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Understanding natural selection

The following observations about patterns in nature have captured the imagination of humans for millennia.

1. **Fit of form and function (*FF&F*)**: different organisms appear remarkably well suited and engineered for their particular environments. The high-crowned molars of zebras and white rhinoceros act as mulching mowers for grinding grass, and protect against the inevitable wear imposed by the silica content of grass. Black rhinos, on the other hand, have lower crowned molars favoring efficient mastication of leaves and foliage. None of these animals has the sharp and stabbing canines like those of lions. Distinct **species**[1] of organisms apply themselves to different ecological tasks using their appropriate sets of tools. For example, zebras and white rhinoceros feed on grass, black rhinos browse leaves from shrubs, and lions kill and eat zebras.
2. **Diversity of life**: we share this planet with a phenomenal array of different life forms. These forms range from delicate mosses and annual flowering plants to awesome whales and fearsome sharks. While many of these forms differ in subtle ways, most can be readily recognized and categorized as types or species quite distinct from others. This is possible because the extant denizens of our planet do not exhibit a continuum of morphological variation from bacteria to redwood tree. Rather, the morphologies and characteristics of living organisms cluster like conspicuous and discrete galaxies in morpho-space.
3. **Procession of life**: despite the variety and discreteness of life, organisms seem connected by design rules of increasing levels of complexity. Notions such as the tree of life identify a regular, yet increasing, sophistication of organisms in terms of size, behavior, and the number and specialization of

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[1] A formal definition of species is given in Subsection 8.2.2.

traits. The early idea of a **bauplan** recognized the fixity of certain design rules among definable groups of species. Linnaeus in his binomial nomenclature used design rules to place organisms in the tree of life. Modern systematics and taxonomy, now more than ever, rely on the hierarchical structuring of traits among collections of species to assign names and position within life's tree.

4. **Distribution and abundance of organisms**: this is the central question of ecology. Paleolithic peoples probably pondered this as the central question of survival. Organisms are not spread randomly in space and time. Furthermore, some organisms seem ubiquitous and excessive in numbers (various species of crow, for their size, are particularly abundant around the globe) while others puzzle us with their rarity (the introduced Eurasian tree sparrow has a toe-hold in the city of St. Louis while its congener, the European house sparrow, occupies the rest of North America).

These observations must predate recorded history. Yet a satisfactory and unified answer to why the above four patterns exist has been available for only about 150 years with the development of Darwin's theory of evolution by natural selection. More recently, game theory (the mathematics used to study conflicts of interest among two or more players) – is being successfully applied to modeling natural selection. The classical game theory of economics, sociology, and engineering has existed as a formal discipline since the 1940s and 1950s, while game theory as a formalism for natural selection has existed since the 1970s.

The objective of this book is to show that the synthesis of Darwin's ideas within the context of an evolutionary game provides a most useful tool for understanding the four patterns of nature. Because the use of evolutionary game theory to model natural selection requires a moderate amount of mathematics, we provide all of the concepts and mathematical tools needed in the chapters that follow.

In this chapter, we start by discussing Darwin's marvelous idea of natural selection, introduce life as an evolutionary game, and explain why we favor a game theoretic approach as a complement to the more familiar and orthodox genetical approaches to natural selection.

1.1 Natural selection

1.1.1 Historical perspective

It is appropriate that well into the Age of Enlightenment the field of evolutionary ecology resided within the intellectual pursuit of Natural Philosophy. Natural

Philosophy encompassed all aspects of the sciences. Then, as today, philosophy (literally the love of wisdom) pursues the facts and principles of reality. Ecology falls into this quest for understanding Nature's reality, and natural philosophers recognized a wisdom to nature. All organisms exhibit in their characteristics excellent engineering in fit of form and function (*FF&F*) and the engineering shows a commonality and connectedness of design across all life from simple to complex (*procession of life*). It is remarkable that, over the ages, the diverse natural philosophies have all recognized a design and engineering component to nature. And, until the mid 1850s, all of these philosophies drew a very logical connection between human tools and organisms as tools designed by nature.

The connection between the tools in the human household and organisms in nature's house is compelling. Hence, essentially all pre-Darwinian natural philosophies took the next logical step. Tools exist because humans design and fashion them with purpose and forethought of intent, a watch is proof of a watchmaker.[2] Commonality of features among watches reflects the watchmaker's trademark and level of technology. It then follows that biodiversity is a reflection of a Creator, of gods, of Mother Earth, or of some other personified force that shows intent and purpose in the conscious design of its organisms. For most cultures over most of history this logical construction held sway. Just as humans make tools so something greater (singular or plural, masculine or feminine) made life. This philosophical view of life provided a seamless blend for people's ecological knowledge and spiritual beliefs. In the nineteenth century (Darwin's Century as Eiseley (1958), aptly calls it) in Western Europe, and in England in particular, this viewpoint began to lose favor as applicable to biology.

Lyell's geology showed how ongoing forces and non-personified natural processes could explain the forms, types, and layering of rocks (Lyell, 1830). And within many of these distinctly non-living rocks were the distinct remains of previous life. Erosion, sedimentation, compression, and volcanism provided for geological changes with time. Could the fates of rocks and life be tied together? Could similarly non-personified natural forces explain the origins and changes of life with time? The essentialists (linked to Greek ideas of life mirroring or manifesting some deeper fixed reality and truth) and biblical creationists (Genesis as scientific treatise) scrambled to make sense of

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[2] Apparently William Paley was the first to use the analogy. "... suppose that I had found a watch upon the ground ... this mechanism being observed the inference we think is inevitable, that the watch must have had a maker ... or shall it, all at once turn us around to an opposite conclusion, namely that no art or skill whatever has been concerned in the business. Can this be maintained without absurdity?" Evidence of evolution reveals a universe without design, hence Dawkins's (1986) useful metaphor of the blind watchmaker.

these new findings and ideas. In its more complex forms, scientific creationism stretched biblical days into millennia, and recognized multiple creations and destructions of life, of which Noah's Flood was but one particularly noteworthy example (Schroeder, 1997). But those seeking a "uniformitarian" explanation for life also had major conceptual and logical hurdles. Yes, geology and life seemed to share a common fate, but erosion, sedimentation, and volcanism do not form the characteristics of organisms. Empirically, life might change its characteristics with time, but what were life's natural processes?

Evolution built around heritable change with time was a potentially attractive force. Most natural philosophers accepted the presence of this force within animal and plant breeding, and many social philosophies emphasized the connections between human bloodlines and human hierarchies. But, as a force for change, it was presumed to be rather limited and in most cases useful only for protecting good blood from bad. Few saw breeding as providing the force or opportunity for truly novel evolutionary change. Early attempts at linking evolution to *FF&F* and *procession of life* still clung to the notion of foreordained or consciously driven improvement. Some espoused a kind of creationist–evolutionist blend: a view that saw God creating life at all levels followed by the evolution of these forms up a chain of being towards humans, angels, and beyond. Lamarck advanced a tenable theory of evolution via "self improvement." Just as an individual can be conditioned physically for a task, perhaps a species can condition their heritable characteristics towards needs and particular tasks, leading to the inheritance of conditioned or acquired traits. Two aspects of this theory of evolution are interesting. First, Darwin did not see Lamarck as incompatible with natural selection and in fact viewed the inheritance of acquired traits as one of several likely ways for introducing heritable variation. Second, Lamarckism could have been correct as a scientific perspective. If **pangenesis** (the equal contributions of all units of the body to the heritable blueprint for the organism's offspring) had been correct, then acquired (or discarded) traits could manifest as heritable change, and natural selection could work within this context. And indeed, in prokaryotes, and some plants where there are fewer clear boundaries between the somatic cell line and the gametic cell line, manifestations of Lamarckian evolution do occur comfortably within the framework of natural selection. But, the raindrops that eroded and formed Lyellian geology still eluded evolutionist thinking.

Darwin found the raindrops in deceptively simple ecological processes – surplus births and subsequent famine. The Struggle for Existence (loosely associated with Malthus (1796)) recognizes a reality of ecology. Organisms are capable of having many more offspring than the environment can possibly

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support. Darwin's genius was in making the link between heritable variation (however it came about!) with the Struggle for Existence in which less satisfactory individuals die. Just as raindrops sculpt landscapes by eroding softer and harder stones at different rates, the ecological raindrops of births and deaths striking the softer and harder rocks of heritable characteristics sculpt life. It is not hard to see how many a natural philosopher would find repugnant the deep social irony of natural selection as beautifully described in "*Darwin's Dangerous Idea*," (Dennett, 1995). This repugnance resonates today in the writings of intellectuals such as Gould (1998). The "noble" excellence exhibited by *FF&F* and *procession of life* is engineered by the scourges put upon it as manifested by "poverty" and "famine."

1.1.2 As Darwin saw it

Evolution is the physical, genetic, or behavioral change in populations of biological organisms over time. Evolution's more interesting and significant manifestations result from **natural selection**, a process that engineers biological systems. Natural selection works within genetic, developmental, and environmental constraints to shape biological organisms in ways that make them appear adapted to their environments. Understanding an evolutionary design has its roots in **Darwin's postulates** (Darwin, 1859). As Sober (1984, p. 21) notes, Darwin's postulates are really two drawn out, discursive propositions. Darwin saw heritable variation leading to evolution, and evolution leading to new species and to new distributions of characteristics within species. Drawing from Lewontin (1974), we will separate Darwin's argument into three postulates:

1. Like tends to beget like and there is heritable variation in traits associated with each type of organism.
2. Among organisms there is a struggle for existence.
3. Heritable traits influence the struggle for existence.

The first postulate was generally well known at the time and had been used by plant and animal breeders for centuries to improve native strains. The second postulate was influenced by Malthus's *Essay on Population* (1976) with the thesis that resources can only increase arithmetically while human populations grow geometrically. Darwin extended this idea into the general phenomenon of competition among individuals of the same or different species for limiting resources. Darwin's last postulate provided the key for understanding the consequences of evolution. For a particular environment, this postulate results in an increase in phenotypically well endowed individuals who are better able to survive and reproduce than less well endowed individuals.

Darwin used logical verbal arguments to model evolution. His views on inheritance were both orthodox for the day and flawed. Today, we think of evolution in terms of genetics, which involves the study of inheritance of genes from one generation to the next. Genetics seems to provide the ultimate tool for studying evolution, yet it is a curious fact that Darwin presented his theory in the absence of any understanding of genes as presented by Mendel (1866). It was not until the 1930s that Fisher (1930), Wright (1931), Haldane (1932), Dobzhansky (1937), and others combined evolution and genetics into what is known as the Modern Synthesis (Mayer and Provine, 1980). Genetics has provided a framework for understanding evolution, yet it need not be the essential core for modeling or understanding evolution by natural selection. Darwin's postulates do not require any specific mechanism of inheritance. This observation is in accordance with the development presented in this book. Since Darwin's three postulates constitute a fundamental principle that can be used to explain and predict evolution, we use these principles in developing a non-genetical mathematical framework for natural selection. The framework is *not* non-genetical in the sense of not having some mechanism for inheritance, and an understanding of the recipe of inheritance, as in the case of modern genetics, is paramount to Darwin's first postulate (as well as to bioengineering, medical genetics, animal and plant breeding programs, taxonomy, DNA fingerprinting, etc.). The framework is non-genetical in the sense that an actual genetic system for allowing natural selection is an auxiliary hypothesis. In the same manner natural selection is merely an auxiliary hypothesis (among several evolutionary forces) for changes to a genetic system. We propose that evolution by natural selection is a dynamic game. Our objective is to develop an evolutionary game theory that can be used as a fundamental modeling tool for understanding natural selection.

1.1.3 The Modern Synthesis

The Modern Synthesis that began in the 1900s and was completed by the 1930s is often viewed as a critical step in formalizing natural selection (Sober, 1984). The lack of a mechanism for inheritance hampered development of rigorous mathematical models of natural selection, which in turn hampered application and advancement. The "rediscovery" of Mendel's Laws in the 1900s (Pearson, 1904; Hardy, 1908) energized work on breeding and inheritance, and drew into question the compatibility of Mendel's particulate inheritance with natural selection. Fisher (1930), Wright (1931), Haldane (1932), and others ushered in a golden age of population genetics by placing the study of evolution on a firm mathematical foundation. In creating this foundation, they showed the compatibility of Mendelian genes, loci, and alleles with natural selection, the evolution of quantitative traits, and systematics. In addition, the recipe of inheritance provided insights into other forces of evolution (mutation and genetic drift) and into interactions that might occur genetically within and between organisms. Genetic interactions within an organism could be **epistatic** (many genes at different loci may contribute non-additively to a particular trait) and **pleiotropic** (a single gene may contribute to the phenotype of several traits). Among individuals, natural selection could be **density dependent** and/or **frequency dependent** depending on whether the population's size and/or gene frequencies influence the success of individuals with particular phenotypes, respectively.

The Modern Synthesis led to the primacy of genes over heritable phenotypes as the objects of evolution. This primacy seems self evident. In the Modern Synthesis, evolution is defined as a change in gene frequency. However, natural selection in terms of *FF&F* must involve the ecological consequences of heritable phenotypes. Can a strictly genetical approach be sufficient for modeling natural selection? Models of gene-frequency dynamics determine what has been selected but cannot necessarily determine what survival or fecundity aptitudes of the organism have been selected for. The *FF&F* requires understanding both what has been selected and why. The "why" requires a focus on heritable phenotypes, particularly when natural selection is frequency dependent. So, while the Modern Synthesis provided a huge advance in our understanding of evolution, taxonomy, and gene dynamics, it may have unwittingly hampered a fuller appreciation of natural selection by subordinating heritable phenotypes to their genetic recipes.

1.2 Genetical approaches to natural selection

Population genetics (modeling changes in the frequency of particular alleles within a population) and **quantitative genetics** (modeling the change with time of quantitative traits under the assumption that many alleles and loci contribute more or less additively to the trait value within an interbreeding population) are the concepts currently used for thinking about and modeling evolution where evolution is defined as a change in gene frequency. This outlook guided research to examine how genetic variability and genetic constraints direct and restrict evolutionary change (Crow and Kimura, 1970).

Viewing evolution as change in gene frequency can produce reasonable results in terms of producing an *FF&F*. For example, consider the case where the fitness conferred by a gene on an individual is **density independent** (independent of the population size) and **frequency independent** (independent of gene frequencies). In this case, the gene dynamics favor the genes that confer the highest per capita rate of growth on the population. In the situation where the fitness conferred by a gene is density dependent and frequency independent, then gene dynamics favors genes that maximize the population's size. In both of these cases the gene dynamics favors survival of the fittest if fitness is defined either as population growth rate or population size. However, as soon as evolution is frequency dependent, that is the fitness conferred by a gene on an individual is influenced by the frequencies of other genes in the population, then the linkage between the consequence of natural selection operating on genes and some corresponding measure of fitness at the population level disappears. The endpoint of the gene dynamics no longer optimizes any obvious measure of ecological success. This will be the most common situation as plausible genetic interactions such as epistasis, pleiotropy, and heterozygote superiority all introduce frequency dependence. The decoupling of change in gene frequency from some measure of ecological success for the individual organism or the population has unintended and unfortunate consequences for the question of *FF&F*. When evolution by natural selection becomes simply the endpoint of genetic dynamics, evolution by natural selection becomes potentially tautological. The fittest genes are those that survive and so survival of the fittest becomes a truism. Or it encourages a view of a life in which genes are the engineers of blindly programmed robots that serve only to reproduce more genes (paraphrased from *The Selfish Gene* (Dawkins, 1976)). The wings of a bird are no longer for flying; rather they are a part of the machinery for proliferating genes. The *FF&F* concept is lost in favor of the dynamical system of gene frequencies.

In this book, the focus will be on the wing rather than the genes coding for the wing. Characters such as wings will be modeled as evolutionary **strategies** (heritable phenotypes). Even under frequency-dependent selection, the resulting game theory analysis will reveal both what has been selected and why. The *FF&F* requires us to study strategies as the outcome of an evolutionary process (accessible using gene-frequency dynamic models), and to study strategies by their function (tricky when using strictly genetical models of frequency-dependent selection). A game theoretic approach is needed because frequency-dependent selection is ubiquitous in natural selection and plays the key role in the *diversity of life* and the *distribution and abundance of organisms*.

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A consequence of the strictly genetical approach used in current textbooks on evolution[3] is a narrow perspective on genetic variability and a decoupling of the concepts of **microevolution** (small evolutionary changes) from concepts of **macroevolution** (large evolutionary changes and the stuff of the *procession of life*). In evolution courses, such traits as tongue rolling and blood type serve to emphasize the idea of genetic variability. Once the genetic variability has been identified, the loci and alleles specified, and the consequences of genes for survival and fecundity defined, then population genetics brings mathematical rigor to subsequent changes in gene frequencies brought about by natural selection. Unwittingly though, the focus on extant genetic variability greatly reduces our appreciation of the complete set of heritable variation on which natural selection operates. Subsequent analyses give the impression that natural selection is a finishing school for microevolution but is inapplicable to macroevolution. Natural selection becomes subordinated to the known and accepted machinery of population and quantitative genetics which then gets subordinated to explaining readily observable evolutionary changes within populations. By not being able to apply the genetical approach to the big interesting evolutionary changes that separate species, families, orders, and classes from each other, evolutionists have proposed macroevolutionary forces such as genetic revolutions, species selection, and phylogenetic constraints and inertia that have little grounding in natural selection (Eldridge and Gould, 1972; Stanely, 1979; Vermeij, 1994). Current evolutionary teaching reflects this split in intellectual thinking. The rigors of population and quantitative genetics are used to show how natural selection can shape characteristics of populations, and then this machinery is discarded and replaced when the course moves on to the really interesting questions of speciation, biogeographic patterns, and the evolution of characters that define and separate the higher taxa of life. Because macroevolution does not fit comfortably within population genetics, natural selection becomes separated from the question of the *diversity of life* and the *procession of life* by virtue of its association with genetical models.

Genetical views of natural selection often ignore the most appealing applications of natural selection to *FF&F*, *diversity of life*, and *procession of life*. This happens because a genetical basis for natural selection cannot comfortably account for the seemingly limitless, though constrained, set of heritable variability available to natural selection, and it subordinates the organism's ecology to the genetic mechanism. But in Darwin's original formulation it is the ecological interactions operating on the set of evolutionarily feasible phenotypes

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[3] Frequency-dependent selection often gets short shrift in these textbooks. Usually the most interesting examples of natural selection cited involve frequency dependence (at least implicitly) even as the formalisms for conceptualizing frequency dependence receive minimal attention.

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that sculpt and refine species towards an *FF&F*. This aspect of Darwin's perspective on natural selection represents an **adaptationist research program** which studies the advantages that particular characters might confer on the individual. Fields such as physiological ecology, functional morphology, and behavioral ecology (particularly in the guise of foraging theory and sociobiology) produce more or less plausible hypotheses for the adaptation of an organism's heritable traits.

The adaptationist approach to natural selection is appealing in that it seems to contain the spirit of Darwin's original idea. However, it is built on a poor foundation. As scathingly noted in "The Spandrels of San Marco" (Gould and Lewontin, 1979), the intuitively appealing explanations for the value of traits to an organism rested on non-rigorous and often indefensible notions of what is valuable to an organism and what is heritably feasible. The adaptationist paradigm in the 1970s lacked formal fitness functions, formal statements of what was feasibly heritable, and formal evolutionary dynamics. Here's the dilemma. Genetical approaches have been successful at modeling what is selected but lack insights into why a character has been selected. Adaptationist approaches have been successful at proposing why a character has been selected for, but often lack a modeling framework.

Here we take another look at the adaptationist approach as embodying the spirit of Darwin's theory of natural selection. While we applaud the formalism and rigor of population genetic and quantitative genetic approaches to evolution, we regard life as a game, and that a game theoretic approach provides the right tools and a sufficient level of rigor for an adaptationist approach to evolution by natural selection. In this book, we present life as a game and develop the formalism necessary to model evolution by natural selection as a game. To make the transition from a strictly genetical perspective to a game theoretic one, we view evolution as a change in heritable phenotypes rather than as a change in gene frequency. From this viewpoint, we recover the sense of natural selection as an optimization process leading to adaptations, and support the engineer's perspective that organisms are designed for a function.

1.3 Natural selection as an evolutionary game

The long loop of Henle within a kangaroo rat's kidney allows it to produce exceedingly concentrated urine. Because of this and other physiological adaptations (Schmidt-Nielson, 1979), the kangaroo rat can inhabit deserts, eat little more than seeds, and never drink a drop of water in its lifetime. Mussels inhabiting inter-tidal habitats have strong abyssal threads that lash them to the