

1 What Are Adaptations?

1.1 Adaptation at the Organismic Level

Picture a woodpecker hanging on a tree. What do you see them doing? They pound their beaks into the bark of the tree at a rate of up to twenty times per second, so hard that the sound carries clearly throughout the neighborhood.

Woodpeckers have a number of special adaptations to aid them in getting the food they eat, which is grubs, insects, and worms that live underneath the bark of trees. What special adaptations help the woodpecker get at these insect foods they like to eat? And how do they escape the expected harm of slamming their heads and beaks up against a hard tree at a rapid rate for tens of minutes at a time? Wouldn't this scramble their brains, damage their eyes, and cause brain injury? Moreover, how do they reach inside the holes once they are made? Their closest relatives, the honeyguides, do not have extended tongues, but they do eat grubs and even beeswax from beehives. Let us consider these adaptive challenges met by the woodpecker.

First, the woodpecker has evolved a chisel-like tip on its beak to help drill holes in the trees in which its food lives. But wouldn't this repeated trauma to the head of the woodpecker damage the brain during this harsh drilling routine? No, because the woodpecker has also evolved a spongy lining to its skull, which has, in addition, thickened to absorb the drilling vibrations.

Moreover, the eyes of the woodpecker have also evolved special membranes to protect them during the harsh, repeated drilling motion. Finally, the woodpecker's tongue has evolved a barb at the end, and sticky saliva so that it can gather the insects inside the wood and bark of the trees after it drills its holes.

And there are additional special adaptations possessed by woodpeckers (also used by hummingbirds for identical purposes): The hyoid apparatus is lengthened. The hyoid apparatus is made up of a series of bones, muscles, and cartilage, connected to the tongue, that allow the tongue to extend to great lengths in nearly all of the woodpecker species. The hyoid apparatus wraps around the base of the skull and over and around the top of the skull, making the "base" of the tongue wrap fully around the skull of the woodpecker. In the red-bellied woodpecker, the tongue extends three times the length of its bill. We can see that the woodpecker species are specially adapted for their ecological niche of eating grubs and insects from trees with a suite of specially adapted traits enabling them to exploit this otherwise inaccessible source of food.

1.2 Evolutionary Models

Our scientific challenge is to explain how the woodpecker evolved all these special adaptations for its life of eating bugs from under the bark of trees. Any study of adaptation in evolution must rely on a very clear understanding of the process of natural selection, and also what kinds of evidence are desirable for demonstrating that a trait is an adaptation. We will review the basics of these selective explanations in this section, as well as the kinds of evidence that support such explanations.

What happens during a simple process of natural selection, according to evolutionary biologists? In all cases, we start with a population of entities, whether they are plants or animals, bacteria within our guts or groups of flour beetles, and variation in traits within that population.

Detailed aspects of the environment then constrain the reproductive success of some of those entities (call them the losing ones), while allowing or encouraging the reproduction of others among the population (call them the winning ones), depending upon their key features that vary. Under conditions where the key features of the winning and losing entities are reliably passed on to the next generation during reproduction, evolution by natural selection will occur within the population. Specifically, the proportion of entities with certain key winning features will grow, while the proportion of entities with the losing key features will shrink, over time (Futuyma & Kirkpatrick 2017; Griffiths et al. 2005). This embodies a simple process of natural selection, though not its only manifestation.

It turns out that selection does not act on traits separately, but rather as clusters or combinations. For example, in the woodpecker, it does no good to have an extra-long tongue if you do not also have the spongy protective skull to protect your brain from repetitive drilling.

One terminological point that we need to get to right away is: What exactly do we mean when we call something an “adaptation”? Do we mean that *any* trait that comes out of a selection process is an adaptation? Or do we mean that only traits that are “engineered” or whose form is changed by selection are adaptations?

Consider some examples to make the meaning of “adaptation” clearer. Many have learned about the case of “industrial melanism” involving the peppered moths in England. The population of moths was exposed to tree trunks blackened by the soot from factories, and the population of peppered moths went from mostly white moths to mostly black moths. This was due to natural selection on variation in traits in the form of birds eating the visible white moths that were resting on the black trees. Thus, the newly black dominance in the population can be considered an adaptation as a result of the selection process. But note that there are no new mechanisms and no new

forms of moth in this case: There is no engineering or cumulative adaptation arising from the bird predation. Giorgio Airoidi calls this a case of “pure selection” (2018). All we have is a change in population distribution of the black and white moths. It is surely correct to call this a process of natural selection, and under the “selection-product” meaning of “adaptation,” also correct to say that the black-dominance in the population is an adaptation. This “product of selection” (or “selection-product”) definition views any outcome of a process that affects fitness in a positive manner as an adaptation. But it seems incorrect to say that there is a cumulative or engineering adaptation arising from this selection process.

Note the contrast with the woodpecker case. In the woodpeckers, we got a whole list of engineering adaptations that resulted, we believe, from natural selection processes and unknown amounts of developmental factors producing additional variation for selection to act on in these ancestral species of insectivores (species that eat insects). This “engineering” definition of adaptation has been dominant in the literature for many years and is the definition used in George C. Williams’ ground-breaking book, *Adaptation and Natural Selection* (1966). Notably, Richard Lewontin (1978) and Stephen Jay Gould,¹ well-known critics of adaptationist research, also used the “engineering” definition of adaptation. The key relevant feature of an engineering adaptation is that it involves a mechanism or complex feature of some kind, built up cumulatively from simpler features, whereas the product of selection or distributive definition of adaptation involves simply a change or shift in allele frequency, one that could be unrelated to building a revised mechanism (Williams 1966, Lewontin 1978, Gould and Vrba 1982).

The “engineering” account requires that the adaptive account explain the adaptive feature(s) or modification(s) acquired through the selective process over time, its “engineering” history of its complex and built-up adaptive traits. Thus, the idea of an evolutionary *function* is tied intimately to the definition of adaptation itself. This is in accordance, for example, with John Maynard Smith’s idea that “the ‘function’ of an organ is taken to mean those of its effects which have been responsible for its evolution by natural selection” (1978, p. 23). This could apply either to selection-product or engineering views of adaptation. But contrary to the usage of some other philosophers, I will be using exclusively the engineering definitions of adaptation and function throughout this Element, unless otherwise noted. See Table 1.1 for a more complete set of definitions below.

Later in this section we will talk about the notion of “function,” but first let us consider some examples.

¹ Gould and Lewontin 1979.

Table 1.1 Definitions²

Term	Definition
Aptation	a trait that increases fitness (aptation for x – by x-ing). (If a trait is an aptation but not an adaptation, then it was not selected in the past for x-ing, and is an exaptation for x-ing).
Non-Aptation	a trait that does not increase fitness (but may do so in future)
“Engineering” Adaptation	a trait that involves a mechanism or complex feature of some kind, built up cumulatively from simpler features through natural selection processes. These types of adaptation involve both the etiological and the systems analysis types of ‘function’ (Williams 1966, Lewontin 1978, Gould and Vrba 1982; Lloyd 1988)
“Product of Selection” Adaptation	a trait that involves simply a change or shift in allele frequency, one that could be unrelated to building a revised mechanism (Williams 1966, Lewontin 1978, Gould and Vrba 1982)
Exaptation	a trait with no direct engineering function for x, which nevertheless increases fitness by x-ing (Gould and Vrba 1982)
Function	a trait has the engineering (evolutionary) function of x-ing, if x-ing increased fitness in evolutionary history, and the increased fitness explains the prevalence of the x-ing complex or engineering trait
Secondary Adaptation	a trait modified by natural selection (for x-ing, say) because of its contribution to fitness (by x-ing), where the trait so-modified existed, before modification, for a different reason than the role it came to have in x-ing
Spandrel	a trait is a “spandrel” if the trait in question (the trait that was pressed into service) for x-ing (where x-ing increases fitness but was not selected for its fitness contributions and hence does not have the function of x-ing) has no direct engineering function at all (a subset of exaptation).

² Thanks to an anonymous reviewer for help with these definitions.

Let's imagine, as Darwin did, a pack of wolves, some of which were swifter and slimmer than others in the pack: "[T]he swiftest and slimmest wolves would have the best chance of surviving, and so be preserved or selected" (Darwin p. 90, 1859).³ They would do better in the evolutionary long run, reproducing more often and having healthier pups, thereby contributing more genes for the structure of their legs for swifter running to future generations through the process of natural selection. That's how the wolves became such swift runners over evolutionary time, able to take down very swift prey. In other words, we are claiming that "swiftness" is an evolutionary engineering set of adaptations in wolves, evolved by natural selection over evolutionary time. We have a type of biological model, in the claim of the process of evolution by natural selection, one that we can sketch and consider for its evidential weight. Or, we can ask, more specifically, what kinds of evidence would we need to establish a trait like swiftness as an evolutionary adaptation in wolves?

Now that we've had a chance to consider some adaptations in nature, we can see the various types of evidence needed to establish a trait as an adaptation. As Darwin argued, and as was later elaborated after the discovery of genetics, the key ingredients of the most basic natural selection model type in evolution are represented in Box 1.1.

We start with a population of organisms (and we fill in that blank in the selection model outline by specifying which population we are considering), and we have descriptions of traits to focus on, as well as claims of how these traits are heritable or based in genetics (filling in the appropriate blanks of the selection model outline). We also need claims about how these traits are related to fitness, usually supplied in the form of a mechanism explaining how the trait

BOX 1.1 NATURAL SELECTION MODEL OUTLINE

population [____]
 variation in trait(s) [____]
 genetic/cellular basis [____]
 connection or mechanism between trait(s) and fitness [____]
 selection pressure or environment [____]

³ "[T]ake the case of a wolf, which preys on various animals, securing some by craft, some by strength, and some by fleetness; and let us suppose that the fleetest prey, a deer for instance, had from any change in the country, increased in numbers, or that other prey had decreased in numbers, during that season of the year when the wolf is hardest pressed for food. I can under such circumstances see no reason to doubt that the swiftest and slimmest wolves would have the best chance of surviving, and so be preserved or selected . . . I can see no more reason to doubt this, than that man can improve the fleetness of his greyhounds by careful and methodical selection" (pp. 90–91, 1859).

increases fitness, as well as a description of a selection scenario that describes how pressure from an environment imposes on a population in a way that leads to changes in trait frequencies over time, as we saw with the fleet wolves and the woodpeckers.

As we can see, a variety of types of evidence might be required to substantiate the claims filling in the blanks of the selection model. Each of these claims, such as how the trait is related to fitness, and what the selection scenario is, needs to be substantiated with empirical or observational evidence.

Evolutionists Barry Sinervo and Alexandra Basolo (1996) offer a helpful discussion of what they think of as important evidence for adaptations. They start with a consideration of whether a particular trait of an organism is “optimal.” Whether a trait is “optimal” is a calculation that depends on a separate model of *optimality*. Each optimal trait is the best-engineered trait it could be, given the constraints of the system, including developmental constraints and genetic constraints, and the job it needs to do, or the function it needs to fulfil.

Perhaps we can understand optimality better by looking at one of its most famous examples: dung fly mating times. Because males of this species of yellow dung fly mate with more than one female, they like to spend as little time as possible with each female, maximizing their chances at multiple matings with other females on other cow pies. However, the males also need to copulate with the females long enough to displace previous males’ sperm inside the female’s reproductive tract. The ability to do this depends on the size of the male. It is in the first male’s interest to stick around after mating and guard her against mating soon with another male. Geoff Parker and colleagues (Charnov and Parker 1995) predicted that how long the male would copulate would depend on how far away the other cow pies were – in other words, how far away the other females were – and on how large the male was. This is an optimality model, in fact, a physical/biological version of an economics model called “marginal value theorem,” and they were assuming that the male would optimize its behavior in terms of mating efficiency. And lo and behold, when they experimentally manipulated the dung fly males and the mating opportunities, they found that the males copulated with the females for the predicted periods of time (Charnov and Parker 1995).

Optimality models obviously make a number of assumptions about the systems they model, not least that the traits they model are engineering adaptations, but these models can be fruitful for research.

If we do assume that these traits are engineering adaptations, we may still want to know what the state of the traits was *before* the evolution of the adaptation in question. What did the species look like before the trait evolved the way it did?

Understanding this involves reconstructing the ancestors of the current population and trying to see what traits they had, without their relying on the adaptation we are studying. This may involve looking back into the ancestral tree of the population and seeing who is closely and more distantly related to the population, to see who had related traits and who did not. By doing this *comparative* work in *phylogenetics* (the study of the relatedness and traits of entities like species and lineages), we can better see what may be new in this species, lineage, or population of entities.

When studying the evolution of an adaptation, it may be ideal to do some experiments, as Sinervo and Basolo do (1996). The best experiments on adaptations often do two things at the same time:

- (1) They manipulate key features of the environment, the very features that the trait is believed to be an adaptation for dealing with.
- (2) And they manipulate the phenotype or appearance of the traits of the species being studied. So, for example, if we are studying the adaptation of the size of organisms, we would want to do an experiment that involves populations of both small- and large-size organisms.

When these experiments are done, it may be possible to determine which phenotype it is best to have in which environment. In other words, an organism may have higher fitness or reproductive success when it is large and living in large ponds, while a smaller organism may have higher fitness or reproductive success when it is living in smaller ponds. Thus, by manipulating both the environment and the phenotype, we are able to determine how the *fitness parameter* varies with the *trait* in a given environment. This is just the information we need in order to fill in the selection model.

Knowing all this, we might be able to discern whether the trait is an adaptation, that is, whether it evolved to serve a particular *function* in that species, given a certain environment. John Maynard Smith's idea is that "the 'function' of an organ is taken to mean those of its effects which have been responsible for its evolution by natural selection" (1978, p. 23).

In his review of the concept, Colin Allen offers us two main philosophical accounts of function:

Etiological approaches to function look to a causal-historical process of selection; functions are identified with those past effects that explain the current presence of a thing by means of a historical selection process (typically natural selection in the case of biological function).

Systems-analysis approaches invoke an ahistorical, engineering style of analysis of a complex system into its components. Functions of components

are identified with their causal contributions to broader capacities of the system. (emphasis added; Allen 2002, p. 375)⁴

Note that both the engineering adaptations and product of selection or effects type of adaptation, introduced above and present in Table 1.1, fall under etiological approaches to function; they both invoke the historical selection process to explain the current presence of a trait. The engineering adaptations also appeal to design analyses often identified with the systems-analysis notion of function. Thus, engineering adaptations in evolution appeal to both etiological and systems-analysis approaches to function in the philosophical senses just presented (Lloyd 1988; Williams 1966; Lewontin 1978; Gould 2002). Knowing all this, in addition, we may also be able to determine whether the trait is being maintained in current populations through current selection.

Adaptation is an “onerous concept,” according to George C. Williams in his 1966 foundational text on the notion. He thought that a burden of proof rested on those claiming an adaptation and that adaptation should not be *assumed* to exist at the outset of biological investigation, just because a benefit could be perceived. We can look at how this burden of proof plays out by considering evidence supporting claims of engineering adaptations in guppies.

1.2 Confirming Evolutionary Models

1.2.1 Model Fit

There are several basic types of supporting evidence and confirmation:

The first type of evidence that can support the type of natural selection model we have just described is “model fit,” that is, where the predictions of, for example, an optimality model “fit” or predict the **outcome** that we find in the real population of organisms. We can have model fit of selective models as well, where, after filling in all the blanks in our natural selection model outline in Box 1.1, we can predict correctly what the model outcome would be. We need an example to help understand this.

Biologists David Reznick, John Endler, and colleagues studied life history traits in guppies (see Figure 1.1). “Life history” traits are simply those traits involving the main stages in life, such as development to maturity, reproduction, and aging (Reznick and Travis 1996; Endler 1978).

⁴ This latter systems definition is most often identified as a “Cummins function” approach (Cummins 1975). See Larry Wright (1973) for more on the etiological approach.



Figure 1.1 Guppies like those studied by Sinervo and Basolo (1996)

They studied the hypothesis that life history traits in the guppies were actually *adaptations to stage-specific predation* that were caused by predators, in other words, adaptations to the rate at which the predators of guppies killed the guppies. Reznick and his colleagues studied two communities that differed in their predators. One type had cichlids as predators – fish that prey heavily on adult-stage guppies – while the other had Rivulus fish that preyed only lightly on guppies, and when they did, it was mostly on juvenile guppies.

Evolutionary theories concerning predation and trade-offs between early and later reproduction made it possible to make predictions about life histories.

The evolutionists investigated the correlation between guppy life histories and the type of predator communities. The first prediction was that an increase in predation on the adults, like that found with the cichlids, would select for a decrease in the age at sexual maturity.

As we can see from Figure 1.2, the measurements from the guppies caught in the wild revealed differences in guppy life histories that were consistent with the predictions. In other words, there was good “model fit.” Guppies from Rivulus localities, where predation was low, were older at maturity than their counterparts from Cichlid localities, where predation was high, which gave the guppies less chance to mature and breed at older ages. Thus, natural selection, according to the hypothesis, evolved guppies that matured earlier and were able to breed at younger ages in the high-predation environment, just as the model predicted. This is an example of directional selection, as illustrated in Figure 1.3. Simple directional or stabilizing selection usually produces *peaks* in the distribution curves of a trait, and with directional selection, the population average moves

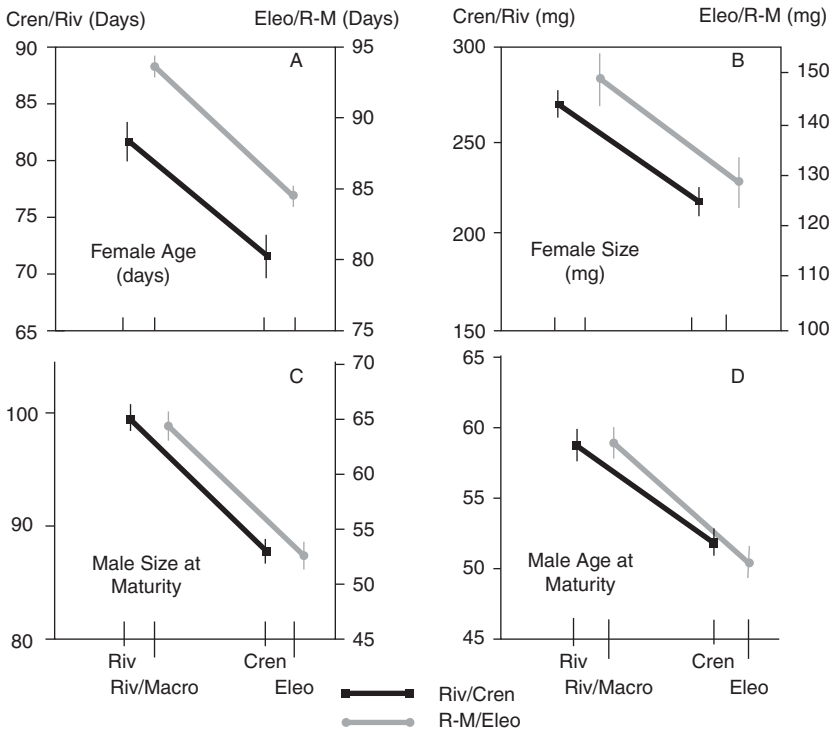


Figure 1.2 Decrease of age at sexual maturity depending on predator (Reznick and Travis 1996, p. 266): Least square means (+1 standard error) for the age and size at maturity and size at first birth in females from high- versus low-predation environments. See caption in Reznick and Travis for more information. Think of the predation rates as going from low to high from left to right on the *x*-axis. The stippled lines represent the means for the Low (Riv/Macro) versus high (Eleo) predation sites. The solid lines are the corresponding values for the high (Cren) and low (Riv) predation sites. All differences between the high- and low-predation sites were significant. (A) Female age at first birth (days). (B) Female size at first birth (wet weight in mg). (C) Male size at maturity (wet weight in mg). (D) Male age at maturity (days).

over to a new, more desirable, value. (We will examine a case of stabilizing selection in Section 4). Note that this account assumes that the traits are genetically controlled rather than arising from phenotypic plasticity.

This guppy reproduction case is a good example of the *good fit* of a selective evolutionary model prediction with the data from animals taken from the wild.