Title
Coevolution in the Classroom

Journal
Evolution: Education and Outreach, 3(1)

ISSN
1936-6434

Author
Thanukos, Anastasia

Publication Date
2010-03-01

DOI
10.1007/s12052-009-0203-7

Peer reviewed

Evo Edu Outreach (2010) 3:71–77
DOI 10.1007/s12052-009-0203-7

Coevolution in the Classroom

Anastasia Thanukos

Keywords Coevolution · Natural selection · Trade-offs · Teaching

In this special issue of *Evolution: Education and Outreach*, many different authors argue for the importance and utility of coevolution as a topic for classroom exploration—and for good reason. Coevolved relationships are likely to impress and interest students: acacias that produce thorny homes for the ants that protect them from voracious insects (Janzen 1966), flowers that exchange nectar for the sexual assistance of a pollinator (e.g., see Nilsson 1998), and newts that have evolved to be so toxic that they can easily kill most any predator—except the resistant snakes that normally feed on them (Brodie and Brodie 1990). Coevolutionary adaptations are often extreme and sometimes weird and wonderful.

From a teacher's perspective, coevolution can be used to illustrate key aspects of natural selection that students frequently miss. Though students tend to think of the environment as an organism's physical surroundings (climate, habitat, etc.), it is important for students to recognize that an organism's environment actually includes both abiotic (nonliving) and biotic (living) components—and that both of these can trigger evolutionary change. Focusing on the biotic components of an organism's environment also highlights how rapidly environments can change. Natural selection doesn't have to wait for tectonic action or the next glacial cycle to shake things up; as organisms evolve, they mutually affect each other, providing constantly shifting opportunities for evolutionary change. This is particularly important because students (and the general public) have a tendency to view evolution as a goal-directed ladder of progress (Fig. 1) that organisms climb as they are changed by natural selection (e.g., see Alters and Nelson 2002; Nehm and Reilly 2007). However, if students grasp just how much environments can change due to coevolutionary and ecological processes—even on short timescales—they are more likely to understand that natural selection acts in relation to an organism's current circumstances. What is most fit today may not be tomorrow. There is no universal scale of evolutionary progress for organisms to climb; it's all relative.

In addition, coevolution offers a perfect way to weave evolution throughout instruction in ecology. Many policymakers and educators have advocated integrating evolution throughout biology instruction so that evolution is not relegated to a discrete unit at the beginning or end of the course, but is accurately portrayed as woven throughout scientific thinking in all areas of biology (e.g., National Academy of Sciences 1998; Alles 2001). Coevolutionary processes and phenomena clearly illustrate the deep ties between evolution and ecology. Using coevolutionary examples, students can understand how ecological relationships result from evolutionary processes and how an understanding of evolution informs ecological research.

In an article in this issue, Thompson (2010) reviews many different forms of coevolution. Here, we will delve into just a few of the processes he addresses (those most likely to come up in classrooms and textbooks), provide summaries of the basic mechanisms involved, give additional examples, and of course, provide relevant teaching resources.

A. Thanukos (✉)
University of California Museum of Paleontology,
1101 Valley Life Sciences Building,
Berkeley, CA 94720-4780, USA
e-mail: thanukos@berkeley.edu
URL: http://evolution.berkeley.edu

Fig. 1 Evolution is not goal directed and does not climb a ladder of progress. An organism's fitness is not absolute but is dependent on its current environment. Illustration modified with permission from the Understanding Evolution website

The Basics

The term coevolution describes a process in which two or more different species reciprocally affect each other's evolution. This may take the form of a tight-knit relationship, in which one species evolves a trait in response to a pressure or opportunity from a second species (e.g., a plant evolving a flower color that attracts a particular bird pollinator), and the second species evolves in response to that change (e.g., the pollinator evolving a beak shape that allows it to better access the nectar of that plant). Coevolutionary relationships may also be more diffuse, involving a web of interactions between many different species (e.g., a plant species evolving a flower color that attracts a whole class of pollinators, which affects the evolution of each of those pollinator species in a slightly different way, which may, in turn, affect other species with which the pollinators interact). We can observe many relationships in the natural world that seem to have coevolved, but working out the details of the evolutionary processes that led up to a particular ecological relationship can take a lot of investigation. Biologists generally look for evidence that each species involved in the hypothesized coevolutionary process has evolved in response to the other(s).

Thompson lists three basic types of ecological interaction that can set the stage for coevolution (see Table 2 in Thompson 2010): trophic antagonism (i.e., predator–prey or parasite–host relationships), competition, and mutualism. We will examine each of these in turn.

Predator vs. Prey

Predator–prey relationships can lead to different sorts of coevolutionary phenomena, but one of the most interesting (and readily graspable by students) is an evolutionary arms race. This is exactly what it sounds like: two parties one-upping each other in terms of defense and counterdefense or attack and counterattack. It works like this: Imagine an insect that feeds on a particular plant species. Any individual plant that happens to carry a mutation coding for, for example, a slightly stronger insect-repellent chemical will be favored by natural selection, and we would expect the mutation to increase in frequency in the population. But, of course, as the mutant gene becomes more common, any insect that happens to have a mutation that provides a slightly higher tolerance for the defensive chemical will be favored, and over many generations, this gene will become more common in the insect population. This sets up another situation in which stronger defensive chemicals are favored in the plants—and if this trait evolves, it sets up another situation favoring stronger tolerance in the insects... and so on. The levels of repellence and tolerance may continue to escalate without either species "winning."

Do arms races continue escalating forever then? No, and the explanation offers instructors a chance to introduce students to another important evolutionary concept: evolutionary trade-offs. Many different traits contribute to an organism's overall fitness, and optimizing one trait often means downgrading another. For example, for our plants and insects, producing stronger chemical defenses and tolerances may take a lot of energy, decreasing the amount of metabolic energy available for reproduction. Eventually, the benefit of producing stronger defenses and tolerances will be outweighed by the detriment of decreased reproduction. At that point, escalating the arms race will no longer be favored by natural selection, and the evolutionary one-upping will stop.

A classic and well-studied example of an arms race (referenced by Thompson 2010) is the rough-skinned newt and its predator, the common garter snake, which live on the West Coast of United States. Some rough-skinned newts are so poisonous that the amount of toxin (called TTX) in a single newt could kill 50,000 mice (Hanifin et al. 2004). This is more than enough to kill virtually all of the newts' potential predators. The few exceptions are the toxin-resistant garter snakes that feed on the newts (Brodie and Brodie 1990). Many different lines of evidence support the idea that these levels of toxicity and toxin resistance evolved through an evolutionary arm race (Fig. 2). First, the researchers studying these organisms showed that the newt's toxin and the snake's resistance are the sort of traits that can evolve via natural selection: they showed that both

Fig. 2 The rough-skinned newt and the common garter snake are engaged in an evolutionary arms race. Illustration reproduced with permission from the Understanding Evolution website

traits vary among individuals in a population, are genetically based, and affect fitness (Brodie 1968; Brodie and Brodie 1990, 1999a; Hanifin et al. 1999; Williams et al. 2003). Then they showed that newt and snake toxicity varies across different regions but that newts and snakes living in the same region have matching levels of toxicity and resistance (Fig. 3), exactly as we would expect if newts and snakes are engaged in an evolutionary arms race that has escalated more quickly in some regions than others (Brodie et al. 2002). The researchers even figured out exactly what trade-off is at stake for the garter snakes: speed. Garter snakes with low resistance are quick—which helps them escape their predators and catch prey—and the more toxin resistance a garter snake has, the slower it moves (Brodie and Brodie 1999b). Too much resistance makes the snake pay a significant price—trouble catching food and escaping from its own predators. This compelling example provides an opportunity to help students learn important evolutionary and ecological concepts while gaining an understanding of the process of science and how biologists investigate questions about the evolutionary past using evidence they gather today (see "In the Classroom" section below for teaching resources on this example).

Competition and Coevolution

Ecological conflicts can arise, not just between the eater and the eaten, but between two species that play the same role in an ecosystem (e.g., eater vs. eater). This occurs when two species compete for food, space, or other limited resources. Thompson explains that this competition can result in a coevolutionary phenomenon called character displacement: when two species compete for the same set of resources, natural selection may favor traits in each species that allow them to specialize, subdividing the resources, or accessing slightly different resources. For an example, imagine two species of bird that wind up on an island together after a hurricane. The species have similarly sized beaks and feed on similarly sized seeds—and so must compete for the same limited resource. One population happens to have a few members with mutations that increase beak size, allowing them to eat slightly larger seeds more efficiently. In that population, these large-beaked birds are likely to reproduce more and spread their genes, since they won't have to compete with as many other birds and will likely be able to get more food. As one species evolves slightly larger beak sizes, the other species is likely to experience selection favoring birds with smaller beak sizes, which allows them to access a resource with less competition. Over many generations, the character (beak size) is likely to be displaced (i.e., likely to diverge) in the two species. In fact, this is almost exactly what biologists think has occurred with two species of Galapagos finch, *Geospiza fuliginosa*, which has evolved a smaller beak and body size, and *Geospiza fortis*, which has evolved the larger beak and body (Schluter et al. 1985). For another example of character displacement involving stickleback fish, see the article of Dolph Schluter in this issue.

Scientists gather many different lines of evidence to determine whether character displacement has occurred.

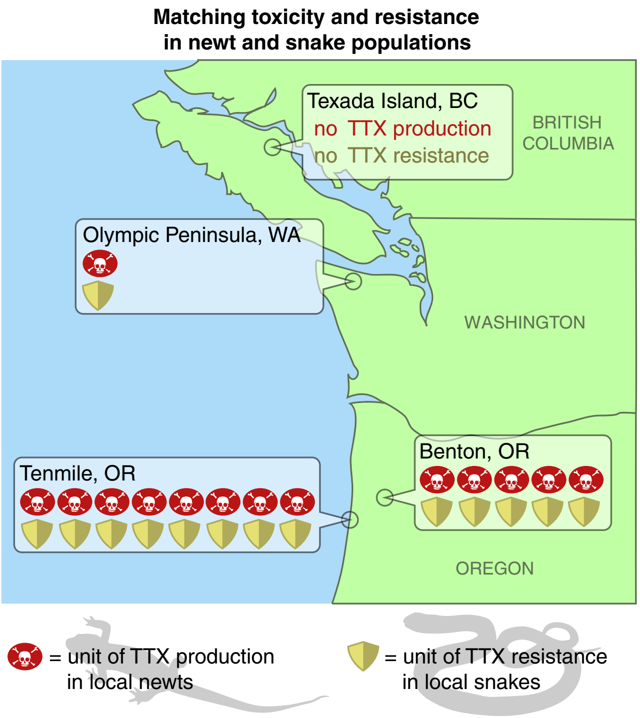

Fig. 3 Levels of newt toxicity and snake resistance are correlated across different geographic regions, supporting the idea of an evolutionary arms race. Illustration modified with permission from the Understanding Evolution website

First, they may study how the character varies over the different locations in which the species are found. If character displacement has occurred, we would expect the trait to be divergent in places where the two species both live, but to be less extreme in places where only one of the species lives. For example, on the Galapagos island where *G. fuliginosa* lives alone (i.e., in the absence of *G. fortis*), the population has a larger beak than it does on the islands where the two species both live. And the reverse is true for populations of *G. fortis* (Lack 1983; Schluter et al. 1985). This is exactly what we would expect to observe if coevolutionary character displacement took place on the islands where the two live together. Scientists may also look for direct evidence that natural selection is operating on the character. For example, biologists were able to observe directly how exploiting small seeds (normally the food of *G. fuliginosa*) increases the fitness of *G. fortis* individuals on the island where *G. fortis* lives alone (Schluter et al. 1985). These observations strongly suggest that having to share resources on the islands where the species both occur depresses fitness and sets up a situation in which we would expect natural selection to act on the species.

Together Forever

Trophic antagonism and competition suit an image of “Nature, red in tooth and claw” (from *In Memoriam A. H. H.*, Tennyson 2007), but coevolution also has a warm, fuzzy side. Coevolution occurs not just as a result of conflict between species, but also as a result of cooperation. In mutualistic relationships, each species involved gets some benefit (i.e., a boost in fitness) as a result of the interaction. A classic example of a mutualism is pollination: the pollinator gets a food source (nectar or pollen), and the plant gets its gametes distributed to other members of the same species. As discussed above in “The Basics” section, coevolution as a result of mutualisms may be diffuse, involving whole groups of species, but Thompson also describes coevolutionary, mutualistic relationships that evolve to be so specific that the participants become completely codependent and cannot live without one another.

Such tight-knit mutualisms often occur when one species actually lives inside another, a situation known as endosymbiosis. This might seem like a rare phenomenon, but in fact, such extreme associations of distantly related organisms are found across the tree of life: Giant clams harness solar energy through their endosymbionts, photosynthetic zooxanthellae (e.g., see Lee et al. 2005). Tubeworms living near deep sea vents have a special organ that harbors their endosymbionts—bacteria that can convert the sulfurous compounds released by the vent into usable energy (Cavanaugh et al. 1981). And like Russian nesting dolls, some termites’ guts are inhabited by wood-digesting flagellates, which are themselves inhabited by bacteria (e.g., see Ikeda-Ohtsubo et al. 2007). Such examples demonstrate that each species involved in such a close relationship must have adapted to the opportunities presented by the other—especially in cases where neither species can live on its own.

The most extreme example of mutual adaptation through endosymbiosis is likely to be compelling to students because it shows how they (and, in fact, all eukaryotes) are the result of ancient coevolutionary events. Several billion years ago, an oxygen-loving bacterium (probably a close relative of modern *Rickettsia* bacteria, which are responsible for typhus) took up residence inside another bacterium and wound up staying forever (Fig. 4; Andersson et al. 1998). Over many generations, the relationship

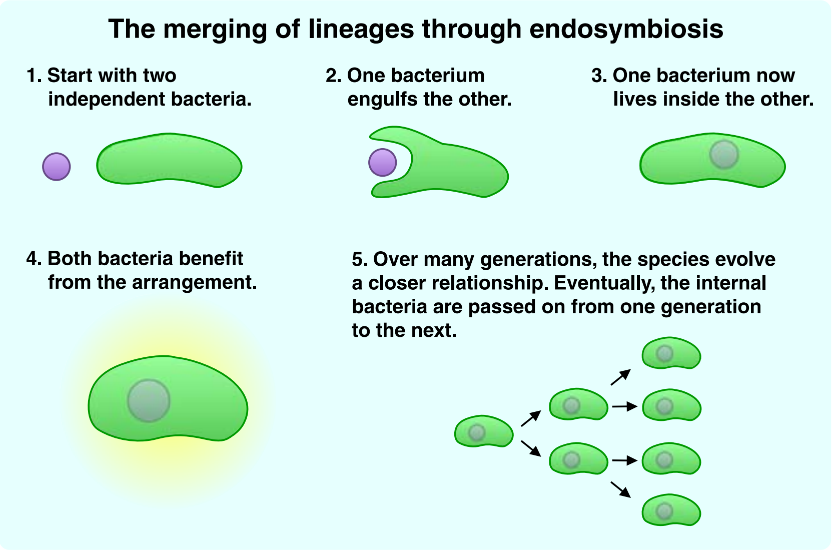

Fig. 4 Over many generations of evolution, endosymbiotic relationships may become so close that the two lineages effectively merge. Eventually, it may become difficult to identify the endosymbiont as the descendent of a free-living organism. Illustration modified with permission from the Understanding Evolution website

became so tight that scientists had trouble identifying mitochondria (the former endosymbiont) as anything other than an integral part of the cell. Of course, many lines of evidence support the idea, and scientists are now confident that our own mitochondria—and those of all eukaryotes—evolved through an ancient endosymbiotic relationship and subsequent coevolution (e.g., see Martin 1999). That subsequent coevolution made the host cells entirely dependent on their mitochondrial endosymbionts, and the mitochondria entirely dependent on their hosts. Many genes that originally belonged to the mitochondrion were transferred to the host's nuclear DNA, and the mitochondrion evolved to become a critical part of the host's metabolism. Two separate evolutionary lineages effectively evolved to become one. This process might seem unusual, but it has almost certainly happened more than once. The plastids (e.g., chloroplasts) inside plant cells evolved via a similar process (e.g., see Martin 1999). These examples are likely to be particularly useful in the classroom because they can be used to tie evolution into a common introductory biology topic—cellular organelles. In addition, the story of how Lynn Margulis resurrected and championed these ideas makes an ideal case study of the process of science in action. Though most of the scientific establishment exhibited its typical (and healthy!) skepticism in response to her hypothesis, they were finally convinced by the many, many lines of evidence that were ultimately found to support the idea.

Conclusion

Coevolution should be a key component of evolution instruction because the process has been so important in shaping the history of life. As Thompson points out, we (and all other complex organisms) are dependent on the coevolved relationships that form the basis of our ecological interactions and even our own metabolism. Just as importantly, coevolution offers many compelling examples for students to sink their teeth into. Coevolution encourages students to think one step beyond an evolutionary scenario, to consider the likely ramifications that one species' evolution is likely to have for other species it interacts with, and in so doing, helps students appreciate the blooming, buzzing complexity that characterizes the natural world.

Give Me an Example of That

Want more examples of coevolution? Check out these resources from the Understanding Evolution website:

- A case study of coevolution: squirrels, birds, and the pinecones they love. In an article in this issue, Benkman (2010) describes the coevolution of pine trees with the squirrels and crossbill birds that eat the trees' seeds. The case study below explains the basic biology of the three players and highlights some of the evidence that has convinced biologists that this interaction represents a case of coevolution. It is written at a level appropriate for high school students. Read it at: http://evolution.berkeley.edu/evolibrary/article/evo_34
- It takes teamwork: how endosymbiosis changed life on Earth. To learn even more about the merging of bacterial lineages through endosymbiosis and coevolution, check out a case study on the topic. Written at a high school level, this resource answers basic questions, such as: What is endosymbiosis? What role did endosymbiosis play in the evolution of eukaryotes? And how did endosymbiosis change our view of the branching pattern on the tree of life? Read it at: http://evolution.berkeley.edu/evolibrary/article/endosymbiosis_01

Branch Out

Thompson's article in this issue briefly describes what recent research has revealed about how parasites and pathogens evolve to be more or less deadly. To learn about the rapid pace at which such coevolutionary interactions can take place, read Brockhurst's article (2010) in this issue on how host–parasite coevolution can be observed over short timescales in the lab. To learn more about how evolutionary biology informs and advances medical science—and to learn more about the evolution of virulence specifically—check out this excerpted chapter from Carl Zimmer's book, *The Tangled Bank*:

- Evolutionary medicine (reprinted on the Understanding Evolution website with the permission of Roberts and Company Publishers, Inc.) http://evolution.berkeley.edu/evolibrary/images/evol_medicine.pdf

You can address these topics in your classroom using a high school level lesson from the National Health Museum, in which students learn about natural selection in rabbits by observing the effects of a virus on the Australian rabbit population:

- Studying living organisms: viruses and host evolution. http://www.accessexcellence.org/AE/AEPC/WWC/1995/viruses.php

Dig Deeper

The process of natural selection is at the root of coevolution. To dig deeper into this topic, visit these Understanding Evolution resources:

- Natural selection: the basics. Darwin's most famous idea, natural selection, explains much of the diversity of

life. Learn how it works, explore examples, and find out how to avoid misconceptions. http://evolution.berkeley.edu/evolibrary/article/evo_25
- Misconceptions about natural selection and adaptation. Natural selection is often misconstrued as a process that perfects organisms and provides them with exactly what they need. Find out the truth. http://evolution.berkeley.edu/evolibrary/article/misconcep_01

In the Classroom

Before students can tackle coevolution, they need to understand the basics of natural selection. The following lessons provide straightforward introductions to the topic:

- Clipbirds. In this lesson for grades 6–12, students learn about variation, reproductive isolation, natural selection, and adaptation through a version of the bird beak activity. http://www.ucmp.berkeley.edu/education/lessons/clipbirds/
- Breeding bunnies. In this lesson for grades 9–12 from WGBH, students simulate breeding bunnies to show the impact that genetics can have on the evolution of a population of organisms. http://www.pbs.org/wgbh/evolution/educators/lessons/lesson4/act1notes.html

Once students understand natural selection, they can begin to reason about situations in which species mutually affect each other's evolution. As described above, evolutionary arms races may be both intuitive and compelling to students, and so provide a good introduction to the topic of coevolution. The arms race between poisonous newts and their garter snake predators is particularly well understood—and entertaining. You might introduce this example with a short video clip from WGBH:

- Toxic newts. This five minute clip from *Evolution: Evolutionary Arms Race* tells the story of a species of newt and its garter snake predator. http://www.pbs.org/wgbh/evolution/library/01/3/l_013_07.html

This can be followed up with a more in-depth case study on the topic:

- Biological warfare and the coevolutionary arms race. This case study for high school and college students explains how an evolutionary arms race has pushed a mild-mannered newt to the extremes of toxicity, and how evolutionary biologists have unraveled its fascinating story. http://evolution.berkeley.edu/evolibrary/article/biowarfare_01

Once you feel students have a basic understanding of coevolution, you can challenge them. Ask them to read the following article and write a short essay response analyzing whether or not human populations have coevolved with dairy cattle. Students may need to do additional research on the evolutionary aspects of domestication.

- Got lactase? This news brief for high school and college students explains that the ability to digest milk is a recent evolutionary innovation that has spread through some human populations. Recent research reveals how evolution has allowed different human populations to take advantage of the nutritional possibilities of dairying. http://evolution.berkeley.edu/evolibrary/news/070401_lactose

Acknowledgments The author wishes to thank Judy Scotchmoor for helpful comments on earlier drafts, as well as David Smith for help developing images.

References

Alles DL. Using evolution as the framework for teaching biology. American Biol Teacher. 2001;63:20–3.
Alters BJ, Nelson CE. Teaching evolution in higher education. Evolution. 2002;56:1891–901.
Andersson SGE, Zomorodipour A, Andersson JO, Sicheritz-Pontén T, Alsmark UCM, Podowski RM, et al. The genome sequence of *Rickettsia prowazekii* and the origin of mitochondria. Nature. 1998;396:133–43.
Benkman C. Diversifying coevolution between crossbills and conifers. Evol Educ Outreach. 2010;2: doi:10.1007/s12052-009-0190-8
Brockhurst MA. Using microbial microcosms to study host-parasite coevolution. Evol Educ Outreach. 2010;2: doi:10.1007/s12052-009-0188-2
Brodie Jr ED. Investigations on the skin toxin of the adult rough-skinned newt, *Taricha granulosa*. Copeia. 1968;1968:307–13.
Brodie III ED, Brodie Jr ED. Tetrodotoxin resistance in garter snakes: an evolutionary response of predators to dangerous prey. Evolution. 1990;44:651–9.
Brodie III ED, Brodie Jr ED. Predator-prey arms races. Bioscience. 1999a;49:557–68.
Brodie III ED, Brodie Jr ED. The cost of exploiting poisonous prey: tradeoffs in a predator-prey arms race. Evolution. 1999b;53:626–31.
Brodie Jr ED, Ridenhour BJ, Brodie III ED. The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between newts and snakes. Evolution. 2002;56:2067–82.
Cavanaugh CM, Gardiner SL, Jones ML, Jannasch HW, Waterbury JB. Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts. Science. 1981;213:340–2.
Hanifin CT, Yotsu-Yamashita M, Yasumoto T, Brodie III ED, Brodie Jr ED. Toxicity of dangerous prey: variation of tetrodotoxin levels within and among populations. J Chem Ecol. 1999;25: 2161–75.
Hanifin CT, Brodie III ED, Brodie Jr ED. A predictive model to estimate total skin tetrodotoxin in the newt *Taricha granulosa*. Toxicon. 2004;43:243–9.

Ikeda-Ohtsubo W, Desai M, Stingl U, Brune A. Phylogenetic diversity of 'Endomicrobia' and their specific affiliation with termite gut flagellates. Microbiology. 2007;153:3458–65.

Janzen DH. Coevolution of mutualism between ants and acacias in Central America. Evolution. 1966;20:249–75.

Lack D. Darwin's finches. Cambridge: Cambridge University Press; 1983.

Lee JJ, Cevasco M, Médor G. Isolation and characterization of the "zooxanthellae" from soritid foraminifera and the giant clam *Tridacna maxima*. J Eukaryotic Biol. 2005;52:7s–27s.

Martin W. A briefly argued case that mitochondria and plastids are descendants of endosymbionts, but that the nuclear compartment is not. Proc R Soc Lond B. 1999;266:1387–95.

National Academy of Sciences. Teaching about evolution and the nature of science. Washington: National Academy Press; 1998.

Nehm RH, Reilly L. Biology majors' knowledge and misconceptions of natural selection. BioScience. 2007;57:263–72.

Nilsson LA. Deep flowers for long tongues. TREE. 1998;13:259–60.

Schluter D, Price TD, Grant PR. Ecological character displacement in Darwin's finches. Science. 1985;227:1056–9.

Tennyson AL. Alfred Lord Tennyson: selected poems. London: The Penguin Group; 2007.

Thompson JN. Four central points about coevolution. Evol Educ Outreach. 2010;2: doi:10.1007/s12052-009-0200-x

Williams BL, Brodie Jr ED, Brodie III ED. Coevolution of deadly toxins and predator resistance: self-assessment of resistance by garter snakes leads to behavioral rejection of toxic newt prey. Herpetologica. 2003;59:155–63.