

[Print](#)by **Dustin R. Rubenstein**

Figure 1.

Dustin Rubenstein is a behavioral and evolutionary ecologist who studies the causes and consequences of sociality in animals. Courtesy of Dustin Rubenstein

The theory of evolution by natural selection is relevant to all fields of modern biology, from **neuroscience** to genomics to **community ecology**. Charles Darwin spent the better part of his life developing the concept of natural selection. From the observations he made on his many travels and the experiments he conducted at his home in England, he noted that individuals in a population vary, most often in the way they look or behave (termed traits), and that not only is much of this variation heritable from parents to offspring, but traits that result in greater reproduction and survival (termed fitness) will increase in frequency over time. Yet throughout the development of his now famous theory, Darwin was puzzled by two observations that seemed at odds with natural selection. First was the observation that some traits, such as the exaggerated weapons and elaborate ornaments that many animals exhibit, surely could not help improve an individual's survival. If anything, these curious and showy traits might lead to a reduction in survival rather than an increase. So how could they be favored by natural selection? Second was the observation that the loss of reproductive ability by some individuals, particularly those in colonies of ants and other insects, surely could not help improve an individual's reproductive success. That is, how could sterility and the inability to reproduce be favored by natural selection? Darwin developed a second theory—the theory of sexual selection—to solve the first puzzle. But it was not until more than 100 years later and the development of another theory—the theory of kin selection—that scientists were able to solve Darwin's second puzzle. As I will discuss here, sexual and kin selection theories are derivations of natural selection theory, and understanding all three is essential for understanding how traits evolve.

Sexual Selection and Conflict

In Darwin's Victorian England, reproduction was thought to be a harmonious act between a man and a woman. Yet, in most animals, nothing can be further from the truth, because the reproductive interests of males and females are rarely aligned. Instead, reproduction can be viewed as a battle between the sexes for maximum genetic advantage. To understand where this idea comes from, we must start at the beginning: the developmental beginning of all **diploid** life, when a sperm fuses to an egg. In an evolutionary sense, sperm are relatively small and cheap—males can produce millions daily for the better part of their adult lives. In contrast, eggs are relatively large and expensive—females are

born with a finite number, and preparing eggs for mating takes an investment of resources. This concept of difference in the relative cost of male and female **gametes**, termed the **fundamental asymmetry of sex**, is one of the primary sex differences, and it underlies many other more familiar sex differences, like those in courtship behavior, ornamentation, or parental care.

Sexual selection is a form of natural selection that acts on traits used to gain access to mates. Members of one sex—typically males—compete with one another for access to the other sex (termed **intrasexual selection**), while the other sex—typically females—chooses among the competitors (termed **intersexual selection**). Sexual selection therefore acts more strongly on male traits used in either male-male competition or the courtship of females. This is why males in most species tend to be bigger, be more ornamented, or have more elaborate traits than females—another primary sex difference (**Fig. 2**). Since females have to invest more resources in their gametes than males do, and also often invest more in parental care once offspring are born, their choice of mate is more critical than that of males to achieving successful reproduction. This means that females are often quite choosy in their mates and show strong preferences for particular traits.

Although male traits of most species tend to be under stronger sexual selection than those of females so that males can gain access to more mates, that is not always the case. A variety of animals exhibit **sexual role reversal**, where females tend to be more elaborately decorated or to compete more aggressively with other females for access to males. In many of these sexually role-reversed species, males also perform the bulk of the parental care duties. Take seahorses, where males are endowed with a pouch for rearing young (**Fig. 3**). Female seahorses lay their eggs inside a male's pouch before swimming off in search of additional mates, leaving the male to rear the young alone.



Figure 2. Intrasexual selection

A female fallow deer (*Dama dama*) stands next to a male who is larger and has large antlers that he uses to fight or scare off rival males. © Patrick Frischknecht/Prisma/AGE Fotostock

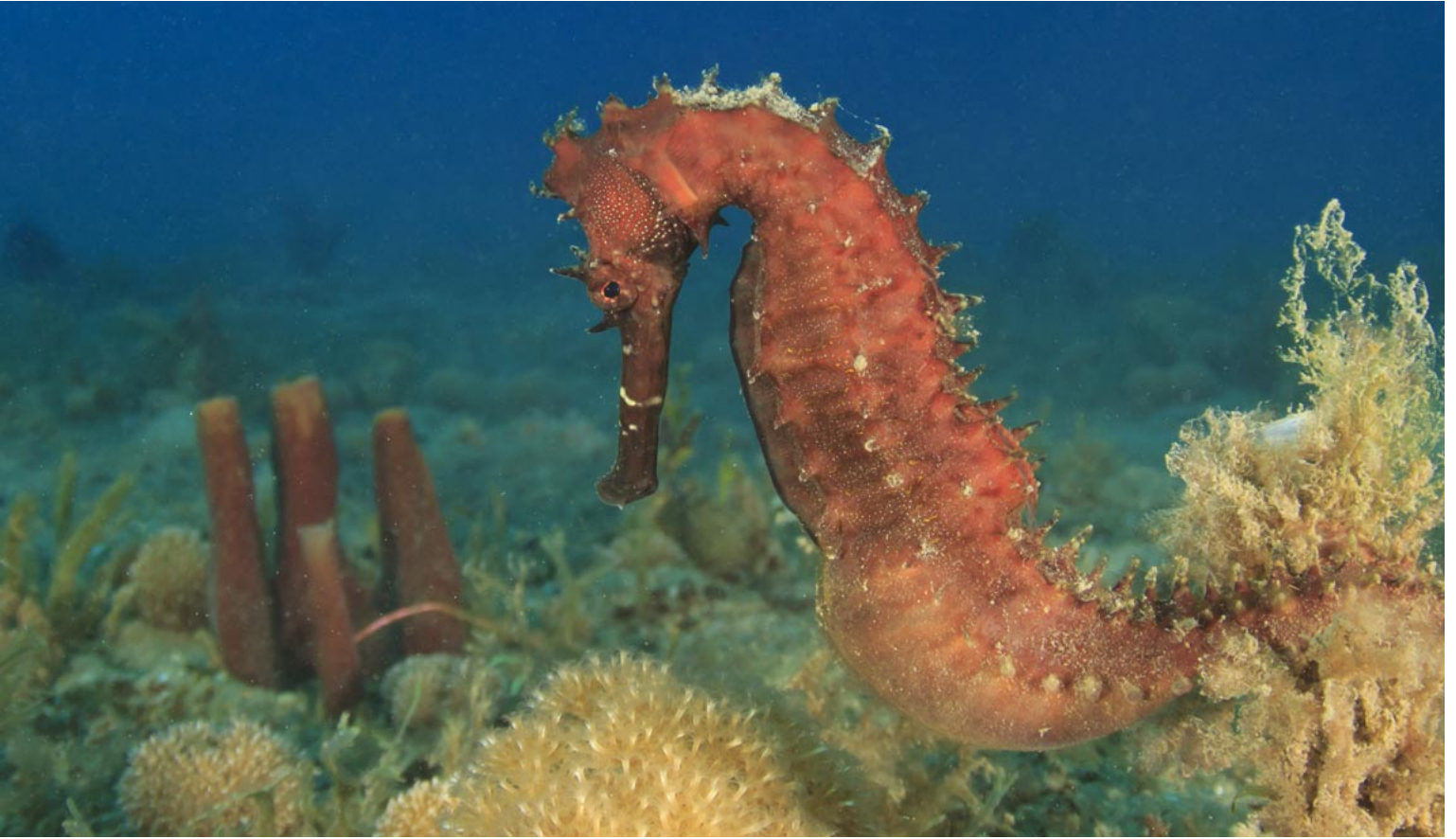


Figure 3. Sexual role reversal

A male thorny seahorse (*Hippocampus histrix*) looks visibly pregnant, which means he is carrying the eggs that a female laid inside of his pouch. © Shutterstock

Although there are many species in which male and female interests are aligned—for example, when both parents raise the young, as do many of the backyards birds common to North America (Fig. 4)—the story of reproduction is often one of **sexual conflict**, or conflict over mating decisions in which males and females have different interests and goals. For example, females typically want to find the highest quality male who will invest the most in her offspring. This investment could take the form of a **direct reproductive benefit**, such as providing parental care for the offspring or providing resources to the female. In the most extreme case, as has been seen in some spiders, males actually provide themselves to females as food after mating. In some species, the benefit that females receive from males comes in the form of an **indirect reproductive benefit**, such as good genes—those that confer vigor, health, or some other trait to her offspring. In contrast, since males often invest little more than their sperm during reproduction, often their goal is to mate as many times as possible with as many different females as they can find, and the quality of their mate is of less importance.



Figure 4. Direct reproductive benefit

A male northern cardinal (*Cardinalis cardinalis*) feeds his babies. In this species, both sexes rear young. © Woodys Photos/AGE Fotostock

To achieve their divergent reproductive goals, females are able to influence male reproductive behavior not only by exerting mate choice, but also by controlling fertilization and altering their investment in the eggs or offspring. By contrast, males can influence female reproduction not only in the way they court or through the resources they provide to females, but also by coercing females and trying to manipulate their choice. Such manipulation by males can often result in a **sexual arms race**, in which strong selection on sexual traits in males to manipulate the reproductive process of females is countered by strong selection on female traits to overcome attempts at manipulation. For example, males in many species of waterfowl have evolved elaborate genitalia that they use to circumvent female choice and achieve mating success, whereas females in these same species have evolved elaborate genitalia alterations of their own to prevent successful insemination when copulation is not by choice.

Kin Selection and Cooperation

Reproduction is not only about conflict and competition. Indeed, cooperation occurs commonly across the animal world in species ranging from microbes to humans. As we just learned, there are numerous cases in which parents work together to raise young, a phenomenon that is not surprising given that they both share genetic material with their offspring. Yet Darwin was puzzled by the observation that some individual insects in a colony help raise young despite being sterile and never having the opportunity to reproduce themselves. This type of **reproductive altruism**, or cooperative behavior that lowers one individual's reproductive success while increasing that of another, occurs not only in many species of **eusocial** insects such as ants or termites where the majority of colony members are sterile and incapable of ever reproducing, but also in a number of **cooperatively breeding** birds, mammals, and fishes where more than two individuals care for young (**Fig. 5**).



Figure 5. Reproductive altruism

Many species of animals live in groups in which some individuals forego their own reproduction to help raise others' young. In the eusocial termite *Macrotermes carbonarius* (left), a single king and queen produce all of the offspring, while other group members tend to the fungus farms that provide food (termed workers) or guard the colony from predators and other termites (termed soldiers). In the cooperatively breeding cichlid fish *Pelvicachromis taeniatus* (right), non-breeding helpers aid in rearing the offspring of a dominant breeding pair, as well as protecting the young from predators. © Budak/CC BY-NC-ND 2.0; Biosphoto/Alamy

We now know that passing on one's genes directly through personal reproduction (termed direct fitness) is not the only way that individuals can achieve fitness. Indeed, if individuals share genetic material with others, they can achieve fitness by helping these non-descendent kin survive and reproduce (termed indirect fitness). Thus, an individual's total contribution of genes passed to the next generation—the sum of direct and indirect fitness—is called inclusive fitness. Behaviors that favor the reproductive success of the relatives that an organism helps, even at a cost to that organism's own fitness, can be favored by a form of natural selection called kin selection. William Hamilton was the first biologist to make the link between inclusive fitness and the presence of sterile workers in ant colonies, something he achieved by formalizing kin selection theory in what has become known as **Hamilton's rule**. According to Hamilton's rule, a rare form of a gene for an altruistic behavior like helping to raise others' offspring will become more common if the indirect fitness gained by the altruist is higher than that direct fitness it loses as a result of the behavior.

Hamilton's rule predicts that individuals that are more closely related to each other are more likely to perform altruistic behaviors, to cooperate, and ultimately, to form societies. Since eusocial insect colonies and cooperatively breeding groups of vertebrates typically consist of parents, offspring, and other relatives, altruistic behavior is more likely to evolve in these settings. In other words, most eusocial insect colonies and many groups of cooperatively breeding vertebrates are extended families where multiple generations live together to help raise relatives. Hamilton's rule can also be extended to predict other types of conditions under which altruistic behaviors are likely to evolve. For example, since ecological conditions influence the costs and benefits of altruism, Hamilton's rule can be used to predict how food resources, habitat availability, or climatic conditions are likely to influence kin selection and the evolution of animal societies, in animals as diverse as amoebae and meerkats.

There is one main difference, however, between societies of insects and those of vertebrates. In insect colonies, like those of the ants that Darwin observed, some individuals are permanently sterile. We call these individuals workers if they help raise the offspring of a queen, or soldiers if they help defend the colony. Over evolutionary time, workers and soldiers have lost the ability to mate and produce offspring, meaning they will never reproduce during their lifetimes. In contrast, in all cooperatively breeding vertebrate societies, individuals that help rear young or defend the group—typically referred to as helpers—retain the ability to reproduce and often will do so at some point during their lives. Thus, although the same theoretical principles—kin selection and inclusive fitness—govern cooperation and the evolution of societies in both vertebrates and invertebrates, variation in the biology, ecology, and life history of different species and taxonomic groups also influences social evolution. In short, understanding why some species form complex societies and others do not requires considering more than just how genetic relationships influence reproductive altruism and cooperation.

Upon first glance, sexual and kin selection seem at odds with natural selection theory. Yet they are not. The theories of sexual and kin selection extend Darwin's idea of natural selection, not only providing explanations for how traits evolve and why conflict and cooperation occur, but also solving mysteries that puzzled Darwin himself. Over a century later, scientists remain intrigued by these questions. Those interested in sexual selection may, for example, ask why certain types of ornaments or weapons have evolved in some species but not others, or how sexual selection contributes to the process of speciation. Those interested in kin selection may explore why species that form cooperative societies tend to dominate the ecosystems in which they occur, or why societies of unrelated individuals form at all. Clearly, there is much more to learn when it comes to solving Darwin's greatest puzzles.

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