# 4. Social evolution and sexual selection

*In which we consider how organisms, even (some) unicellular organisms have evolved to cooperate with one another, leading to the formation of multicellular organisms composed of distinct cell types. Similar evolutionary mechanisms have produced a range of cooperative (social) behaviors. One particularly important such behavior is sexual reproduction and we consider its effects on the morphology and behavior of organisms.*
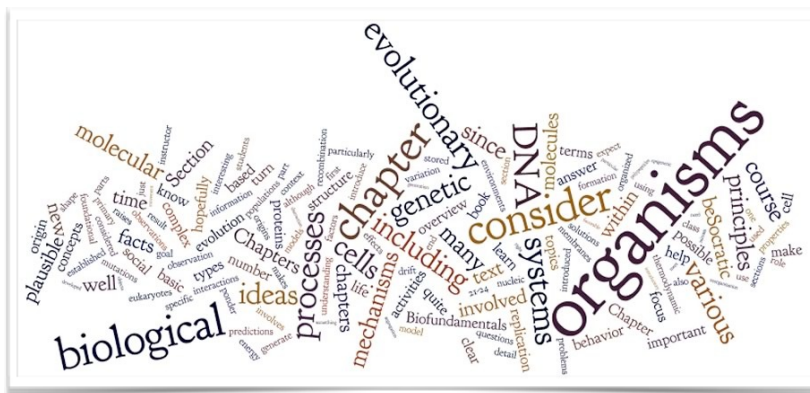


The naturalist Ernst Mayr made an important point when thinking about biology compared to physics and chemistry. The history of an electron, an atom, or a molecule is irrelevant to its physical and chemical properties. Each carbon isotope, for example, is identical to all others - one could be replaced by another and you could never, in theory or in practice, tell the difference. In contrast, each organism, how it is built, how it behaves, how it interacts with other organisms, and the future evolution of its descendants is the result of a continuous evolutionary process involving both selective and adaptive and non-selective and non-adaptive processes stretching back approximately 3.5 billion years. This history encompasses an unimaginable number of random events (mutations, accidents, environmental disasters, isolated and merging populations). Because of their molecular and cellular level complexity and their distinct histories, each organism is unique and distinguishable from all others.

We normally talk about organisms, but this may be too simplistic. When does an organism begin?  What are its boundaries. The answers can seem obvious, but then again, perhaps not. When a single celled organism reproduces it goes through some form of cell division, and when division is complete, one of two organisms present is considered a new organism and the other the old (preexisting) one, but generally it is not clear which is which. When an organism reproduces sexually, the new organism arises from the fusion of pre-existing cells and it itself produces cells that fuse to form the next generation. But if we trace the steps backward from any modern organism, where would we draw the lines between the different "types" of organisms. The answer is necessarily arbitrary, since cellular continuity is never interrupted. In a similar manner, we typically define the boundaries of an organism in physical terms, but organisms interact with one another, often in remarkably complex ways. A dramatic example of this are the eusocial organisms. While many of us are familiar with ants and bees, fewer (we suspect) are aware of the naked (*Heterocephalus glaber*) and the Damaraland (*Cryptomys damarensis*) mole rats. In these organisms, reproduction occurs at the group level; only selected individuals, termed queens because the tend to be large and female, produce offspring. Most members of the group are (often sterile female) workers, and a few males to inseminate the queen.[93] So what, exactly, is the organism, the social group or the individuals that make it up. From an

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[93]An Introduction to Eusociality: http://www.nature.com/scitable/knowledge/library/an-introduction-to-eusociality-15788128

evolutionary perspective, selection is occurring at a social level, rather than an organismic level. Or consider yourself and other multicellular animals (and plants). Most of the cells in your body (known as the soma) do not directly contribute to the next generation, rather they cooperate to insure that a subset of cells, known as the germ line, have a chance to form a new organism. In a real sense, the somatic cells are sacrificing themselves so that the germ line cells can reproduce a new organism. They are the sterile workers to the germ line's queen.

We find examples of social behavior at the level of unicellular organisms as well. For example think about a unicellular organism that divides but in which the offspring of that division stick together. As this process continues, we get what we might term of colony. Is it one or many organisms? If all of the cells within the group can produce new colonies, we could consider it a colony of organisms. So where does a colony of organisms turn into a colonial organism? The distinction is certainly not unambiguous, but we can adopt a set of guidelines or "rules of thumb".[94]  One criterion would be that a colony becomes an organism when it displays traits that are more than just sticking together or failure to separate, that is, when it acts more like an individual or a coordinated group. Conventionally this involves the differentiation of cells, one from the other, so that certain cells within the group become specialized to carry out specific roles, and reproducing the next generation is one such specialized role. Other cells may become specialized for feeding or defense. This differentiation of cells from one another has moved a colony of organisms to a multicellular organism. What is tricky about this process is that originally reproductively competent cells have given up their ability to reproduce, and are now acting, in essence, to defend or support the cells that do reproduce. This is a social event and is similar (analogous) to the behavior of naked mole rats. Given that natural selection acts on reproductive success, one might expect that the evolution of this type of cellular and organismic behavior would be strongly selected against or simply impossible to produce, yet multicellularity and social interactions have arisen independently dozens (or more likely millions) of times during the history of life on earth.[95] Is this a violation of evolutionary theory, or do we have to get a little more sophisticated in our thinking?

## Selecting social (cooperative) traits

The answer is that the origins and evolution of multicellularity do not violate evolutionary theory, but they do require us to approach evolutionary processes more broadly. The first new idea we need to integrate into our theoretical framework is that of inclusive fitness, which is sometimes referred to as kin selection. For the moment, let us think about traits that favor the formation of a multicellular organism - later we will consider traits that have a favorable effect on other, related organisms, whether or not they directly benefit the cell/organism that expresses that trait.



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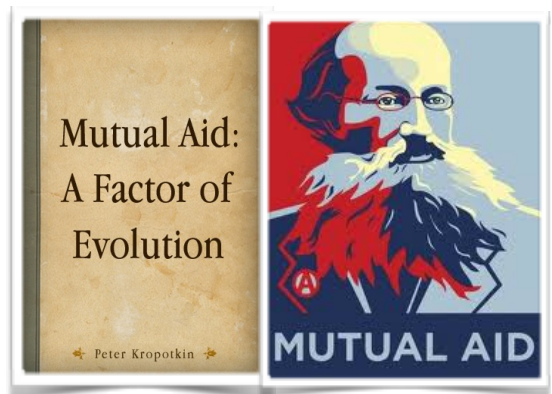
[94]A twelve-step program for evolving multicellularity and a division of labor: http://onlinelibrary.wiley.com/doi/10.1002/bies.20197/full

[95] The Origins of Multicellularity:  https://bcrc.bio.umass.edu/courses/fall2010/biol/biolh100-03/sites/default/files/bonner_multicellularity_1998.pdf

Finally, we will consider social situations in which behaviors have become "fixed" to various extents, and are extended to strangers (humans can, but do not always, display such behaviors). The importance of "mutual aid" in evolutionary thinking, that is the roles of cooperation, empathy, and altruism in social populations, was a point emphasize by the early evolutionary biologist (and anarchist) (Prince) Peter Kropotkin (1842 – 1921).

All traits can be considered from an economic "cost-benefit" perspective. There is the cost (let us call that term "c") in terms of energetics needed to produce the trait and the risks associated with expressing the trait, and a benefit ('b') in terms of effects on reproductive success. To be evolutionarily preferred (or selected), the benefit b must be greater than the cost c (b > c). Previously we had tacitly assumed that both cost and benefit applied to a single organism, but in cooperative behaviors and traits, this is not the case. We can therefore extend our thinking as follows. Assume that an organism displays a trait. That trait has a cost to produce and yet may have little or no direct benefit to the organism and may even harm it, but this same trait benefits neighboring cells. This is like (but not exactly the same as) the fireman who risks their life to save an unrelated child in a burning building. How is it possible for a biological system (the fireman), the produce of evolutionary processes, to display this type of behavior?

Let us consider some examples of this type of behavior. A classic example is provided by social amoebae of the genus *Dictyostelium*.[96] These organisms have a complex life style that includes a stage in which unicellular amoeba-like organisms crawl around in the soil eating bacteria and dividing (watch http://youtu.be/bkVhLJLG7ug). These cells can divide asexually in what is known as a vegetative cycle (as if vegetables don't have sex, but we will come back to that!) If the environment turns hostile, the isolated amoeba begin to secrete a small molecule that influences their own and their neighbor's behaviors. They begin to migrate toward one another, forming aggregates of thousands of cells. Now something rather amazing happens, these aggregates begin to act as coordinated entities, they migrate around as "slugs" for a number of hours. Within the soil they respond to environmental signals, for example moving toward light, and then settle down and undergo a rather spectacular process of differentiation.[97]  All through the cellular aggregation and slug migration stage, the original amoeboid cells remain as distinct cells. Upon differentiation approximately 20% of the cells in the slug differentiate to form stalk cells,



which lift the rest of the cells above the soil. The stalk cells can no longer divide, in fact, they die; they

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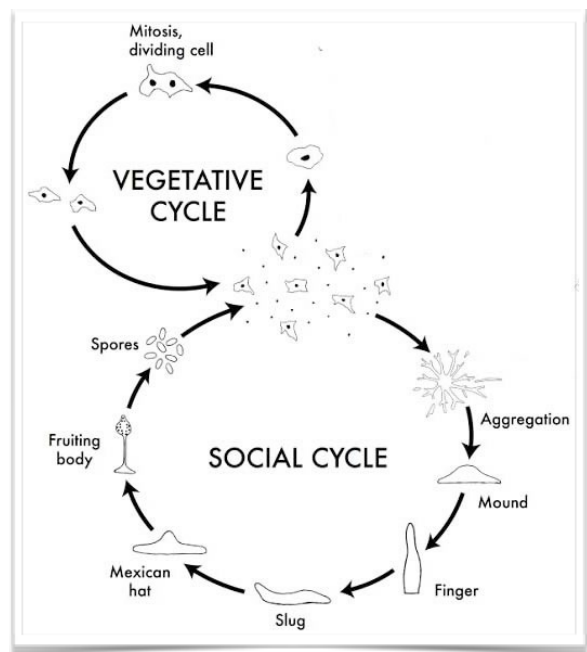
96 Molecular phylogeny and evolution of morphology in the social amoebas: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2173941/#!po=38.8889 and A Simple Mechanism for Complex Social Behavior: http://youtu.be/vjRPIa0BONA

97 Behavior of cellular slime molds in the soil: http://www.mycologia.org/content/97/1/178.full

have "sacrificed them selves" for other cells, which go on to form spores. These spores are specialized cells that can survive harsh conditions and can be moved by the wind and other mechanisms into new environments. Once these spore cells land in a new environment, they convert back into unicellular amoeba that begin to feed and reproduce. The evidence indicates that within the slug, the "decision" on whether a cell will form a stalk or a spore cell is stochastic rather than innate. By stochastic we mean that the decision is controlled by underlying random processes, processes that we will consider in greater detail later on. What is important at this point is that this stochastic process is not based on genetic (genotypic) differences between the cells within a slug - two genotypically identical cells may both form spores, both stalk cells, or one might become a stalk and one a spore cell.

## Quorum sensing

Another type of behavior at the unicellular level involves a behavior known as quorum sensing. This is a process by which such organisms can sense the density of other organisms in their immediate environment. Each individual secretes a molecule which they can also respond to, but their response is dependent upon the concentration of the secreted molecule and their response is non-linear. So what does that mean? As the concentration of signaling molecules increases, there is a discrete "threshold" concentration below which the cells/organisms do not change their behavior in response to the secreted compound and above which they do. When the cells/organisms are present at a low density, the concentration of the signaling molecule never reaches the threshold concentration. When the density (organisms per unit volume) increases sufficiently, the concentration of the signaling molecule rises above threshold and the cells/organisms change their behavior. Often this involves changes in the expression of specific genes (we will consider what that means exactly later on).[98]
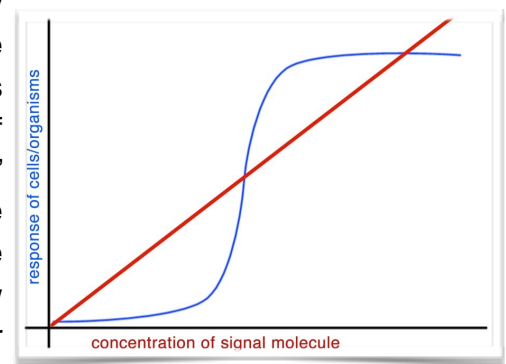
A classic example of a number of cooperative and quorum sensing behaviors is provided by the light emitting marine bacteria *Vibro fischeri. These* are marine bacteria that form a symbiotic arrangement with the squid *Euprymna scolopes*.[99] In these squid, the *V. fischeri* bacteria colonize a special organ known as a light organ. The squid uses light emitted from this organ to confuse and hide from its own predators as it hunts its prey. While their are many steps in the colonization process, and its regulation is complex, we will just consider a few to indicate how cooperative behaviors between the bacteria are critical. For the colonization of the squid's light organs the *V. fisherei* bacteria must bind to a specific region of the juvenile squid. As they divide, they sense the presence of their neighbors and begin to secrete molecules that form of gooey matrix - this leads to the formation of a specialized aggregate of cells (a type of biofilm) that is essential for the bacteria to colonize the squid's light organs. Within the biofilm, the bacteria acquire the ability to follow chemical signals produced by the squid's

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[98] Quorum sensing in bacteria: http://www.ncbi.nlm.nih.gov/pubmed/11544353

[99] Gimme shelter: how Vibrio fischeri successfully navigates an animal's multiple environments: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3843225/pdf/fmicb-04-00356.pdf

light organ cells. The bacteria swim (through a process known as chemotaxis) toward these signals, thereby entering and colonizing the light organs.

The bacteria in the light organs can emit light through a reaction involving the luciferin molecule. This reaction is catalyzed (that is, speeded up) by the protein luciferase, which is encoded by one of the bacteria's genes. We will discuss in some detail the thermodynamics of such reactions in the next section of the course. Given that bacteria are small, you can imagine that very little light would be emitted from a single bacteria. If there are only a small number of bacteria within the light organ, it would be ineffectual to carry out the light emitting reaction. The light emitting reaction occurs only when the number of bacteria within a light organ becomes sufficiently high. But how do the bacteria know that they are in the presence of sufficient numbers of neighbors? Here is where quorum sensing comes into play. The light reaction components are regulated by a molecule secreted by the bacteria. At high concentrations of bacteria, the concentration of the secreted molecule rises above a threshold, and the bacteria respond by turning on their light emitting system.
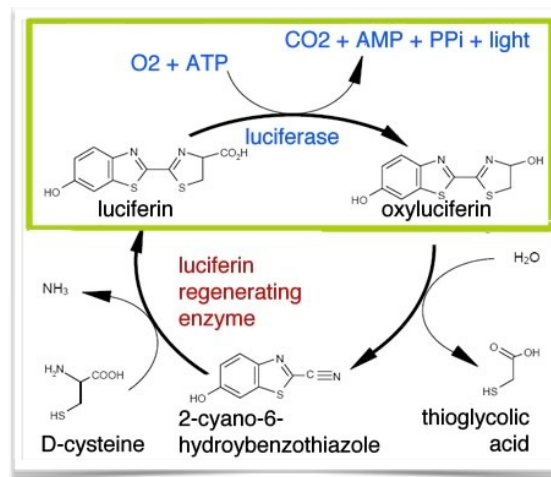


Mechanistically similar systems are involved in a range of processes including the generation of toxins (virulence factors and antibiotics directed against other types of organisms). These are produced only when the density of the bacteria rises above a threshold concentration. This insures that when an "expensive" toxin or other secreted molecule is made, it is effective – that is, it is produced at a level high enough to carry out its intended role. These high levels can only be attained through cooperative behaviors involving many individuals.
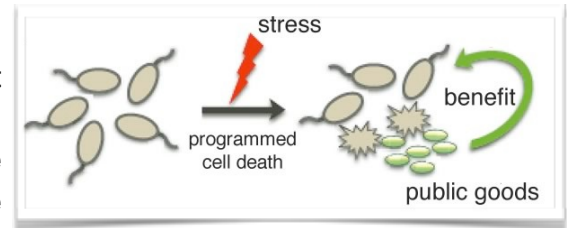
## Active (altruistic) cell death

One type of behavior you might think would be impossible for evolutionary processes to produce would be the active, "intentional" or programmed death of a cell or an organism. Yet, such behaviors are found in a wide range of systems.[100] The death and release of leaves from deciduous trees in the autumn is an example of a programmed cell death process known generically as **apoptosis**. The process amounts to cellular suicide. It plays important roles in the formation of various structures within multicellular organisms, such as the fingers of your hands, which would develop as paddles without it, as well as playing a critical role in development of the immune and nervous systems, topics beyond the scope of this book. The process of programmed cell death is distinct from accidental cell death, such as occurs when a splinter impales a cell or you burn your skin. Such accidental death leads to what is known as necrosis, in which cellular contents are spilled out of the dying cell. It often provokes various organismic defense systems to migrate into the damaged area, primarily to fight off bacterial infections. The swelling and inflammation associated with injury is an indirect result of necrotic cell death. In contrast, apoptotic cell death occurs by a well defined pathway and requires energy to carry out. Cell

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[100] see On the paradigm of altruistic suicide in the unicellular world http://www.ncbi.nlm.nih.gov/pubmed/20722725

contents are retained during the process, and no inflammatory, immune system response is provoked. In general it appears to play specific and important roles within the context of the organism. Commitment to active cell death is generally very tightly controlled. A detailed discussion of the molecular mechanisms involved in apoptosis is beyond the scope of this course.

Here we will consider active/programmed cell death in the context of simpler systems, specifically those formed by unicellular organisms. In unicellular organisms, active cell death is a process triggered by environmental stresses together with quorum sensing. In this situation, a subset of the cells will "decide" to undergo active cell death by activating a pathway that will lead to the death of the cell. Now when one cell in a densely populated environment dies, its contents are released and can be used by the living cells that remain. These living cells gain a benefit, and we would predict that the increase in nutrients would increase their chances of their survival and successful reproduction. This strategy works because as the environment becomes hostile, not all cell die at the same time. As we will see later on, this type of individualistic behavior can occur even in a group of genetically identical cells through the action of stochastic processes.



So how do cells kill themselves (on purpose)?  Many use a similar strategy. They contain a gene that directs the expression of a toxin molecule, which by itself will kill the cell. This gene is expressed in a continuous manner. Many distinct toxin molecules have been identified, so they appear to be analogous rather than homologous. Now you may well wonder how such a gene could exist, how does the cell survive in the presence of a gene that encodes a toxin. The answer is that the cell also has a gene that encodes an anti-toxin molecule, which typically binds to the toxin and renders it inactive. Within the cell, the toxin-anti-toxin complex forms exists but does no harm, since it is inactive (the toxin's activity is inhibited by the binding to the anti-toxin molecule.)  The toxin and anti-toxin molecules differ however in one particularly important way. The toxin molecule is relatively stabile - once made it exists for a substantial period of time before it is degraded by other molecular systems within the cell. In contrast, the anti-toxin molecule is unstable. It is rapidly degraded. It can be maintained at a high enough level to inhibit the toxin only if new anti-toxin molecules are continually synthesized.  In a sense the cell has become addicted to the toxin-anti-toxin module.

Now, what happens if the cell is stressed, either by changes in its environment or perhaps infection by a virus. Often the synthesis of cellular components slows or stops. Now can you predict what happens? The level of the stable toxin molecule within the cell remains high and only slowly decreases, while the level of the unstable anti-toxin drops rapidly. It quickly drops below the threshold level required to keep the toxin inactive, so that the now active toxin initiates the process of active cell death.

In addition to the dying cell sharing its resources with its neighbors, active cell death can be used as a population-wide defense mechanism against viral infection. One of the key characteristics of viruses is that they must replicate within a living cell. Once a virus enters a cell, it typically disassembles itself and sets out to reprogram the cell's biosynthetic machines to generate new copies of the virus. During the period between viral disassembly and the appearance of newly synthesized

viruses, the infectious virus disappears - it is said to be latent. If the cell were to kill itself before new viruses were synthesized, it would also kill the infecting virus. By killing the virus (and itself) the infected cell acts to protect its neighbors from viral infection - this can be seen as the ultimate kind of altruistic, self-sacrificing behavior we have been considering.[101]

**Inclusive fitness, group selection, and social evolution**

**Kin selection**:So the question that troubled Darwin and others was, how can evolutionary processes produce this type of social, self-sacrificing behavior? Consider, for example, the behavior of bees. Worker bees, who are sterile females, "sacrificed themselves to protect their hives" even though they do not themselves reproduce.[102] Another example, taken from the work of R.A. Fisher (1890 – 1962) involved the evolution of noxious taste as a defense against predators. Assuming that the organisms that were eaten by predators did not benefit from this trait, how could the trait of "distastefulness" arise in the first place? If evolution via natural selection is about an individuals differential reproductive success, how are such traits possible? The formal answer was provided by W.D. Hamilton (1936 – 2000) who expressed the answer in the equation $r \times b > c$ (defined by Sewall Wright (1889 – 1988)), where "b" stands for the benefit of the trait to the organism and others, "c" stands for the cost of the trait to the individual and "r" indicates the extent to which two organisms within the population are related to one another.

Let us think some more about what this means. How might active cell death in bacterial cells be beneficial evolutionarily? In this case reproduction is asexual and the cell's/organism's neighbors are likely to be closely related. They are likely to be a clone, that is sets of cells or organisms derived from a common parent in an asexual manner. Aside from occasional mutations, the cells/organisms within a clone are genotypically identical. Their genotypic similarity arises from the molecular processes by which the genetic material (DNA) is replicated and delivered to the two daughter cells. We can characterize the degree of relationship or genotypic similarity through their r or coefficient of relationship. In two genetically identical organisms, $r = 1$. Two unrelated organisms, with minimum possible genotypic similarity would have an r very close to, but slightly larger than 0 (you should be able to explain why r is not equal to 0). Now let us return to our cost-benefit analysis of a trait's effect on reproductive success. As we introduced before, each trait has a cost = c to the organism that produces it, as well as a potential benefit = b in terms of reproductive success. Selection leads to a trait becoming prevalent or fixed within a population if $b > c$. But this equation ignores the effects of a trait on other, related and neighboring organisms. In this case, we have to consider the benefits accrued by these organisms as well. Let us call the benefit to the cooperative/altruistic = $b_i$ while the benefit to others/ neighbors = $b_o$ . To generate our social equation, known as Hamilton's rule (see above) we need to consider what is known as the inclusive fitness, namely the benefits provided to others as a function of their relationship to the cooperator. So $b > c$ becomes $b_i + r \times b_o > c$. This leads to the conclusion that a trait can evolve if the cost to the cell or organism that displays it, in terms of metabolic, structural or behavioral impact on its own reproductive ability, is offset by a sufficiently large increase in the

[101] The evolution of eusociality: http://www.ncbi.nlm.nih.gov/pubmed/20740005.1

[102] Dugatkin, L.A. 2007. Inclusive Fitness Theory from Darwin to Hamilton.  http://www.genetics.org/content/176/3/1375.full

reproductive success of individuals related to it. The tendency of an organism to sacrifice itself for another will increase (be selected for) provided that the reproductive success of closely enough related organisms is increased sufficiently. We will see that we can apply this logic to a wide range of situations, and it provides an evolutionary mechanism driving the appearance and preservation of various social behaviors.

That said, the situation can be rather more complex. Typically, to work, inclusive fitness requires a close relationship to the recipient of the beneficial act. So how is this relationship assessed? How does one individual know that it is making a sacrifice for its relatives and not just a bunch of (semi-) complete strangers? As social groups get increasingly large, this becomes a more and more difficult task. One approach is to genetically link the social trait (e.g. altruistic behavior) to a physically discernible trait, like smell or a detectable structure. This is sometimes called a "green beard" trait. Individuals that cooperate (that is, display social behavior) with other organisms do so only when the green beard trait is present. The presence of the green beard trait indicates that the organism is related to the cooperator. Assume a close linkage between the two traits (social and visible), one can expect social behavior from an apparent (distantly related) stranger. In some cases, a trait may evolve to such a degree that it becomes part of an interconnected set of behaviors. Once, for example, humans developed a brain sufficiently complex to do what it was originally selected for (assuming that it was brain complexity that was selected, something we might never know for sure), this complexity may have produced various unintended byproducts. Empathy, self-consciousness, and a tendency to neurosis may not be directly selected for, but could be a side effect of behavioral processes or tendencies that were. As a completely unsupported (but plausible) example, the development of good memory as an aid to hunting might leave us susceptible to nightmares. Assume, for the moment since we are speculating here, that empathy and imagination are "unintended" products of selective processes. Once present, they themselves can alter future selection pressures and they might not be easy to evolve away from, particularly it they are mechanistically linked to a trait that is highly valued (that is, selected). The idea that such traits have a basis in one's genotype is strongly supported by the effects of various genetic mutations on personality and behavior. That said, this is a topic far beyond the scope of this book.

## Group selection

A proposed alternative to inclusive fitness has been the concept of group selection. In this type of evolutionary scenario, small groups of organisms of the same species are effectively acting as single (perhaps colonial) organisms and it is the reproductive success of the group compared to other groups of the organism, that benefit from the presence of cooperative and altruistic traits. Again the mathematical analysis is similar (and it is claimed that mathematically group and kin selection are equivalent).[103] The costs of a trait must be offset by the benefits, but now the key factor is membership in a particular group (and typically, members of a group tend to be related to one another). The life cycle of the bacterium *Myxococcus xanthus* provides an example of this type of behavior. When environmental conditions are harsh, the cells aggregate into dense, 100 μm diameter, "fruiting bodies"

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[103] Mathematics of kin- and group-selection: formally equivalent? http://www.ncbi.nlm.nih.gov/pubmed/19929970

containing about 100,000 stress resistant spores each. When the environment improves, and prey becomes available the spores are released en mass and return to active life. They move and feed in a cooperative manner through the release of digestive enzymes, which because they are acting in a quorum mode, can reach high levels.[104] A well coordinated group is expected to have a significant reproductive advantage compared to a more anarchic collection of cells.

While their functional roles are clearly different, analogous types of behavior are seen in flocks of birds, schools (or shoals) of fish, swarms of bees, and blooms of algae.[105] They represent a cooperative strategy by which organisms can gain a reproductive advantage over those that do not display this behavior. While the original behavior is likely the result of kin selection. In the wild it is possible that different groups (communities) could be in competition with one another, and the group that produces the most offspring, that is, reproductively successful groups, will come to dominate.
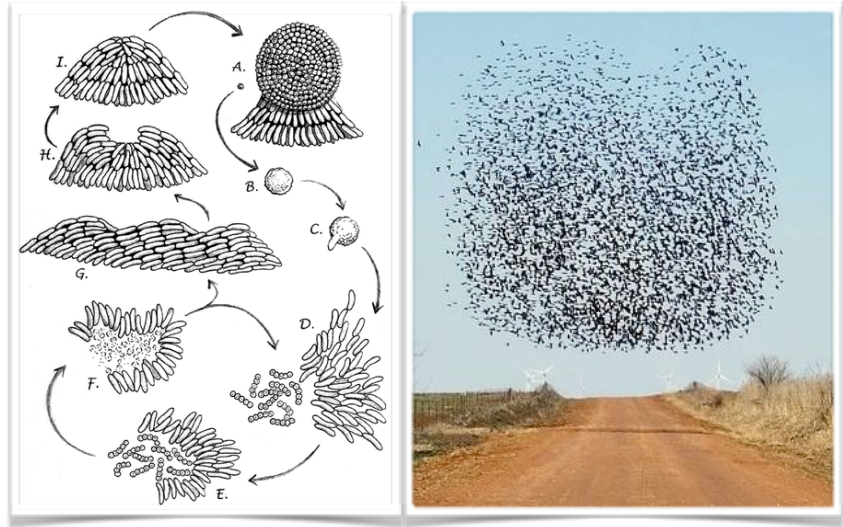


## Defense against social cheaters

Now an interesting question arises, within a social organization, such as a group of cooperating microbes or hunters,[106] we can expect that, through mutation (or through other behavioral mechanisms), cheaters will arise. What do we mean by a cheater? Imagine a bacterium within a swarm, a cell in an organism, or a animal in a social group that fails to obey the "rules." In the case of slime mold aggregates, imagine that a cell can avoid becoming a non-reproductive stalk, but rather always differentiates to form a reproductively competent spore. What happens over time. One plausible scenario would be that this spore cell begins its own clone of migratory amoeba, but when conditions change so that aggregation and fruiting body formation occur, most of the cells, avoid forming the stalk. We would predict that the resulting stalk, required to lift the spore forming region above the soil and necessary for spore dispersal, would be short or non-existent, and so would reduce the efficiency of dispersion between different aggregates, as a function of the number of individuals with a cheater phenotype present. If dispersion is important for reproductive success, there would be selection for those who maintain it, and against cheaters.

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[104] Evolution of sensory complexity recorded in a myxobacterial genome: http://www.ncbi.nlm.nih.gov/pubmed/17015832

[105] How Does Social Behavior Evolve? http://www.nature.com/scitable/knowledge/library/how-does-social-behavior-evolve-13260245

[106] An interesting read: The stag hunt and the evolution of social structure. http://bilder.buecher.de/zusatz/22/22362/22362426_lese_1.pdf

Now the question is, once a social behavior has evolved, under what conditions can evolutionary mechanisms maintain it. One approach is to link the ability to join a social group with various internal and external mechanisms.  This makes "cooperators" recognizable and works to maintain a cooperative or altruistic trait even in the face of with individual costs. There are a number of plausible mechanisms associated with specific social traits.  This is, however, a topic that can be easily expanded into an entire course. We will focus on common strategies with occasional references to specific situations. To illustrate these mechanisms, we will use human tissues as an example. We can consider the multicellular organism as a social system. The cells that compose it have given up their ability to reproduce a new organism for the ability to enhance the reproductive success of the whole organism. In this context, cancer is a disease that arises from mutations that lead to a loss of social control. Cells whose survival and reproduction is normally strictly controlled, lose that control; they become anti-social. They begin to divide in an uncontrolled manner, disrupt the normal organization of the tissue in which they find themselves, and can even breakaway, migrate and colonize other areas of the body, a process known as metastasis. The controlled growth of the primary tumor and these metastatic colonies leads eventually to the death of the organism as a whole.

When we think about maintaining a social behavior, we can think of two general mechanisms: intrinsic and extrinsic policing. For example, assume that a trait associated with the social behavior is also linked to, or required for cellular survival. In this case, a mutation that leads to the loss of the social trait may lead to cell death. Consider this in the context of cancer. Normal cells can be considered to be addicted to normality. When their normality is disrupted they undergo a type of active cell death, known as apoptosis. A cell carrying a mutation that would enable it to grow in an uncontrolled, inappropriate manner will likely kill itself before it can produce significant damage.[107] For a tumor to grow and progress, other mutations must somehow disrupt and inactivate the apoptotic process. The apoptotic process reflects an intrinsic-mode of social control. It is a little like the guilt experienced by (some) people when they break social rules or transgress social norms. The loss of social guilt or embarrassment is analogous to the inhibition of apoptosis in response to various cues associated with abnormal behavior.

In humans, and a number of other organisms, there is also an extrinsic social control system. This is analogous to the presence of external policeman (guilt and apoptosis are the internal policemen). Mutations associated with the loss of social integration, that is the transformation of a cell to a cancerous state can lead to changes in the character of the cell. These changes can be recognized by specialized cells of the organism's immune system; these cells recognize the mutant cell and kill it.[108]  Of course, given that tumors occur and kill people, we can assume that there are mutations that enable tumor cells to avoid what is known as "immune system surveillance". As we will see, one part of the cancerous phenotype is often a loss of normal mutation and genome repair systems; in effect the mutant cell has increased the number of mutations, and consequently the genetic variation in the cancer cell population. While many of these variants are lethal, the overall effect is to increase the rate of cancer cell evolution. This leads to an evolutionary race. If the cancer is killed by intrinsic and

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[107] Apoptosis in cancer: http://carcin.oxfordjournals.org/content/21/3/485.full

[108] Immune recognition of self in immunity against cancer: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC503781/

extrinsic control systems, no disease occurs. If, however, the cancer evolves fast enough to avoid death by these systems, the cancer will progress and spread. As we look at a range of social systems, from cooperating bacteria to complex societies, we see examples of these two types of control, intrinsic and extrinsic.

**Driving the evolutionary appearance of multicellular organisms**

Now that we have some idea about cooperative behaviors and how evolutionary mechanisms can select and maintain them, we can begin to consider their role in the evolution of multicellular organisms.[109] As we have mentioned there are a number of strategies that organisms take to exploit their environment. Most prokaryotes are unicellular, but some can grow to gigantic sizes. For example, the bacterium *Epulopiscium fishelsoni*, inhabits the gut of brown surgeonfish (*Acanthurus nigrofuscus*); it can grow to more than 600 μm in length. As we will see (from an experimental perspective) the cells of the unicellular eukaryotic algae of the genus *Acetabularia* can be more than 10 cm in length. On the other hand, a number of multicellular prokaryotes have been described, some exhibit quite complex behaviors. A particularly interesting one is a species of bacteria that form multicellular colonial organisms that sense and migrate in response to magnetic fields.[110]  Within the eukaryotes, there are both unicellular and microscopic species (although most are significantly larger than the unicellular prokaryotes) as well as a range of macroscopic and multicellular species, includes those we are most likely to be familiar, namely animals, plants, and fungi.

A question arises, what drove the appearance of multicellular organisms. A number of theoretical and empirically supported models have been proposed. It has been suggested that predation is an important driver, either enabling the organisms to become better (or more specific) predators or to avoid predation. For example, Borass et al.,[111] reported that the unicellular algae *Chlorella vulgaris* (5-6 μm in diameter) is driven into a multicellular form when grown together with a unicellular predator *Ochromonas vallescia,* which typically engulfs its prey. They observed that over time, *Chlorella* were found in colonies that *Ochromonas* could not ingest.

At this point, however, what we have is more like a colony of organisms rather than a colonial organism or a true multicellular organism. The change from colony to organism appears to involve cellular specialization, so that different types of cells within the organism come to carry out different functions. The most dramatic specialization being that which gives rise to the next generation of organisms, the germ cells, and those that function solely within a particular organism, the somatic cells. At the other extreme, instead of producing distinct types of specialized cells, a number of unicellular eukaryotes, known as protists, have highly complex cells that display complex complex behaviors such as directed motility, predation, osmotic



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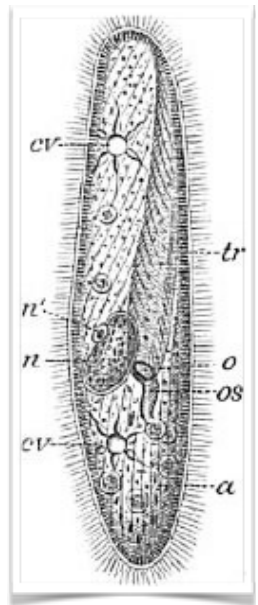
[109] The evolutionary-developmental origins of multicellularity:  http://www.amjbot.org/content/101/1/6.long

[110] A novel species of ellipsoidal multicellular magnetotactic prokaryotes from Lake Yuehu in China. http://www.ncbi.nlm.nih.gov/pubmed/24725306

[111] Phagotrophy by a flagellate selects for colonial prey: A possible origin of multicellularity:  http://link.springer.com/article/10.1023%2FA%3A1006527528063

regulation, and digestion. But such specialization can be carried out much further in multicellular organisms, where there is a socially based "division of labor." A classic example are the stinging cells of jellyfish, which are specialized to deliver poison to any organism that touches them through a harpoon-like mechanism. The specialization of this cell makes processes such as cell division impossible and typically the cell dies after it discharges. Such cells are produced by a process known as terminal differentiation, which we will consider later but only in passing. While we are used to thinking about individual organisms, the same logic can apply to groups of distinct organisms. The presence of cooperation extends beyond a single species, into ecological interactions in which organisms work together to various degrees. From a related perspective, one can view cancer as a disease in which the cooperative behavior of cells breaks down.
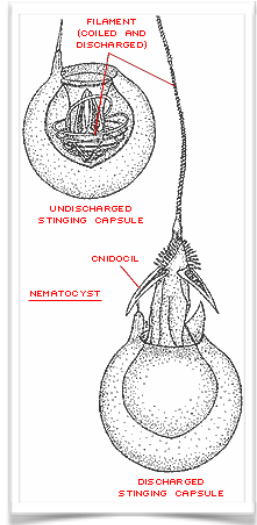
Based on the study of organisms and their genetic information, which is passed with various changes from generation to generation, we have begun to clarify the origins of multicellular organisms. Such studies indicate that multicellularity has arisen independently in a number of eukaryotic lineages. This strongly suggests that in a number of contexts, becoming multicellular is a successful way to establish an effective relationship with the environment.

**Questions to answer & to ponder:**
• Why does a quorum signal need to be secreted (released) from the organism?
• What components are necessary for quorum signaling?
• Why is r (the relationship between organisms) never 0 (although it can be quite small)?
• What types of mechanisms can be used to address the effects of cheaters in a population?
• How would these mechanisms apply to social interactions?
• Make a model of the mechanisms that can lead to the evolution of social interactions within an organism and within a population.

**Origins and implications of sexual reproduction**

One type of social interaction that we have mentioned in passing is sex. In many of unicellular eukaryotes, there are a number of distinct "mating types". Reproduction involves cooperative interactions between organisms of different mating types. Through mechanisms we will consider later, the outcome of sexual reproduction leads to increased diversity among offspring. So what are the common hallmarks of sexual reproduction? Let us return to the slime mold *Dictyostelium* as a exemplar.  We have already considered its asexual life cycle, but *Dictyostelium* also has a sexual life cycle. Under specific conditions, two
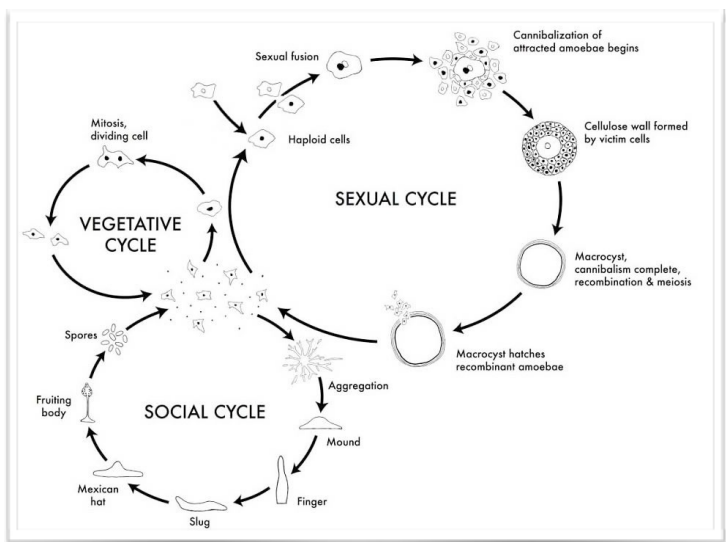
amoeboid cells of different mating types will fuse. These cells will be haploid, meaning that they have a single copy of their genome. The resulting fused cell will have two copies of the genetic material, it is diploid. This diploid cell will go through a series of events, eventually producing four haploid cells through the process known as meiosis. During meiosis there is a shuffling of genetic material, so that the genotypes of the haploid cells that emerge from the sexual process are different from those of the haploid cells that originally fused with one another.

## Sexual dimorphism

So by now you might be wondering what, biologically, defines whether an organism is female or male, and why does it matter. The question is largely irrelevant in unicellular organisms with multiple mating types. For example, the microbe *Tetrahymena* has seven different mating types, all of which appear morphologically identical. A individual *Tetrahymena* cell can mate with another individual of a different mating type but not of the same mating type as itself. Mating involves fusion and so the identity of the parents is lost. There is a cost of a sexual mode of reproduction in unicellular organisms, since they need to find a partner, something that is unnecessary in the asexual state.

In multicellular organisms, the parents do not themselves fuse with one another. Rather they produce cells, known as gametes, that do. Also, instead of two or more mating types, there are two sexes, male and female. This, of course, leads to the question, how do we define male and female? The answer is superficially simple, but its implications are profound. Which sex is which is defined by the relative size of the fusing cells the organism's produce. The larger fusing cell is termed the egg and the organism that produces it is termed a female, while the smaller is termed a sperm and the organism that produces it is termed a male. At this point, we should note the limits of these definitions. There are organisms that can change their sex, which is known generically as sequential hermaphroditism. For example, in a number of fish it is common that all individuals originally develop into males, but based on environmental cues, the largest of these males changes its sex to become a female. Alternatively, one organism can produce both eggs and sperm; such an organism is known as a constitutive hermaphrodite.

The size difference between male and female gametes changes the stakes for the two sexes. Because of the larger size of the egg, the female invests more energy in its production (per egg) than a male invests in the production of a sperm cell. It is therefore relatively more important, from the perspective of reproductive success, that each egg produce a viable and fertile offspring. As the cost to the female of generating an egg increases, the more important the eggs reproductive success becomes. Because sperm are relatively cheap to produce, the selection pressure associated with their production is relatively less than that associated with producing an egg. The end result is that there emerges a conflict of interest between females and males. This conflict of interest increases as the disparity in the relative investment per gamete or offspring increases.

This is the beginning of an evolutionary economics cost-benefit analysis. First there is what is known as the "two-fold cost of sex", which is associated with the fact that each asexual organism can produce offspring, but two sexually reproducing individuals must cooperate to produce offspring. Other,

more specific factors influence an individual's reproductive costs. For example, the cost to a large female laying a small number of small eggs that develop independently is less than that of a small female laying a large number of large eggs. Similarly, the cost to an organism that feeds and defends its young for some period of time after they are born (that is, leave the body of the female) is larger than the cost to an organism that lays eggs and leaves them to fend for themselves. Similarly, the investment of a female that raises its young on its own is different from that of the male that simply supply sperm and leaves. As you can imagine, there are many many different reproductive strategies (many more than we can consider), and they all have implications. For example, a contributing factor in social evolution is that where raising offspring is particularly "expensive", cooperation between the sexes or groups of organisms  in child rearing can improve success, and increase the return on the investment of the organisms involved. But what is important to remember (and be able to apply in specific situations) is that the reproductive investments, and so evolutionary interests, of the two sexes often diverge dramatically from one another.

Consider, for example, the situation in placental mammals, in which fertilization occurs within the female and relatively few new organisms are born from any one female. The female must commit resources to supporting the new organisms from the period from fertilization to birth. In addition, female mammals both protect their young and feed them with milk, using specialized glands (mammary glands.) Depending on the species, the young are born at various stages of development, from the active and frisky (such as goats) to the relatively helpless (humans).   During the period when the offspring are fed and protected by the female, the female is more stressed and vulnerable than other times. Under specific conditions, cooperation with other females (as can occur within a pack) or with a specific male (typically the father) can greatly increase the rate of survival of both mother and offspring, as well as the reproductive success of the male. But consider this, how does a cooperating male know that the offspring he is helping to protect and nurture are his? Spending time protecting, and gathering food for, unrelated offspring is time when the male cannot produce new offspring. It will greatly reduce the male's reproductive success. Carrying this logic out to its conclusion can lead to behaviors such as male guarding of females from interactions with other males.

As we look at the natural world, we see a wide range of sexual behaviors, from males who sexually monopolize multiple females (polygyny) to polyandry, where the female has multiple male "husbands." There are situations where no pair bond forms between male and female to situations in which male and female pairs are stable and (largely) exclusive. In some cases these pairs last for extremely long times, in others there is what has been called serial monogamy where pairs form for a while, break up, and new pairs form (this seems relatively common among performing arts celebrities). There are situations in which females will mate with multiple males, a behavior that is thought to confuse males (they cannot know which offspring are theirs) and so reduces infanticide by males.[112]

It is common that while caring for their young, females are generally reproductively inactive. Where a male monopolizes a female, the arrival of a new male who displaces the previous male can lead to behaviors such as infanticide. By killing the young, the female becomes reproductively active and able to produce offspring related to the new male. There are situations, for example in some

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[112] Promiscuous females protect their offspring. http://www.ncbi.nlm.nih.gov/pubmed/16701243

spiders, in which the male will allow itself to be eaten during the course of sexual intercourse as a type of "nuptial gift", which both blocks other males from mating with a female (who is busy eating) and increases the number of offspring that result from the mating. This is an effective reproductive strategy for the male if its odds of mating with a female are low; better (evolutionarily) to mate and die than never to have mated at all.  An interesting variation on this behavior is described in a paper by Albo et al.[113] Male *Pisaura mirablis* spiders offer females nuptial gifts, in part perhaps to avoid being eaten during intercourse. Of course, where there is a strategy, there are counter strategies. In some cases, instead of an insect wrapped in silk, the males offers a worthless gift, an inedible object wrapped in silk. Females cannot initially tell that the gift is worthless, but quickly terminate mating when they discover it is. This reduces the odds of a male's reproductive success.  As deceptive male strategies become common, females are likely to display counter strategies.  For example, a number of female organisms store sperm from a mating, and can eject that sperm and replace it with that of another male (or multiple males) obtained from subsequent mating events.[114] There is even evidence that in some organisms, such as the wild fowl *Gallus gallus*, females can bias against fertilization from closely related males, a situation known as cryptic female choice, cryptic since it is not overtly visible in terms of who the female does or does not mate with.[115] And so it goes, each reproductive strategy can lead to counter measures.[116] For example, in species in which a male guards a set of females (its harem), groups of males can work together to distract the male, allowing members of their group to mate with the females. But be clear, these are only a few of the mating and reproductive strategies that exist in the living world.[117]  Molecular studies that can distinguish an offspring's parents suggest that "cheating" by both males and females is not unknown even among highly monogamous species. The extent of cheating will, of course, depend on the stakes. The more negative the effects on reproductive success, the more cheating will be selected against.

In humans, a female can have at most one pregnancy a year, while a totally irresponsible male could, in theory at least, make a rather large number of females pregnant during this same period of time. Moreover, the biological cost of generating offspring is substantially greater for the female, compared to the male.[118] There is a low, but real danger of the death of the mother during pregnancy, whereas males are not so vulnerable, at least in this context. So, if the female is going to have offspring, it would be in their evolutionary interest that those offspring be as robust as possible, meaning that they are likely to survive and reproduce. How can the female influence that outcome? One approach is to control fertility, that is the probability that a "reproductive encounter" results in

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[113] Worthless donations: male deception and female counter play in a nuptial gift-giving spider: http://www.biomedcentral.com/1471-2148/11/329

[114] Evolution: Sperm Ejection Near and Far: http://www.sciencedirect.com/science/article/pii/S0960982204004452

[115] Cryptic female choice favors sperm from major histocompatibility complex-dissimilar males: http://rspb.royalsocietypublishing.org/content/280/1769/20131296.full

[116] Sperm Competition and the Evolution of Animal Mating Systems: http://www.sciencedirect.com/science/book/9780126525700

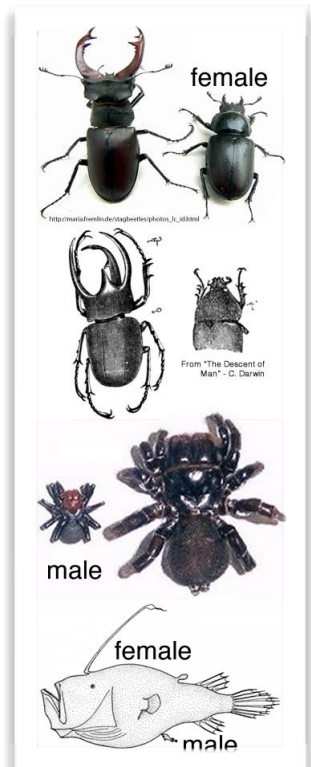[117] The Evolution of Alternative Reproductive Strategies: Fitness Differential, Heritability, and Genetic Correlation Between the Sexes: http://jhered.oxfordjournals.org/content/92/2/198.full

[118] 'Parental investment: http://www.anthro.utah.edu/PDFs/maynardsmith77parenting.pdf

pregnancy. This is accomplished physiologically, so that the odds of pregnancy increase when the female has enough resources to successfully carry the pregnancy to term. It should be noted that these are not conscious decisions on the part of the female, but physiological responses to various cues. There are a number of examples within the biological world where females can control whether a particular mating is successful (that is, produces offspring). For example, female wild fowl are able to bias the success of a mating event in favor of dominant males by actively ejecting the sperm of subdominant males.[119]  One might argue that the development of various forms of contraception are yet another facet of this type of behavior, but one in which females (and males) consciously control reproductive outcomes.

**Sexual selection**

As we have already noted it is not uncommon to see morphological and behavioral differences between the two sexes. Sometimes the sexual dimorphism and associated behavioral differences between the sexes are profound; they can even obscure the fact that the two sexes are actually members of the same species. In some cases, specific traits associated with one sex can appear to be maladaptive, that is, they might be expected to reduce rather than enhance an organism's reproductive potential.[120] The male peacock's tail, the gigantic antlers of male moose, or the bright body colors displayed by some male birds are classic examples. Darwin recognized the seriousness of this problem for evolutionary theory and addressed it in his book "The Descent of Man and Selection in Relation to Sex" (1871). Where the "investment" of the two sexes in successful reproduction is not the same, as is often the case, the two sexes may have different and potentially antagonistic reproductive strategies. Organisms of different sexes may be "looking" for different traits in their mates. In general, the larger parental investment in the production and rearing of offspring, the less random is mating and the more prominent are the effects of sexual selection.[121] It is difficult not to place these behaviors in the context of conscious behaviors, looking, wanting, etc., whereas in fact these are generally the result of evolved behaviors and do not imply self-conscious decision making.  This may even be the case among organisms, like humans, who are self-conscious. What is happening is an interaction between costs, benefits, and specific behaviors.



female

http://mariafrenlin.de/stagbeetles/photos_lc_id.html

From "The Descent of Man" - C. Darwin

male

female

male

Consider an example in which the female does not require help in raising offspring, but in which the cost to the female is high. Selection would be expected to favor a behavior in which females mate preferentially with the most robust males available. Females will select their mates based on male phenotype on the (quite reasonable) assumption that the most robust appearing male will be the most

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[119] Female feral fowl eject sperm of subdominant males: http://www.ncbi.nlm.nih.gov/pubmed/10866198

[120] Flaunting It' - Sexual Selection and the Art of Courtship: http://youtu.be/g3B8hS80k6A

likely to produce the most robust offspring.  In the context of this behavior, the reproductive success of a male would be enhanced if they could "advertise" their genetic robustness, generally through visible and unambiguous features.[122] To be a true sign of the male's robustness, this advertisement needs to be difficult to fake and so reflects the true state of the male. For example consider scenarios involving territoriality. Individuals, typically males, establish and defend territories. Since there are a limited number of such territories and females only mate with males that have a territory, only the most robust, as defined in terms of the ability to establish and defend a territory, are reproductively successful. An alternative scenario involves males monopolizing female's sexually. Because access to females is central to their reproductive success, males will interact with one another to establish a dominance hierarchy, typically in the form of one or more "alpha males".  Again, the most robust males are likely to emerge as alpha males, which in turn serves the reproductive interests of the females. This type of dominance behavior is difficult or impossible to fake. But, cooperation between non-alpha males can be used to thwart the alpha males monopolization of females.

Now consider how strategies change if the odds of successful reproduction are significantly improved if the male "stays around" and helps the female raise their offspring. In this situation, there is a significant reproductive advantage if females can accurately identify those males that display this type of reproductive loyalty.[123] Under these conditions, that is the shared rearing of offspring with a "committed" male, females will be competing with other females for access to these males.  Moreover, it is in the male's interest to cooperate with fertile females, and often females (but not human females) advertise their state of fertility (that is the probability that mating with them will produce offspring) through external signals. There are of course, alternative strategies. For example, groups of females (sisters, mothers, daughters, aunts, and grandmothers) can cooperate with one another, thereby reducing the importance of male cooperation. At the same time, there may be what could be termed selection conflicts. What happens if the most robust male is not the most committed male? A female could maximize their reproductive success by mating with a robust male and bonding with a committed male, who helps rear another male's offspring. Of course this is not in the committed male's reproductive interest. Now selection might favor male's that cooperate with one another to ward off robust but promiscuous and "transient" males. Since these "loyal" males already bond and cooperate with females, it may well be a simple matter for them to bond and cooperate with each other.  In a semi-counter intuitive manner, the ability to bond with males could be selected for based on its effect on reproductive success with females. On the other hand a male that commits themselves to a cooperative (loyal and exclusive) arrangement with a female necessarily limits their interactions with other females. This implies that they would attempt to insure that the offspring they were raising were genetically related to them.

Clearly the situation quickly gets complex and many competing strategies are possible. Different species make different choices depending upon their evolutionary history and environmental constraints. As we have noted above, various signals are advertised through what are known as

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[122] In Male Rhinoceros Beetle, Horn Size Signals Healthy Mate: http://www.aaas.org/news/releases/2012/0726sp_plumage.shtml

[123] http://www.madsci.org/posts/archives/2012-05/1336600952.Ev.r.html

"secondary sexual characteristics". These are traits that tend to vary dramatically between the two sexes since they are meant to advertise different thing (loyalty, robustness, fertility). The size and symmetry of a beetle's or an elk's antlers, or a grasshopper's song communicate rather clearly their state of health.[124] The tail of the male peacock is a common example, you either have a large, colorful and symmetrical tail, all signs of a healthy male, or you do not – there is little room for doubt. Moreover, these predictions have been confirmed in a number of systems experimentally; the robustness of offspring does correlate with the robustness of the male, a "win" for evolutionary logic.[125]

*One of the most robust and reliable findings in the scientific literature on interpersonal attraction is the overwhelming role played by physical attractiveness in defining the ideal romantic partner (Hatfield & Sprecher, 1986; Jackson, 1992). Both men and women express marked preference for an attractive partner in a noncommitted short-term (casual, one night stand) relationship (Buss & Schmitt, 1993).*

It is critical that both females and males can correct "read" various traits. For example, males can often read the traits of other males in order to determine whether they are likely to win a fight with another male, a fight that could end up crippling both males. A more complex question is how does a female determine whether a male is committed, and vice versa? As with advertisements of overall robustness, we might expect the female to look for behaviors that are difficult to fake. So how does one unambiguously signal one's propensity to loyalty and willingness to cooperate? As noted above, one could use the size and value of "nuptial gifts". The more valuable, that is, the more expensive and difficult the gift is to attain, the more loyal the female can be expected the gift giver to be. On the other hand, once valuable gift giving is established, one can expect the evolution of traits in which the cost of the gift given is reduced and by which the receiver needs to be skeptical about the actual nature of the gift.

*For committed long-term relationships, females appear to be willing to relax their demand for a partner's attractiveness, especially for males with high social status or good financial prospects (for a review see Buss, 1999).*

*Males also look for various personality qualities (kindness, understanding, good parental skills) in their search for long-term mating partners, but unlike females, they assign disproportionately greater importance to attractiveness compared to other personal qualities (Buss, 1999).*

This points out a general pattern. When it comes to sexual (and social) interactions, organisms have evolved to "know" the rules involved. If the signs an organism must make to another are expensive, there will be selective pressure to cheat. Cheating can be suppressed by making the sign difficult or impossible to fake, or by generating counter-strategies that can be used to identify fakes. These biological realities produce many behaviors, some of which are disconcerting. These include "sexual cannibalism" and male infanticide mentioned above. What we have not considered as yet is the conflict between parents and offspring. Where the female makes a major and potentially debilitating investment in its offspring, it

*The paramount importance of attractiveness in males' mate choices has been recently demonstrated by using the distinction between necessities (i.e., essential needs, such as food and shelter) and luxuries (i.e., objects that are sought after essential needs have been satisfied, such as a yacht or expensive car) made by economists.*

*Using this method, Li et al., (2002) reported that males treat female attractiveness as a necessity in romantic relationships; given a limited "mating budget," males allocate the largest proportion of their budget to physical attractiveness rather than to other attributes such as an exciting personality, liveliness, and sense of humor. - from Mating strategies for young women by Devendra Singh (2004).*

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[124] Attractiveness of grasshopper songs correlates with their robustness against noise:http://beheco.oxfordjournals.org/content/early/2011/05/08/beheco.arr064.full

[125] Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1688278/pdf/2UET8WJ5TD06WFUT_264_297.pdf

may respond to signs of reproductive distress that might threaten the survival of the female, by spontaneously aborting the offspring. Of course, this is not in the interest of the offspring, and there will be mechanisms to maintain pregnancy, even if it risks the life of the mother. There are many variations of reproductive behavior to be found in the biological world and a full discussion is beyond the scope of this course, but it is a fascinating subject with clear but complex implications for human behavior. Part of the complexity arises from the fact that the human brain (and the mind it generates) can respond in a wide range of individualistic behaviors, not all of which seem particularly rational. It may well be many of these are emergent behaviors. That means that they were not directly selected for. but emerged in the course of evolution and once present, play a important roles in subsequent organismic behavior (and presumably evolution).

## Curbing runaway selection

Sexual selection can lead to what has been termed "runaway selection". For example, the more prominent the peacock male's tail the more likely he will find a mate, even though it may also have negative effects. There will be positive selection for larger and larger tales. Of course, selection does not really run away, but begins to settle down when the positive (in terms of sexual success) and negative (in turns of various costs) of a trait come to equal each other. Sufficient numbers of male peacocks emerge as reproductively successful, even if many males are handicapped by their tails and fall prey to predators. For another example, consider the evolution of the extremely large antlers associated with male dominance and mate accessibility such as occurred in *Megaloceros giganteous;* these antlers could also act to inhibit their ability to move through heavily wooded areas. In a stable environment, the costs and benefits associated with the development of sexual advertising would be expected to balance out; selection would produce an optimal solution. But if the environment changes, pre-existing behavior and phenotypes could act to limit an organisms ability to adapt or to adapt fast enough to avoid extinction. In the end, as with all adaptations, there is a balance between the positive effects of a trait, which lead to increased reproductive success and their negative effects, which can influence survival. The optimal form of a trait may not be stable over time, particularly if the environment is changing.

**Summary**: Social and ecological interactions apply to all organisms, from bacteria to humans. They serve as a counter-balance to the common caricature of evolution as a ruthless and never ceasing competition between organisms. This hyper-competitive view, often known as the struggle for existence or Social Darwinism, was not in fact supported by Darwin or by scientifically established evolutionary mechanisms, but rather by a number of pundits who used it to justify various political positions, particularly arguing against social programs that helped the poor at the "expense" of the wealthy. Assuming that certain organisms were inherently less fit, and that they could be identified, this view of the world gave rise to Eugenics, the view that inferior people should be killed, removed, or sterilized, less they overwhelm a particular culture. Eugenics was a particularly influential idea in the United States in the early part of the 20th century, and inspired the Nazis in Germany. What is particularly odd

about this "evolutionary" perspective is that it is actually anti-evolutionary, since if the unfit are actually unfit, they could not possibly take over a population.


### Questions to answer & ponder

• What does it mean to cheat, in terms of sexual selection - is the "cheating" organism actually being consciously deceptive?
• Why do the different sexes (of the same species) often display different secondary sexual traits?
• If the two sexes appear phenotypically identical, what might you conclude about their reproductive behaviors?
• What types of "cheating" behaviors do females use with males; or males with females?
• What are the costs involved when a male tries to monopolize multiple females? what are the advantages?
• What limits "runaway selection"?
• Why would you expect female infanticide to be extremely rare?  When might it make evolutionary sense?
• Is Devendra Singh right about "mating budgets"?
• Is the "schooling" or "herd" behavior seen in various types of animals (such as fish and cows) a homologous or an analogous trait?