapid evolutionary change in a sexual signal: genetic control of the mutation 'flatwing' that renders male field crickets (*Teleogryllus oceanicus*) mute. *Heredity.* 2008;100:161–267.
- Tinghitella RM, Zuk M. Asymmetric mating preferences accommodated the rapid evolutionary loss of a sexual signal. *Evolution.* 2009;63:2087–98.
- Tinghitella RM, Wang JM, Zuk M. Preexisting behavior renders a mutation adaptive: flexibility in male phonotaxis behavior and the loss of singing ability in the field cricket *Teleogryllus oceanicus*. *Behav Ecol.* 2009;20:722–8.
- Wiens JJ. Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends Ecol Evol.* 2001;16:517–23.
- Wiens JJ, Brandley MC, Reeder TW. Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution.* 2006;60:123–41.
- Wilkens H, Strecker U. Convergent evolution of the cavefish *Astyanax* (Characidae, Telesotei): genetic evidence from reduced eye-size and pigmentation. *Biol J Linn Soc.* 2003;80:545–854.
- Williams GC. *Adaptation and natural selection*. Princeton: Princeton University Press; 1966.
- Xiong Y, Brandley MC, Xu SX, Zhou KY, Yang G. Seven new dolphin mitochondrial genomes and a time-calibrated phylogeny of whales. *BMC Evol Biol.* 2009;9:20.
- Yamamoto, Stock DW, Jeffrey WR. Pleiotropic functions of embryonic sonic hedgehog expression link jaw and taste bud amplification with eye loss during cavefish evolution. *Dev Biol.* 2009;330:200–11.
- Zeigler D. Relevance in education? *Evol: Educ Outreach.* 2008;1:517–9.
- Zimmerman, M. Social Darwinism: a bad idea with a worse name. http://www.huffingtonpost.com/michael-zimmerman/social-darwinism-a-bad-id_b_489197.html; 2010.
- Zuk M, Rotenberry JT, Tinghitella RM. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biol Lett.* 2006;2:521–4.