CHAPTER 14

Niko Tinbergen & the Mating Behavior of Sticklebacks

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INTRODUCTION

If you visited a lake as a child, you may remember being fascinated by the bluegill and pumpkinseed sunfish swimming under the dock. Sometimes floating almost motionless in the shade, other times darting away from some unseen disturbance, their behavior probably appeared completely random. Careful study, however, reveals that each of these closely related species has a distinctive pattern of behavior, particularly during the breeding season. Male pumpkinseeds are solitary animals. Equipped with hard, bony mouthparts well adapted for nipping potential predators, each male is able to protect his own nest site from marauding catfish who might eat the eggs. In contrast, the small, delicate mouthparts of bluegills pose little threat to nest-raiding predators. For protection, bluegills join together in breeding colonies of 50 to 100 males. Strength in numbers may be a good strategy against nest-raiding catfish, but being social poses other problems for male bluegills. Each male vigorously defends a small territory surrounding his nest from the other males, who might slip in and fertilize the female's eggs first.

The threat of having another male fertilize the eggs in his nest is a serious problem for territorial males. Some male bluegills who don't build nests specialize in sneaking into other males' nests to spawn. Perhaps not surprisingly, these interlopers are often small and furtive. Another type of male mimics female coloration and behavior to prevent detection by nest-building males.

How have these alternative forms of behavior evolved and how are they adaptive? Are complex forms of social behavior learned or do they have some genetic basis? Are there principles of animal behavior that can be generally applied, perhaps even to humans? Such questions intrigued the Dutch biologist Niko Tinbergen, and he devoted his career to answering them. Together with Konrad Lorenz, he developed the new field of *ethology* to study the biological basis of behavior. For their pioneering studies of animal behavior, Tinbergen, Lorenz, and another ethologist, Karl von Frisch, were awarded a Nobel Prize in 1973.

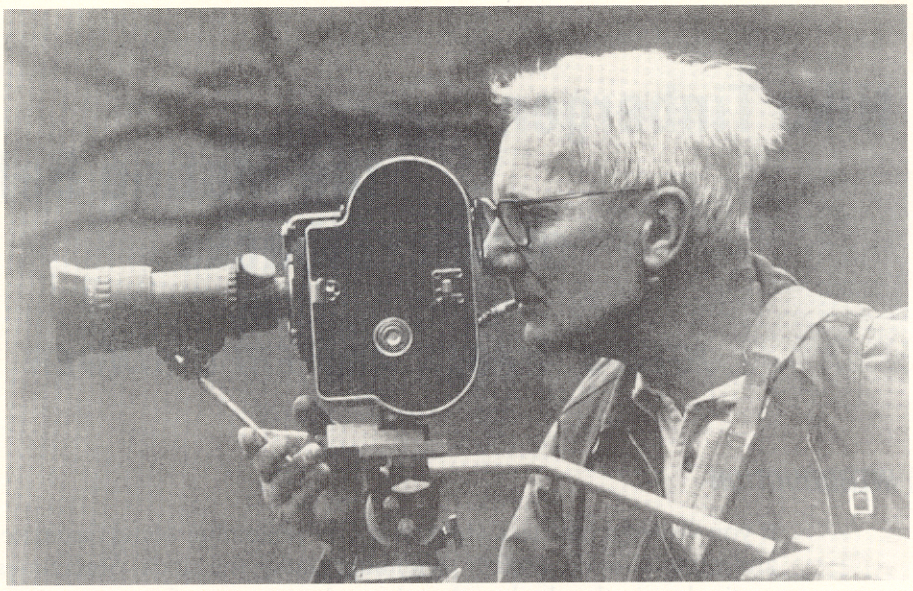

FIGURE 14.1 Niko Tinbergen. *Source:* M. S. Dawkins, T. R. Halliday, and R. Dawkins, eds., *The Tinbergen Legacy*, 1991.

THE MAKING OF AN ETHOLOGIST

Niko Tinbergen (Figure 14.1) was born into a family where learning was encouraged. The family had the unique distinction of having two children win Nobel Prizes. Older brother Jan won the prize for economics in 1969, four years before Niko was awarded his prize.

Despite his intellectual abilities, Tinbergen was a somewhat indifferent student. He excelled in courses that interested him but ignored those he found boring. Two other activities competed for his attention. Tinbergen was an avid athlete, competing internationally in field hockey. Throughout his career, he remained physically active, and he always enjoyed working outdoors. Like many animal behaviorists, he was also drawn to natural history at an early age. His family encouraged this extracurricular interest, and as a boy he spent much of his time on field trips collecting animals.

His interest in natural history took a serious turn when he entered the University of Leiden. His teachers quickly recognized his abilities, and Tinbergen joined a small, but active, group of Dutch animal behaviorists. After completing his Ph.D., he taught zoology at the university. Although still in his twenties, Tinbergen was already building an international reputation as a talented scientist.

During the early 1930s Tinbergen met the Austrian biologist Konrad Lorenz. At the time, Lorenz was trying to establish a new approach to animal behavior, which he called **ethology**. Tinbergen's observational and experimental skills complemented Lorenz's more theoretical approach. The two men forged a lifelong friendship, and together they made ethology an important field of biological study.

This activity was temporarily interrupted during World War II, when Tinbergen was imprisoned for his resistance to the Nazis. After the war, Tinbergen left Holland to take a teaching position at Oxford University. This was an important move for Tinbergen, because Oxford had become a center of field biology. There he joined an outstanding group of biologists who were interested in animal behavior, ecology, and population genetics (see Chapter 1).

SEX AND STICKLEBACKS

Choosing the right organism to study is an important ingredient in research. Although Tinbergen studied many species, one of his favorite subjects was the three-spined stickleback (*Gasterosteus aculeatus*), a small fish named for its protective dorsal spines. As a boy, Tinbergen had often caught sticklebacks in ditches near his home, and, he later recalled, "I soon discovered that in choosing these former pets I had struck oil." Sticklebacks are hardy animals, easy to collect and keep in the laboratory. Unlike mammals whose behavioral characteristics are complicated by learning, this fish always seemed to respond in a predictable way to stimuli. According to Tinbergen, sticklebacks provided excellent examples of what he referred to as "automatic" or "purely instinctive" behavior. For all of these reasons, they were a good choice for behavioral experiments. Perhaps with tongue in cheek, Tinbergen claimed that "to us this little fish is what the rat is to many American psychologists."

Tinbergen was particularly interested in the mating behavior of sticklebacks. During most of the year sticklebacks live together in schools. At the beginning of the breeding season, however, males become territorial. On the bottom of the stream, each male builds a nest out of algae and plant material, and he actively drives all

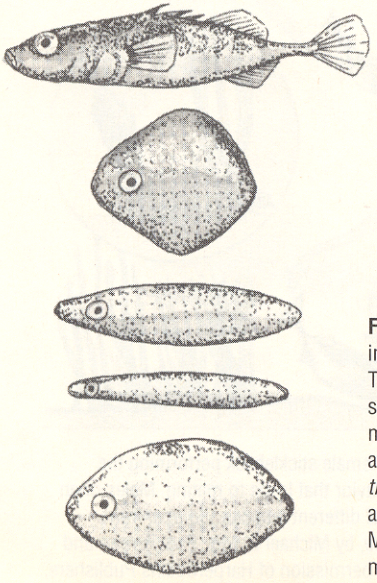

FIGURE 14.2 Models used in experiments on fighting behavior in territorial male sticklebacks. Territorial males attacked models with red undersides, even if they did not look like fish. Realistic models without the red coloration were rarely attacked by territorial males. *Source:* from *Biology: the Network of Life*, by Michael C. Mix, Paul Farber, and Keith I. King. Copyright ©1992 by Michael C. Mix, Paul Farber and Keith I. King. Reprinted by permission of HarperCollins Publishers.

other males and nonreceptive females away from the surrounding area. Physiological changes accompany this change from nonaggressive schooling to aggressive territoriality. The abdomens of territorial males turn bright red. In contrast, egg-bearing females turn glossy silver, and their abdomens become swollen with eggs.

Through a series of elegantly simple experiments, Tinbergen demonstrated that the color red serves as a stimulus for aggressive behavior. Almost any red object placed in front of a territorial male elicited an aggressive display. Wooden models, which bore little resemblance to male sticklebacks, provided this stimulus as long as they had red undersides (Figure 14.2). In fact, Tinbergen noticed that males often reacted aggressively when red mail trucks passed by the window of his laboratory. In contrast, perfectly shaped models of male fish that lacked red coloration were rarely attacked.

PROBLEM

Consider the models shown in Figure 14.2. What characteristics of male fish are represented by these models? What male characteristics might be missing in a wooden model? How could Tinbergen modify his models to test whether the missing characteristics also stimulated territorial behavior?

According to Tinbergen, the aggressive, territorial behavior of male sticklebacks illustrated two important characteristics common to all innate behavior. First, the behavior had a physiological basis. Males acted aggressively only when their

FIGURE 14.3 A male and female stickleback performing the sequence of courtship behavior that leads to mating. Males often court and mate with several different females. *Source:* from *Biology: the Network of Life*, by Michael C. Mix, Paul Farber, and Keith I. King. Reprinted by permission of HarperCollins Publishers.

abdomens turned red and they were physiologically ready to breed. Second, the behavior was always a response to a specific stimulus. A single male trait, red coloration, stimulated attacks. All other male characteristics seemed to be irrelevant.

Even some very complex forms of behavior could be thought of as chain reactions of simple stimulus-response mechanisms. The zigzag courtship dance between a male and a receptive female illustrated this more complex mechanical pattern (Figure 14.3). When a female enters a breeding territory, the male swims vigorously toward her. Such an aggressive approach causes most nonreceptive females to flee, but an egg-bearing female responds by facing the approaching male and exposing her swollen abdomen. This simple response acts as a new stimulus that switches the male from aggression to courtship. He responds by leading the female in a zigzag pattern toward the nest.

Once the pair arrive at the nest, the male turns on his side and points to the entrance with his snout. The female enters the nest and remains there with her head and tail protruding from either end. Trembling, the male prods the female's tail several times, which causes her to release her eggs. After spawning, the female swims out of the nest and the male enters to fertilize the eggs.

After mating is complete, the male again becomes aggressive and chases the female out of the territory. He then begins to court other egg-bearing females that enter his nest site. After fertilizing several clutches of eggs, the male stops courting and begins to show parenting behavior. The eggs seem to provide a stimulus for fanning, which the male does to provide them with oxygen. After the eggs hatch, the male protects the young. Females take no part in this parenting behavior.

PROBLEM

Propose a testable hypothesis about what characteristic of the eggs stimulates the switch from courtship to parenting behavior (fanning eggs) in male sticklebacks. How would you test this hypothesis?

Tinbergen's careful description of the courtship dance highlighted several important features of mating behavior. The dance was complicated, but it comprised a series of quite simple steps. Each step involved a specific stimulus from one fish followed by an equally specific response from the other. Finally, the type of response depended not only upon the stimulus but also upon the physiological state of the fish. For example, the color red was an important stimulus, but it caused different responses in males and females. Males would attack red-colored models, even those that did not look like fish. Gravid females would follow these same unrealistic red models through the zigzag courtship dance, even if a nest was not present.

THE ETHOLOGICAL METHOD

Unraveling the details of the zigzag dance required several different scientific methods. Careful observation is the starting point for all behavioral research, and it was particularly important for ethologists. Tinbergen cautioned his students not to begin experiments until they thoroughly understood the natural behavior of the animals

they studied. This meant spending hours watching behavior without disturbing the animals in any way. Often this was done in the field, but in the case of the sticklebacks, Tinbergen was able to observe the fish in aquaria.

After becoming thoroughly familiar with a complex behavior, the ethologist could begin to analyze its component parts. Often this involved creating an **ethogram**, which was a detailed list or description of the types of behavior performed by a species. Ethograms generated questions about the frequency, intensity, sequence, and duration of simple behavioral characteristics. At this point in the study, the ethologist might design experiments to test hypotheses. Although experiments played a critical role in discovering the causes of behavior, Tinbergen stressed that experimentation must always be balanced with careful observation.

PROBLEM

Reconsider the simple behavior of fanning eggs that males perform after mating. This behavior, which provides the eggs with oxygen, is crucial for the survival and development of embryos. Propose a testable hypothesis about how eggs stimulate the frequency, intensity, or duration of this behavior. Design a simple experiment to test your hypothesis.

The final step in the ethological method was comparing the same types of behavior among closely related species. By comparing similarities and differences among species, ethologists could sometimes draw inferences about how the behavioral characteristics evolved. Behavioral characteristics could also sometimes be used as important pieces of evidence for determining evolutionary relationships among related species.

NATURE VERSUS NURTURE

Ethologists believed that all behavior had a genetic component that is passed from parent to offspring. Some simple behavioral characteristics seemed so rigid and uniform that they appeared to be inherited much like fins, gills, or spines. Just as all of the sticklebacks that Tinbergen studied had three dorsal spines, all males and females seemed to perform the courtship dance in the same way. In both cases, the characteristics were adaptive, and natural selection tended to eliminate unusual variants. Just as a mutant stickleback with missing spines would be quite defenseless against predators, a stickleback that could not correctly perform the courtship dance would be unsuccessful at mating.

Tinbergen thought that courtship rituals had evolved by natural selection. Consequently individuals almost always mate with members of their own species and avoid mating with members of other species. For example, ten-spined sticklebacks (*Pungitius pungitius*) performed a courtship dance very similar to that of three-spined sticklebacks. Rather than having red abdomens, however, male ten-spined sticklebacks had black undersides. Several of the individual dance steps were also slightly different in this species. Thus both anatomical and behavioral characteristics were adaptations to prevent interbreeding. In order for this reproductive isolation to work, all members of each species would have to perform the

appropriate courtship ritual. A female three-spined stickleback would produce no offspring if she mistakenly responded to the black abdomen and courtship behavior of a male ten-spined stickleback.

In many simpler animals, almost all behavioral characteristics seemed to be instinctive. Tinbergen often spoke of sticklebacks as if they were machines that automatically reacted to stimuli. Using a modern figure of speech, ethologists believed that each species was "hardwired" to perform characteristic innate forms of behavior. Even in humans, which Tinbergen also studied, one could find some simple, instinctive behavioral characteristics. For example, breast-sucking seems to be an instinct that is automatically done by all newborn infants. Perhaps even complex forms of learned behavior had evolved from such instincts.

This emphasis on instinct put ethologists at odds with many American psychologists, who were primarily interested in learning. Using rewards and punishments, experimental psychologists could drastically modify behavior. Rats and pigeons could be trained to push buttons or pull levers to receive food or avoid electrical shocks. Impressed with these results, some psychologists believed that all behavior was learned in this way. They proposed that at birth the animal's brain was like a blank slate. Through experience, both painful (punishments) and pleasant (rewards), the animal learned to behave in appropriate ways.

This "nature versus nurture" controversy polarized animal behaviorists during the 1950s. Ethologists criticized psychologists for using highly artificial experiments and for studying only a few species of animals: rats, pigeons, chickens, and primates. What could be learned about natural behavior from timing rats as they ran through mazes? Psychologists criticized ethologists for ignoring the development of behavior as young animals grew into adults. How could ethologists be so sure that learning did not occur, even in many simple animals?

PROBLEM

Behavioral psychologists stressed two forms of learning that might be used even by simple animals: copying and trial and error. Design an experiment to test whether copying is involved in the development of stickleback courtship behavior. Design another experiment to test whether trial-and-error learning plays a role in the development of stickleback courtship behavior.

By the 1960s, the nature versus nurture controversy had largely subsided. Both ethologists and psychologists realized that a sharp distinction between instinct and learning was misleading. Almost all forms of behavior involved both elements. Tinbergen himself pointed out that four different questions could be asked about behavior. How was it caused by nerves and hormones? How did it develop in the growing organism? How was it adaptive in a particular environment? And how had it evolved? These questions were equally important, but a single scientist might not be able to answer all of them. Studying each question required a different set of methods and, perhaps, a slightly different perspective on what was important about animal behavior.

Like all great scientific achievements, Tinbergen's early studies of sticklebacks raised interesting new questions as they answered old ones. By posing these questions, his books and articles continue to stimulate creative research. A new group of

behavioral ecologists, many of them Tinbergen's students, has criticized, expanded, and refined his explanations of the adaptive function of courtship behavior and how it evolved in different environments. This ongoing research tradition is perhaps Tinbergen's greatest legacy.

☐ EPILOGUE

Unlike Tinbergen, who emphasized the ways in which courtship behavior was the same in all male or female sticklebacks, behavioral ecologists are now more interested in behavioral differences among individuals of each sex. Thus the focus of study has shifted from the level of the species to the level of individuals within a population or species. What caused this change from traditional ethology to behavioral ecology?

Beginning in the mid-1960s, evolutionary biologists began to emphasize that natural selection usually operates at the level of individuals rather than whole populations or species. If the individual is the unit of selection, it makes sense to ask whether behavioral differences among individuals are due to genetic differences. If there is a genetic basis for behavioral differences, we would expect that natural selection would favor some behavioral traits over others. Like physical characteristics, behavior should contribute to individual fitness.

This emphasis on natural selection and individual fitness was accompanied by new research methods. Behavioral ecologists, including Tinbergen later in his career, studied large numbers of animals in natural populations. In many cases they marked or tagged individuals. This method allowed the scientists to study variation in behavior among individuals and quantify its consequences for survival and reproductive success. This was quite different from Tinbergen's early study of sticklebacks, which involved observing only a small number of fish living in aquaria.

Tinbergen generally adopted a cooperative world view in which males and females harmoniously courted, mated, and raised offspring. The primary focus of this complex process was the male's behavior. Females were portrayed as passively following the male's lead during the zigzag dance. Although he recognized conflicting drives (as evidenced by the aggressive components of the zigzag dance), Tinbergen emphasized the coordination of male and female behaviors, leading to successful reproduction. Courting and mating always seemed to take place in a predictable way.

Behavioral ecologists view courtship behavior quite differently. By focusing on how different individuals may benefit from different types of behavior, biologists now realize that there is often a strong element of competition between males and females. When male and female interests don't converge, the two sexes may not always work harmoniously. In contrast to Tinbergen's view of females as followers, behavioral ecologists now recognize that female sticklebacks play an active role in determining the reproductive success of both sexes.

Females actively choose males on the basis of where their nests are located. Males who build nests in well-protected areas that are relatively free of predators tend to be most successful in attracting mates. Because the quality of territories is so important, males must compete for areas camouflaged by protective layers of filamentous green algae. The red coloration of territorial males that Tinbergen empha-

sized may be correlated with a male's competitive abilities, but it is the quality of the territory that first attracts the female.

A more dramatic female behavior that Tinbergen did not discuss is egg cannibalism. Females often attack males' nests and eat eggs or developing young. This benefits the female because she gets a nutritious meal and eliminates the eggs of her rivals. It appears that cannibalistic females are very successful in mating with males whose nests they have previously raided. Egg cannibalism, however, is always detrimental to the male's reproductive success. Not surprisingly, males have evolved several types of behavior to deter egg cannibalism. Males frequently attack marauding females with vigorous bites and threatening displays. A male may also distract cannibalistic females by feeding outside his territory. Finally, because egg cannibals often travel in roving gangs, males often court single females while avoiding females in groups.

Egg cannibalism is a striking example of how stickleback behavior may depart from Tinbergen's simple description of male-female cooperation. Other recent studies call into question Tinbergen's description of the zigzag dance as a "species-specific" behavior pattern. When behavioral ecologists studied five genetically distinct populations of three-spined sticklebacks, they discovered important differences in the courtship ritual. In two populations, females rather than males initiated courtship, and the zigzag component was either missing or very inconspicuous. In both of these populations, groups of up to 300 females and immature males attacked the nests and cannibalized the young. Presumably, a history of cannibalism by females in these two populations has favored males who do not advertise their nest sites with conspicuous courtship displays.

In three other populations where the males did initiate courtship with the conspicuous zigzag dance described by Tinbergen, cannibalism was never observed. In this social environment, males can use conspicuous courtship displays without the risk of losing their fertilized eggs. Thus courtship behavior appears to be an adaptive characteristic that may evolve differently in different social environments. By comparing different populations within a species, behavioral ecologists have successfully tested hypotheses about the adaptive significance of behavior.

QUESTIONS AND ACTIVITIES

1. What does this case show about the following aspects of doing biology?
   — experimental and nonexperimental methods
   — disciplinary boundaries and interdisciplinary problems
   — how different theoretical perspectives may influence the interpretation of data
   — how research problems and methods change
2. Tinbergen was a very careful observer, so he probably saw individual variation in the way different sticklebacks performed the courtship dance. Why do you think he did not emphasize this variation when he described the behavior?

3. In his descriptions of courtship behavior, Tinbergen emphasized cooperation between the male and female to ensure successful reproduction. Behavioral ecologists often emphasize competition between the sexes. How have both of these perspectives contributed to understanding courtship behavior?
4. Unlike his laboratory studies of sticklebacks, Tinbergen's equally famous research on seagulls and other birds was done on wild populations. These studies involved carefully observing the behavior of many individual birds in their natural habitats. What might be the advantages and disadvantages of studying animal behavior in the field versus the laboratory?
5. Tinbergen and other ethologists used terms like "courtship" and "dance" to describe certain aspects of mating behavior in sticklebacks. More recently, some behavioral ecologists have used the term "cuckoldry" to describe the situation where the eggs in one male's nest are fertilized by another male. The male who fertilizes the eggs is sometimes referred to as a "sneaker." How appropriate are these analogies to human behavior? What are some possible benefits or dangers in using such analogies?
6. Although Tinbergen and other ethologists usually studied nonhuman animals, they believed that their research might provide some insights into human behavior. How might studying bluegill sunfish or sticklebacks help us to understand human behavior?

SUGGESTED READING

Baerends, G., C. Beer, and A. Manning. (eds.) 1975. *Function and Evolution in Behaviour: Essays in Honour of Professor Niko Tinbergen, F.R.S.* Oxford, England: Clarendon Press.

Burkhardt, R. W. 1981. "On the Emergence of Ethology as a Scientific Discipline." *Conspectus of History* 1: 62–81.

Dewsbury, D. (ed.) 1989. *Leaders in the Study of Animal Behavior: Autobiographies of the Founders.* Chicago: University of Chicago Press.

FitzGerald, G. J. 1993. "The Reproductive Behavior of the Stickleback." *Scientific American* 268(4): 80–85.

Tinbergen, N. 1951. *The Study of Instinct.* Oxford, England: Clarendon Press.

Tinbergen, N. 1952. "The Curious Behavior of the Stickleback." *Scientific American* 187(6): 22–26.