## The Evolution of Animal Societies

Social behavior evolves when cooperation among conspecifics produces, on average, higher rates of survival and reproduction than solitary individuals can achieve. Associations for reproduction may consist of little more than a coming together of eggs and sperm, but individuals of many species associate for longer times to provide care for their offspring. Associating with conspecifics may also improve survival in ways unrelated to reproduction, such as by reducing the risk of being captured by a predator.

The social systems of many animals are very simple: Males court females, the fertilized females disperse and lay eggs, and the eggs and larvae grow to maturity untended. Other systems—such as the elaborate colonies of ants, bees, and wasps or the social groups of lions and primates—are very complex. How did these complex animal societies evolve? Although today's social systems are the result of long periods of evolution, behavior leaves few traces in the fossil record. Biologists must infer possible routes of the evolution of social systems by studying current patterns of social organization. Fortunately, many degrees of social system complexity exist among living species; the simpler systems suggest stages through which the more complex ones may have passed.

We will describe only a few animal social systems, but as we look at these examples, we will keep in mind three important concepts:

- Social systems are best understood not by asking how they benefit the species as a whole, but by asking how the individuals that join together benefit by the association.
- Social systems are dynamic; individuals constantly communicate with one another and adjust their relationships.
- The costs and benefits experienced by individuals in a social system differ according to their age, sex, physiological condition, and status.
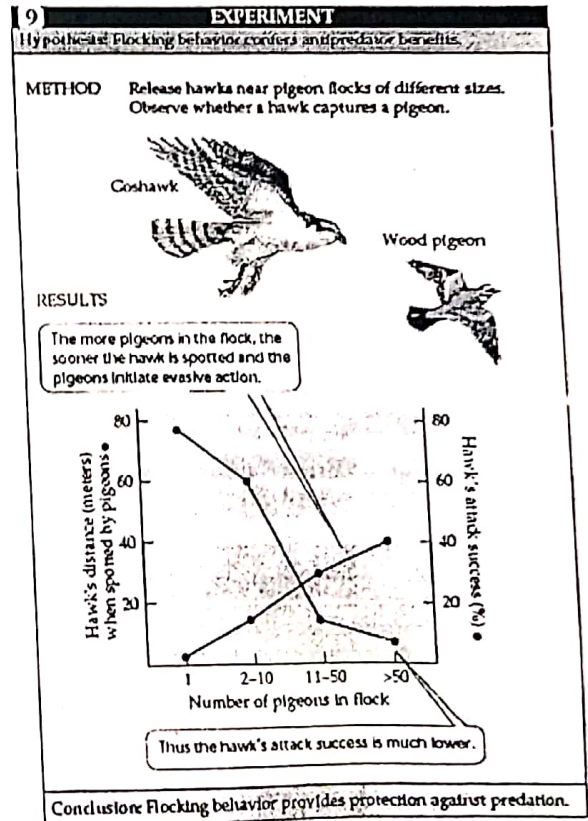
### Altruism

V. C. Wynne-Edwards published a book in 1962 entitled *Animal Dispersion in Relation to Social Behavior*. In it, he suggested that animals regulate their own population density through altruistic behavior. For example, under crowded conditions, many birds cease reproducing. The interpretation of this phenomenon was that these birds were being altruistic: Their failure to breed was for the ultimate good of the species. (Altruism means risking loss of fitness in an act that could improve the fitness of another individual.)

Wynne-Edwards suggested a mechanism called **group selection**: groups that had altruistic behavior would have a survival advantage over groups that did not.

## Group living confers benefits but also imposes costs

Living in groups may confer many types of benefits. It may improve hunting success or expand the range of prey that can be captured. For example, by hunting in groups, our ancestors were able to kill large mammals they could not have subdued as individual hunters. These social humans could also defend their prey and themselves from other carnivores, and could tell one another about, for example, the locations of food and predators.

Many small birds forage in flocks. To test whether flocking provides protection against predators, an investigator released a trained goshawk near wood pigeons in England. The hawk was most successful when it attacked solitary pigeons. Its success in capturing a pigeon decreased as the number of pigeons in the flock increased (Figure 9). The larger the flock of pigeons, the sooner some individual in the flock spotted the hawk and flew away. This escape behavior stimulated other individuals in the flock to take flight as well. But foraging in a flock also imposes a cost: The pigeons in a flock interfere with one another's ability to find seeds.



**9  EXPERIMENT**

**Hypothesis:** Flocking behavior confers antipredation benefits.

**METHOD** Release hawks near pigeon flocks of different sizes. Observe whether a hawk captures a pigeon.

Goshawk

Wood pigeon

**RESULTS**

The more pigeons in the flock, the sooner the hawk is spotted and the pigeons initiate evasive action.

*(Graph: Hawk's distance (meters) when spotted by pigeons, and Hawk's attack success (%), versus Number of pigeons in flock: 1, 2-10, 11-50, >50)*

Thus the hawk's attack success is much lower.

**Conclusion:** Flocking behavior provides protection against predation.

Social behavior has many costs as well as benefits. In some social species, individuals inhibit one another's reproduction or injure one another's offspring. An almost universal cost associated with group living is higher exposure to diseases and parasites. Long before the causes of diseases were known, people knew that association with sick persons increased their chances of getting sick. Quarantine has been used to combat the spread of illness for as long as we have written records.

The diseases of wild animals are not as well known, but they too are spread mostly by close contact.

Table 1 summarizes the benefits and costs of group living.

| Benefits | Cost |
|---|---|
| • Aggregative response to prey density means that groups indicate rich sources of food<br>• Individual risk of predation diluted by joining a group<br>• Groups can tackle larger prey than single individuals<br>• Grouping confuses predators, making it harder for them to target prey<br>• Huddling in groups helps thermoregulation<br>• Energetic advantages to swimming or flying in a group through 'slipstreaming'. | • Greater interference from competitors<br>• Greater risk of contracting disease<br>• Greater chance of being cuckolded, or<br>• mistakenly feeding someone else's<br>• offspring<br>• Investment in foraging, courtship, or other activities exploited by other group members<br>• Young may be cannibalised by neighbours<br>• Greater risk of inbreeding |

Many social groups are characterised by sustained aggressive/submissive competitive relationships between individuals. Where encounters are frequent enough, individuals can often be ranked according to their tendency to win or lose against each of the others in the group. Such **rank orders** are referred to as **social or dominance hierarchies**. Within a hierarchy, an 'alpha' individual is dominant to all the others in the group, a 'beta' individual is dominant to all but the 'alpha', and so on down to the lowest ranker who is dominant to no one, though there are often triangular relationships (e.g. A beats B, B beats C, but C beats A) that disrupt the linearity (transitivity) of the hierarchy.

## In some species, parents care for their offspring

The most widespread form of social system is the family, an association of one or more adults and their dependent offspring. If parental care lasts a long time, or if the breeding season is longer than the time it takes for offspring to mature, adults may still be caring for younger offspring when older offspring reach parenting age. These older offspring may help their parents care for their younger siblings. Among birds, many communal breeding systems probably evolved by this route. Florida scrub jays live all year on territories, each of which contains a breeding pair and up to six helpers that bring food to the nest. Nearly all helpers are offspring from the previous breeding season that remain with their parents.

Most mammals also evolved social systems via an extended family. In simple mammalian social systems, solitary females or male–female pairs care for their young. As the period of parental care increases, older offspring are still present when the next generation is born, and they often help rear their younger siblings. In most social mammal species, female offspring remain in the group in which they were born, but males tend to leave, or are driven out, and must seek other social groups. Therefore, among mammals, most helpers are females.

Raising a family involves tremendous costs for parents and helpers. Animals who provide food for their young may sacrifice food for themselves, and protecting the young may involve the animal putting itself in danger. Acts that benefit another individual at a cost to the performer are altruistic acts. How can behavior that inflicts a cost on the performer evolve?

## Concept of Kin Selection and Inclusive Fitness

In 1964, W. D. Hamilton developed concepts that explained altruistic acts without resorting to group selection. Starting with the known fact that relatives have alleles in common, Hamilton suggested that natural selection would favor an allele that promoted altruistic behavior toward relatives because the result might be an increase in copies of that allele in the next generation. The proportion of alleles shared by two individuals can be defined as a **coefficient of relationship, r.** If an individual has a certain allele, the probability that a particular relative also has that allele is $r$. Siblings have an $r = 1/2$. A squirrel is likely to have virtually all its alleles still viable if it sacrifices itself for two or more siblings. In fact, natural selection should definitely favor altruism of an individual toward three siblings because, in a sense, natural selection is weighing 1 copy of an individual's alleles (the individual itself) versus 1.5 copies (three siblings). This sort of reasoning has been termed the **calculus of the genes.** it does not imply that individuals actually think these things out; rather, natural selection has favored the individuals that behave this way.

*Individual fitness + fitness effects of alleles*

Hamilton referred to the sum of an individual's fitness plus the fitness effects of alleles that relatives share as **inclusive fitness.** He referred to the way natural selection acts on inclusive fitness as **kin selection.**

## Hamilton's rule

Hamilton worked through several examples, and eventually realised that the number that kept falling out of his calculations was Sewall Wright's coefficient of relationship. This became **Hamilton's rule: in each behaviour-evoking situation, the individual assesses his neighbours' fitness against his own according to the coefficients of relationship appropriate to the situation.** Algebraically, the rule posits that a costly action should be performed if:

$$C < r \times B$$

Where,
**C** = the reproductive cost to the individual of performing the act.
**r** = the genetic relatedness of the recipient to the actor, often defined as the probability that a gene picked randomly from each at the same locus is identical by descent.
**B** = the additional reproductive benefit gained by the recipient of the altruistic act,

This inequality is known as Hamilton's rule after W. D. Hamilton who published, in 1964, the first formal quantitative treatment of kin selection to deal with the evolution of apparently altruistic acts. Altruistic acts are those that benefit the recipient but harm the actor. Fitness costs and benefits are measured in fecundity.

Altruistic behaviors exhibited by parents toward their offspring are easily understood in terms of close genetic relatedness. Genetic relatedness extends beyond the parent–offspring relationship, allowing an individual to influence its fitness in two different ways. First, it may produce its own offspring, contributing to its own individual fitness. Second, it may help relatives (who bear some of the same genes) in ways that increase their fitness.

Because relatives are descended from a common ancestor, they are likely to bear some of the same alleles. In diploid organisms, two offspring of the same parents share on average 50 percent of the same alleles; an individual is likely to share 25 percent of its alleles with its sibling's offspring. Therefore, by helping its relatives, an individual can increase the representation of some of its own alleles in the population. This process is called kin selection. Together, individual fitness and fitness gained through helping non-descendent kin determine the inclusive fitness of an individual. Occasional altruistic acts may eventually evolve into altruistic behavior patterns if the benefits of increasing the reproductive success of relatives exceed the costs of decreasing the altruist's own reproductive success.

Many social groups consist of some individuals that are close relatives and others that are unrelated or distantly related. Individuals of some species recognize their relatives and adjust their behavior accordingly. White-fronted beeeaters are African birds that nest colonially. Most breeding pairs are assisted by nonbreeding adults that help incubate eggs and feed nestlings. Nearly all of these helpers assist close relatives (Figure 10). When helpers have a choice of two nests at which to help, about 95 percent of the time they choose the nest with the young more closely related to them. Several other pieces of evidence suggest that the helping behavior of white-fronted bee-eaters evolved through kin selection. First, both males and females help to care for nestlings, but males help more often than females. Males remain in the social group in which they were born, but females join other social groups when they mature. Therefore, females typically live in social groups composed primarily of nonrelatives.

Second, individual bee-eaters do not appear to gain anything in addition to inclusive fitness by helping helpers do not gain experience that improves their performances when they become breeders. Finally, nests with helpers produce more fledglings than do nests without helpers, showing that helpers do increase the number of fledglings produced by their close relatives. Notice that all these patterns are → unexperienced

consistent with the principle that bee-eaters behave in ways that improve their individual fitness, not in ways that benefit the species.
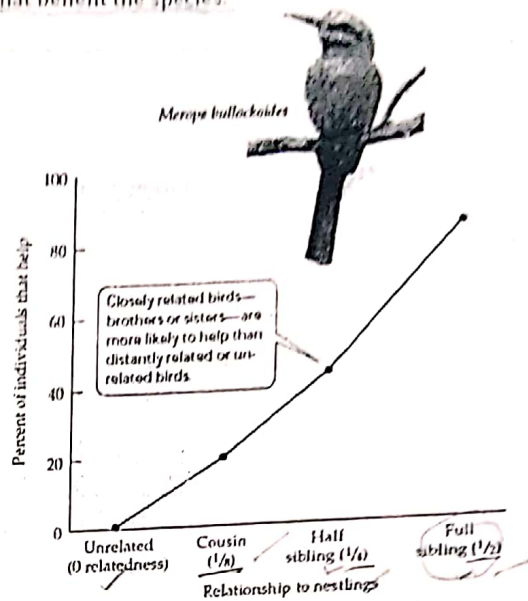


Figure 10   White-Fronted Bee-Eaters are Altruists

## Reciprocal Altruism:

The concept of "reciprocal altruism", suggests that altruism, defined as an act of helping someone else although incurring some cost for this act, could have evolved since it might be beneficial to incur this cost if there is a chance of being in a reverse situation where the person whom I helped before may perform an altruistic act towards me. Researchers seeking to understand the evolution of reciprocal altruism have turned to mathematical models based on game theory.

Conditions necessary for reciprocal altruism:

1. the behaviour must reduce a donor's fitness relative to a selfish alternative;
2. the fitness of the recipient must be elevated relative to non-recipients;
3. the performance of the behaviour must not depend on the receipt of an immediate benefit:
4. A mechanism for detecting 'cheaters' must exist.
5. A large (indefinite) number of opportunities to exchange aid must exist.

The first two conditions are necessary for altruism as such, while the third is distinguishing reciprocal altruism from simple mutualism. Conditions 1, 2, and 3 must apply to both individuals engaging in reciprocal helping. The fourth condition makes the interaction reciprocal. Condition number five is required as otherwise non-altruists may always exploit altruistic behaviour without any consequences and therefore evolution of reciprocal altruism would not be possible. However, it is pointed out that this "conditioning device" does not need to be conscious. Condition number six is required to avoid cooperation breakdown through backwards induction—a possibility suggested by game theoretical models.

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## Example of Reciprocal altruism: Warning calls in birds

Warning calls, although exposing a bird and putting it in danger, are frequently given by birds. An explanation in terms of altruistic behaviour is given by Trivers. It has been shown that predators learn specific localities and specialize individually on prey types and hunting techniques. It is therefore disadvantageous for a bird to have a predator eat a conspecific, because the experienced predator may then be more likely to eat him. Alarming another bird by giving a warning call tends to prevent predators from specializing on the caller's species and locality. In this way, birds in areas in which warning calls are given will be at a selective advantage relative to birds in areas free from warning calls.

Nevertheless, this presentation lacks important elements of reciprocity. It is very hard to detect cheaters. Also, there is no evidence that a bird refrains from giving calls when another bird is not reciprocating. And there is no evidence that individuals interact repeatedly. Another explanation for warning calls is that these are not warning calls at all: A bird, once it has detected a bird of prey, calls to signal to the bird of prey that it was detected, and that there is no use trying to attack the calling bird.

Two facts support this hypothesis:
- The call frequencies match the hearing range of the predator bird.
- Calling birds are less attacked—predator birds attack calling birds less frequently than other birds.

### Eusociality

Species whose social groups include sterile individuals are said to be **eusocial**. This extreme form of social behavior has evolved in termites and many hymenopterans (ants, bees, and wasps). In these species, most females are *workers* that forage for the colony and/or defend it against predators, but do not reproduce. Workers may include soldiers with large, specialized defensive weapons, which may be killed while defending the colony. Only a few females, known as *queens*, are fertile, and they produce all the offspring of the colony.

Both genetic and environmental factors facilitate the evolution of eusociality. The British evolutionist W. D. Hamilton first suggested that eusociality evolved among the Hymenoptera because its members have an unusual sex determination system in which males are haploid but females are diploid. Among the Hymenoptera, a fertilized (diploid) egg hatches into a female; an unfertilized (haploid) egg hatches into a male.

If a female copulates with only one male, all the sperm she receives are identical because a haploid male has only one set of chromosomes, all of which are transmitted to every sperm cell. Therefore, a

female's daughters share all of their father's genes. They also share, on average, half of the genes they receive from their mother. As a result, they share 75 percent of their alleles on average, rather than the 50 percent they would share if both parents were diploid. Since workers are more genetically similar to their sisters than they would be to their own offspring, they can increase their fitness more by caring for their sisters than by producing and caring for their own offspring.

## Conditions favoring Eusociality:

Eusociality may also be favored if establishment of new colonies is difficult and dangerous. Nearly all eusocial animals construct elaborate nests or burrow systems within which their offspring are reared. Naked mole-rats—the most eusocial mammals—live in underground colonies containing 70 to 80 individuals. The colony's tunnel systems are maintained by sterile workers. Breeding is restricted to a single queen and several kings that live in a nest chamber in the center of the colony. Individuals attempting to found new colonies are at high risk of being captured by predators, and most founding events fail. Thus, high predation rates, which favor cooperation among founding individuals, may facilitate the evolution of eusociality.

Inbreeding—the mating of individuals who are genetically related—can generate increased genetic relatedness within a group. Even if two parents are unrelated, but each is the product of generations of intense inbreeding, all of their offspring may be genetically nearly identical. Such offspring would increase their fitness by helping to rear siblings. Genetic similarity generated by inbreeding could explain the evolution of eusociality among the many hymenopteran species in which queens mate with many males and among termites and naked mole-rats in which both sexes are diploid.

Hamilton applied his ideas of inclusive fitness and kin selection to explain sterile castes in the eusocial (truly social) hymenoptera (bees, ants, and wasps).The workers in these colonies are sterile females. Why do they forsake their ability to reproduce in order to help maintain the hive or colony? The answer seems to come from haplodiploidy, the unusual sex-determining mechanism of these species. In the eusocial hymenoptera with sterile castes, fertilized eggs produce diploid females, whereas unfertilized eggs produce haploid males (drones).The difference between a reproductive queen and a sterile worker in bees is larval nutrition: larvae fed "royal jelly" can become queens. Hamilton showed that since a worker is more closely related to her sisters than to her own potential offspring, kin selection could favor a worker who helps her sisters at the expense of her own reproduction.

Figure 11 shows a queen (female) with alleles $A_1$ and $A_2$ at the $A$ locus and a haploid drone (male) with the $A3$ allele. A daughter will have either the $A_1A_3$ or $A_2A_3$ genotype. If we compare one of these daughters with

her sisters,we see that the average $r = 0.75$—half of the time, $r = 1.0$, and the other half of the time, $r = 0.5$. A queen and her daughters have an $r = 0.5$. Thus, we see that workers (females) are more closely related to their sisters, and hence are at a reproductive advantage by raising them rather than their own young. Wilson has pointed out that sterile caste systems have evolved among insects in only one other group beside the eusocial hymenoptera, the termites. Although eusocial hymenoptera make up only 6% of insects, sterile castes have independently evolved at least eleven times. This is compelling evidence for the validity of Hamilton's analysis. Only one non insect example of a caste has been discovered: the naked mole rat, a small subterranean rodent living in Africa, has this type of social system.
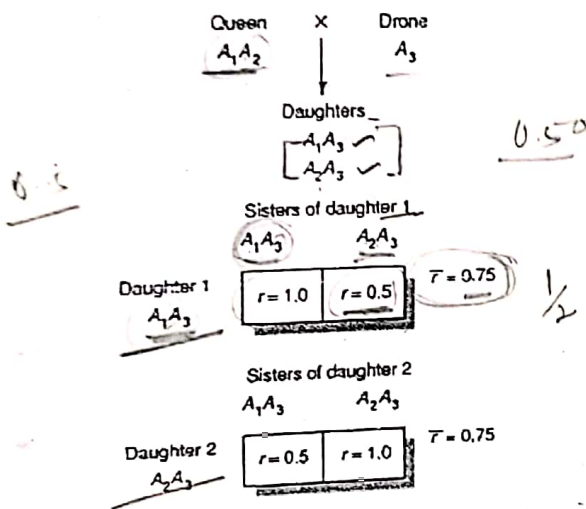


Figure 11    Haplodiploidy in eusocial hymenoptera produces sisters with an average $r$ of 0.75. Because drones (males) are haploid, queens produce daughters of only two genotypes at any locus. A given daughter has an $r$ of 1.0 with sisters of identical genotype and an $r$ of 0.5 with sisters of the other genotype, for an average $r$ of 0.75. In other words, females have a 75% genetic similarity with their sisters but only a 50% similarity with their own offspring.

Many studies concerned with apparently altruistic acts have provided a large body of support for Hamilton's theory of kin selection and inclusive fitness. P. Sherman, working with ground squirrels, for example, has observed that the individuals that make the alarm calls have the most to gain from the standpoint of inclusive fitness; these individuals are resident females surrounded by kin.

One other explanation for altruism is also consistent with benefits to individual fitness. It is that many apparently altruistic acts are in reality selfish—they just look altruistic. To be altruistic, an individual must risk reducing its fitness to potentially benefit the fitness of others. We may, in fact, misinterpret some acts as altruistic that simply are not. This turnaround in thought, from group selection to individual selection, has been an intellectual revolution in modern evolutionary biology. Before this revolution, many of the behaviors in nature that involved apparent altruism were difficult to explain. Now sociobiological reasoning provides an explanation.

The reason so much controversy has sprung up over the theory of genetic control of social behavior is because of the implications the theory has for human social, political, and legal issues. Human husband-wife, parent-child, and child-child conflicts, for example, may be built into the genes. Altruism, our highest form of nobility, may be mere selfishness. Many critics fear that sociobiological concepts can be used to support sexism and racism. For human beings, the alternative to the theory of sociobiology is the theory that most human behavior, including cultural learning, is determined by the environment. At present, although much evidence remains to be gathered, the sociobiology concept is compelling to much evolution.

### Social animals may achieve great abundances

The abundances achieved by some social animals are impressive. For example, up to 94 percent of the individuals and 86 percent of the biomass of arthropods in the *canopies* (tree-tops) of tropical rainforests are social ants. Termites (also social insects) are the primary consumers of plant tissues in the savannas of Africa. They live in and build large mounds, within which many other species of animals live. Termites may extract nutrients from the soil at depths as great as 80 meters. In parts of Australia, termite density may reach 1,000 colonies per hectare.

Ants and termites have achieved these remarkable abundances in part because their social organization allows them to exploit the services of other organisms in harvesting vital resources. The most abundant and highly productive ants and termites actively cultivate fungi that break down difficult-to digest plant tissues, including wood. Some ants tend aphids and other insects that tap phloem fluids, protecting the phloem-suckers from predators. Because phloem is rich in carbohydrates but poor in proteins, phloem-suckers ingest more carbohydrates than they can use. They eject the excess in the form of sugar-rich anal drops, which the ants eat. Because the ants can easily obtain enough carbohydrates in this manner, they need to get only proteins in other ways, such as by eating other insects. Moreover, with their high, sugar-based metabolic rates, the ants can expend the energy needed to drive other predatory insects away from their food sources. In this way, ants strongly influence the community of insects in tropical forest canopies.

Social living also enables organisms to find and use temporally and spatially patchy foods. The wildebeest, which travels in large herds, is the most abundant large mammal in Africa. More than a million individuals are found in the herd that migrates between the Masai Mara in Kenya and the Serengeti in Tanzania to feed on the rapidly growing grass that follows seasonal rains in each area. Even more striking is the abundance achieved by our own species. Social living enabled members of human groups to specialize in different activities. Among the benefits of specialization were domestication of plants and animals and cultivation of land. These innovations enabled our ancestors to increase the resources at their disposal dramatically. Those increases, in turn, stimulated rapid population

growth up to the limit determined by the agricultural productivity that was possible with human- and animal powered tools. Agricultural machines and artificial fertilizers, made possible by the tapping of fossil fuels, greatly increased agricultural productivity and removed that earlier limit. In addition, the development of modern medicine reduced the mortality rate in human populations. Medicine and better hygiene have also allowed people to live in large numbers in areas where diseases formerly kept numbers very low. However, these successes have been accompanied by many problems.

**Interspecific interactions influence animal distributions**

As we have seen, animals assess habitat quality and settle preferentially in better places. They also select the food items that give them the best return for the time and energy they expend in getting them. The optimality modeling approach used to develop and test hypotheses about how such choices are made has yielded an important general "rule of thumb" of behavioral ecology: As much as possible, organisms concentrate on doing what they do best and avoid doing what they do poorly.

However, inter-specific interactions may prevent animals from living in those environments in which they would do best. Individuals of a behaviorally dominant species may be able to exclude individuals of a subordinate species from its preferred foraging areas. How such behavioral dominance influences use of foraging areas can be illustrated by observing hummingbird behavior.

Hummingbirds extract nectar from flowers and often defend patches of flowers from other hummingbirds. In an experiment done in southeastern Arizona, investigators created artificial "flower patches" by setting up an array of feeders. Some feeders contained artificial nectar that was rich in sucrose; others contained a more dilute solution that was a poorer source of sucrose. Hummingbirds quickly learned which were the high-quality feeders because the rich ones had blue bee guards; the poor ones had yellow bee guards.

Males of three hummingbird species visited the feeders. Interactions were strongest between two of them: Male blue-throated hummingbirds, which weigh about 8.3 g on average, behaviorally dominated the smaller male black-chinned hummingbirds, which weighed only about 3.2 g. When no male blue-throats were present, black-chinned males fed almost exclusively at the rich feeders; but when male blue-hroats were present, black-chinned males fed at poor feeders as often as they fed at rich feeders. Even though the nectar at the poor feeders was more dilute, the black-chins achieved about the same rate of energy from them as from the rich feeders because they were able to feed longer at the poor feeders without being chased away by the larger blue-throat males.

These kinds of observations show us that the ways in which animals choose what to eat, where to seek food, and with whom to associate influence the sizes and distributions of populations of many species and how they interact in nature.

## The Timing of Behavior: Biological Rhythms

Among the important proximate regulators of behavior are those that control its organization through time. The study of biological rhythms has led to major discoveries about brain mechanisms at the molecular level that enable animals to organize their behavior in time.

**Circadian rhythms control the daily cycle of behavior**

Our planet turns on its axis once every 24 hours, creating a cycle of environmental conditions that has existed throughout the evolution of life. Daily biological cycles are characteristic of almost all organisms. What is surprising, however, is that this daily rhythmicity does not depend on the 24-hour cycle of light and dark.

If animals are kept in constant darkness, at a constant temperature with food and water available all the time, they still demonstrate daily cycles of activities such as sleeping, eating, drinking, and just about anything else that can be measured. The persistence of these daily cycles in the absence of environmental time cues suggests that animals have an endogenous (internal) clock. Without time cues from the environment, however, these daily cycles are not exactly 24 hours long. They are therefore called **circadian rhythms** (from the Latin *circa*, "about," and *dies*, "day").

A biological rhythm can be thought of as a series of cycles, and the length of one of those cycles is the period of the rhythm (Figure 12). Any point on the cycle is a *phase* of that cycle: Hence, when two rhythms completely match, they are *in phase*, and if a rhythm is shifted (as in the resetting of a clock), it is *phase-advanced* or *phase-delayed*. Since the period of a circadian rhythm is not exactly 24 hours, it must be phase-advanced or phase-delayed every day to remain in phase with the daily cycle of the environment. In other words, the rhythm has to be *entrained* to the cycle of light and dark in the environment.

**ENTRAINMENT:**

The resetting of the circadian rhythm by environmental cues is called **entrainment**. An animal kept in constant conditions will not be entrained to the 24-hour cycle of the environment, and its circadian clock will run according to its natural period—it will be free-running. If its period is less than 24 hours, the animal will begin its activity a little earlier each day (see the middle panel of Figure 12). The free-running circadian rhythm is under genetic control. Different species may have different average periods, and within a species, mutations can lead to different period lengths.