

Chapter 11

Non-Random Evolution

11.1 Introduction

I have emphasized that the evolution of life on Earth is not at all an entirely random occurrence. We can comprehend it in terms of what we know about nature. Randomness and non-randomness play important parts. The randomness I am talking about are the genetic and symbiotic innovations presented in chapter 9 (not in this edition) But into what are these innovations introduced? They come to be in consistent yet limited environments of one form or another. Consistent environments represent the non-random ecological components of non-random evolution. So we can say that innovations, however random their origins, either live or die depending upon how well they cope with their environment. This chapter describes how non-random ecological circumstances can yield non-random evolutionary results.

First, the big picture perspective. Non-random evolution is a consequence of the four following things:

1. the presence of life
2. The continuance of life for long periods of time
3. Opportunities to introduce innovations
4. Non-random environments that 'test' each innovation

It will take some doing to get from this big picture viewpoint to the details. So, let me give you an idea of the logic behind this chapter.

1. First I want to talk about the essence of a living existence
2. Then I want to talk about how reproduction with inheritance gives to life the property of continuance and also provides opportunities in which innovations can be introduced.
3. Then I want to present ideas on what a consistent and stressful environment is and what it means to the things that live and reproduce in them.
4. Then I want to describe how non-random evolutionary results occur as a consequence of unique individuals living in consistent and stressful environments.
5. Then I want to talk about how different kinds of environments result in different kinds of non-random survival, non-random reproductive success, evolution and adaptations.

11.2 Reproduction continues life and provides opportunities to introduce innovations

I want to present three concepts related to the idea of life as it relates to evolution. The concepts are: 1) the properties of life; 2) how reproduction assures the continuance of life; and 3) how reproduction provides opportunities to introduce innovations.

First, let's review the essential properties of an individual living thing? A living thing is a exploitative system that sustains itself at a complex thermodynamic state — a system which reacts to changing environmental circumstances. Living things assemble, operate and maintain themselves by using resources in their surrounding environment. Once assembled, as long as an individual is able to operate and maintain itself, it continues to *be*. Once it stops, the living thing no longer *is*. It's dead. Which brings me to the idea of the continuance of life.

If individuals could live forever, then the continuance of life would be assured. But living things do not live forever. Living individuals have short lifetimes. Let's consider the consequences of the idea of limited life spans. If all things eventually die, then it would seem that the planet eventually would become lifeless. But life is still present after billions of years. One way that life can persist when represented by short-lived individuals is the process of reproduction. Some living individuals successfully make copies of themselves before they die. Then, after they are dead, their offspring also will make copies of *themselves*, and so on.

Each round of reproduction provides opportunities to introduce innovations.

Reproduction with inheritance gives life the potential to lead to complex life forms by providing a mechanism in which information can be copied and modified. Let's think about the idea of information for a second. The very orderly and non-random pattern of atoms in a molecule is a form of information. The barcode on the back cover of this book is a form of information. Living individuals are produced by and hosts to the information they inherited from their parents. In this scenario, although the individuals are mortal, the information that made them in the first place is

Panel II.1 The basics on non-random survival and non-random reproductive success

Circumstances	Comments	Random or Non-random Circumstance
1. Genetic information. Genes code for the traits that make up individual living things.	This is a basic biological property of life.	Not applicable
2. Genetic Inheritance. Copies of a parent's genes are passed to its offspring.	This is a basic biological property of life. So, although all individuals eventually die, their traits can live on and on -- <i>if</i> they reproduce.	Not applicable
3. Genetic Uniqueness. All individuals of a generation are genetically unique.	This is a basic biological property of life, for sexually reproducing species. Because of random assortment of genes during gamete formation, each new individual will have a unique suite of traits.	Random
4. Discriminating environment. Only a small fraction of the total number of individuals from each generation will actually survive long enough to reach the threshold of sexual maturity.	<p>This circumstance is most applicable in preparation for <i>non-random survival</i>. This is because the natural environment is limited or otherwise stressful and cannot support all new individuals. The reproductive process cares not about stressful, limited environments and the huge mortality that follows reproductive output. Therefore, abundant reproduction inevitably and automatically creates a resource shortage crisis for individuals in the environment.</p> <p>This circumstance does not apply to <i>artificial, non-random reproductive success</i>. This is because survival to reproductive maturity often is guaranteed by human intervention such as agricultural practices that try to get all individuals to maturity.</p> <p>This circumstance also does not apply to <i>artificial, non-random reproductive success</i> because <i>artificial, non-random reproductive success</i> usually kicks in only after individuals have reached sexual maturity.</p>	Non-random
5. Non-random survival and non-random reproductive success. Some traits will enable some Individuals who survive and reproduce will do so because they possess certain traits that help them to do so better than other individuals who do not possess such traits.	<p>In <i>non-random survival</i> individuals resolve the resource shortage crisis as they bring their unique, inherited suite of traits to bear as best they can. By virtue of their unique mix of traits, some individuals will be able to cope with resource shortages and other environmental stresses better than will others.</p> <p>In <i>artificial, non-random reproductive success</i>, humans choose which individuals will breed and which ones will not. Individuals who possess traits that human breeders want stand a greater chance of being allowed to reproduce.</p> <p>In <i>natural, non-random reproductive success</i>, traits that aid in survival may be irrelevant. Non-random reproductive success results when mating is non-random. It takes two general forms: 1) male competition; and 2) female choice. Males who have traits that help them fight off other males, or attract females will have a better chance to reproduce.</p> <p>These circumstances mean that not everybody wins and there is a reason that the winners win and the losers lose.</p>	Non-random
6. Therefore, certain traits that increase chances for survival and reproduction will tend to: 1) become more abundant in future generations; and 2) become more refined to fit the environment after many generations of non-random survival and non-random reproductive success.	<p>The outcome of these circumstances is that the traits and the genes that code for them will tend to become more consistent for their particular selective environment. Traits and genes not suitable for the particular selective environment will tend to be reduced or eliminated.</p> <p>As a result, evolution by non-random survival and non-random reproductive success non-randomly shape the species along a path that leads to features</p>	Non-random

immortal — but not entirely immune from change. Each time the information gets copied, this is an opportunity to introduce change into the information of life.

To summarize, life is a form of orderly existence in which matter actively assembles, operates and maintains itself in a state of elevated complexity (self-sustaining, exploitative, reactive complex systems). Reproduction is not a necessary component to define the living state alone, but it is important in the continuance of life (because life is short). Also, each instance of reproduction represents an opportunity to introduce innovative modifications to the information that defines the type of living thing.

11.3 Living things operate in two main modes, survival, and reproduction

For the purposes of this chapter, we can think of living individuals as operating in two main modes: 1) survival mode; and 2) reproductive mode. Survival is the inherent and constant mode of the individual. This is the primary mission of the individual – to maintain the living state. Generally, individuals are always in survival mode, even when reproductive mode kicks in. During reproductive mode, individuals still dealing with the challenges of mere survival must endure the additional hardships that accompany reproduction.

Let's think about the idea of the development of living things in relation to their environment. Once instantiated ('born?') an individual living thing possesses the genetic information necessary for the participation in reproduction activities. BUT, the new individual does not instantly possess the anatomical, physiological and behavioral features it needs to actually participate in reproductive activities. And it won't until it becomes sexually mature. This takes time. As the individual develops toward a state of sexual maturity, it tries to stay alive – despite the stresses imposed upon it from the surrounding environment.

To the extent that any living individual is able to cope with the stresses in its environment (survive), it will successfully copy itself, yielding offspring (reproduction). But reproductive success is not automatic. Often, because of insurmountable environmental stresses, some living individuals will be unable to survive to sexual maturity. Therefore, the environment has a discriminating influence on any living individual. In other words, survival to sexual maturity and reproductive success are constrained by the environment.

More about survival mode. In any non-random environment, an individual will bring its particular mix of traits to bear on that environment — with the aim of continued existence. Just surviving to adulthood is hard enough. Which brings us to the topic of reproduction mode. The entire ritual of reproduction is clearly not in the best interest of the individual — except to the extent that the individual benefited from the fact that its parents suffered the hardships of reproduction. I use the word, 'hardship', because the process of reproduction overlays costly stresses onto the difficulties individuals normally face in life. The reproductive mode operates simultaneously with the survival mode. But the reproductive mode makes survival harder because of the additional resources required.

For example, flowering plants dedicate enormous resources to the production of flowers and nectar as part of the sperm distribution phase of their reproductive process. Then, they plow huge quantities of resources into the manufacture of nutrient rich seeds surrounded by thick layers of fruit. This is very expensive. Female mammals grow embryos internally for a time, then spend months or years afterwards providing for their young. Reproduction is by no means a goal of the individual. I want to emphasize the point that individuals would be far better off in their environments if they never had the urge to reproduce. So, if reproduction does the individual no good (except in creating the individual in the first place), then why is it present in the lives of individuals?

It turns out that, although it is hard on adult individuals, reproduction is the only way the species can continue to field live representatives in the environment, since the life of the individual is short. Reproduction is the only way to replace the individuals who die. And all individuals eventually die for one reason or another. Considering this reality, all species have some kind of reproductive process programmed into the life cycle of their individuals. Even though reproduction is hard on the individuals, it is the unavoidable price of existence. A costly overhead expense that replaces dead members of a species with fresh new ones.

We could look at it this way. A species remains extant because individuals of that species reproduce. To the extent that individuals successfully reproduce, the species will thrive. If all individuals of a species fail to reproduce, then the species will go extinct – no more living representatives of the type. We can think that individuals are the beneficiaries of reproduction, having been produced by it. But having reached sexual maturity, genetic programming causes the individual is to pay back its debt to the species. They pay this debt by engaging in costly and inconvenient reproduction activities. For nearly all species, individuals cannot

override or disable the genetic programming that triggers the reproductive urge. And so, reproduction is not the goal of the individual because it serves no benefit to the individual. But it is a biological requirement imposed upon the individual to the benefit of the species as a whole.

In his book, *The Selfish Gene*, Richard Dawkins considered reproduction in a similar way. Individuals are the temporary repositories of physical bits of information called genes. The genes hold the information that is used to direct the development, operation, maintenance and reproduction of a particular kind of living thing. The genes attain a form of immortality by getting themselves copied into one generation after the next. This is done by the process of reproduction. But in many complex species, the ability to reproduce only is possible after long delays while the individual develops to sexual maturity. Therefore, genes program the development of robust 'survival machines' that help the individual cope with its environment while it develops to sexual maturity. The genes that produce successful survival machines get copied into the future.

Dawkins's view sees individuals as sorts of remarkable biological robots constructed and directed by their internal genetic cargo enabling them to overcome two important challenges: 1) survival in the environment while the individual develops toward sexual maturity; and 2) reproduction, triggered by genes after having reached sexual maturity. Keeping in mind that reproduction is the ultimate test of a species, a species exists because individuals are able to complete these two challenges. So the persistence of living representatives of a species is more than just the survival of individuals. To use a sexist medieval metaphor, slaying the dragon is the first challenge, but what if the princess doesn't like you?

However we think about the life of individuals and species, it is clear that survival and reproduction are important challenges for living things on Earth. Non-randomness can act separately during each of these challenging modes. Non-random survival generally acts on the survival mode as individuals try to cope with their surrounding environment during their entire lives. And in many species, non-random reproductive success happens amongst sexually mature adults during the reproduction mode of their lives.

Non-random survival and non-random reproductive success both are ecological outcomes that happen in nature, but they can lead to very different results. Non-random survival may lead to natural adaptations that help individuals cope with their surrounding physical and biological environment. Non-random

reproductive success may actually lead to features that make survival more difficult, but which may increase reproductive opportunity. These are sexual adaptations. More about these later.

11.4 Consistent and stressful environments establish the terms of a living existence

Let us explore the idea of environment as it relates to non-random evolution. Living things are constrained by their environment because they need certain materials and certain physical conditions from their environment. We can define the environment as any material situation in which any living thing exists. An environment can be composed of physical and biological components. A *consistent environment* is an ecological setting that remains more or less the same as time goes on. It can have dynamic qualities, such as with the changes in the seasons or the cycle of day and night.

The idea of a consistent environment is an important one especially in comparison to a purely random environment. A purely random environment would frequently change its physical and biological characteristics randomly such that it would be impossible to describe, or live in. Random environments are not good for life. If one day the environment were like Earth, the next like Uranus, the next like the Sun, the range of stresses would be so great that life would be quite impossible. Life is a very conservative process that depends upon consistent and stable environments. Therefore, consistent environments are necessary for life. But they also impose restrictions on life.

Here is where the idea of stress comes in. Consistent environments present a set of limited, non-random circumstances that living individuals must experience. Living things have no choice, that's where they live. Let's settle the big question about who is in charge here. It is largely the environment, and not the living individual that sets forth the terms of survival. Ironically, living things themselves and unintentionally create a host of environmental stresses as they seek to satisfy their own internal biosynthetic needs (as we saw in chapter 4). These stresses are exacerbated because reproductive output can eventually exceed environmental capacity.

In any case, environments represent a limited set of physical and biological characteristics. They cannot be all things to all individuals and they cannot support infinite growth. At some point the responsibility for survival falls upon the individual. If an individual living thing is to successfully exist and reproduce, it is obliged to do so on the terms of its environment. The environment quite automatically enforces those terms.

In this way, environments discriminate against most new individuals. But some new individuals are able to survive to sexual maturity and successfully contribute their genetic information to the next generation.

A word about environmental stress. Natural environments do not actively seek to create stress for individuals. Natural environments simply present a limited set of physical and biological circumstances to the individual. Then, the individual either is able to cope with these circumstances or isn't able to cope. Here is an example of what I mean. Imagine that your doctor puts you on a strict diet in which you can eat only enchiladas. Then, you wander into a Chinese restaurant for lunch. There are no enchiladas on the menu, so you cannot eat. The restaurant is not actively trying to create stress for you. It is just that you have entered an environment that presents to you a set of limited circumstances that are incompatible with your pre-determined needs.

So we have seen that environments must have two important qualities for them to contribute to non-random evolution: 1) they must be consistent and non-random in their conduct; and 2) they must be stressful by presenting a limited set of circumstances that living things are obliged to experience.

11.5 Non-random survival, and non-random reproductive success happen as a consequence of unique individuals living in consistent and stressful environments

(Note: I use the term, 'non-random survival' instead of the more traditional, 'natural selection.' In addition, I use the term 'non-random reproductive success' instead of the more traditional terms, 'artificial selection' and 'sexual selection.' Non-random survival is the outcome of individuals surviving to adulthood in natural environments. Non-random reproductive success happens in artificial environments like the breeding of domestic animals, and under some natural sexual environmental conditions.)

Genetically unique individuals experience consistent and stressful environments in unique ways. Some individuals will successfully cope with the environment and live to become sexually mature. Many individuals will perish before achieving sexual maturity. If this differential death happens in an environment that is otherwise stable, are the survivors just lucky? Or could it be that they have survived to adulthood by virtue of their particular mix of inherited traits? Evolution theory predicts the phenomenon of evolution by non-random survival (my alternative expression for the traditional, 'natural selection') in which some individuals, by virtue of their particular mix of inherited traits, survive to adulthood because they were better able to tolerate the stresses

imposed upon them by the environment. And other individuals die before reaching adulthood because they were less able to negotiate the same stressful environment. Let's see how it comes about.

11.6 Evolution by non-random survival or non-random reproductive success can result in two main outcomes

Non-random survival and non-random reproductive success are important ecological outcomes that can produce non-random evolution. Evolution by non-random survival or non-random reproductive success can result in two main outcomes: 1) Change in the distribution of existing alleles in a population; and 2) the development and enhancement of adaptations. First, in the absence of innovations, evolution by non-random survival or non-random reproductive success will tend to increase the presence of alleles that code for useful traits, and decrease the presence of alleles that code for less useful traits. This is pure population genetics - just a redistribution of existing traits (alleles) within the population. The result is a shift in the genetic profile of the population. Such a shift will change the future characteristics of the typical individual.

If factions of an ancestral population become physically separated from each other (genetic isolation), then, given enough time, evolution by non-random survival or non-random reproductive success could change the distribution and composition of alleles in each sub-population such that they become reproductively separate. That is, if members of each sub-population later interbreed and are unable to produce viable offspring, it is because they have changed so much genetically that they have become two distinct species. An important outcome, but the development of new species doesn't necessarily have to involve the development of special adaptations.

In order to lead to adaptations, useful traits must be enhanced by the repeated introduction of new kinds of innovations. Occasionally an innovation enhances the effectiveness of a trait. When such innovations appear (all things being equal — theoretically), evolution by non-random survival or non-random reproductive success (depending on the circumstances) will tend to preserve the innovation. Later, new innovations will contribute additional enhancements. Repeated rounds of this type of evolution by non-random survival or non-random reproductive success can lead to refined natural or sexual adaptations.

Panel II.2 A brute force innovation engine

Let's compare a logic-based innovation engine to a brute force innovation engine. The creative potential of a logic-based innovation engine is constrained by logical concerns over losses and conservative patterns of past success. Our human mind produces creations based on a logic-based innovation system. It allows us to cut losses, and improve our chances for success. It is conservative in nature – which is a good thing for us because we want to stay alive, right? As logic-based innovation engines work to avoid large losses, they forego some creative opportunities because they are seen as too risky. Logic-based innovation systems assume environmental uniformitarianism in which it expects the future to be much like the past. So in short, a logic-based innovation engine is less risky, less wasteful, less creative and more dependent upon a predictable future overall than a brute force innovation system, and requires the presence and integration of a logic processing system.

A brute force innovation engine is different from a logic-based innovation engine. The creative potential of a brute force innovation engine is limited only by the physical constraints of the environment in which it operates. There are no logical or historical constraints imposed upon a brute force innovation engine. Brute force innovation engines are free to create any kind of innovation within its physical capacity (creating outside the box, as it were). And because there is no logical dependence upon or awareness of predictable past and future environments, brute force innovation engines operate independently of the past and future. This means that when the future cannot be predicted, the creative output of brute force innovation engines will not be affected. But given unpredictable futures, the creative output from logic-based innovation engines will be severely reduced. So in short, a brute force innovation engine is more risky, more wasteful, more creative and less dependent upon a predictable future overall than a logic-based innovation engine, and requires no logic processing system.

Life has been successful on Earth because it has been able to meet the environment's terms — but at quite a cost. Living things have done this not by planning and strategy, but by brute force and uniqueness. Let's continue with the idea of a brute force innovation engine. The reproductive output of a population of living things typically exceeds environmental capacity (NOTE: this is not always the case). Without any foresight or planning, life aggressively floods the environment with an over abundance of genetically unique individuals. This is what I mean by brute force. When brute force is used, a focused strategy is not necessary as long as enormous losses are acceptable.

The brute force approach forces a situation in which some individuals will survive to reproduce and most will not. Survival and non-survival will be a non-random outcome because all individuals are unique. It reasonably follows that some individuals will survive to adulthood as a result of more effective use of their inherited traits on their stressful environment. As a result, perhaps only a few siblings will be able to cope long enough in their environment to reach sexual maturity and reproduce. The overwhelming majority of others will die before reaching reproductive age. A wasteful, inefficient and indifferent situation — but in the long run, successful just the same.

Based on these circumstances, survival to reproductive age generally is a non-random outcome because the stressful environments tend to be non-random. The main point is that non-random survival is a consequence of an abundance of genetically unique individuals seeking to live in a consistent yet stressful environment. The importance of non-random survival is that, overall, it has the potential to produce non-random evolutionary results and can give evolution a consistent, non-random and directional quality.

II.7 Evolution by non-random survival can cause a directional redistribution of existing alleles

Let's consider an example of how non-random survival contributes to evolution by redistributing existing alleles in a non-random way. In this classic example, I will track how non-random survival has acted on many generations of the peppered moth, *Biston betularia*, living in the United Kingdom. The moth comes in two shades of gray, light and dark. Color is controlled by a single genetic locus. There are two alleles that influence coloration in the moth. The *C* allele codes for the dark form and is dominant over the *c* allele that codes for the light gray form.

In the 1950s, English physician and amateur butterfly and moth collector, H.B.D. Kettlewell, began to investigate the population genetics of the peppered moth. By studying old moth collections made by earlier biologists, Kettlewell noted that until the early 1800s, the light form of the moth was typical and the dark form of the moth was extremely rare. But since that time, the dark form became ever more present in moth collections. Kettlewell's own observations in the British countryside confirmed that the dark form of the moth was indeed the typical form of the moth during his day — especially in regions near industrial cities. It occurred to Kettlewell that the moth had undergone a rapid shift from a species of almost entirely light

forms to a species of almost entirely dark forms. Kettlewell's explanation for this apparent evolution was that it was brought about by non-random survival. But how?

Kettlewell had observed that the moth is preyed upon by birds such as spotted flycatchers, robins and thrushes that pluck the moths from the trunks and branches of trees. In wooded areas away from industrial population centers, a gray lichen grows on the birch and beech trees of the forest. Light gray moths alighting on such a tree are camouflaged. But in the last 200 years, severe air pollution from the burning of coal had killed the lichens and darkened the tree trunks with soot making them almost black. Kettlewell studied moth coloration in terms of bird predation. He observed that birds are more likely to eat poorly camouflaged moths. That is, near cities, dark moths had greater chances of surviving to sexual maturity than did light moths because birds more easily saw the light moths. Light coloration readily exposed the light moths against the blackened trees. Meanwhile, dark coloration gave the dark moths a measure of protection against the birds.

Given these observations, Kettlewell reasoned that non-random survival was the principle cause for the color shift in peppered moths. Before the widespread burning of coal, the dark form existed in small numbers in the species but its genetic influence was hindered by low survival rates. Then, as the environment changed from predominantly gray, lichen-covered trees to blackened trees, the fitness of the *C* allele (dark) increased as visually-hunting birds more easily spotted light moths (*cc*). Since dark moths (*CC* or *Cc*) tended to survive to sexual maturity more often, their contribution of alleles into each new generation steadily increased. After many generations of non-random survival in this environment, the *C* allele (dark) became more abundant in populations near industrial centers and the *c* allele (light) became less abundant.

More. Starting in the middle of the twentieth century, air pollution control devices have nearly eliminated the black soot emissions from coal-fired power plants in the United Kingdom. The previously blackened forests are becoming lighter again. And the dark form of the peppered moth is showing signs of decline, while the lighter form is becoming more widespread. Evolution by non-random survival can modify a species on the time scale of several decades.

Let's do a reality check this example. In 1980, laboratory studies by Creed, Lees, and Bulmer showed that for moths raised safely in the laboratory, the dark homozygote (*CC*) was better than the light homozygote (*cc*) at survival and reproduction. This result suggests that the dark allele (*C*) has inherent advantages to the

life of moths that are unrelated to its obvious camouflage effect. Also, it has been observed that the pattern of moth distribution relative to polluted areas in the United Kingdom is not neatly what you would expect. G. S. Mani demonstrated that migration of moths between polluted and non-polluted areas is partially to blame. Despite these qualifications, the effect of non-random survival on differentially camouflaged moths in different environments remains at the core of our understanding of the peppered moth.

Please note that in this case, the allele coding for dark coloration already existed in the population. Although the dark allele may not have been adaptive in pre-industrial Britain, it defaulted to adaptation status as the trees grew black. In this case, neither genetic innovation nor evolution by non-random survival created or enhanced this dark adaptation. It only redistributed it, making the adaptation more widespread in the population. The next section discusses how evolution by non-random survival can *enhance* a feature that already is adaptive.

11.8 Different kinds of environments result in different kinds of adaptations.

Evolution by non-random survival, and evolution by non-random reproductive success can happen in different ways depending on the type of non-random environment. Below, we will consider three main types of non-random environments: 1) artificial; 2) natural; and 3) sexual. All three non-random environments can generate adaptations. Typically, these adaptations are useful only in the context of the non-random environment that produced them. Wiener dogs may be successful in living rooms and dog shows, but probably less successful in the open savanna. In the wild, natural non-random environments can produce non-random survival leading to the production of natural adaptations. These are the kinds of features that help individuals survive to adulthood.

In many species, the sexually mature adults must bear the enormous hardships of reproduction. But survival to adulthood doesn't automatically confer reproductive rights. Some are denied this 'privilege' because of a thing called non-random reproductive success. I will briefly present how non-random survival, and non-random reproductive success can yield different kinds of adaptations in artificial, natural, and sexual environments.

11.9 Evolution by non-random survival can result in natural adaptations

In natural ecological settings, non-random survival can lead to natural adaptations after many generations. Non-random survival is an ecological outcome that acts when the individual primarily is in

'survival' mode, as opposed to 'reproductive' mode. Let's consider the evolution of natural adaptations by non-random survival. There are certain principles we need to keep in mind.

Adaptations must be considered in the context of their environment.

The useful features that evolve as a consequence of non-random survival do so because of the effects of the environment on the survivability of unique beings. But should that environment change, or should the survivors disperse to a new geographic location, their 'adaptation' may no longer be any good. As we saw above in the example of the Galapagos finches, consistent environments are subject to dynamical cycles. First drought, then flood. The drought environment selected finches with large beaks. The rainy environment selected finches with smaller beaks.

The swiftly spreading dark coloration in peppered moths is another example. What good was dark color for a moth before the coal-fired industrialization of Britain? Probably little good, if not downright harmful. If harmful, the dark coloration could hardly be called an adaptation. A deleterious mutation would be a better description. Still, this deleterious innovation had latent potential that became important as trees turned black under the rain of modern soot. Perhaps it saved the species from dangerously severe predation that might have occurred as a once-adaptive gray camouflage betrayed the moths on the dark trees. Life is so unpredictable and indifferent. Now as the trees of the United Kingdom return to their native color, grayness is again flourishing and dark moths are in decline.

Adaptations often are complicated.

Take the well studied case of the European land snail, *Cepaea nemoralis*. This snail lives throughout Europe and it occurs in a variety of colors and patterns. Background colors include yellow, brown or pink. The tip of the shell also may have distinctly colored bands. The snails appear in nature in any combination of coloration and banding — a polymorphic trait. For years, biologist naturally wondered if the complex coloration in this snail could be adaptive. But how do you study a trait that has so many different phenotypes? In 1954, biologists A. J. Cain and P. M. Sheppard presented evidence showing that non-random survival could explain this variation. First, they noted that birds like to eat the snails. They discovered that banded snail types were eaten more readily in habitats such as open fields where the environmental background coloration was fairly uniform and bland. But where environmental background coloration was more diverse, it was the opposite. In places like mixed hedgerows, the birds preferred the unbanded snails. So, the multitude of

coloration and patterns could be partially explained as a consequence of non-random survival at the beaks of visually hunting birds. But the story is more complicated than this.

In 1977, biologists, Jones, Leith, and Rawlings showed that predation is just one of eight different forces acting directly on shell color and banding polymorphisms in the European land snail. For example, shell color will influence heat uptake from the sun. Light-colored shells will slow heat gain, while dark shells will increase it. Researchers looked at the distribution of snails in Europe with respect to shell lightness or darkness. They found that the frequency of the darker version of the snail increases steadily as you move from hot southern Europe to chilly northern Europe. The same is true with habitats of higher elevation. Another twist has to do with the search patterns by predators hunting for a similar snail, *C. hortensis*. If banded *C. hortensis* snails are abundant, then the birds will tend to search for banded snails, regardless of the species. This is called frequency-dependent selection. But the hunt can spill over from one species to another. Because of the abundance of banded *C. hortensis*, banded *C. nemoralis* will be preferentially preyed upon even if they are better camouflaged or occur at lower frequencies than unbanded snails.

Continuing this discussion about the complexities of adaptations, let me comment on non-random survival in terms of the development of an individual toward adulthood. Even a constant environment acts on the individual in different ways at each stage of development. Although the environment may remain constant, the growing individual goes through many changes. As a result of this growing process, the individual experiences the environment in different ways at different stages of its life. Here is an obvious example. The adult African elephant is so large that no predator dares to attack a vigorous healthy one. Yet as a species, African elephants do suffer from a modest amount of predation. How could this be? Lions will prey on infant elephants if they can separate the baby elephants from the herd. Lions pose the same kind of threat to rhinos and hippos. Large size is a natural adaptation that guards against lion attack, but it only appears when the elephant reaches adulthood. In the meantime, the predatory environment is very stressful to young elephants.

Staying on this topic, vertebrate predators prefer to exploit the young. Ravens raid mockingbird nests for eggs or young hatchlings. The eaves of my roof are inhabited every spring by house finches tucked away in tiny hidey holes hoping to avoid the watchful gaze of ravens perched in the nearby eucalyptus tree. Ravens are so methodical. Numerous times I have watched as they systematically stroll along roof edge poking

inquisitive beaks into likely nesting spots. Although an adult finch may be able to escape raven predation, an egg or a hatchling is no match for an adult raven. And the beat goes on.

In the case of the Galapagos finches, let's reexamine the offspring from the drought survivors. Remember that the larger adult finches with larger, deeper beaks tended to do better during drought. This was thought to be because their larger beaks allowed them to crack larger and harder seeds. The smaller finches could not. And since larger seeds were more abundant than small seeds during episodes of drought, clearly the larger finches had a selective advantage over the smaller finches. The result of the drought was that most of the finch population died of starvation. The larger finches tended to survive. This is a classic case of non-random survival in action. The survivors' offspring inherited the large traits from their parents and were large too. But the traits that helped their parents survive actually became a hindrance for young finches.

Here is the reason why. Bigger juveniles require more food than do smaller juveniles. The problem is that the beaks of the larger juvenile finches are still too soft to help them crack the large seeds so beneficial to their adult parents. As a result, the larger juvenile finches had increased energy demands, but had to compete directly with smaller finches that had lower energy demands. This situation put the larger juvenile finches at a distinct disadvantage compared to their smaller counterparts — at least during this stage of their life.

Adaptations are compromises

All adaptations must be paid for, biologically. So, I will make the general statement that individuals will have the most refined adaptation they can afford. An individual must divvy up its resources to pay for all of its operations. But it has to strike a balance. For example, let's think about leaf size in relation to climate. First, leaves are useful adaptations in that they are the main sites of photosynthesis for the tree. The bigger the leaf, the more sun they can collect, and the more photosynthesis they can support. So, trees will have the biggest leaves they can afford. So why don't all trees have extremely large leaves?

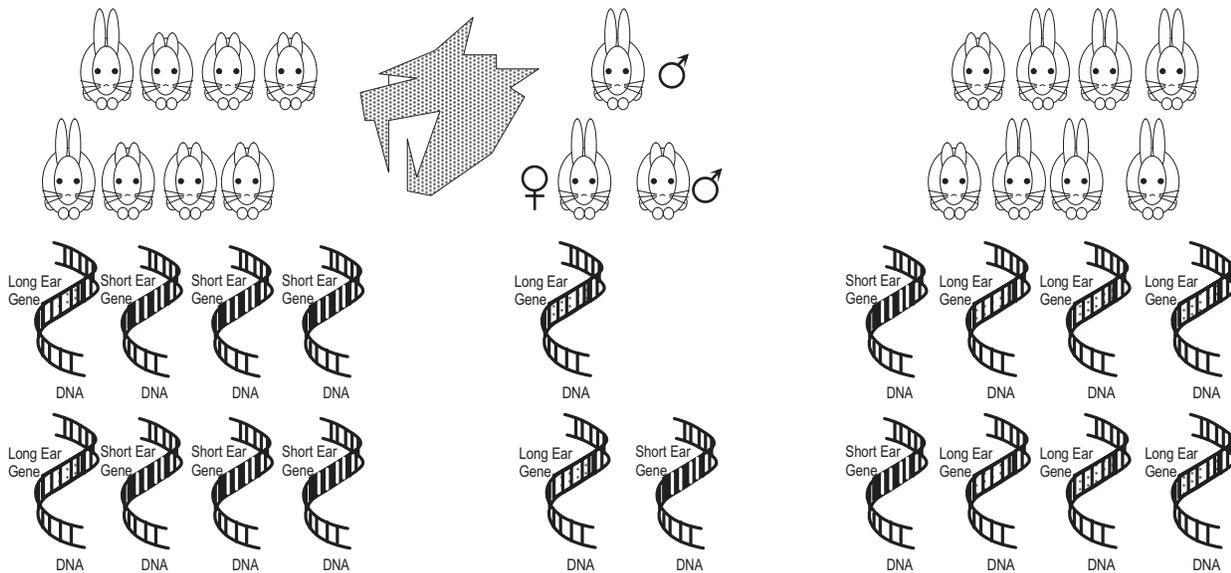
It turns out that leaves are expensive, especially in dry climates. For a plant, leaves are the main sites of water loss. The bigger the leaf, the more water it will lose. Plants living in arid climates like the desert or savanna strike a compromise. They balance their sugar production with water conservation. The result is smaller leaves. Here is an example. The tree, Palo Verde (*Cercidium floridum*), lives in washes throughout the Colorado Desert of southern California (see Schoenherr, p. 465). Now, trees are not that common

in any desert mainly because trees are large plants that have huge water requirements. And yet, there is Palo Verde. When it is in its leafy stage, you would hardly know it, the leaves are so small. Its delicate leaflets are only about an eighth of an inch wide and about half an inch long. Good for conserving water, but at the cost of reduced sun uptake. But even these tiny leaves may lose too much water. So, Palo Verde drops its leaves altogether and hunkers down, leafless, through the hot, dry desert summer. Still, Palo Verde has another ingenious adaptation that allows it to photosynthesize even when it has no leaves at all. Throughout the thin bark of the tree are chlorophyll-containing cells of such abundance that the whole tree looks green. It has a green trunk and green branches, which accounts for its name. Palo Verde is Spanish for 'green stick'. Stems and branches are much more possessive of water than are leaves. So by virtue of its green bark, Palo Verde is still able to perform some photosynthesis while doing its best to conserve water.

Another example of compromise has to do with the wild grass, *Agrostis tenuis* that lives in open and disturbed areas in the United Kingdom and Europe. A host of investigators, including S. Jain and A. D. Bradshaw, and T McNeily, wondered how the plant could survive in the copper-contaminated soils at copper mines. They noticed that the copper-tolerant plants were a distinct variety of the species. The researchers demonstrated that copper tolerance was an adaptation that was common to copper mine plants but not to plants living in otherwise normal conditions. How do tolerant and nontolerant plants compare with each other? Nontolerant plants died within seven weeks of being planted in copper-contaminated soil. Tolerant plants thrived in clean soil, but were not as vigorous as the nontolerant plants in the same soil. Why were they different? Perhaps tolerance comes at some biological cost. The tolerant varieties have higher overhead expenses in maintaining their adaptation. The nontolerant varieties don't have this expense and therefore have more resources available for growth than do the tolerant plants. Tolerance is an adaptation that enables some individuals to find refuge from the competitive world beyond. Tolerant individuals can inhabit stressful places where other cannot follow. But the bridges that lead to these new environments are burned behind them.

11.10 Evolution by non-random survival can produce adaptations in two ways

Adaptations can arise in two general ways: 1) either by the repeated introduction of innovations that enhance the usefulness of a trait; or 2) for traits that are controlled by multiple loci, adaptations can arise following the non-random reorganization of alleles at all loci such that they influence the trait in similar ways.



Generation 1

This example shows a starting generation with eight individuals. Two of the individuals possess the gene for long ears. The other six possess the gene for short ears.

Individuals from Generation 1 Who Lived Long Enough to Reproduce

A greater proportion of long-eared hares survived predation pressures (non-random survival). So, more long-eared genes will be passed on to the next generation.

Generation 2

The offspring of the surviving individuals will inherit their parents' genes. Since a greater proportion of the survivors have long-eared genes, Generation 2 will have a greater proportion of long-eared hares than Generation 1 did.

The long-eared hares have experienced non-random survival. Since the genetic makeup of the snowshoe hare population in this NEXT generation is different from the genetic makeup of the population from the previous generation, this is an evolutionary result. And since this result appears to be a consequence of non-random predation, we can label this result as 'evolution by non-random survival'.

Figure 11.1. A simple model showing the results of non-random survival.

Let's consider the first case. Adaptations can arise following repeated rounds of non-random survival on ever newer and slightly different innovations. For the purposes of this discussion, let's consider a trait controlled by a single genetic locus. Also, let's assume an innovation that enhances this particular trait. Remember that the chances are very slim that any innovation will actually be an improvement. As we saw in chapter ??, innovations can come in several different ways. For example, mutations can produce new alleles. New alleles also can be introduced into the population by immigrants from distant populations. Or, new alleles can be transferred from completely different species. Adjustments in symbiotic relationships between species also can represent an innovation that is available for non-random survival to act on. But we will ignore symbiotic relationships for now. Instead, we will confine our discussion to alleles.

Let us consider a case in which a new allele (A) results in a phenotypic improvement and is preserved by non-random survival. But what are the consequences of non-random survival on a single beneficial allele? If non-random survival simply

increases the presence of the beneficial new A allele and reduces the presence of the less useful old a allele, this is evolution. But if the trait produced by the A allele is only slightly different from the trait of the a allele, then the species won't change much. Still, this may not be the final improvement. Newer alleles may be introduced later that offer still more improvements. In each instance, non-random survival preserves and distributes these genetic enhancements throughout later generations of the population. As a result, adaptations evolve following the accumulation of dozens of incremental genetic improvements that appear occasionally over many thousands of generations. Therefore, non-random survival repeatedly acts on new innovations that enhance the usefulness of traits — adaptations are refined and distributed.

Let's consider this idea in the context of the eye. The eyes of living things have always been a favorite point of controversy amongst creationists and evolutionists. In 1802, theologian, William Paley, argued that the

human eye must have a designer, like a watch has a designer, like a telescope has a designer. How does the theory of evolution by non-random survival explain such a complicated adaptation as an eye?

In his books, *The Blind Watchmaker* and *Climbing Mount Improbable*, Oxford zoologist, Richard Dawkins, presents compelling arguments that the eye and all other adaptations are chiefly the result of the accumulation of tiny improvements over many generations. Since this accumulation process has so far eluded scientists seeking first-hand evidence, investigators have turned to computer models for help. In 1994, D. E. Nilsson and S. Pelger constructed a computer model that simulated evolution by non-random survival. They wondered if many generations and accumulations of tiny improvements could produce an eye. They started their simulation with a single, flat layer of light-sensitive cells against a black background and covered it with a thin layer of transparent cells. Light-sensitive cells are themselves a mutation that even if they are only slightly functional, might convey an advantage. Nilsson and Pelger established this simple 'organ' as their starting point and programmed the selection simulation to do what it would from such meager beginnings. Maybe an eye would result, maybe something completely different, maybe nothing at all.

The program was designed to consider the benefit to the individual should small changes happen to any of the components in this system. They allowed random changes in size, thickness, transparency and refractive index. The team provided conservative assumptions for the program to work with. They assumed that an organ of greater sensitivity and focusing power was more adaptive and would assist its possessor in survival. However, they assumed that any improvement would only confer a 1 percent advantage. They assumed that any surviving mutation had only a 50 percent chance at making it to the next generation. And they assumed that only one part of the eye could change in each generation.

The result of the Nilsson and Pelger simulation was astonishing. From such simple beginnings, the accumulation of tiny improvements, each improvement selected for, resulted in an eye comparable to that of a fish. The simulated eye evolved in just 364,000 generations. If this kind of evolution had happened in nature, it would have taken less than half a million years — a mere instant in the history of life on Earth.

Now let's think about the second case in which evolution by non-random survival can produce adaptations. The situation is slightly different for traits that are controlled by multiple genes. In this case, I will refer to the example of the medium ground finch, *Geospiza fortis*, that lives on one of the

Galapagos islands, Daphne Major. This finch, along with others, was studied by Princeton biologists, Peter and Rosemary Grant. Their work was chronicled by Jonathan Weiner in his book, *The Beak of the Finch*. The Grants and their team of scientists trapped and tagged thousands of birds from 1973 to 1993. Their findings revealed a surprisingly rapid pace of evolution by non-random survival.

For two decades, the team accumulated data on such bird features as beak length, beak depth, wing length, and other body dimensions. Features such as these occur in a continuous range of magnitude, rather than in discrete blocks. For example, the depth of the finch's beak can range between 9-10 millimeters, with hundreds of continuous intermediates. Geneticists argue that continuous traits like these are controlled not by a single genetic locus (as was the case in our peppered moth study) but by many loci. In turn, each locus may have several alleles that influence beak depth in different ways. Some alleles will act to increase beak depth. Some alleles will act to decrease beak depth. So, the actual beak depth is a sort of average of the multiple and competing alleles all acting simultaneously. A random assemblage of these alleles would result in a beak depth in between the 9-10 millimeter range. Evolution by non-random survival can shift the assemblage of alleles to a group of alleles that influence slightly larger beaks or to a group of alleles that influence slightly smaller beaks.

Starting in 1976 through 1977, Daphne Major was plagued with over a year of drought. This had an immediate and negative impact on the food supply and the finches. At the start of the drought, there were 1200 *G. fortis* finches. At the end of the drought, there were only 180 left. During the drought, the total amount of food from seeds went down, and the average seed size and hardness went up. In other words, there were far fewer seeds, and those seeds that were available tended to be bigger but much harder to crack. The drought had created a slightly new set of environmental stresses that only a small fraction of the finches were able to cope with.

The finches that survived the drought tended to be bigger and had deeper beaks than the finches killed by the drought. The survivors were about 5 percent larger. The average beak depth before the drought was 9.42 mm. After the drought, the average depth was 9.96 mm. Based on these and other measurements, the Grant team concluded that non-random survival had favored larger finches with larger and deeper beaks. But why?

Their explanation had to do with the relationship of beak size and seed characteristics. Finches with larger beaks are better at cracking larger and harder seeds. The drought shifted the available food supply from an

abundance of small seeds to smaller quantities of larger, harder seeds. As a result, finches with just slightly smaller than average beaks had a much tougher time trying to get something to eat simply because they were unable to crack the larger seeds. In the end, most small-beak finches were unsuccessful. The instantaneous result from this non-random survival event was a smaller finch population but one with a greater presence of alleles coding for larger beaks. In this case, the possession of a larger than average beak was a fortuitous adaptation. But can evolution by non-random survival enhance this adaptation?

In the following year after the end of the drought, the Grant team noted that the survivors mated and produced a large crop of offspring. Evolution theory argues that the offspring should inherit traits from their parents. So, since the parental population had somewhat larger than average beaks, we should expect the offspring to have beaks of similar size. It turns out that the offspring actually were larger on average than their parents. Beak depth in the offspring population was deeper than that of their parents. This additional increase was due to non-random sexual success (discussed below) as picky females chose the largest of the male survivors. As a result, in just a single generation, evolution by non-random survival had increased the average beak depth by 5 percent.

In this case, greater beak depth is an adaptation during and immediately after drought years. Evolution by non-random survival enhanced this polygenic trait making what was already a useful adaptation more useful and more widespread. But what is useful today may not be useful tomorrow.

Later, Lisle Gibbs, a graduate student and part of the Grant team, followed the finches after a deluge of rain started falling on the island of Daphne Major in December 1982. Brought on by the most intense El Niño ever recorded, the rain lasted for several months. And the vegetation responded. By June, the total mass of seeds on the island was more than 10 times than before. The seed size distribution shifted dramatically, producing a wealth of small seeds and few large seeds. Presented with this horn of plenty, mating amongst the finches was frenzied. The finch population increased by four times. But Lisle noted something else. The big birds with deep beaks were dying at a greater rate than the small birds with small beaks. The selective environment had shifted and what was once an adaptation now was a handicap, and vice versa.

The rainfall had reduced the large seed crop by 90 %. Large-beaked finches accustomed to feeding on large seeds eventually ran out of them. In the rainy aftermath, smaller beaks were adaptive, larger beaks

were not. Which leads us to remember one of the most important principles in the study of adaptations. The usefulness of an adaptation can only be determined in the context of its environment.

In this case, beak depth (deep or shallow, depending upon the environment) is an adaptation that evolved not because of innovation, but through a non-random redistribution of many existing alleles. Keep in mind that although all of the alleles previously did exist in the population, their distribution within individual finches may have been random such that average beak depth was neither deep nor shallow. What evolution by non-random survival did was reorganize these alleles such that individual finches inherited non-random assortments of alleles that coded mostly for large, deep beaks (after dry years) or small, shallow beaks (following rainy years). It is this non-random presence of similar acting multiple alleles for polygenic traits which constitutes an adaptation.

II.11 Evolution by non-random reproductive success in artificial environments can result in artificial adaptations

An artificial environment is an environment set up by humans. And it is the humans who consciously select which individuals will reproduce and which individuals will not reproduce. Artificial, non-random reproductive success is controlled by animal and plant breeders in a variety of ways.

You are familiar with the many breeds of domestic dogs and cats. The variety in the domestic dog and cat world is the result of artificial non-random reproductive success. For example, let's consider the adorable dachshund, otherwise known as the wiener dog. How did this dog come to be? The word 'dachshund' means 'badger dog' in German. The dachshund was bred as a special hunting dog that would be able to pursue prey into burrows. Before setting about to breed the dachshund, dog breeders saw that burrowing animals had elongated trunks and short legs. The ground squirrel, mole and badger are examples. Dog breeders observed that these characteristics are adaptations to underground life. The breeders reasoned that a hunting dog with similar characteristics would be more effective against burrowing prey. So dog breeders set out with a goal in mind — to breed a dog with an elongated trunk and short legs for the purpose of helping in the hunt for burrowing animals.

About 300 years ago, German dog breeders started by cross-breeding a mix of European breeds. Each generation they selected the individuals with the most elongated bodies but with the shortest legs. After many generations of selective breeding, the dachshund

had evolved. For the dachshund, we can consider its elongated body and short legs as adaptations. But these are *artificial* adaptations brought about by artificial non-random reproductive success.

Plant breeders also use selective breeding to accentuate desirable characteristics. For example, roses have been fancied by gardeners for over 4000 years. They are prized for their handsome colors and delicate fragrances. Rose breeders control artificial non-random reproductive success to create new varieties from existing varieties of roses. They do this by the simple and widespread practice of cross-pollination. Garden clubs around the world hold annual competitions in which amateur and professional gardener alike seek to produce the most fragrant and colorful rose. All made possible by evolution by artificial non-random reproductive success.

On a more economically important note, artificial non-random reproductive success is one of the pillars of modern agriculture. For example, most of the western world's wheat crop is produced by just a few varieties of wheat. Those few varieties are the result of many generations of artificial non-random reproductive success. Crop breeders carefully selected characteristics such as large grain size, fast growth speed, and high pest resistance. Today's modern food crops are exquisite examples of artificial non-random reproductive success acting on genetic variety in a way that amplifies desired traits.

Agricultural animals also have been shaped by artificial non-random reproductive success. Dairy cows were bred for maximum milk production. Beef cattle, pigs, chickens and turkeys were artificially selected for meat production.

But nowhere is artificial non-random reproductive success more exciting than in the sport of horse racing. In addition to the purses gathered by winning races, there is great money to be made in stud fees. A horse with a history of winning races is highly sought after by horse breeders. They will pay hundreds of thousands of dollars for stud services from winning horses whose offspring are likely to inherit the speed of their father.

As a result of evolution by artificial non-random reproductive success, we have more distinct varieties of dogs and cats, more colorful and fragrant roses, more productive agricultural plants and animals, and faster horses. In this case, non-random reproductive success is the result of conscious decisions made by humans. Humans have a desired outcome in mind and

they select for breeding only those individuals that lean toward that outcome. After many generations, small improvements in the desired traits eventually accumulate to produce big changes.

11.12 Evolution by non-random reproductive success in natural environments can result in sexual adaptations

I will attempt to keep my comments on non-random reproductive success as brief as possible, although it is more vexing than is non-random survival. Let me say that the issue of non-random reproductive success remains a topic of lively debate amongst evolutionary biologists. The details of those debates are far beyond the scope of this book. Therefore, the purpose of this section is to present a general description of non-random reproductive success and to contrast it with non-random survival.

Non-random reproductive success occurs when the individual is in reproductive mode. Remember that reproductive mode is a simultaneous add-on to survival mode making survival much more difficult. Non-random reproductive success is a consequence of non-random reproductive environments. That is, not all individuals who survive to sexual maturity are able to mate. Instead, only a fraction of sexually mature adults actually participate in reproduction. Usually, the males are the ones who are denied, while most sexually mature females participate fully. So, non-random reproductive success mostly is about non-random and restricted access of males to females. In most species where non-random reproductive success occurs, nearly all sexually mature females get their genes into the next generation, but only a fraction of the males do.

As far as we know, non-random reproductive success happens in animals only — and most obviously in vertebrates, particularly birds and mammals. Non-random reproductive success is not generally observable in plants, fungi, algae, protozoans, bacteria or archaea.

The idea of non-random reproductive success arose in the 1800s amongst naturalists, including Charles Darwin and A. R. Wallace. They wondered why certain animals had robust anatomical features and behaviors that seemed completely unrelated to survival. Extreme features like peacock tails and ram horns not only do not appear to be natural adaptations, they appear to make survival much more burdensome. But naturalists observed that such deleterious features seemed to be related to some part of the reproductive cycle of the species. For example, the peacock's tail is an

important courtship ornament that helps in attracting a female. The ram's bulky horns help it physically subdue other males seeking exclusive reproductive rights with all the females of a group.

So, we can consider two general types of non-random reproductive success: 1) female choice; and 2) male competition.

The idea of non-random reproductive success by female choice concerns certain features in the male that are neither adaptive nor useful in fighting other males for breeding rights. Panel ? gives several examples of features that are best explained by non-random reproductive success. I will use the example of the peacock's tail (I beg for forgiveness from biology professors for selecting the peacock, but it really is a good example).

The sexually mature peacock (the male sex of peafowl; the female is the peahen) is adorned with a massive and colorful tail. The male spreads out his tail feathers in an impressive display when in the presence of a sexually mature peahen. Naturalists generally do not think the peacock's huge tail feathers have any real survival value. In fact, because they are so costly to produce and maintain, they appear to hurt the individual peacock's chances for survival. So, how do we explain them?

Darwin wondered about the peacock too. In his *Descent of Man*, Darwin devoted much of the book to the idea of non-random reproductive success (what he called, sexual selection). In it he explored examples of non-random reproductive success in dozens of insects, reptiles, birds and mammals. It occurred to him that the peacock's rich display of feathers helped the male attract a mate (many knights may slay dragons to survive, but given a choice, the princess will choose the knight with the shiniest armor). Darwin theorized that in order for this system to work, the female must exert some freedom of choice in mate selection. And the female chooses based upon her preference for long tail feathers.

Evolutionary geneticist, R. A. Fisher speculated on how this peculiar system came about. Fisher's explanation was that two things were going on separately in the males and females. First, males with longer tails had greater chances for survival. Hence, the genetic hardware for tail elongation became established. Next females developed a preference for males with longer tails (the explanations for how this might have come about are beyond the scope of this book. For a provocative theory, refer to Zahavi (1975). Also, see Dawkins, *The Selfish Gene*, new edition pages

308-313 for a discussion of Zahavi's handicap theory). Now we have the makings for a positive feedback loop that will cause the male tails to get longer and longer with each generation.

The process can be speeded up if the alleles for longer tails become linked with the alleles for long tail preference. In this scenario, the offspring of a long-tailed male and a female who prefers long-tailed males each will possess the alleles that produce long tails as well as the alleles that produce preference for long tails. Let me try to simplify this. The long tail trait is expressed only in males, and the long tail preference trait is expressed only in females. But both traits can be carried by either male or female. Imagine a peacock with a long tail. Obviously, he has alleles that code for long tails. But what we can't see is that he is also a carrier of alleles that code for female preference of long-tailed males. Next, imagine a female that prefers long-tailed males. Obviously, she has alleles that code for female preference of long-tailed males. But what we can't see is that she is also a carrier of alleles that produce long tails in males. That is both males and females carry the same alleles. Now, when these two mate, all of the male offspring will produce long tails, and all of the female offspring will prefer males with long tails.

Another way to think about it is that when the female chooses a long-tailed male, she is also choosing long-tailed preference. This ensures more of the same. And when the male grows a long tail, this assures more long-tailed males in the future, because any female that chooses him also carries alleles for producing long tails.

This kind of thinking attempts to explain how features related to non-random reproductive success can become so extreme. Eventually, there are limits. Tails cannot keep getting longer forever. At some point the costs for producing ever longer tails will get so high that they will reduce the ability of their owners to survive to sexual maturity. At some point premature death caused by excessive tail length will outweigh any reproductive advantage such a long tail would give (What good is shining armor that's too heavy to stand up in?).

Let's move on to the topic of non-random reproductive success by male competition. Naturalists have observed in many species of animals that males compete with one another for mating rights. This competition often is quite direct and shows up as males fight with each other. Such competitions are more prevalent in mammals than are displays and female choice.

In many cases where male competition prevails, the males have developed special weapons for dealing with each other. For example, the stag deer has huge antlers, the bull elephant has giant tusks. The big horn sheep of the California desert uses its formidable horns as weapons against male opponents. Although these features are useful weapons against other males, would they not also be useful in helping the males to survive in its environment otherwise? The answer is probably yes, but that does not explain the primary cause of their origin. In other words, are these weapons primarily the result of non-random reproductive success or non-random survival? The reason there is some doubt is that such weapons are not always present in such robust form in the females.

For example, female African elephants and wild boars have tusks that are much smaller than the tusks of males. Compared to females, horns are larger in the male sheep, goat, musk oxen, elk and moose. Male chameleons have prominent horns while horns are absent in females. Canine teeth are formidable weapons too. Female baboons, camels, dogs and mountain gorillas generally have smaller canine teeth than do their male counterparts.

These sexual differences are present in species where males fight with each other for mating privileges. The victor of the fight gets to mate. The loser of the fight does not. In such cases, the males with the hardest weapons tend to win more fights and therefore mate more often. As a result of this form of non-random reproductive success, alleles that code for more powerful weapons get passed on more frequently. alleles that code for less powerful weapons get passed on less frequently.

This concludes the section on non-random reproductive success. Keep in mind, there is much more to this theory than what I have presented here. It is potentially more complex and subtle than the activities of non-random survival.

11.13 Concluding remarks about evolution

All of the random and non-random factors I have discussed involving evolution are free to fluctuate independently of one another. Random activities like gene flow and genetic drift can be happening simultaneously with the different kinds of non-random survival and non-random reproductive success — all the while, the biological and physical environments fluctuate like a soap bubble in the wind. This makes possible an infinite variety of circumstances and outcomes. The result is that evolution can be a very complicated affair that has enormous potential.

My goal for these chapters on evolution was to present to you the aspects of the science that are relevant to our understanding planetary biology. Evolution, in its many forms, is a natural consequence of the circumstances of living things on this planet. Many of those circumstances are products of life itself. In any case, life is an extremely versatile, exploitive and complex happening. The science of evolution seeks to understand the diversity and dynamics of life on its own terms. The more we learn about life, the more we understand its immense arsenal of survival techniques, the statistical subtleties of genetics, the genius of sexual reproduction, and the surprising interception of harmful genetic damage as an unlikely mechanism for improvement. Ironically, the evolution of life is mostly about death, as non-random death mortally reaps its crop of the unprepared with a bold indifference that sentient beings like ourselves find hard to accept. How could such a heartless state of affairs exist? As we probe deeper, we scientists discover that it can be no other way. Life just is, and what is, has helped create a world like no other.

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