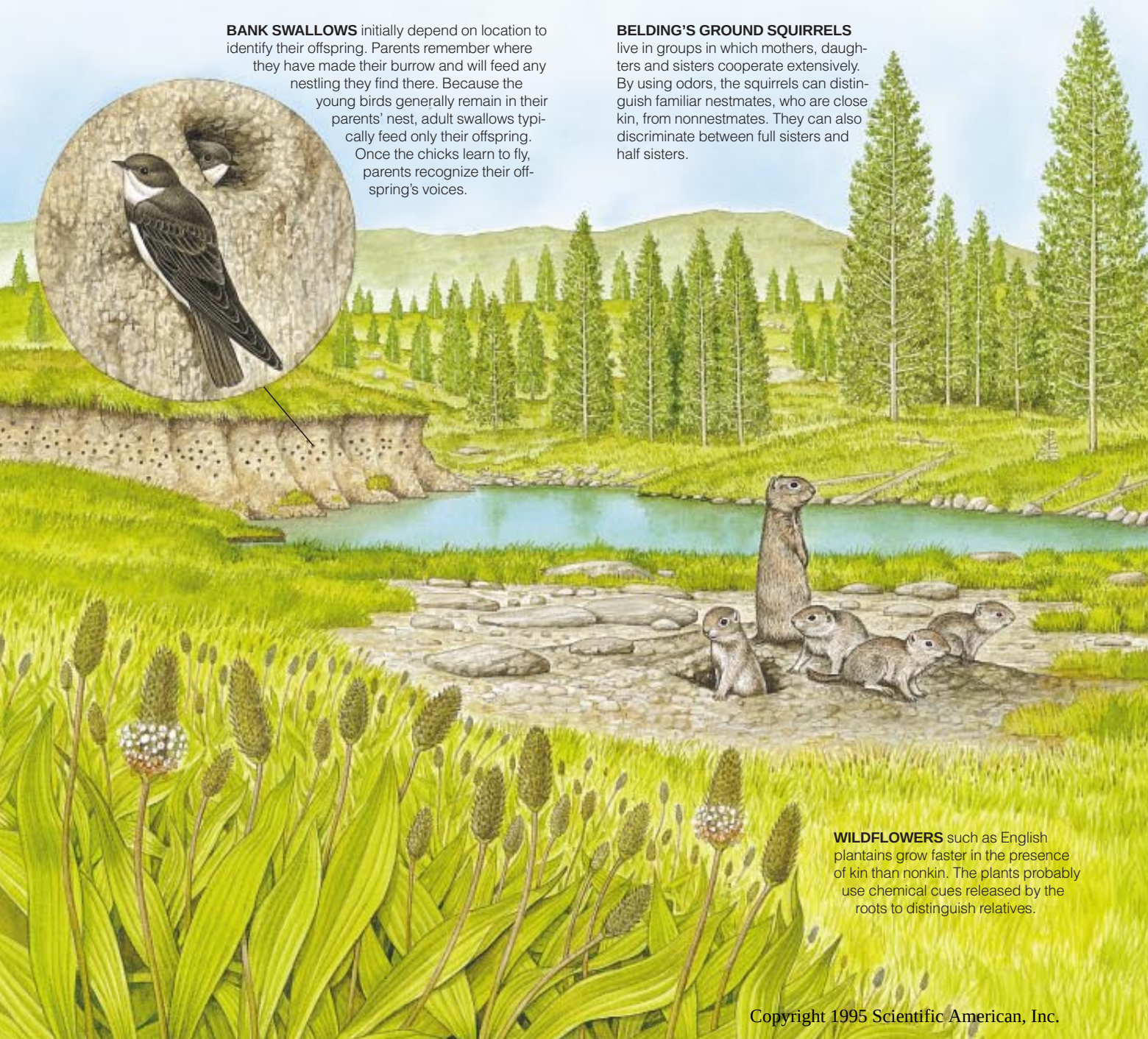
Kin Recognition

Many organisms, from sea squirts to primates, can identify their relatives. Understanding how and why they do so has prompted new thinking about the evolution of social behavior

by David W. Pfennig and Paul W. Sherman



BANK SWALLOWS initially depend on location to identify their offspring. Parents remember where they have made their burrow and will feed any nestling they find there. Because the young birds generally remain in their parents' nest, adult swallows typically feed only their offspring. Once the chicks learn to fly, parents recognize their offspring's voices.

BELDING'S GROUND SQUIRRELS live in groups in which mothers, daughters and sisters cooperate extensively. By using odors, the squirrels can distinguish familiar nestmates, who are close kin, from nonnestmates. They can also discriminate between full sisters and half sisters.

WILDFLOWERS such as English plantains grow faster in the presence of kin than nonkin. The plants probably use chemical cues released by the roots to distinguish relatives.

Kinship is a basic organizing principle of all societies. Humans possess elaborate means by which to identify relatives, such as using surnames and maintaining detailed genealogies. Mechanisms for distinguishing kin also occur throughout the plant and animal kingdoms regardless of an organism's social or mental complexity, in creatures as diverse as wildflowers and wasps. Scientists are beginning to discover that an understanding of the origin and mechanisms of kin recognition offers fresh insights into such diverse topics as how living things choose their mates, how they learn and how their immune system works.

The current interest in kin recognition can be traced back to two theories. In 1964 William D. Hamilton of the University of Oxford realized that in the competition for survival and genetic reproduction, evolution makes no distinction between copies of

PAPER WASPS utilize odors to determine whether visiting wasps are related. All colony members have an identifying smell that results from the unique blend of plant fibers used to construct the nest.

ROBERTO OSTI

WESTERN TOAD TADPOLES congregate in schools composed of siblings. Apparently the tadpoles recognize their brothers and sisters as well as their home environment by smell.

MOUNTAIN DELPHINIUMS distinguish relatives from nonrelatives based on pollen. The plants use kin recognition to avoid breeding with close relatives or with plants that are extremely different genetically.

ACORN WOODPECKER females live in communal nests with several sisters. One female will remove her sisters' eggs from the nest and destroy them until she starts laying her own eggs. The birds rely on these timing clues to determine which eggs are not their offspring. After a female lays eggs, however, she cannot distinguish among them and will not disturb any eggs in the nest.

SWEAT BEES must be able to recognize kin to defend their nest. At the entrance of each colony, a worker bee stands guard. When another bee approaches, the sentry determines by smell whether the visitor is familiar, and thus related, and allowed to enter.

alternative forms of genes, known as alleles, that are transmitted through direct descendants, such as offspring, and those propagated through nondescendant kin, such as siblings. Whereas the traditional view held that natural selection favored individuals that produced the greatest number of offspring, Hamilton shifted the emphasis to genes. He concluded that natural selection must favor organisms that help any relative, because by doing so they increase their total genetic representation.

Hamilton termed this idea inclusive fitness, because it includes both the genes an organism transmits through its offspring as well as copies of those genes it helps to propagate in reproductive relatives. Inclusive fitness theory can explain the evolution of nepotism, particularly in the unusual instances in which some members of certain species—ants, bees or naked mole rats, for example—have no offspring and exist only to nurture other relatives [see "Naked Mole Rats," by Paul W. Sherman, Jennifer U. M. Jarvis and Stanton H. Braude; SCIENTIFIC AMERICAN, August 1992].

A second explanation, optimal outbreeding theory, was developed in the early 1970s by Patrick Bateson of the University of Cambridge and William M. Shields of the SUNY College of Environmental Science and Forestry in Syracuse. Their hypothesis draws on the well-known fact that inbreeding between very close relatives, such as siblings, often causes offspring to display detrimental characteristics. All organisms possess a few deleterious alleles that are normally not expressed. The same rare versions of these genes are likely to be carried by close relatives. With close inbreeding, offspring can inherit such alleles from both parents, resulting in their harmful expression. Conversely, mating with individuals that are very different genetically can produce detrimental effects by breaking up gene combinations that produce favorable traits. Optimal outbreeding theory explains why many organisms prefer to mate with those to whom they are neither too closely nor too distantly related.

RICHARD K. GROSBERG

SEA SQUIRTS are marine animals that lack brains but can nonetheless identify their kin using chemical cues. Two organisms occasionally attempt to join together, an endeavor that is successful only if the two animals are related.

Two Forms of Recognition

More recent work has brought up additional ideas for why kin recognition takes place. But the evolutionary reasons for this ability are only part of the story, one to which we will return later. We turn first to the intriguing question of *how* organisms distinguish their relatives. In general, plants and animals use two mechanisms to identify kin. In some cases, physical features, known as phenotypes, allow individuals to recognize their relatives directly. Alternatively, kin can be identified indirectly without reference to phenotypes but by clues related to time or place.

Often organisms rely on a combination of direct and indirect techniques. For example, bank swallows (*Riparia riparia*), birds that nest in colonies on sandbanks, identify their young using both kinds of clues. John L. Hoogland of the University of Maryland and one of us (Sherman) found that bank swallow parents will feed any nestling that appears in their burrow. This behavior indicates that adult swallows recognize their young indirectly by learning the location of the burrow they have excavated. The flightless chicks usually remain in the burrow where they were born for three weeks after hatching, so during this time parents generally feed only their own young. After the chicks learn to fly, however, broods mix extensively, so parents must use direct clues to ensure that they continue to provide only for their own offspring. Michael D. Beecher and his colleagues at the University of Washington discovered that by the time bank swallow chicks are 20 days old, they have distinct vocal signatures that indicate to parents which young are their own.

To understand how these discriminations take place, researchers have divided the process of kin recognition into three components. Initially, a recognition cue is produced. Next, another individual perceives it. Finally, that individual interprets the cue and takes appropriate action. In indirect recognition the signal is external to the plant or animal; in direct recognition the label is produced by the organism itself. Communities of social animals, in which kin and nonkin frequently mix, are especially likely to use the direct method. Thus, scientists have become intrigued with the complex interplay of factors that takes place in the process of direct kin recognition.

A direct kin-recognition signal can be any physical characteristic that correlates reliably with relatedness. Such labels vary widely among species. Visual references are common among animals, such as primates, whose most prominent sense is sight. Organisms that must attract mates across a distance in the dark, such as frogs, use auditory signals. And, of course, chemical odors are important distinguishing labels for many animals.

In general, chemical markers convey information accurately while requiring less effort to produce than other signals, particularly sounds. An organism must expend a considerable amount of energy compressing air to create sound. In contrast, chemical labels often consist of a few molecules of a substance the body produces naturally during daily activities. Furthermore, a system is already in place to detect and decipher chemical substances: such signals are readily interpreted by the body's immune system. Some speculate that the physiological machinery used in kin recognition was borrowed from the immune system in the course of evolution.

Source of the Signals

Recognition labels differ not only according to which sense they draw on but also in their origin. These cues can reflect specific genetic traits; they can be acquired from the environment, or they can be a result of both. Studies of certain tunicates, or sea squirts, specifically *Botryllus schlosseri,* show that these marine animals use genetic labels to identify relatives. Tunicates lack a brain, thus proving that kin recognition does not depend on mental complexity.

Sea squirts begin life as planktonic larvae that eventually settle on a rock and multiply asexually to form an in-

terconnected colony of structurally and genetically identical animals. Occasionally, two colonies will attempt to fuse; large organisms survive better than small ones, so combining with others is apparently beneficial. Richard K. Grosberg and James F. Quinn of the University of California at Davis discovered that the larvae settle near and merge with genetically similar organisms. If a tunicate attempts to join another, unrelated colony, the second tunicate emits toxic substances that repel the invader.

Grosberg and Quinn have also determined the area on the chromosomes that controls this recognition response. They noticed that larvae settle near others that carry the same allele in the location known as the histocompatibility complex. This region of the chromosome encodes for the chemicals that enable an organism to distinguish self from nonself as part of the immune system. The researchers also discovered that tunicates settle closer to nonrelatives that were bred in the laboratory to have the same version of the gene at this location in preference to establishing themselves near true kin that were bred to carry an alternative allele.

In nature, the chances of mistaking nonrelatives for kin are minuscule. For reasons that are not totally clear, the types of genes found at the histocompatibility complex are so variable across a species that if two organisms share the same allele there, they must have acquired it from a recent ancestor. So when one tunicate attempts to fuse its tissues with another, the immune system can recognize the encroaching tissue as being either foreign or similar—in other words, related or not—depending on the genetic makeup at the histocompatibility complex.

House mice (*Mus musculus*) also rely on the histocompatibility complex to identify kin. Because the genes there affect body odor, mice can depend on this trait to distinguish relatives. Just as was the case for tunicates, the genes in mice found at the histocompatibility complex are highly variable, but among family members the alleles tend to be the same. Therefore, individuals that smell alike are usually related. C. Jo Manning of the University of Nebraska and Wayne K. Potts and Edward K. Wakeland of the University of Florida observed that female mice tend to mate with males that smell different, apparently in order to avoid inbreeding. But they nest communally with females that smell similar, such as sisters, which helps to ensure the survival of nieces and nephews as well as offspring.

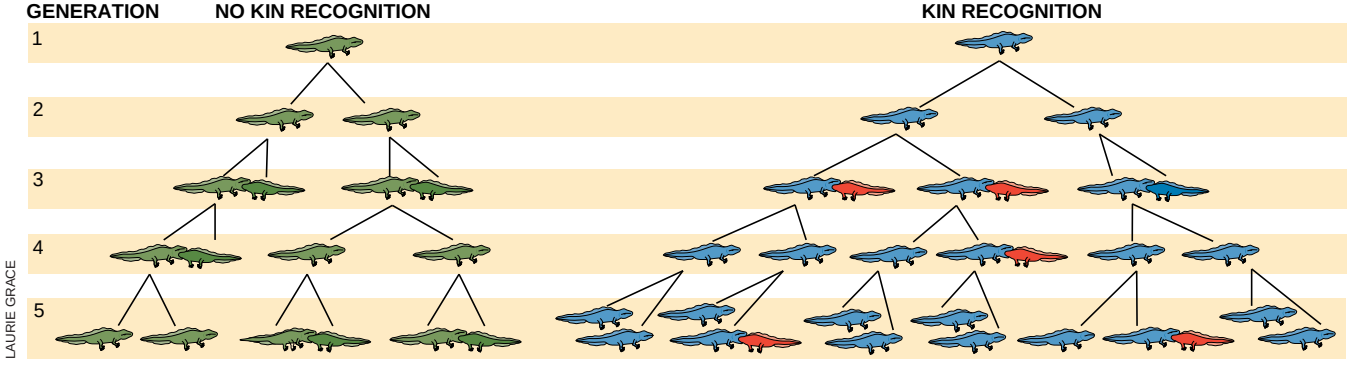
The Smell of Paper Wasps

In contrast to tunicates and mice, other organisms use labels acquired from their environment to recognize relatives. One of us (Pfennig) has studied such signals in certain paper wasps, specifically *Polistes fuscatus*. These common garden insects construct open comb nests composed of wafer-thin plant fibers. Colonies typically consist of a queen and her daughter workers.

Kin recognition is crucial because nests are frequently visited by other wasps with various intentions. In some cases, the visitors are homeless relatives whose nests were destroyed by predators, such as birds. In others, the intruding wasps come to steal eggs to feed the larvae in their own active colonies. Before allowing invaders on their nest, wasps must distinguish between orphaned kin, which will be helpers, and unrelated wasps, which are threats to the nest.

Paper wasps make this distinction directly using chemical odors. Pfennig, George J. Gamboa of Oakland University, Hudson K. Reeve and Janet Shellman-Reeve of Cornell University discovered that each wasp assimilates from its nest an odor specific to the insects that live there. This smell, which serves as the recognition cue, is locked into the wasp's epicuticle, or skin, before it hardens. Karl E. Espelie of the University of Georgia and his colleagues determined that the source of the smell is odoriferous hydrocarbons. These compounds are derived from the plant fibers that make up the nest paper as well as from secretions produced by the wasps that constructed the nest. Because each colony uses a unique mixture of plants in nest construction, family members often are more likely to share this environmentally acquired label than a genetic one. The mixing and recombination of genes that happen during sexual reproduction ensure that family members, though genetically similar, will not be identical.

Both genetic labels and environmentally acquired ones can lead to mistakes, however. Relying solely on signals picked up from the environment might cause acceptance errors, in which an individual mistakenly assists nonrelatives that live in similar surroundings. Such cheaters could then reap the rewards of misplaced beneficence without reciprocating and so become predominant in the population. Depending only on gene products also might cause an individual to accept nonrelatives that carry "outlaw alleles" that encode just the recognition trait. Again, the renegade alleles will spread throughout a population. Finally, relying on genetic cues increases the risk of committing rejection errors, in which relatives are mistakenly treated as nonkin because they do not, by chance, possess the recognition trait.



LAURIE GRACE

KIN RECOGNITION can help make one group of organisms more successful than others. In this example, each salamander produces two offspring (only one parent is shown), but not all of them survive, because these animals resort to cannibalism when faced with a food shortage. For instance, in the third generation, only half of the salamanders that cannot recognize kin (*green*) survive to reproduce; the others are eaten by siblings. But three out of four salamanders survive in the family that can identify relatives (*blue*) because half of them ate salamanders from another family (*red*). By the fifth generation, the family that is genetically disposed to distinguish kin predominates.

The likelihood that these types of mistakes will occur depends on the genetic makeup of the organisms involved as well as their surroundings. Organisms such as tunicates and mice minimize the chance that two nonrelatives will share similar genetic traits by exploiting regions of the chromosomes that are variable within a species but relatively constant in families. These genetic labels are most useful for organisms that inhabit a fairly uniform chemical environment, such as a rock where several colonies of tunicates might live. For organisms such as paper wasps that live in more diverse areas, environmentally acquired labels can provide more accurate clues.

Acting on a Cue

After a recognition cue has been produced, how do others use it to assess relatedness? As far as we know, these signals are always learned. Even the immune system must learn to recognize the self [see "How the Immune System Learns about Self," by Harald von Boehmer and Pawel Kisielow; SCIENTIFIC AMERICAN, October 1991]. Indeed, without learning how to make that distinction, the immune system would attack every tissue in the body.

Organisms learn labels from themselves, their relatives or their environment. Individuals form a template of these labels, much like the templates that are thought to be involved in birdsong learning. In most creatures the process of learning takes place early in life, when they are likely to be living among relatives. Memories of companions are durable, ensuring that throughout its life an organism can compare the remembered image with another individual's physical characteristics. In addition, many creatures update their templates from time to time, enabling them to recognize kin as their labels change with age, for instance.

To illustrate the role of learning in kin recognition, consider the part that the nest plays for paper wasps. In experiments done in the laboratory, wasps removed from their nest and nestmates later recognized nonrelatives as well as relatives as kin. Wasps isolated only from their nest but not from their nestmates still treated all wasps as kin. Furthermore, ones exposed to a nest other than their own learned to treat wasps emerging from that nest as their relatives. Only in the presence of their own nest did the insects learn the chemical signal that allows them to distinguish kin from nonkin.

In contrast to paper wasps, honeybees (*Apis mellifera*) can learn identification cues from their nestmates and from themselves. One reason for this difference between honeybees and paper wasps may be the mating patterns of the queens. Honeybee hives often contain workers sired by more than a dozen drones, whereas paper wasp workers are sired primarily by only one male. In consequence, honeybee hivemates are a mixture of full and half sisters, and paper wasp nestmates are mostly full sisters.

To distinguish between full and half siblings, a worker honeybee must have knowledge of the genes received from its father, as well as such information about the bee under examination. Thus, some mechanism of self-inspection is required—a phenomenon Richard Dawkins of the University of Oxford has dubbed the "armpit effect." Wayne M. Getz and Katherine B. Smith of the University of California at Berkeley showed that bees raised in isolation learned their own odor and then favored similarly smelling full sisters over maternal half sisters whose slightly different genetic makeup resulted in a different odor. Whether honeybees learn from themselves under crowded hive conditions is unclear.

Once recognition has taken place, the individual must decide what action to take, depending on the context of the encounter. For example, paper wasp workers are more intolerant of unrelated wasps when they invade the nest—where they might try to steal eggs—than they are when they meet the same nonkin elsewhere. According to a theoretical model developed by Reeve, for discrimination to occur, the similarity between the observed individuals' physical characteristics and the observer's template must be above some critical value. This value reflects how often organisms encounter relatives as opposed to nonrelatives as well as the costs of rejecting kin compared with those of accepting nonkin.

This model helps to explain certain errors in discrimination. For example, Anne B. Clark of SUNY at Binghamton and David F. Westneat, Jr., of the University of Kentucky have found that male red-winged blackbirds (*Agelaius phoeniceus*) feed all the chicks in their nest, even though—because females mate with more than one male—about one in four chicks is not their offspring. Presumably, it is more efficient in a reproductive sense for a male parent to feed all the chicks in its nest, which wastes only a little effort on unrelated young, than to risk allowing one of its progeny to starve.

Cannibalistic Kin

Let us now return to the question of why many organisms can distinguish their relatives. The evolutionary significance of kin recognition is dramatically illustrated by species in which some individuals have the potential to harm their relatives. Certain protozoans, rotifers, nematodes and amphibian larvae exist in two distinct forms that differ in dietary preference—they can be either cannibalistic or omnivorous. Which path an individual takes depends mainly on the environment in which it was raised, although both types can be found within one family.

Cannibalistic animals also return us to inclusive fitness theory. According to this line of thinking, cannibals should have evolved to avoid eating their own kin because of the genetic costs of such a practice: any family that exhibited such behavior would probably not survive very long.

To test this prediction, we studied patterns of kin recognition in spadefoot toad tadpoles (*Scaphiopus bombifrons*), which develop in temporary ponds in the desert. These tadpoles possess a special means of acquiring extra nourishment in order to hasten their growth so they can escape their rapidly drying ponds.

All spadefoot tadpoles begin life as omnivores, feeding primarily on detritus. Occasionally, however, one eats another tadpole or a freshwater shrimp. This event can trigger a series of changes in the tadpole's size, shape and musculature and, most important, in dietary preference. These changed tadpoles become exclusively carnivorous, feast-

LARRY DITTO *Bruce Coleman Inc.*

RED-WINGED BLACKBIRD males feed all chicks in the nest. Most of these young birds are indeed offspring, so the adults benefit in a reproductive sense by taking care of all the birds in their nests rather than risk letting kin starve.

Family Matters

After four barren years at the Philadelphia Zoo, Jessica, a rare Lowland gorilla (*right*), was moved to the San Diego Zoo. Jessica became pregnant right away and gave birth to Michael on Christmas Eve in 1991.

Kin discrimination may explain why Jessica did not mate until she was introduced to males other than those she had lived around since birth. In nature, such familiar individuals would usually be relatives, and Jessica may have viewed her companions as such. To avoid potential inbreeding, animals generally do not have much sexual interest in their close relatives.

In species that have dwindled to a single small population, identifying familiar nonrelatives as kin can be a particular problem. With an understanding of kin recognition, zookeepers can prevent animals from making such mistakes and perhaps facilitate breeding in endangered species.

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ing on other animals—including members of their own species.

Whether a tadpole will actually eat members of its own family depends on the balance between the costs and benefits of such discriminating taste. This balance changes depending on the tadpole's development and its hunger level. For example, if the tadpole remains an omnivore, it tends to congregate in schools that consist primarily of siblings. Its cannibalistic brothers and sisters, however, most often associate with and eat nonsiblings.

Carnivores nip at other tadpoles, and after this "taste test," they either eat the animals if they are not related or release them unharmed if they are siblings. Interestingly, carnivores are less likely to avoid eating brothers and sisters when they are hungry than when full. Apparently the tadpoles stop discriminating kin when their own survival is threatened—after all, a carnivorous tadpole is always more closely related to itself than to its sibling.

Arizona tiger salamanders (*Ambystoma tigrinum*) also come in two types: a small-headed omnivore that eats mostly invertebrates and a large-headed carnivore that feeds mainly on other salamanders. All larvae start off as omnivores, and they typically stay that way if they grow up among siblings. But the larvae often transform into cannibals if they grow up among nonkin. By not developing into a cannibal in the presence of siblings, the salamanders reduce their chances of harming relatives. Together with James P. Collins of Arizona State University, we found that cannibals prefer not to dine on close kin when also offered smaller larvae that are distantly related. By temporarily blocking the animals' noses, we determined that the discrimination is based on chemical cues.

New Challenges

In addition to the standard inclusive fitness theory arguments, there may be other reasons why organisms recognize kin. For example, Pfennig and his graduate student Michael Loeb, along with Collins, ascertained that tiger salamander larvae are afflicted in nature with a deadly bacterium. Furthermore, the team determined that cannibals are especially likely to be infected when they eat diseased members of their species. Perhaps natural selection favors cannibals that avoid eating kin and thereby avoid pathogens that are transmitted more easily among close relatives with similar immune systems. Such reasoning implies that kin recognition may have evolved not only to ensure relatives' survival but also simply to preserve an animal's own life.

These recent results have challenged traditional understandings of kin recognition and have demonstrated that biologists have much more to learn about the process. In the course of such work, we hope to gain more insights into the evolution of social interactions as varied as nepotism and cannibalism. Because of the fundamental connection between the immune system and the mechanism of kin recognition, we also hope further study will reveal details on how these systems operate.

Research on kin recognition also may have practical uses. Mary V. Price and Nickolas M. Waser of the University of California at Riverside have discovered that mountain delphinium (*Delphinium nelsonii*) can recognize pollen of related plants. Also, Stephen J. Tonsor of Michigan State University and Mary F. Wilson of the Forestry Sciences Laboratory in Juneau, Alaska, found that some flowering plants, such as pokeweeds (*Phytolacca americana*) and English plantains (*Plantago lanceolata*), grow faster when potted with full or half siblings than when potted with nonrelatives. If these kinship effects are widespread, they could be used to advantage in planting crops.

Scientists have been investigating kin recognition for more than half a century, and we now have a good deal of information about a variety of plants and animals. Ongoing work will allow us to formulate a broad understanding of the significance of this phenomenon.

The Authors

DAVID W. PFENNIG and PAUL W. SHERMAN have shared an interest in kin recognition for more than a decade. Pfennig received his Ph.D. from the University of Texas before joining Sherman as a National Science Foundation postdoctoral fellow at Cornell University. Currently Pfennig is assistant professor of ecology, ethology and evolution at the University of Illinois, where his research focuses on the evolution of kin recognition and developmental polymorphism. Sherman, who received his Ph.D. from the University of Michigan, is professor of animal behavior at Cornell. He studies the social behavior of various vertebrates, including ground squirrels and naked mole rats.

Further Reading

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