Evolution: The Unifying Theory of the Biological Sciences

“Nothing in biology makes sense, except in the light of evolution”

Evolution shapes all interactions between organisms and their environment. Consequently, human anatomy and physiology can be understood only in the context of evolutionary theory. Indeed, the theory of evolution is the foundation of all that we understand about living systems, from elementary principles of taxonomic classification to the most advanced aspects of medicine and psychology. As the noted geneticist, Theodosius Dobzhansky once stated, “Nothing in biology makes sense, except in the light of evolution.” Thus, our final goal in BIOL 189 is to understand the process of evolutionary change and the principal mechanism by which it occurs – natural selection.

For all practical purposes, Charles Darwin first proposed the theory of evolution in his book On the Origin of Species by Means of Natural Selection. Specifically Darwin argued that:

1) individuals within a population differ in their morphology (i.e., anatomy), physiology, and behavior;
2) some of this variation is heritable (offspring resemble their parents more than they resemble other individuals in the population);
3) organisms have tremendous capacity for increase that is not realized;
4) resources such as food, water, space, and access to mates are limited, thus there must be competition for resources among individuals;
5) as a result of this competition, some variants will survive and reproduce better than others;
6) characteristics of successful variants will increase in frequency in future generations.

Darwin further argued that via this mechanism, which he termed natural selection, species could change, or evolve, through time. Darwin’s arguments are embodied in what we now refer to as the general theory of evolution. This theory describes evolution as the process by which living organisms have descended from ancestors unlike themselves through the gradual acquisition and modification of heritable characteristics, or traits. The general theory of evolution also states that all organisms can ultimately trace a common ancestry to nonliving material.

Evolution by natural selection requires that the traits possessed by individual organisms can be modified and passed from one generation to the next – i.e., traits must be mutable and heritable. When he wrote “The Origin,” Darwin was ignorant of the mechanism of heredity; and the lack of such a mechanism was the most serious criticism leveled at the theory of evolution by natural selection. Consequently, the most important addition to evolutionary thinking came at the beginning of the 20th century with the discovery of Gregor Mendel’s work on heritability in garden peas and the development of genetics as a biological sub-discipline. We now know that morphological, physiological, and behavioral traits are passed from parents to offspring via units of genetic material termed genes; and that evolution occurs when individuals with certain alternative forms of genes termed
alleles survive, grow and/or reproduce better than individuals with different alleles.

A review of genetics

Genes are the most important component of living systems because they are the only elements that can exist in an indefinite number of discreet, reproducible forms. Due to the second law of thermodynamics, all living systems have finite existences. However, if they are faithfully replicated and transmitted from parent to offspring, genes can (theoretically) be immortal. Of course, the second law of thermodynamics ensures that replication is not always faithful. Errors in replication or mutations can occur. As a rule, mutant genes are detrimental to the organism that posses them. However, in some cases, mutant genes may be replicated and transmitted at higher rates than their parents. Through time, these mutant genes will increase in number with respect to their parents.

These four properties of genes (replication, variation, heredity, and reproductive advantage) underlie the concept of the selfish gene and the definition of biological evolution as a change in the gene pool of a population. The selfish gene is a particularly important concept to grasp. When attempting to understand the evolution of a complex trait such as cooperative behavior, it is tempting to explain the trait in terms of ultimate advantages to the group or species. However, such traits must be explained in terms of the immediate benefits they provide to the replication and transmission of individual genes.

At the molecular level, genes are specific numbers of DNA nucleotides (or RNA nucleotides in some viruses) that act as:

1. Templates for their own replication,
2. Templates for the synthesis of functional molecules in cells.

Typically, the functional products of genes are polypeptides that are proteins, or parts of proteins. Other functional products include sequences of RNA (transfer-RNA and ribosomal-RNA) that play vital roles in the chemical synthesis of polypeptides and, hence, proteins. Proteins act as transporters, structural molecules, signaling molecules, and regulatory molecules (see the section on development). However, the most important function of proteins is to act as enzymes. Enzymes catalyze (accelerate) the chemical reactions of cellular metabolism.

In all eukaryotic cells, DNA exists as discrete, linear molecules termed chromosomes. A gene occupies a specific region on a specific chromosome termed a locus (plural: loci).

Most animals are diploid: their somatic cells (non-gametes) contain two sets of chromosomes, one that is maternally inherited and one that is paternally inherited. Consequently, each somatic cell has two copies of each gene; and these copies may differ slightly in their sequences. Alternative sequences of a gene are termed alleles. Different alleles are produced by mutations; and different alleles result in slightly different functional products.

The structure and functioning of a cell emerges from interactions among the functional products of its alleles. Hence, cells with different mixtures of alleles will tend to exhibit different structures and dynamics. The complete set of alleles within a cell is referred to as its genotype. The cell structure and functioning that emerge from interactions among the functional products of these alleles constitute the phenotype.

In multicellular organisms, gross anatomical, physiological, and behavioral traits emerge from interactions among numerous somatic cells. Over the course of an organism’s life,
these cells can accumulate mutations by a variety of mechanisms such as exposure to ultraviolet radiation. Thus, the genotypes of two somatic cells in the same organism can differ. However, because somatic mutations are not transmitted to offspring (i.e., they are not heritable), we do not account for them when describing the genotype of a multicellular individual. Thus, the genotype of a multicellular organism is based on the genotype of totiopotent stem cells from which all of its somatic cells are descended (a fertilized egg, or zygote, is a totiopotent stem cell). Individuals that develop from totiopotent stem cells with different genotypes will tend to exhibit different morphological, physiological, and behavioral traits. Thus, the complete set of alleles contained in totiopotent stem cells constitute the genotype of a multicellular organism; the morphological, physiological, and traits that emerge from the interactions among somatic cells constitute the phenotype of a multicellular organism. In effect, a phenotype is equivalent to an individual organism or Darwinian individual. Darwinian individuals can be thought of as compartments or receptacles that are “designed” to replicate and transmit their underlying alleles to maximum effect. This is an extremely important point to keep in mind.

Theoretically, we can inspect the chromosomes of a totiopotent stem cell and identify every distinct locus (this was the goal of the human genome project). We can then classify each locus with respect to the functional product/products that it produces – i.e., we can classify each locus with respect to its genetic identity. Finally, we can classify each locus with respect to its specific sequence of DNA nucleotides – i.e., we can classify each locus with respect to its allelic identity. If we follow this procedure for every individual in a population, we can determine: 1) the number of unique genes in the population; 2) the number of unique alleles for each gene; and 3) the number of copies for each unique allele. In combination, these numbers describe the gene pool of the population. Any change in this pool constitutes biological evolution.

Consider a human population living in equatorial Africa. Suppose that a specific gene termed β, codes for the β-subunit of hemoglobin. As we have noted in class, this gene has at least two alleles. The B-allele is completely dominant to the b-allele. People who are homozygous recessive have a serious genetic disease, Sickle Cell Anemia. People who are homozygous dominant have an advantage over people who are homozygous recessive. However, people who are homozygous dominant are at a disadvantage to people who are heterozygous because heterozygous individuals have an increased resistance to Malaria.

Suppose that, at some time, t, we inspect the chromosomes of all people in the population and find that the DNA sequence corresponding to the B-allele occupies 50% of all β-loci. We repeat the process at some later time t+1 and find that the B-allele now occupies 75% of all β-loci. We can thus say that the human population has evolved.

**Development and phenotypic plasticity**

A phenotype arises from its underlying genotype via a process of development that occurs continuously from the point of conception to the point of death. Development is based on the regulation of gene expression in single cells. Gene expression describes the process by which the sequence of nucleotides defining a gene is converted into a functional product such as a protein. It is a multi-step process that begins with transcription of DNA into RNA. In some cases (e.g., transfer-RNA and ribosomal-RNA) the newly transcribed RNA may itself be a functional product. However, most RNA is messenger RNA that is used as a template for the synthesis of proteins. After it has been transcribed, messenger RNA is chemically modified in various ways, and then translated into proteins. Once a protein has been
translated, it may be chemically modified in a fashion similar to messenger RNA. Completed proteins are then transported to specific locations in the cell where they assume their functional roles.

The expression of a gene can be started, stopped, accelerated, or decelerated at each stage listed above. In combination, these actions constitute the regulation of gene expression. Regulation of gene expression determines the timing with which different functional products appear in a cell and the rates at which those products are synthesized. Through time, changes in the relative concentrations of different functional products determine the metabolism of a cell. Thus, regulation of gene expression determines a cell’s structure and function including: 1) its degree of specialization; 2) its rate of growth; and 3) its rate of division.

In general, functional genes are regulated by “binding proteins.” These proteins are coded for by regulatory genes. Some regulatory genes act like a thermostat. If concentrations of certain functional products are low, the regulatory genes are turned on – i.e., they are transcribed and translated thus producing binding proteins. The binding proteins then turn on the genes that code for the functional products in reduced supply. As the concentrations of these products increase, the regulatory genes are turned off. Thus, the regulatory genes are regulated by the genes they regulate. In addition to regulating functional genes, some regulatory genes control other regulatory genes. Consequently, genes are grouped into complex regulatory networks. Genes in a network interact with each other and chemical substances in the cell to govern the rates at which related groups of functional products are synthesized.

A small number of master regulatory genes can be activated by certain signals or stimuli that a cell receives from its ambient environment such as the receipt of a growth factor. Receipt of a signal initiates a chain of biochemical reactions that activates the master regulatory genes. Activation of these genes then activates multiple regulatory networks. Thus, a signal received from ambient environment can initiate a complex cascade of effects that significantly alters the structure and function of a cell.

In a multicellular animal, the adult phenotype develops from a single zygote via the process of morphogenesis. The zygote divides to become two cells, which divide to become four cells, which divide to become eight cells, and so on. This process continues until the developing embryo consists of 128 cells. At this point, individual cells begin to grow, migrate to new positions, and differentiate, ultimately forming the embryonic tissues of the ectoderm, endoderm, and mesoderm. The cells of the ectoderm, endoderm, and mesoderm then grow, divide, and differentiate, ultimately developing into functional organs and body parts. All of these processes are governed by the expression of genes in individual cells. In each cell, expression of genes is governed by: 1) changes in the concentrations of functional products that reflect its genetic programming; 2) physical and chemical signals sent from other cells; and 3) physical and chemical stimuli associated with substances in the external environment. Thus, conditions in the ambient environment can have a large influence on the gross morphological, physiological, and behavioral traits of an adult phenotype.

Because signals from the ambient environment influence the regulation of gene expression, a single genotype can produce distinct phenotypes when exposed to different environmental conditions. This phenomenon is referred to as phenotypic plasticity.

For evolution by natural selection to occur, phenotypic traits must be heritable. At first glance, traits that are induced by conditions in the ambient environment appear to be un-
heritable. Thus, phenotypic plasticity seems to pose a problem for the theory of evolution by natural selection. However, that is not the case. In a multicellular animal, the receipt of environmental signals depends on specialized cells; the receipt of environmental signals by these cells depends on the presence of specialized receptor proteins; and these proteins are the functional products of genes. Hence, phenotypic plasticity is itself a heritable phenotypic trait, and is thus subject to evolutionary change.

Natural selection and adaptation

Phenotypes interact with the ambient environment. These interactions mediate the survival, growth, and reproduction of phenotypes; and the survival, growth, and reproduction of phenotypes mediates the replication and transmission of their underlying alleles. Within a population, different phenotypes will meet the challenges of the ambient environment with different degrees of success. Phenotypes that interact more successfully will tend to survive for longer periods of time, grow faster, and/or produce more offspring than those that interact less successfully. This process is termed natural selection. Through time, alleles that give rise to more successful phenotypes will increase in frequency with respect to alleles that give rise to less successful phenotypes. This process is referred to as evolution by natural selection.

Imagine a population of mule deer that occurs in an environment characterized by severe winters: winter temperatures are extremely low and food is limited. Within this population, certain deer have an enzyme that allows them to store fat more efficiently than other individuals. When temperatures are low and food is scarce, fat can be metabolized to maintain body temperature and provide life-sustaining energy. Thus, deer that enter the winter with a high percentage of body fat have a better chance of surviving than deer that enter the winter with a low percentage of body fat. Moreover, mule deer typically breed in the late fall/early winter. Because they have more energy, males with a high percentage of body fat breed with more females than males with a low percentage of body fat; and females with a high percentage of body fat are more likely to carry their pregnancies to term and give birth to healthy fawns. Consequently, deer that are more efficient at storing fat will contribute more alleles to succeeding generations, than deer that are less efficient at storing fat. Across generations, both the enzyme that allows more efficient fat storage and its underlying allele will increase in frequency. Thus, the population of deer will evolve by natural selection.

While natural selection acts via the differential survival and reproduction of phenotypes, it is the replication and transmission of the underlying alleles that matters. Fitness measures the ability of a phenotype to transmit its alleles to succeeding generations across its entire lifespan with respect to competing phenotypes. Natural selection always increases the average fitness in a population; it cannot decrease the average fitness. Moreover, because fitness depends on a phenotype’s ability to meet environmental challenges to survival, growth, and reproduction, natural selection always increases the average ability to meet these challenges. Environmental challenges to survival and reproduction are referred to as selection pressures. Traits that allow phenotypes to meet these challenges are referred to as adaptations. The process by which natural selection produces adaptations is referred to as adaptation. In the example above, the severe winters constitute a selection pressure. The enzyme that allows more efficient fat storage is an adaptation. Across generations, a greater and percentage of the deer will possess the enzyme. Consequently, the population will become increasingly capable of meeting the challenges imposed by severe winters.
Mechanisms other than natural selection can lead to biological evolution. For example, across generations, the frequency of an allele can shift due to chance alone – a process termed genetic drift. However, natural selection is the most important evolutionary process because it is the only one that produces adaptation. Forces such as genetic drift do not mold populations to conditions in the environment.

Three axioms of adaptation

**Natural selection is constrained by the past**

Adaptation leads to specialization. As selection molds a population to its ambient environment, specific alleles are lost; and, once they have been lost, alleles are unlikely to reappear.

In addition, the evolutionary history of an organism is embodied in its program of development. Complex phenotypic traits tend to be modular: they consist of multiple, interacting parts that are functionally specialized. Modularity is made possible by the subdivision of developing embryos into semiautonomous units that occurs during development. As a rule, mutations that significantly disrupt developmental networks are highly deleterious; and the alleles that cause such changes are quickly weeded out of the population. This principle has two important consequences. The first consequence is that modular traits tend to evolve in small steps in which functionally new parts are jury-rigged to existing parts. Exceptions do occur, for example when mutations occur in regulatory genes. However, such exceptions are extremely rare. The second consequence is that existing traits are unlikely to be lost unless they have a strong negative effect on fitness. The alleles that code for such traits are fully integrated into regulatory networks. Hence losing them would tend to produce a cascade of developmental changes, most of which would be lethal.

In combination, loss of genetic variation and developmental constraints limit the trajectory along which a species can evolve: **what a population was limits what it can be** – at least in the short term.

**Natural selection does not predict the future**

Natural selection is based on the ability of phenotypes to meet environmental challenges in the present; it cannot “pre-adapt” the members of a population to challenges that might occur in the future. Indeed, adaptation leads to increasing specialization; and greater specialization makes organisms vulnerable to changes in the conditions to which they have become adapted. In this sense, specialization is the ultimate basis of all extinctions, whether they are natural or human induced.

**Natural selection does not produce perfection**

The only constant in nature is constant change. A perpetually changing environment precludes natural selection from perfectly matching a population to its ambient environment. In addition, every phenotypic trait is associated with costs as well as benefits; and the benefits of a trait must be balanced against its costs. For example, the long tails of peacocks provide a benefit with respect to the attraction of peahens. However, they carry a cost in terms of increased predation risk that must be balanced against the benefit. In addition the costs and benefits of a particular trait must be balanced against the costs and benefits of other traits. For example, aggressive defense of the nest by some songbirds is advantageous only if they can select nest-sites that are
defendable. In other words, natural selection is an “optimizing process” and optimization is not equivalent to “perfection.”

Some important kinds of adaptation

**Life history strategies**

Obviously, a phenotype that does not survive long enough to reproduce will transmit no alleles to succeeding generations. Similarly, a phenotype that survives for a long period but does not reproduce will transmit no alleles to succeeding generations. Thus, a phenotype that can maximize both survival and reproduction will maximize its fitness. However, survival and reproduction require energy and materials; and the second law of thermodynamics ensures that, for any phenotype, energy and materials are limited. Moreover, energy and materials devoted to the demands of survival cannot be devoted to the demands of reproduction, and vice versa. Consequently, phenotypes face a tradeoff with respect to how they allocate energy and materials to these competing demands. This principle is the basis of life history evolution.

The life history of an organism describes how an average phenotype allocates energy and materials to the competing demands of survival and reproduction. In essence, natural selection acts to balance the survival and reproduction of phenotypes in a population such that the average phenotype transmits the maximum number of alleles possible to succeeding generations. There are many strategies for optimizing survival and reproduction. At one extreme, there are organisms that trade survival for reproduction (r-selected species). Such organisms tend to be characterized by: 1) short life spans; 2) frequent bouts of reproduction; 3) large numbers of offspring in each bout; and 4) little to no parental care. At the other extreme, there are organisms that trade reproduction for survival (K-selected species). Such organisms tend to be characterized by: 1) long life spans; 2) infrequent bouts of reproduction; small numbers of offspring in each bout; and 4) extensive parental care.

**Phenotypic plasticity**

Recall that phenotypic plasticity is a heritable trait that natural selection can act on. It requires many generations for natural selection to change the frequency of alleles within a population. Thus, for adaptation to occur, environmental challenges must remain relatively constant across many generations. Variation in the environment that occurs within the lifespan of a single phenotype can thus present a serious problem. In the face of such variation, phenotypes that can “assess” new challenges and respond accordingly would gain a significant benefit in fitness. Such benefits constitute the adaptive basis for phenotypic plasticity.

**Animal behavior** is simply an extreme form of phenotypic plasticity. A change in the external environment acts as a signal or stimulus that is received by specialized receptor cells. Receipt of the stimulus causes a cascade of physiological changes that alter the animal’s internal condition. Changes in internal condition then induce physiological and anatomical reactions or responses. Complex behavior based on nervous systems gives animals a degree of flexibility that plants do not have. In the face of environmental change, a terrestrial plant has one option: it can alter its growth. If this option proves inadequate the plant’s survival and or reproduction is reduced. In contrast, an animal faced with
environmental change can move to a new location where environmental conditions are more favorable.

Behavior that can be rapidly modified on the basis of past experience, or learned behavior, is particularly advantageous when changes in the environment are rapid. Consequently, many aquatic and terrestrial vertebrates exhibit some degree of learned behavior. An organism that can use its past experiences to predict the future and prepare for changes that might occur would have a particularly large advantage. Such behavior, termed reasoning, is exhibited by only a few species, of which humans are the most obvious example.

**Cooperation**

Fitness is a relative measure: the fitness of a phenotype is defined as its ability to transmit its alleles to succeeding generations with respect to competing phenotypes. Thus, a phenotype that is very good at replicating and transmitting its alleles in absolute terms will still have low fitness if competing phenotypes replicate and transmit their alleles better. This is an extremely important point to grasp! In evolutionary terms, intraspecific competition (competition between members of the same species) is arguably the most powerful selection pressure that exists. Indeed, intraspecific competition ensures that natural selection will always favor phenotypes that are genetically selfish. True altruism cannot exist. Individual organisms always act in their own best interest or, more appropriately, in the best interest of their selfish genes. They do not act for the good of the group or the good of the species unless doing so benefits their own fitness. This principle poses a major barrier to the evolution of cooperation.

Most forms of stable cooperation are based on inclusive fitness. Closely related phenotypes share a large percentage of their genes. For example, in a sexually reproducing, diploid species, parents and their offspring share 50% of their alleles. On average, full siblings also share 50% of their alleles. Hence, a phenotype that helps its parents, offspring, or full siblings survive and reproduce and thus replicate and transmit their alleles will increase its inclusive fitness. Inclusive fitness is responsible for most forms of stable cooperation because related phenotypes almost always benefit from cooperating. For example, many ants, wasps, and bees are haplodiploid: males develop from an unfertilized egg and have one set of chromosomes (they are haploid); females develop from a fertilized egg and have two sets of chromosomes (they are diploid). This system of inheritance ensures that haplodiploid relatives share an unusual percentage (50-100%) of their genes. These unusually close genetic relationships have contributed to a reproductive division of labor where only a few individuals (Kings and Queens) in the colony can reproduce. Most individuals in the colony sacrifice their own reproduction and devote themselves to foraging, nest construction, nest defense, and brood rearing to enhance reproduction by the Kings and Queens.

Distantly related phenotypes cooperate only when the benefits to personal fitness that accrue from the success of the group are greater than the personal benefits of fitness that accrue from acting alone – i.e., when cooperation provides a mutual advantage. Mutual benefits include: 1) more efficient exploitation of presently utilized resources; 2) exploitation of novel resources; 3) more effective defense from enemies; and 4) more effective response to challenges posed by the physical environment, including manipulation and/or control of the physical environment. However, any phenotype in a cooperative alliance will always gain the maximum benefit from “cheating,” or gaining the benefits of cooperation without actually cooperating, as much as it can get away with. Moreover, for
non-relatives, the benefits of cooperation tend to vary through time. At some points phenotypes gain a mutual benefit from cooperating, at other points they do not. Consequently, cooperation among non-relatives is highly unstable.

**Exploitation, competition, and the evolution of ecosystems**

The fitness of predators depends on their ability to capture prey. Thus, selection tends to favor predators that are better at capturing prey. This presents a problem for the prey. As the predator population adapts and the average predator becomes more efficient at capturing prey, fitness of the average prey declines. Consequently, selection tends to favor prey organisms that are better at avoiding predators. As the prey population adapts and the average prey organisms become better at escaping, the fitness of an average predator declines. Consequently, selection tends to favor predators that are even better at capturing prey, and so on... In essence, predators and their prey are engaged in an evolutionary arms race in which each population must constantly adapt to keep pace with the other population. Such arms races are termed evolutionary Red Queens or The Red Queen Effect. Red Queens are not limited to predators and prey. They occur with equal or greater intensity among conspecific and heterospecific organisms that compete for limited resources including food, water, security, and access to mates. As a consequence of The Red Queen effect, the dynamics of coexisting populations can become linked such that ecological and evolutionary changes in one population prompt ecological and evolutionary changes in many others. When the dynamics of coexisting populations become linked in this way, the populations begin to change as a single interactive unit; and a higher-order system of systems – the community or food web - emerges.

Via their life sustaining activities, the organisms in a food web modify the physical environment at many different scales of space and time. For example, to maintain themselves, certain kinds of bacteria assimilate molecular nitrogen and convert it into a form that other organisms can use. Fixation of molecular nitrogen by one bacterium constitutes a local modification of the physical environment or disturbance. The effects of single bacterium are inconsequential. However, the effects of “billions and billions” of bacteria are considerable: they form the base of the nitrogen cycle. Similarly, an individual elk compacts soil and erodes geologic substrates as it walks. In general, the disturbance caused by a single elk has little meaning. However, the effects of many elk can compact stream banks and alter the hydrology of entire watersheds. Biological modifications of the physical environment combine with physical processes such as the flow of water, erosion, and volcanism to produce an overall disturbance regime. When the dynamics of the physical environment become linked to the dynamics of communities in this way, physical and biotic aspects of the environment begin to change as single interactive unit and another higher order system of systems – the ecosystem – emerges.

In many ways, ecosystems are comparable to individual organisms. They have a physical structure that is maintained via a continuous flow of low-entropy free energy that is transformed into high-entropy thermal energy. However, ecosystems differ fundamentally from individual organisms in the sense that have no goal or purpose. Individual organisms exist to replicate and transmit their prescribing genes to succeeding generations. Ecosystems do not exist to replicate and transmit their constituent species and physical structures: they are not super-organisms.
Cooperation, symbioses, and evolutionary transitions in individuality

Cooperation evolves when the average fitness of phenotypes that cooperate is greater than the average fitness of phenotypes that act alone. As a rule, cooperation is more efficient when there is a division of labor among the cooperating phenotypes. Thus, once cooperation is established, selection tends to favor specialization. At some point, the division of labor may become so extreme that the cooperating phenotypes are no longer capable of surviving and reproducing on their own: they can replicate and transmit their genes only as part of a larger whole. At this point, the cooperative alliance effectively becomes a new individual, or super-organism on which natural selection can act.

Such transitions in individuality appear to have been necessary steps in the evolution of complex phenotypes. The major transitions include:

1) The origin of chromosomes from independently replicating strands of genetic material.
2) The origin of organelles such as mitochondria and chloroplasts from free living prokaryotic cells that were consumed by ancestral eukaryotic cells.
3) The origin of sexual reproduction from eukaryotic cells that reproduced asexually.
4) The origin of multicellular organisms from cooperative groups of unicellular organisms.
5) The origin of eusocial groups such the colonies of ants, bees, wasps, and termites.

Transitions in individuality are by no means common. They require sustained selection for specialization; and sustained selection for specialization can occur only if the advantages of cooperation are stable across many generations. Such stability is extremely rare. As long as the genotypes of cooperating individuals can vary (via mutations, recombination of chromosomes, etc.) independently of one another, competition among individuals within groups will tend to be stronger than competition among groups. As a result, selfish, competitive phenotypes will tend to contribute more genes to succeeding generations than cooperative phenotypes.

Thus, evolutionary transitions in individuality are always associated with the presence of mechanisms for controlling cheaters or free riders and minimizing the destabilizing effects of within group competition. Five such mechanisms have been identified: 1) symbioses; 2) shared genes/inclusive fitness; 3) shared advantage or mutualism (including reciprocal altruism or reciprocity); 4) dominance; and 5) culture. No single control mechanism appears to be sufficient for a transition in individuality to occur: most transitions have involved two or more mechanisms.

For example, lichens consist of two distinct species: a fungus and an alga. The fungus encloses the alga in a sheath of protective cells; it also extracts inorganic nutrients from difficult substrates (e.g., rock) and converts them to forms that the alga can use. The photosynthetic alga extracts carbon dioxide from the atmosphere and converts it to carbohydrates that the fungus requires. The division of labor between fungus and the alga allows them to exploit inhospitable environments that they could not exploit on their own. Such environments are largely free of competitors. Hence, cooperation is maintained on the basis of a stable, mutual advantage that is a function of the high degree of specialization between the cooperating organisms. Note, however, that the division of labor in lichens is not completely equitable. The fungus benefits more than the alga. Consequently, lichens are, perhaps, more appropriately viewed as limited parasitism of the alga by the fungus.
Indeed, symbiotic relationships such as lichens appear to lead to transitions in individuality only when one partner directly dominates, or controls the other, typically by enclosing it in a physical boundary such as a cell membrane.

Unlike eusocial insects, individuals in mammalian social groups do not share large percentages of their genes; and, unlike symbiotic associations such as lichens, cooperating individuals are not highly specialized to begin with. Thus, the mutual advantages of cooperation are highly unstable in space and time. Such instability can be reduced via dominance hierarchies which are central to all complex mammalian societies.

Dominant individuals can serve as "policemen," punishing cheaters and enforcing cooperation by defectors. Such activity is costly in terms of time and energy to the dominant individuals. However, these costs are outweighed by the advantages of being dominant. For example, in wolf packs, dominant individuals do most of the breeding. Indeed, in virtually all mammalian societies, humans included, individuals with high status tend to have significantly higher survival and reproduction. Thus, in social groups with dominance hierarchies, status becomes a kind of resource for which individuals compete. Indeed, the potential of being dominant can ensure cooperation from individuals that would otherwise defect.

While dominance can stabilize cooperation, it can also destabilize it. Dominant individuals are no less subject to the temptations of cheating than subordinates. Consequently, dominants can become despots, hijacking cooperation to serve their own selfish purposes, typically to the detriment of the group as a whole. In human social groups, despotism tends to be limited by the disbursement of status among multiple individuals (e.g., tribal elders, city councils, etc.). Despotism is also limited by cultural traits such as morals, values, customs, and laws (e.g., democracy) that serve to disburse control and discourage cheating.

However, the tendencies to cheat and compete for status cannot be eliminated. Human social groups sit on the fence between disorganized collections of selfish individuals and fully integrated evolutionary transitions in individuality. Indeed this duality is mirrored in the neural mechanisms by which we perceive environmental stimuli and make decisions. It is thus, the ultimate source of the inner conflict between the needs and desires of self and the needs and desires of others that we all experience.

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References


